

A cladistic analysis of subfamilial relationships in the Chrysomelidae *sensu lato* (Chrysomeloidea)

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Abstract. A phylogeny of the subfamilies traditionally assigned to the Chrysomelidae and Bruchidae is suggested, based on cladistic relationships of 29 family-rank taxa and 71 characters. The analysis is primarily based on a review of published morphological characters of adults and larvae. Various plesiomorphic Cerambycidae and allied taxa (a lineage within Chrysomeloidea) and Curculionoidea are used for out-group comparison. The hypothesis of monophyly of the Chrysomelidae (including Megalopodidae and Bruchinae) is tested.

The Chrysomeloidea is divided into four groups: (1) the families of the cerambycid lineage; (2) Megalopodidae (with subfamilies Megalopodinae, Palophaginae and Zeugophorinae); (3) Orsodacnidae (with subfamilies Aulacoscelidinae and Orsodacninae); (4) Chrysomelidae (with subfamilies Bruchinae, Chrysomelinae, Criocerinae, Cryptocephalinae, Donaciinae, Eumolpinae, Galerucinae, Hispinae, Lamprosomatinae and Sagrinae). Evidence is given for monophyly of the following: Megalopodidae + (Orsodacnidae + Chrysomelidae); Palophaginae + (Megalopodinae + Zeugophorinae); Orsodacnidae + Chrysomelidae; Aulacoscelidinae + Orsodacninae; Sagrinae + Bruchinae; Chrysomelinae + Galerucinae; Eumolpinae + (Lamprosomatinae + Cryptocephalinae). Various possible arrangements of subfamilies of Chrysomelidae are discussed. Support is given for subsuming Cassidinae under Hispinae, Alticinae in Galerucinae, Synetinae and Megascelidinae in Eumolpinae, Sphaerocharitinae in Lamprosomatinae and Clytrinae and Chlamisinae in Cryptocephalinae. Keys are given for the identification of larvae and adults of the families and subfamilies of Chrysomeloidea. Host association and biogeography are discussed briefly and compared with the proposed phylogeny.

Introduction

The traditionally circumscribed family Chrysomelidae (leaf beetles) is one of the largest in the Coleoptera, with approximately 35,000 described species

J. Pakaluk and S.A. Ślipiński (eds.): Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson.

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worldwide (Jolivet 1988). Many species remain to be discovered and described, for example, an estimated 30% of the Australian fauna is undescribed (Lawrence and Britton 1991), and the total world fauna may exceed 60,000 species. There are also many synonyms because this is a popular group for the philatelic fraternity. For example, in Australia at least 10% of the currently valid species names, listed in the *Coleopterorum Catalogus* and subsequent taxonomic works, are junior synonyms. All leaf beetles are phytophagous, particularly on Angiospermae; species diversity is therefore greatest where angiosperm diversity is greatest—in tropical rain forests (*see* Farrell and Erwin 1988). A large number of species are important pests in agriculture and forestry and many other species are finding use as biological control agents of weeds (at least 30 species have been introduced into Australia for this purpose (Julien 1992; A. Sheppard, *personal communication*).

The nomenclature of all chrysomeloid family rank taxa used in this paper is given in Table 1. I also use "cerambycid lineage" or Cerambycidae *s.lat.* for Anoplodermatidae, Cerambycidae, Disteniidae, Oxypeltidae and Vesperidae, and "chrysomelid lineage" or Chrysomelidae *s.lat.* for Chrysomelidae, Megalopodidae and Orsodacnidae. The following family group names have been corrected to take the genitive stems of the nouns on which they are based: Aulacoscelinae = Aulacoscelidinae and Megascelini = Megascelidini, from Greek *skelis*, *skelidos* (rib); Sphaerocharini = Sphaerocharitini, from Greek *charis*, *charitos* (loveliness).

At present the definition of the Chrysomelidae is controversial. The relationships of "Bruchidae" and Megalopodidae to other Chrysomeloidea and the cerambycid lineage have not been resolved, and there is little consensus on the internal classification of the family. There has never been much nomenclatural stability in the family rank taxa of the Chrysomeloidea, due to both variation in allocation of rank and inconsistency in determination of boundaries. Part of the problem is the difference in attitudes between systematists with a broad knowledge of the Coleoptera and specialists working on their favourite subfamily. For example, 40 years ago good reasons were given by Crowson (1955) for the amalgamation of Bruchidae and Chrysomelidae, Cryptocephalinae and allies, Hispinae and Cassidinae, and Galerucinae and Alticinae, yet these suggestions are still not followed by the majority of chrysomelid taxonomists.

Until the work of Crowson, theories of classification of the subfamilies were based on very limited character analyses. The most important of the early classifications (Chapuis 1874, 1875) was based on a comprehensive review of all known genera and, for internal arrangement of the subfamilies, remains little changed to this day (Seeno and Wilcox 1982). For convenience, the subfamilies were placed in "sections" indicating supposed similarity. Chapuis' system depended on a linear model of "progress" from simple to complicated adult body form, with genera of crudely similar body form linking the subfamilies (*e.g.*, *Oides* linking Galerucinae to Chrysomelinae, *Iphimeis* linking Eumolpinae

to Lamprosomatinae). This early system involved extant taxa evolving from extant taxa, a concept still in use (Jolivet 1957, 1988; Medvedev 1971; Borowiec 1984, 1987; Suzuki 1988). Sharp and Muir (1912) looked at male genitalia and made some interesting speculations on the evolution of the family (Crowson 1955). Analysis of larval characters by Böving and Craighead (1931) allowed a radical reclassification of the Chrysomelidae, but these ideas have still not been widely adopted by chrysomelid workers. Larval morphology suggested new relationships between subfamilies, with inclusion of Bruchinae for the first time.

Roy Crowson and his students have systematically examined and analysed the following features of chrysomelid morphology: metendosternite (Crowson 1938, 1944), plesiomorphic character states (Crowson 1946, 1955), tarsal setae (Mann and Crowson 1981), nervous system (Mann and Crowson 1983c), gut (Mann and Crowson 1983b), male genitalia (Mann and Crowson 1983a, 1992), and female genitalia (Kasap and Crowson 1985).

Since 1950 there have been many published morphological phylogenies of the chrysomelid lineage, with very little agreement between them. The reasons for this disagreement are partly found in the different analytical methods. Some studies are based on unquantified assessments of similarity, producing a maze of cross-linkages and living ancestors (*e.g.*, Jolivet 1988), or dissimilarity (*e.g.*, Suzuki (1988), who identified eight dissociated groups). Character systems may be considered unique portents of relationship (genitalia – Iablokoff-Khnzorian (1966) and Suzuki (1988); wings – Jolivet (1957, 1959) and Suzuki (1994)). “Evolutionary trends”, in which the taxa are aligned from “primitive” to “advanced”, may be constructed by ingroup comparison alone, without reference to any other taxa (*e.g.*, in Alticini: Furth 1988; Konstantinov 1994).

Other studies have constructed phylogenies from hierarchical patterns in living taxa, using evolutionary principles. There have been various approaches, some of which can be faulted philosophically (*e.g.*, use of the “bauplan”, undue deference to fossils, emphasis on retention of plesiomorphies), but these are testable scientific hypotheses of relationship, not axiomatic truths. All of these studies are based on either very limited numbers of characters or a limited range of taxa; indeed, as Crowson’s familiarity with chrysomelid morphology has increased so his cladograms have changed shape. This is not a fault but an acknowledgement that additional information is useful (Eernisse and Kluge 1993). The most recent study is based on larval characters of a few Japanese taxa (Lee 1993)¹.

¹) I have analysed Lee’s original data set (p.417) using PAUP 3.1.1 and have found that his proposed phylogeny based on this data set is 7 steps longer (103 steps) than the 70 trees with a minimum length of 96 steps (this includes making character 13 ordered). A strict consensus of these 70 trees pairs Galerucinae *s. lat.* with Chrysomelinae, and Cryptocephalinae (but excluding Chlamisini) with Lamprosomatinae, and places Bruchinae as the sister group of all other Chrysomelidae. However, several taxa are erroneously described in the data matrix.

There is a considerable corpus of morphological information for larvae and adults of Chrysomeloidea and the time is ripe for a systematic analysis of this information. This is especially important now that molecular phylogenies of the Chrysomeloidea are beginning to appear (Hsiao 1994)². DNA will not replace morphology as a provider of phylogenies—the two should be considered complementary and ideally should be used in combination (Eernisse and Kluge 1993). It should be noted that the analysis of base-pair sequences has just as many problems as the analysis of morphological data (Lake 1991; Clark and Whittam 1992; Smith 1994).

Here I present a cladistic analysis of adult and larval morphological characters, with two principal aims: (1) defining the Chrysomelidae as a monophyletic group; (2) determining the relationships of the included subfamilies. This analysis is used to justify a revised classification, although none of the taxonomic decisions are new. Problems of homology, host relationships and biogeography are discussed. It is hoped that this study will allow refutation of some of the more implausible chrysomelid classifications and will provide a framework for further phylogenetic studies.

Monophyly of the Chrysomeloidea

There appears to be general agreement that the Chrysomeloidea form a monophyletic group (Crowson 1955, 1960; Lawrence and Newton 1982; Lawrence and Britton 1991), with at least the following shared character states (including plesiomorphies): adult—antennae filiform or at least without 3-segmented club, gular sutures separated, remnant of RP_{3+4} present (= r-m spur; rare exceptions); larva—lack of mandibular mola (also lacking in most Curculionoidea: May 1994), lack of hypopharyngeal bracon (rarely also lacking in Curculionidae: May 1994). Most authors also identify the Curculionoidea as the monophyletic sister group of the Chrysomeloidea – recent dissent is due to exaggerated claims for the significance of fossils (Kiretjtshuk 1992). The two superfamilies share: adult—pseudotetramerous tarsi on all legs (except taxa which are clearly derived from this state), tegmen of aedeagus without articulated parameres. It is notable that plesiomorphic members of each of the three groups may be quite similar morphologically.

² If the unrooted PAUP derived tree (Hsiao 1994: 244) is rooted at *Orsodacne* (as it should on morphological evidence), the following hierarchy is produced: (Orsodacnidae + (Hispinidae + (Eumolpinae + (Cryptocephalinae + (Galerucinae (part) + Chrysomelinae + (Criocerinae + Galerucinae (part)))))). Only monophyly of each of Hispinidae and Cryptocephalinae concurs with the morphological evidence presented here. How many morphologists would be allowed to publish a phylogeny based on examination of one species of each subfamily, and not even all subfamilies?

Table 1. Family-rank taxa of Chrysomeloidea used in this paper.

This work (*para- or polyphyletic?)	Lawrence and Britton 1991	Seeno and Wilcox 1982	Crowson 1955
Chrysomeloidea	Chrysomeloidea	—	Chrysomeloidea
Vesperidae	Vesperidae	—	Lepturinae (part)
Anoplodermatidae	Anoplodermatidae	—	Anoplodermatinae [sic]
Disteniidae	Disteniidae	—	Disteniinae
Cerambycidae	Cerambycidae	—	Cerambycidae (part)
Cerambycinae	Cerambycinae	—	Cerambycinae
Lepturinae	—	—	Lepturinae (part)
Prioninae	Prioninae	—	Prioninae
Parandrinae	Parandrinae	—	Parandrinae
Megalopodidae	Chrysomelidae (part)	Chrysomelidae (part)	Chrysomelidae (part)
Megalopodinae	Megalopodinae	Megalopodinae	Megalopodinae
Palophaginae	Megalopodinae	Orsodacninae (part)	?Orsodacninae (part)
Zeugophorinae	Megalopodinae	Zeugophorinae	Megalopodinae
Orsodacnidae	—	Chrysomelidae (part)	Chrysomelidae (part)
Aulacoscelidinae	—	Aulacoscelinae [sic]	Aulacoscelinae [sic]
Orsodacninae	—	Orsodacninae (part)	Orsodacninae
Chrysomelidae	Chrysomelidae (part)	Chrysomelidae (part)	Chrysomelidae (part)
Bruchinae	Bruchinae	Bruchidae	Bruchidae
Chrysomelinae	Chrysomelinae	Chrysomelinae	Chrysomelinae
Chrysomelini	Chrysomelini	Chrysomelini	—
Timarchini	Timarchini	Timarchini	—
Criocerinae	Criocerinae	Criocerinae	Criocerinae
Cryptocephalinae	Cryptocephalinae (part)	Cryptocephalinae, Clytrinae & Chlamisinae	Clytrinae (part)
*Cryptocephalini	Cryptocephalini	Cryptocephalinae	—
Clytrini	Clytrini	Clytrinae	—
Chlamisini	Chlamisini	Chlamisinae	—
Donaciinae	Donaciinae	Donaciinae	Donaciinae
Eumolpinae	Eumolpinae	Eumolpinae, Synet- inae & Megascalinae	Eumolpinae & Clytrinae (part)
*Eumolpini	—	Eumolpinae (part)	—
Megascalidini	—	Megascalinae [sic]	Clytrinae (part)
Spilopyrini	—	Spilopyrini [sic] Hornibiini & Stenomelini	—
Synetini	—	Synetinae	?
Galerucinae	Galerucinae	Galerucinae & Alticinae	Galerucinae
*Alticini	—	Alticinae	—
Galerucini	—	Galerucinae	—
Hispininae	Hispininae	Hispininae & Cassidinae	Hispininae
Cassidini	—	Cassidinae	—
*Hispini	—	Hispininae	—
Lamprosomatinae	Cryptocephalinae	Lamprosomatinae	Clytrinae (part)
Sagrinae	Sagrinae	Sagrinae	Sagrinae

Monophyly of the Chrysomelidae

At present the status of the Chrysomelidae is controversial and needs to be resolved. Until Böving and Craighead (1931) placed the Bruchinae within the Chrysomelidae there was general agreement on the composition of the family, with only minor arguments about rank. Since 1931 many authors have continued to omit Bruchinae, which were not considered in the two recent books on Chrysomelidae (Jolivet *et al.* 1988, 1994); *see* comments by Crowson (1994). Furthermore, the relationship of Megalopodidae to other chrysomeloids has been questioned (Schmitt 1992, *in press*), and there has been the startling suggestion that Megalopodidae and Orsodacninae are derived from two different lineages within the Cerambycidae *s.str.* (Suzuki 1988). In order to resolve these problems, several taxa of Cerambycoidea need to be included in any phylogenetic analysis of chrysomelid subfamilies—at least the subfamilies of Cerambycidae mentioned by Suzuki (1988) plus members of the more plesiomorphic groups (*e.g.*, *Vesperus*, *Distenia*, *Philus*) (Crowson 1955; Svachá and Danilevsky 1987). *Philus* has not been included in my analyses because the larva is unknown, but the adult does not differ greatly from the other two genera listed above.

Methods

For general morphological nomenclature I have followed Lawrence and Britton (1991) except for wing venation which follows a more recent review (Kukalová-Peck and Lawrence 1993). Specific terms, applicable to a few taxa in this analysis, are explained in the definition of character states.

There are clearly hundreds of potential characters with thousands of potential terminal taxa. Why choose the following list? Some reasons are discussed separately below, but in general I have accepted that the subfamilies, or tribes, if this rank is considered important, are in themselves valid taxa. I have tried to choose characters which do not vary within these groups and are not simply confined to one terminal taxon. The characters are primarily chosen from the literature; if Chapuis or Crowson or some other chrysomelid worker has indicated that a certain character is diagnostic for a group of higher taxa, then I have tried to use that character in this study. In practice, many characters considered diagnostic for higher taxa are evidently variable and both states may occur in a taxon of relatively minor rank. A classic example is the presence or absence of the lateral pronotal border (Character 13), in which both states have been considered plesiomorphic yet are generally scattered throughout the taxa considered here. Other character states, considered diagnostic for a taxon, may only apply to the majority but not all of a higher taxon. In cases of wing vein characters which obviously involve loss or reduction, I have only scored the

most complete venation known to be present in any taxon. The most plesiomorphic states of reduction sequences in larval characters are treated similarly (stemmata, antennal segments and so on). Several other characters are included for which only a few species have been examined, especially from non-ectodermal morphology, and morphology of the nerve cord was not examined at all (Mann and Crowson 1983c). The value of my study is constrained by all the qualifications listed above.

I tried to examine as many species as possible, especially those which appeared to be or have been described as morphologically plesiomorphic within each subfamily. Whole adults were disarticulated after maceration in dilute KOH. The material studied, from the Australian National Insect Collection, CSIRO Division of Entomology, Canberra, included representatives of every subfamily discussed.

Analysis of the morphological characters of adults and larvae was performed with the cladistic programs PAUP 3.1.1 (Swofford 1993) and MacClade 3 (Maddison and Maddison 1992). The analyses and different options used are described under Cladistic Analysis.

OUTGROUP

Reasons for using an outgroup in any analysis have been cogently argued by Maddison *et al.* (1984). The characters used for testing monophyly of Chrysomelidae *s.lat.*, with respect to the cerambycid lineage, can be polarised by reference to basal taxa of the sister group, Curculionoidea, *e.g.*, Nemonychidae, Anthribidae and Belidae which are treated as a single monophyletic outgroup. Fortunately, for such a comparison, an excellent review of curculionoid larval morphology has recently been published (May 1994). In practice, some of the characters of weevils are so derived that ancestral states can only be determined by reference to other Polyphaga.

INGROUP

The ingroup includes a selection of cerambycoid taxa and representatives of all traditional chrysomelid subfamilies plus Bruchinae, described from available descriptions and specimens. Only a little new information is included, primarily concerning the first-instar larva of Sagrinae and data from my unpublished analyses of the Camptosomata (Reid 1990), Chrysomelinae and Eumolpinae *s.lat.*

The family group names of the taxa studied are listed in Table 1. The following groups are treated as single taxa, with the name used in this paper in brackets: Cryptocephalinae–Clytrinae–Chlamisinae [Cryptocephalinae], Lamprosomatinae–Sphaerocharitinae [Lamprosomatinae], Galerucinae–Alticinae [Galerucinae], Hispinae–Cassidinae [Hispinae]. There are good characters for

a broadly defined Cryptocephalinae, including both the Clytrini and Chlamisini as highly autapomorphic monophyletic groups whose character states can be derived from cryptocephaline-like ancestors (Reid 1990). Clytrini are particularly close to *Pachybrachis* and allied genera. However, the distinction between Lamprosomatinae and Cryptocephalinae is maintained because each has well-defined synapomorphies. Lamprosomatinae includes the tribe Sphaerocharitini. Two of the three features used to define Sphaerocharitinae + Cryptocephalinae (Kasap and Crowson 1976) do not occur in all Cryptocephalinae and the third is reduced wing venation which is a weak character throughout the Chrysomeloidea. The status of Sphaerocharitini needs to be reconsidered, but subfamily status is unlikely to be justifiable. Crowson seems to have recognised this in later studies (Mann and Crowson 1981). Recognition of Galerucinae and Alticinae as separate subfamilies by previous authors has been based on a single character, presence or absence of a metafemoral spring, which does not correlate with other morphological features of the adult or larva. Both groups are probably polyphyletic as presently circumscribed (Reid 1992c). Recognition of the Hispinae and Cassidinae as two well-defined entities is similar to the galerucine-alticine problem. It is likely that there is a monophyletic core group of Cassidini within a paraphyletic Hispini, including the residue of Cassidini. This problem is treated elsewhere (Borowiec 1995).

The Sagraeae are treated as a monophyletic subfamily here, although previous authors have considered them a living "stem group" to all other subfamilies (Medvedev 1971; Jolivet 1978) and a more recent study has suggested they may be paraphyletic with regard to Donaciinae (Askevold 1990b). I have seen virtually all described species of Sagraeae and have no problems with monophyly of this subfamily. Askevold's study is based on a small sample of taxa and adult characters and includes erroneously scored characters (tibial spurs, pronotal margins). Sagraeae paraphyly was suggested because of male internal sac characters which Askevold relies on in all his taxonomic studies (Askevold *et al.* 1994) and which he uses to exclude Bruchinae from the clade including Criocerinae, Donaciinae and Sagraeae. In my experience of Chrysomelidae the internal sac varies considerably in structure, even between allied genera, and should not be unduly relied upon to resolve phylogenies.

Two taxa which normally have tribal rank are treated separately. The tribe Timarchini, represented by the single genus *Timarcha* (Seeno and Wilcox 1982), has adults and larvae which look like fat bumbling Chrysomelinae. However, among the latter they are unique in retaining plesiomorphic features of the aedeagus and ovipositor. To test whether this indicates different ancestry I have treated the two tribes of Chrysomelinae separately: Timarchini and Chrysomelini. Among the Eumolpinae there are several genera which I consider to belong to the tribe Spilopyrini and which retain many plesiomorphies (Reid, in preparation). This tribe, including *Cheiloxena*, *Macrolema*, *Spilopyra*, *Richmondia* (Reid 1992b), *Bohumiljanina*, *Hornibius* and *Stenomela*, is distinct

in the Eumolpinae but similar in some respects to Synetini. The traditional Eumolpinae are therefore treated as two groups: Spilopyrini and Eumolpini *s.lat.* (remaining genera). At present, the non-spilopyrine Eumolpinae are listed under 11 tribes. The definitions of these are so feeble that treating them all under Eumolpini seems a reasonable option. The traditional subfamilies Synetinae and Megascelidinae are considered separately, but named as tribes of Eumolpinae in accordance with the proposed phylogeny. Classification of Synetini within Eumolpinae has already been implied by Crowson (1992) and the Megascelidini were placed in Eumolpinae by Bechyné and Bechyné (1969).

Character analysis

In the following discussion, the characters are numbered according to sequence in the data matrix and the designated states are numbered in brackets. The complete matrix of taxa and assigned character states is given in Table 2.

ADULT MORPHOLOGY (CHARACTERS 1–46)

HEAD. — (characters 1–11). There are two basic types of mouthparts for all taxa in this study: either pollen (granule) feeding in both adult and larva, considered plesiomorphic by Mann and Crowson (1981), or flower or foliage feeding. Mandibular structures in Chrysomelidae were reviewed by (Sakai 1983) who noted important and consistent differences between the higher taxa. Mouthparts for granule consumption are relatively complex, with a mandibular mola, large bilobed membranous ligula and densely fringed labium, galea and lacinia. Leaf-chewing mouthparts have lost these features.

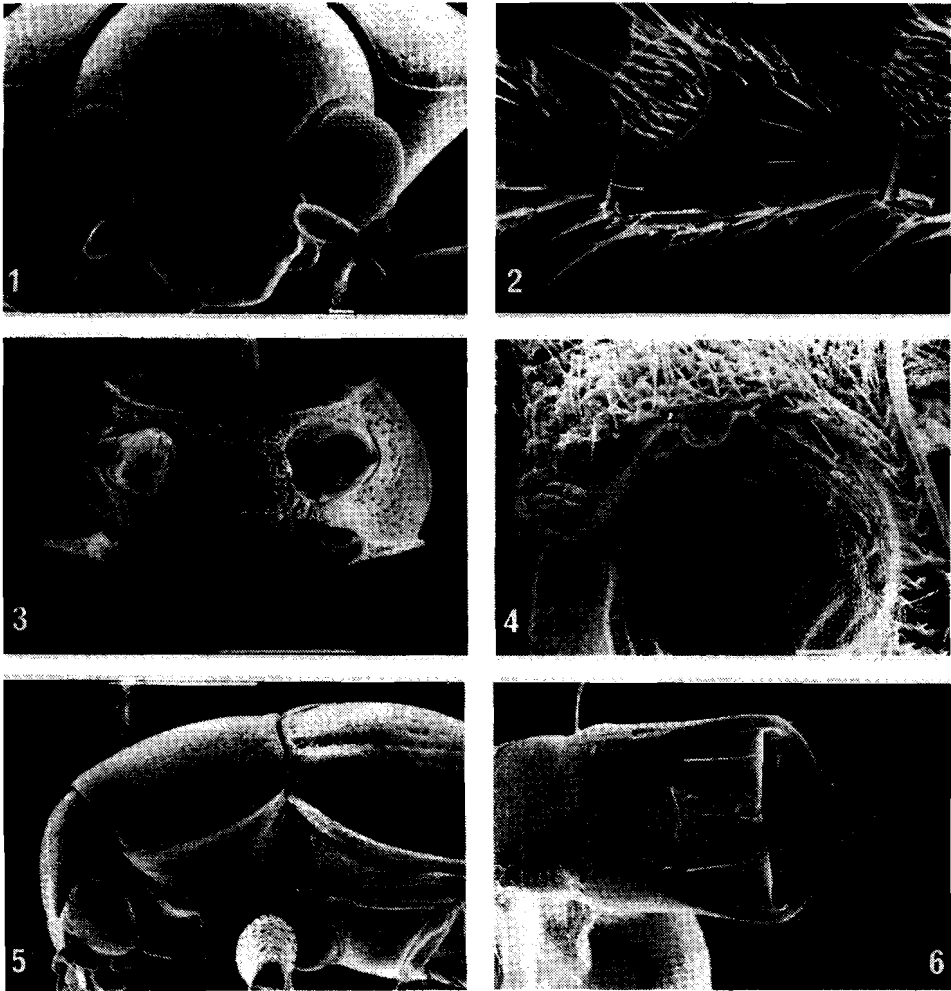
- 1: elongate internal mandibular prosthema strongly setose (0), membranous with setose fringe (1) or absent (2). The mandibles of *Orsodacne* and *Aulacoscelis* have setose membranes, not indicated by Mann and Crowson (1981).
- 2: basal prosthecal lobe present (0) or absent (1). In some taxa a small lobe or tuft of setae is present at the base of the internal face (Fig. 13).
- 3: mandibular mola present (0) or absent (1). The mola is a prominent flattened area at the base of the internal margin.
- 4: ligula not free or at most a single membranous sheet (0; Fig. 14) or large and bilobed (1; Fig. 15). The ligula is frequently not expressed or is split but fused to the floor of the mouth, or is prominent but as a single lobe. I have coded all these states as (0).
- 5: labiomaxillary complex free (0) or mentum fused to gula (1). The derived state is confined to the outgroup.

The last segment of the maxillary palp has digitiform sensilla on the outer face (Honomichl 1980, Mann and Crowson 1984): sets of grooves, each with an elongate sensillum slotted into it. Attempts have been made to make use of

the patterns of these sensilla for phylogenetic analysis, but there is a problem of definition of pattern. Furthermore this is yet another character in which the derived state is a reduction.

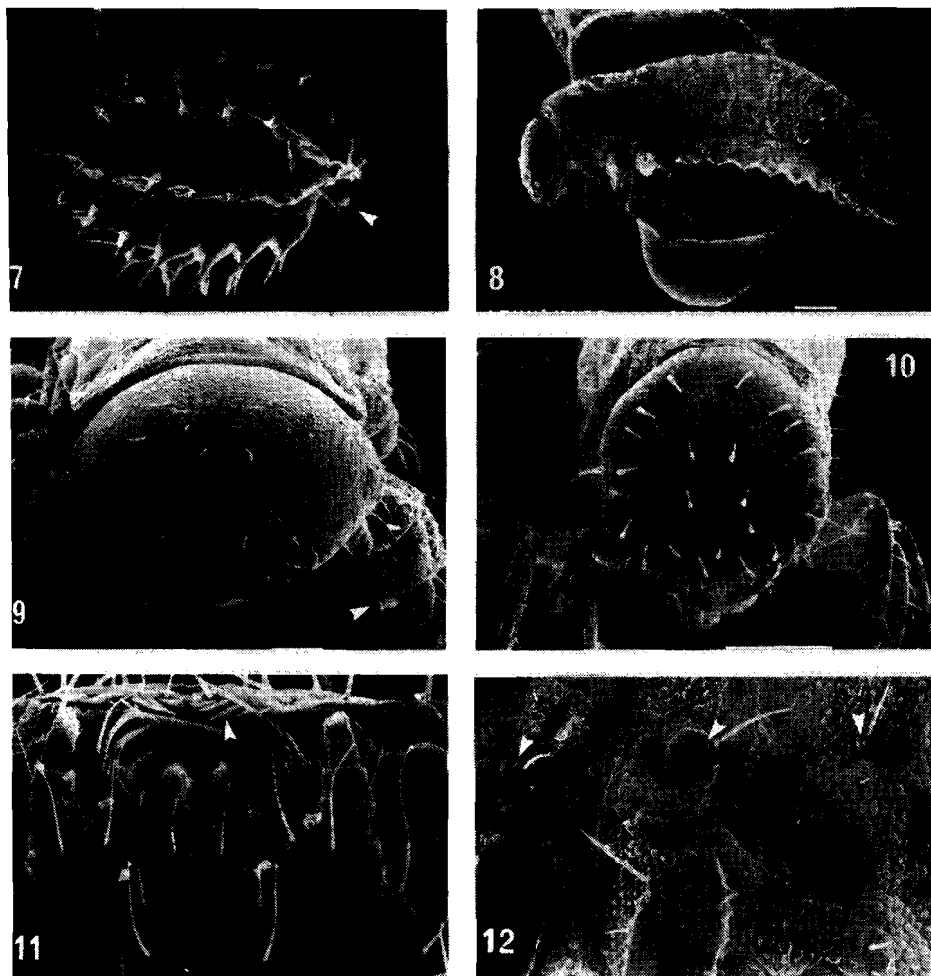
6: digitiform sensilla on apical maxillary palp segment in U-shaped arrangement (0) or otherwise arranged, sometimes reduced to less than 5 (1).

The structure of the front and middle of the head capsule is an obvious and apparently important source of variation in the Chrysomeloidea. Presence or



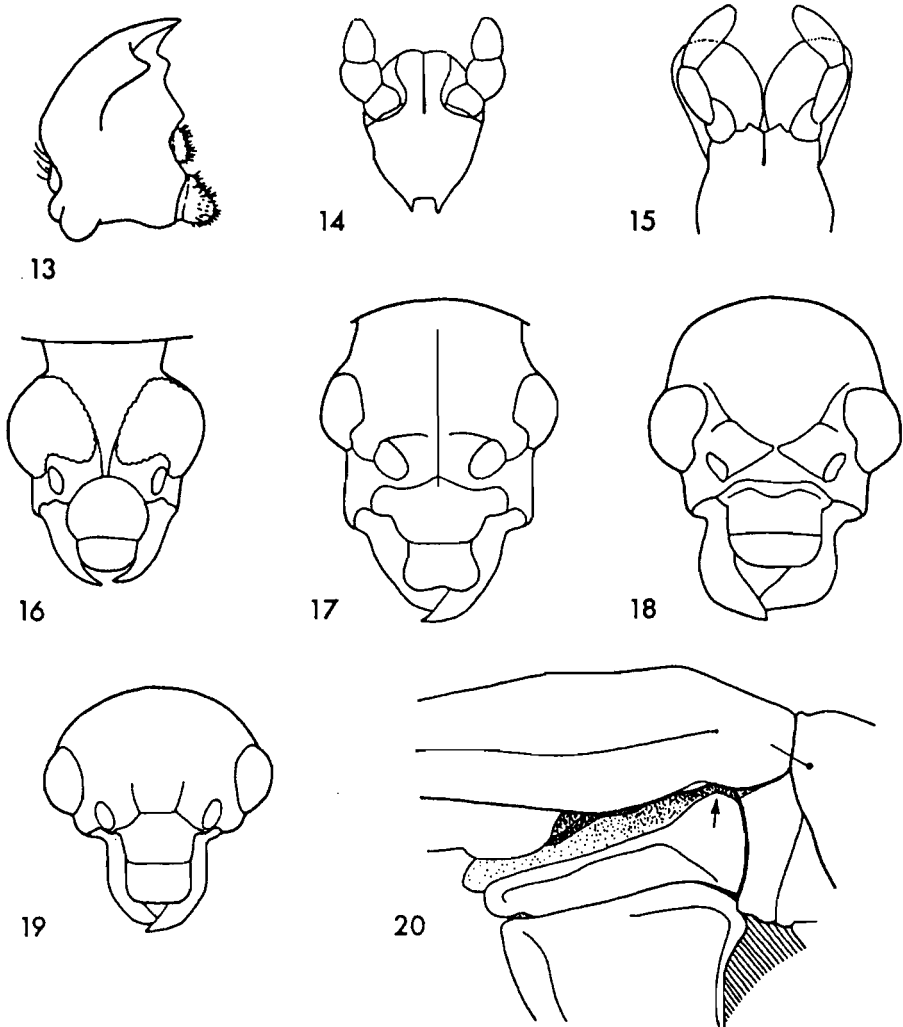
Figures 1-6. (1) Head of *Deretrichia* sp., anterior. (2) *Ditropidus* sp., antennal segment 8. 3-4. *Colasposoma sellatum* Baly: (3) prothorax, ventral; (4) interior of left coxal cavity. (5) Anterior part of *Deretrichia* sp., lateral. (6) Penis of *Leasia* sp., dorsal. Not to scale.

absence of a membranous anteclypeus, supposedly diagnostic for Galerucinae and Chrysomelinae, has not been included, because this character is hard to distinguish and appears to be present in some Cerambycidae, Eumolpinae, Cryptocephalinae and Hispinae. The presence of raised tubercles at the antennal bases is often used to define the Cerambycidae *s.lat.*, although similar structures are seen in Donaciinae and Parandrinae and a species of *Pseudotoxotus* (Sagrinae) lacks these tubercles.



Figures 7-12. (7) Egg-capsule (scatoshell) of *Diandichus* sp. (head of first-instar arrowed). (8) First-instar larva, *Edusella* sp., lateral. (9) First-instar larva, *Pyrgoides* sp., anterior (paronychial appendix arrowed). (10) First-instar larva, *Diandichus* sp., anterior. (11) First-instar larva, *Ditropidus* sp., mouth, ventral (apical epipharyngeal setae arrowed). (12) First-instar larva, *Aporocera* sp., eggburst, left side (note linear-cribriform spiracle on abdominal segment 1). Not to scale.

7: clypeus transverse, at or behind base of mandibles (0; Fig. 1), transverse to quadrate, projecting between mandibles (1; Fig. 16) or fused with frons and not distinguishable or at least not functioning as a separate sclerite (2). State (2) is confined to the outgroup.



Figures 13–20. (13) Right mandible of *Spilopyra* sp. 14–15. Ligula: (14) *Syneta* sp.; (15) *Aulacoscelis* sp. 16–19. Head capsules: (16) *Pachymerus* sp.; (17) *Strangalia* sp.; (18) *Megamerus* sp.; (19) *Orsodacne* sp. (20) Right lateral view of meso- and metathorax, *Lema* sp. (metepisternal spur arrowed). Figures 14–15 redrawn from Mann and Crowson (1981). Not to scale.

- 8: antennal tubercles separate, without median or X-grooves (0; Fig. 1), adjacent with median groove between (1; Fig. 17), adjacent with X-grooves between (2; Fig. 18) or separate with a quadrate depression between (3; Fig. 19). These are mutually exclusive states, but are not obviously related to each other. Similar H- or W-shaped grooves are seen in a few species of Chrysomelinae and Eumolpinae but in these the antennae are widely separated (Fig. 1).
- 9: no rostrum (0) or rostrum present, or at least both prolongation and expansion of frontoclypeus anterior to antennal insertions (1). A rostrum is almost always present in the outgroup taxa Nemonychidae (Kuschel 1994) and Belidae (Zimmerman 1994), and usually in Anthribidae (Zimmerman 1994).

Eye shape has not been used in analyses. All or many representatives of certain taxa may have either a deep invagination or canthus on the inner margin of the eye (Fig. 18), or have simple eye margins (Fig. 19), but in most larger subfamilies both states are present. Eye structure has also been ignored. Schmitt *et al.* (1982) studied the rhabdom in 108 species of Chrysomeloidea and Cerambycoidea. Two patterns in arrangement of microvilli were discriminated (1) "insula" = Lepturinae, Cerambycinae (part), Lamiinae (part), Bruchinae, Megalopodinae, Orsodacninae, Donaciinae, Criocerinae, Clytrinae, Cryptocephalinae, Galerucinae, Eumolpinae, Hispini, Cassidini, and (2) "ponticulus" = Prioninae, Disteniidae, Aseminae, Cerambycinae (part), Lamiinae (part), Timarchini, Chrysomelinae. They noted that the ponticulus pattern is better for low light activity and is correlated with nocturnal taxa, for example nocturnal Prioninae, Cerambycinae, Chrysomelinae. Subpatterns of rhabdomeres are scattered through both Cerambycidae and Chrysomelidae or are unique types. For phylogenetic studies there is nothing new or useful in this because of the simple correlation between rhabdom pattern and nocturnal or diurnal activity in individual taxa.

The antennae are variably structured, but rarely in a way that is common to all members of a subfamily. Frequently morphological variation is due to secondary sexual characters. Proportions of the first three segments, frequently used for delimiting genera, are correlated with the method of flexure of the antennae and often with the length of the genae. Other conspicuous features, such as well-defined sensillary pits at the apices of segments, may be present or absent in both Eumolpinae and Cryptocephalinae (Fig. 2). Antennal shape has been a traditional character in chrysomelid classification, and I have tried to represent this in Characters 10–11.

- 10: at least segments 4–8 similar in width to 1–3 (0) or segments 4–8 expanded at their apices, broader than 2–3, *i.e.*, antennae serrate from segment 4 (1).
- 11: last 3 segments of antennae same as others (0) or all expanded or elongated (usually as a club) (1). The derived state is only present in the outgroup.

THORAX. — (characters 12–30). The glandular defence system in the pronotum and elytra has been extensively reviewed recently (Pasteels and Rowell-Rahier 1989) and the following summary is from this work. Chemical defences probably evolved independently in larvae and adults. In adults, glandular morphology and secretion chemistry are not intrinsically related. Gland structure in chrysomelids is unusual for insects (no common reservoir, large numbers, particular distribution on pronotum and elytra), which strongly argues for common origin of the glands (Pasteels and Rowell-Rahier 1989). Glands are present in Criocerinae, Chrysomelinae, Alticinae (not all), Galerucinae (not all). Glands are absent from Donaciinae, Zeugophorinae, Clytrini, Cryptocephalini, Hispini, Cassidini. I have looked unsuccessfully for glands in Megalopodinae, Orsodacninae, Aulacoscelidinae and Sagrinae.

12: defence glands in pronotal and elytral cuticle absent (0), or present, of the type noted above (1).

Absence of lateral pronotal margins has been considered an apomorphy for the Curculionoidea, Cerambycoidea and Chrysomeloidea (Crowson 1955), with numerous subsequent reversals. The argument for this polarity is circular: the supposedly primitive taxa do not have lateral margins therefore lateral margins are primitive to the whole group. In fact lateral margins are present in at least one taxon of many plesiomorphic subfamilies (e.g., *Palophagus* in Palophaginae; *Carpophagus* in Sagrinae; widely in Anthribidae) and may be both present and absent within a genus (*Microdonacia*: Reid 1992c). Crowson (1981: 676–7) notes the presence of lateral margins in early fossils of Curculionoidea and Chrysomeloidea.

13: pronotum laterally margined (Fig. 5) or at least partially so (0) or not laterally margined (1).

The shapes of the procoxal cavities and the associated prosternal process are extremely variable in Chrysomeloidea, often within subfamilies. Most taxa include members with externally closed procoxal cavities, with closure effected by the hypomerall lobe slotting into the prosternal process (Fig. 4). The procoxae may vary in shape and prominence, depending largely on convexity of the prosternal process, but because of difficulties in determining discrete states I have not included such characters. In some taxa with antennal slots on the prosternal process, the lateral prosternal spurs may be obliterated.

14: middle of prosternal process simple (0) or with a lateral spur into each coxa and coxae therefore internally excavate (1; Figs. 3–4). This spur may be difficult to see because it is internally deflexed (Fig. 4)

15: pronotal hypomerall lobes short or locking into prosternal process (0) or lobes long and overlapping behind short prosternal process (1).

The stridulatory file of the mesoscutum is discussed under “stridulation” below.

Crowson has noted the presence of lateral spurs from the apex of the mesosternal process into the mesocoxae in some taxa (Crowson 1992).

16: mesosternal process simple (0), or with lateral spurs into coxae (1).

17: mesocoxal cavities open (0) or closed, through junction of mesosternum and metasternum (1; Figs. 5, 20). The derived state is confined to the out-group.

Elytral structure has not been used in this analysis. Possible useful sources of phylogenetic information include distribution of wing-folding spicule patches (Hammond 1979) and the type of locking mechanism along the suture. There is generally a well-marked epipleuron, a raised margin along the suture which may flatten out to form a line parallel to the suture, and a scutellary striole. Underneath the base of the elytra, the metanotum appears to be almost constant in structure, except that it may be absent in apterous species.

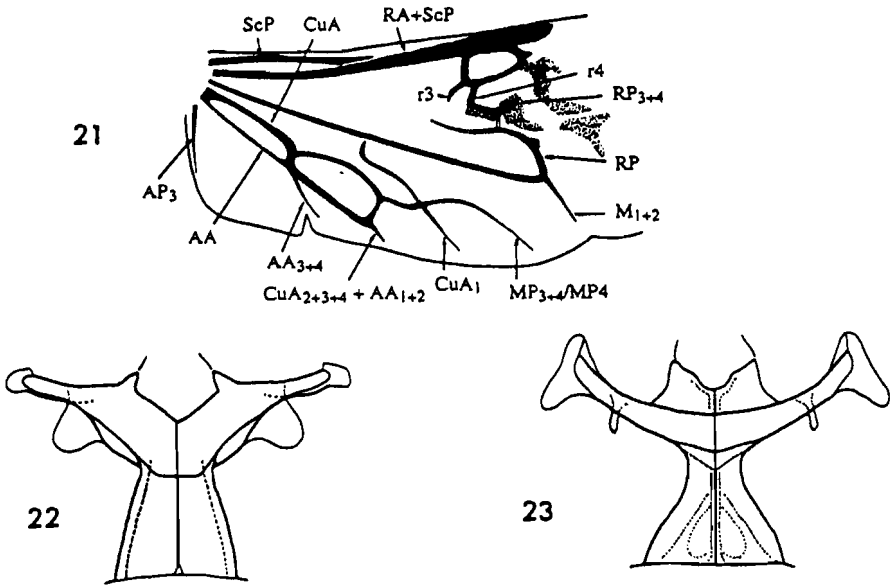
Wing venation has fortunately been mapped for almost all genera of the chrysomelid lineage by Jolivet (1957, 1959) and wings of the plesiomorphic weevils have recently been illustrated (Zimmerman 1994). A modern nomenclature for coleopteran wing structures which allows comparison with other insect orders is provided by Kukalová-Peck and Lawrence (1993). An appropriately labelled wing of *Megascelis* is shown here (Fig. 21), which should be compared with a similarly structured wing illustrated by Suzuki (1994). The most important part of the wing has previously been referred to as the anal region, but the multibranched veins in this area originate from the Median, Cubitus and Anal veins. The problems of using wing venation for phylogenetic analysis include: (a) character coevolution – the aerodynamic function of the wing probably requires that the veins do not exist in isolation from each other, and that any reduced venation will require the same pattern of veins for structural stability; (b) a few taxa lack wings; (c) wing venation is another set of progressively lost features, which may be non-homologous, and which are presumably irreversible. Close relatives may show markedly dissimilar venation, for example *Cucujopsis* and *Palophagus* (Kuschel and May 1990), and in Eumolpinae (Jolivet 1959). There is a widespread “complete” wing venation which is almost identical in many taxa of different subfamilies (Fig. 21), which is quite clearly plesiomorphic by comparison with other Polyphaga (Crowson 1955; Kukalová-Peck and Lawrence 1993). This venation is notably completely lacking in some chrysomelid taxa, including whole subfamilies, which usually have a much reduced anal area (area posterior to MP_{1+2}). In subfamilies with both types of venation, I have used the most plesiomorphic set of venation known for each group.

18: 2 cubito-anal cells, i.e. including wedge cell, present (0) at most 1 elongate basal cell present (1).

19: apical branches of “anal” veins 5 (0), 4 (1), 3 (2) or 2 (3).

20: MP_{3+4} connected to MP_{1+2} or almost so (0) or not connected (1).

- 21: AA₃₊₄ present (0) or absent (1).
 22: CuA₁ + MP₄/MP₃₊₄ forked, *i.e.* fused at base (0), both free (1) or reduced to single vein (2).
 23: CuA₁ connected to cubito-anal cell(s) (0) or not connected (1).
 24: RP₃₊₄ spur absent (0) or present (1). The plesiomorphic state is almost confined to the outgroup.



Figures 21–23. (20) Basal half of wing of *Megascelis* sp., with major veins labelled after Kukulová-Peck & Lawrence (1993). 22–23. Metendosternite, posterior view: (22) *Spilopyra sumptuosa* Baly; (23) *Pachybrachis* sp. Not to scale.

The sclerites between the elytra and metasternum are variably shaped and often ridged at the margins. Internally there are spiculate patches which lock the wings or elytra and which have not been studied in Chrysomeloidea.

- 25: dorsal margin of metepisternum simple (0; Fig. 5) or with a short spur or keel slightly overlapping and usually projecting into eytral epipleuron (1; Fig. 20).
 26: surface of metepisternum simple (0; Fig. 5) or with anterior corner demarcated by a curved keel or raised area (1; Fig. 20).

There are internally projecting endosternites raised from the posterior margin of the floor of each thoracic segment. In the prothorax the endosternite is a pair of short lobes each with a short external branch (often lost). In the mesothorax the endosternite is a pair of thin twisted rods, more obviously laterally bran-

ched and close to the mesocoxal cavities. In the metathorax the paired lobes or arms are set on a basal stalk. At the base of the arms there may be a transverse lamellar plate or, more often, this plate is reduced to subsidiary lobes situated along the arms, or is absent. The metendosternite of various Chrysomeloidea has been studied by Crowson (1938, 1944). However, this is yet another character reduction sequence and the more plesiomorphic taxa in various subfamilies often have the more complex metendosternite (e.g., *Spilopyra* in Eumolpinae, Fig. 22, *Pachybrachis* in Cryptocephalinae, Fig. 23).

27: metendosternite, at its most complete, with broad lamellar plate at base of arms (0), with apical lamellar lobes, usually small (Fig. 23), rarely larger (Fig. 22) (1) or reduced to simple T or Y shape (2).

Leg structure is relatively invariable in the Chrysomeloidea and few characters have been examined. The presence of swollen hind femora is scattered but is not universal in subfamilies and is hard to define. In a few species the femora may be sexually dimorphic. The pair of articulated spurs on each tibia (plesiomorphic in Coleoptera) may be reduced in number or lost. At least one spur is present on one pair of tibiae in more taxa than indicated by Crowson (1955, 1992), for example many Eumolpinae (e.g., *Lypesthes*) including Megascelidini (one spur on hind tibia), and Cryptocephalinae (e.g., *Pachybrachis*). Presence or absence of tibial spurs was therefore discarded as a character. The presence of an articulated tarsal empodium is included here, but is not always easy to identify. It is a setose lobe between the claws (Crowson 1955).

28: tarsal empodium absent (0) or present (1).

The structure of the tarsal ventral setae has been reviewed for Chrysomeloidea by Stork (1980) and Mann and Crowson (1981). Bifid setae are found on the tarsi of Sagrinae, Bruchinae, Donaciinae, Criocerinae and Hispinae. The occurrence of these setae on individual tarsomeres is variable in Bruchinae, Sagrinae and Criocerinae, in which bifid setae may be confined to the third tarsomere (*Caryedon*, *Sagra*, *Oulema*) or present on all (*Bruchus*, *Carpophagus*, [contra Mann and Crowson] and *Lilioceris*). Bifid setae are on the third tarsomere only in all Donaciinae and on all 3 basal segments in all Hispinae. For Schmitt (1989: 531) there "is no argument in favour of convergency [sic]", therefore this group of taxa is treated by him as a monophyletic unit. Setulose spatulate setae, i.e. spatulate setae with small prominences on the apical surface (Stork 1980) are distinct when present, but also occur in the Cerambycidae.

29: bifid tarsal setae absent (0) or present (1).

30: setulose spatulate adhesive setae absent (0) or present (1).

ABDOMEN.— (characters 31–32). The abdomen and its contents, apart from sexual structures, has not been studied in great detail in Chrysomeloidea. At extremes, the tergites and pleurites may be almost rigidly connected or lacking

(apterous species). Position of the spiracles varies more than has been suggested (Kasap and Crowson 1976)— they may be in the pleural membrane or the tergite in both Clytrini and Cryptocephalini (Reid 1990). Fusion of sternites is sufficiently rare to provide only autapomorphies for individual subfamilies.

31: sternites 6–7 free (0) or fused, although line of junction may be distinct (1).

The gut and nervous systems of Curculionoidea have recently been reviewed (Calder 1989). These systems were studied by Mann and Crowson in Chrysomelidae (nerve cord: Mann and Crowson 1983c; gut: Mann and Crowson 1983b). There is a tendency for apical abdominal ganglia to fuse, but it should be noted that relatively few taxa have been examined. Gut morphology has been examined for a few taxa. In Curculionoidea there is variation within subfamily of anterior insertion of Malpighian tubules and development of midgut papillae and similar variation is evident in the few Chrysomeloidea studied. Midgut caecae are present in a few taxa of Chrysomeloidea (including Spilopyrini) and midgut papillae are both present and absent in Spilopyrini. None of these gut characters are included here because too little information is available. The structure of the rectum is discussed under female abdomen.

32: abdominal ganglia 7–8 fused (0), 6–8 fused (1) or 5–8 fused (2).

MALE ABDOMEN. — (characters 33–41). The externally visible sternites of the male abdomen are often modified, but in ways that are most appropriate for species-group recognition. There appears to be a relatively consistent rectangular invagination (often only visible by dissection) in some taxa.

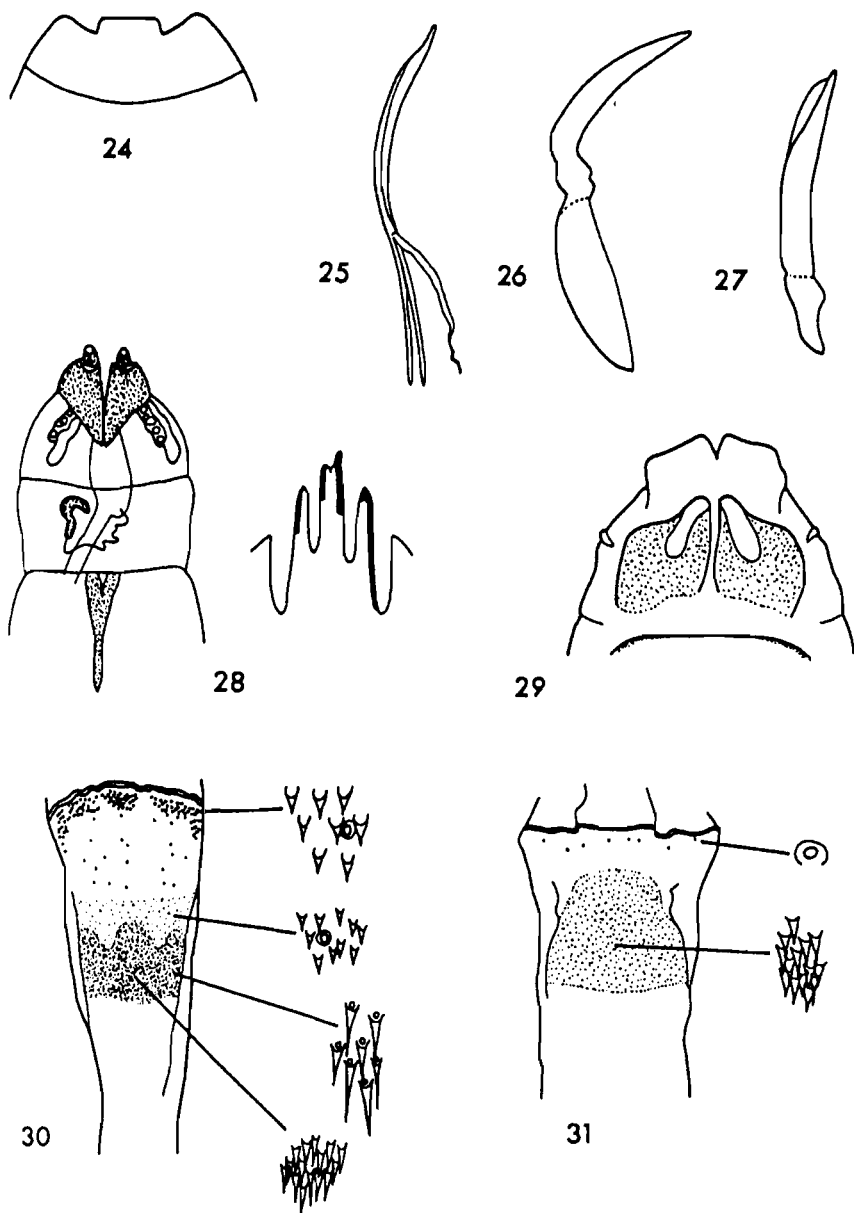
33: apex of last male ventrite simple (0) or with rectangular extension or invagination (1; Fig. 24).

Aedeagal morphology has been reviewed by several workers and recently diagnoses were given of the three families recognized here, based largely on aedeagal structure (Kuschel and May 1990). The form of the tegmen varies enormously, from a complete sheath with bilobed apex enclosing the penis to two tiny ventral struts. The tegminal manubrium, a keel at the base of the tegmen, is difficult to define, but present in more taxa than has been suggested by Schmitt (1985).

34: tegmen with complete ring around penis (0) or reduced to ventral Y or V (1).

35: base of tegmen simple (0) or deeply keeled (1).

The structure of the penis is also diverse, especially in those taxa with fusion of the median struts which has allowed strengthening of the whole organ and diversification of the apex. Setae on the apex of the penis, supposedly diagnostic for Camptosomata, are also present, but rare, in Galerucinae (Reid 1992c) and Eumolpinae (Reid 1993b). The transverse ridge present at the anterior margin of the foramen in some taxa (Chen 1985) is not included because it is



Figures 24–31. (24) Apex of male abdomen, *Calomela* sp. 25–27. Penis: (25) *Palophagus* sp.; (26) *Megascelis* sp.; (27), *Micrantipha* sp. (28) Ovipositor *Megascelis* sp., ventral (extruded) and lateral (retracted). (29) Ovipositor *Syneta*, ventral. 30–31. Rectum, dorsal view, kotpresse stippled: (30) *Syneta adamsi* Baly; (31) *Eupales ulema* Germar. Figure 25 redrawn from Kuschel and May (1990). Not to scale.

difficult to quantify and may only be of patchy occurrence in the larger taxa.

36: aedeagal median struts free (0; Fig. 25) or fused (1; Fig. 26).

37: penis setae absent (0) or present on apex (1; Fig. 6).

38: base of penis with foramen roughly equal to apical lobe (0; Fig. 26) or foramen much shorter than apical lobe (1; Fig. 27).

Soft parts of chrysomelid male and female genitalia have been studied by Mann and Crowson (1983a, b) and Suzuki (1988) and have recently been reviewed for Curculionoidea (Calder 1990). From these character systems Suzuki diagnosed seven 'phyletic lineages' for the Chrysomeloidea.

39: lobes of testes 2 + 2 (0), 1 + 1 (1) or fused together as 1 (2).

40: vas deferens long, accessory gland distant from testis (0) or accessory gland adjacent to testis (1).

41: one accessory gland (0) or more than one accessory gland (1).

Sperm structure has been investigated in a few species of Chrysomeloidea (Baccetti and Daccordi 1988) and there is evidently considerable variation, but not enough information is available to make any phylogenetic sense of this variation.

FEMALE ABDOMEN.— (characters 42–46). Externally, the female abdomen is rarely specially modified. The apex may be shallowly or deeply hollowed. In Cryptocephalinae and Lamprosomatinae this is the point of rotation of the egg as it is coated in faeces, but the function in other taxa is unknown.

42: female apical ventrite simple (0), with small deep non-setose apical hollow, less than third length of segment (1) or with large deep usually densely setose hollow (2).

Internally, segments 8–9 provide various sclerites for the ovipositor which varies greatly in development (Kasap and Crowson 1985). In some taxa the whole ovipositor has stout sclerites and is relatively rigid. Reduction of the vaginal palp (coxite plus stylus) to a single fused segment is common in several subfamilies.

43: ovipositor telescopic, sclerites elongate (0; Fig. 28) or not telescopic, with broad sclerites in a rigid structure (1; Fig. 29).

44: spiculum gastrale of ovipositor present (0) or absent (1; Fig. 28).

The spermatheca is generally strongly sclerotised and falcate, with a gland arising from the base. There are many deviations from this form, but they rarely characterise a subfamily.

In some taxa, the rectum is specially modified with a kotpresse (Erber 1968), with at least dense patches of posteriorly directed spines, to provide a coating for the egg (for example *Syneta*, Fig. 30, and *Eupales*, Fig. 31, in Eumolpinae).

Sclerotised rectal plates are unique to the Cryptocephalinae (Erber 1968; Reid 1990).

45: kotpresse absent (0) or present (1; Figs. 30–31).

In some taxa, vaginal pouches are present, which are possible storage organs for microbes or are secretory (colleterial) glands for the egg-coverings (Mann and Crowson 1983b; Becker 1994). Mann and Crowson suggested that they are symplesiomorphic for Chrysomeloidea, but they may not be homologous and may also be present but not expressed as morphologically distinct organs, as in Hispinae (Hinton 1981).

46: vaginal pouches present (0; Fig. 28) or absent (1).

Ovariole number is too variable within subfamilies and even genera to be useful for phylogenetic study (Mann and Singh 1979).

STRIDULATION (character 47)

Stridulation is widespread in the taxa included here and has been recently reviewed (Schmitt 1992, 1994). The most common type involves the mesoscutum as the transversely grooved field (*pars stridens*) with the posterior margin of the pronotum as *plectrum*. This is found in scattered taxa: some Nemonychidae (Kuschel 1994), some Cerambycoidea, Megalopodinae, Zeugophorinae, Palophaginae (Schmitt 1992, 1994) and Clytrini (Reid 1990). In Clytrini the *pars stridens* is derived from flattening of lateral ridges and is clearly not homologous with the medially smooth type of the others. In all Criocerinae examined the *pars stridens* is on the pygidium, with the elytral apex as *plectrum* (Schmitt and Traue 1990; Schmitt 1992, 1994). A few Bruchinae have a *pars stridens* on the metepisternum, rubbed by the ventral tooth of the hind femora (Kingsolver *et al.* 1993). In some Hispinae, especially Hispini, there is a *pars stridens* on the posterior of the vertex, with the anterior of the pronotum as the *plectrum* (Schmitt 1985, 1992, 1994).

47: median mesonotal stridulatory files absent (0) or present (1).

KARYOLOGY

There are excellent reviews of the karyology of Chrysomeloidea by Petitpierre (1988) and Petitpierre *et al.* (1988). Some genera in various subfamilies show invariant or almost invariant chromosome number and combination type, whereas other genera display striking variation. Such variation includes: broad range of chromosome size including total complement length variation; total amount of DNA, even between related species; centromeres median or submedian; male sex-determining system Xyp being predominant and present in almost every subfamily. Karyologists tend to consider "common" as "primitive", but this is unacceptable for several reasons, including sample bias and failure to distinguish an ancestral state from one shared by a recent radiation of spe-

cies (Reid 1992a). At present levels of study, karyology is useless for chrysomelid phylogeny except at trivial levels, as already noted by Crowson (1994).

PALAEONTOLOGY

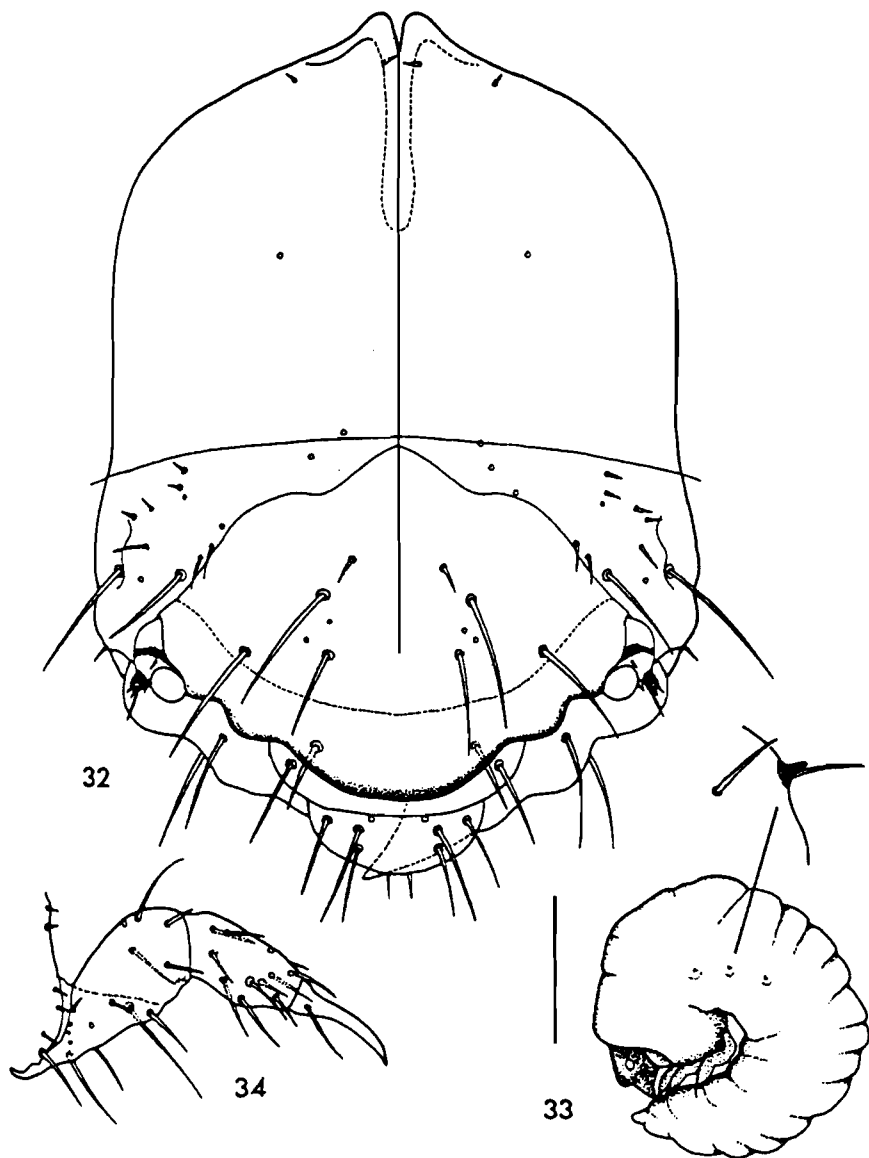
Fossils of Chrysomelidae have been reviewed (Santiago-Blay 1994) and my comments here largely refer to the illustrations in that review. Fossils are uncommon and either old and unrecognisable, or recent and clearly belonging to extant groups. Most fossils are very poorly described. They provide almost no information for phylogenetic studies because they rarely show any of the morphological features that provide synapomorphies in a cladistic analysis. A supposedly extinct subfamily, Protoscelidinae, which has been proposed as the stem group for the Chrysomeloidea (Medvedev 1971) does not show any features that exclude it from the Cerambycoidea. Other Mesozoic fossils are equally unrecognisable as Chrysomelidae. *Cerambyomima*, placed with Aulacoscelidinae by Kuschel and May (1990), has a longitudinally grooved frons, which excludes it from that subfamily. From the early to mid Caenozoic, *Eosagra*, a supposed sagrine from the Eocene of Europe, may equally belong to the Criocerinae or to some unknown extinct group. It has not been shown to display diagnostic characters of the Sagraeae. Mid-Caenozoic Baltic amber fossils are relatively common, but mostly are described in extant genera and are at least easily placed in chrysomelid subfamilies (Spahr 1981). These amber fossils need to be revised. Donaciine fossils are relatively plentiful and easily recognised, but they say almost nothing about the origin of the group except that it was certainly pre-Tertiary (Askevold 1990a). Phylogenetic problems in the Chrysomelidae can be resolved by reference to present day morphology and distribution (*e.g.*, Spilopyrini *q.v. infra*), without reference to fossils, although well preserved specimens may provide interesting phylogenetic and especially biogeographical information (Eucnemidae: Muona 1993). Fossils are not used in this analysis.

EGGS (character 48)

Chrysomeloid eggs are rarely studied in detail, as noted by Hinton (1981) who reviewed the early literature. In a few species they are stalked (Hispininae: Buzzi 1988; Cryptocephalinae: Erber 1988). The chorionic sculpture of *Cryptocephalus* (Cryptocephalinae: LeSage 1986a) and *Diabrotica balteata* LeConte (Galerucinae: Krysan 1987) is remarkably similar, yet the variation exhibited by different species of *Diabrotica* (Krysan 1987) suggests that chorionic sculpture would be difficult to analyse. Furthermore, the chorion is commonly coated in a smooth layer of spumaline (Credland 1992). A complete case constructed around each egg (scatoshell) from plates of faeces and other material produced by rectal compression is characteristic of two subfamilies. This egg protection is similar to the ootheca provided by some Hispininae, but in the latter

the faecal plates are produced by dorsoventral compression of the ninth segment (Hinton 1981), not by special rectal modification.

48: egg exposed or covered at site of attachment to substrate (0) or in scato-shell, which may be attached to substrate (1; Fig. 7).



Figures 32-34. First-instar larva of Sagrinae. (32) Head, dorsal. (33) Lateral view, with detail of egg-burster. (34), Fore leg. Scale line = 1mm.

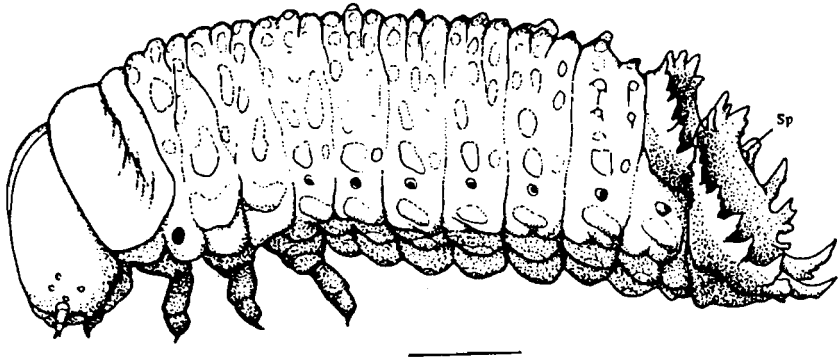


Figure 35. Late instar larva of *Allocharis* sp., New Zealand. Sp = spiracle. Scale line = 1 mm.

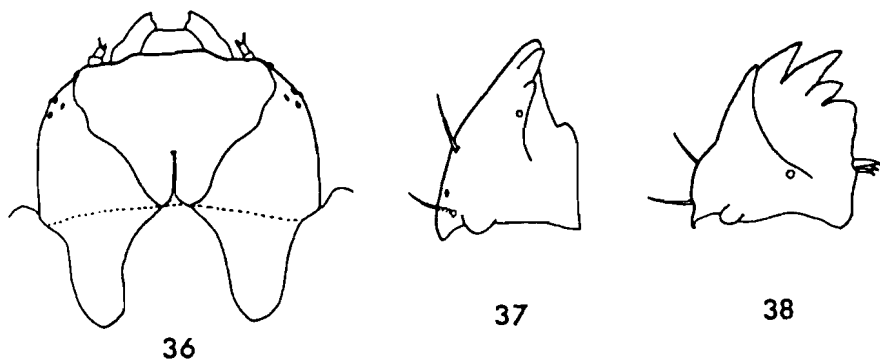
LARVAL MORPHOLOGY (CHARACTERS 49–71)

Larvae of Aulacoscelidinae, Megascelidini and Spilopyrini are unknown, and the larvae of Megalopodinae are relatively poorly described. There are excellent recent reviews of the larval morphology of the cerambycid lineage (Svachá and Danilevsky 1987) and Curculionoidea (May 1994), but there are no comprehensive reviews of larval structure for the Chrysomelidae *s. lat.* except studies of gross morphology (for example, Böving and Craighead 1931; Peterson 1951; Medvedev and Zaitsev 1978). Attempts have been made to determine homologies of setae and sclerites in individual subfamilies (Galerucinae: Takizawa 1972, LeSage 1986b; Chrysomelinae: Kimoto 1962; Cryptocephalinae: LeSage 1982, 1984a, 1984b, 1985, 1986a), but these have not been systematically compared. Most head capsule nomenclature (for example in LeSage 1982; Kuschel and May 1990) is derived from the work of Anderson (1947) on Curculionoidea, but a major problem with establishing setal homology on the head capsule is the change in setal configuration and loss of geographic markers associated with loss of stemmata as has occurred in Curculionoidea. It may also be difficult to determine homology of setae on the frontoclypeus and labrum, especially if these are fused. Furthermore, in some Chrysomelinae and Cryptocephalinae individual specimens often show bilateral asymmetry and variation in position and number of head setae (Fig. 10). Alternative setal nomenclatures, mostly derived from Paterson (1931), give no indication of how setae are to be identified. The naming of setae in the two systems for chrysomelids in current use is inconsistent; there are differences in the nomenclature of the vertical and genal setae between *Orsodacne* (Cox 1981) and *Phaedon* (Cox 1982) and between *Exema* (LeSage 1982) and *Cryptocephalus* (LeSage 1986a). A comprehensive review of larval setal patterns is required, but this is not the appropriate place. Another problem is in the comparison of different instars; in many fea-

tures the first instar is the least derived state and therefore most informative, but most published descriptions are of later instars, which frequently have different mandibles, spiracles or setal patterns. Head capsule sensilla patterns may also be useful for phylogenetic analysis but are at present little studied.

Larval gut morphology may provide useful characters (Mann and Crowson 1983b; May 1994), but as yet little information is available.

Each larval mode of life is associated with particular morphological types: the flattened leaf-miner with excavate posterior of the head; the fat bodied externally feeding caterpillar; the C-shaped inhabitant of galls, seeds or capsules of excrement. Have these modes of life evolved several times independently?



Figures 36–38. Larval structures. (36) Head of *Notosacantha* sp. 37–38. First-instar mandible: (37) *Edusella*; (38) *Geomela*. Not to scale.

HEAD.— Segmentation of the antennae and palpi, numbers of stemmata, structures of the mouthparts and formation of the capsule all provide useful characters (Fig. 32). Apart from mandible shape, these are features which rarely vary with instar. Head shape is apparently dependent on the life habit of the larva, e.g., broad and ovate in leaf-feeders (Fig. 9), operculate in scatoshell inhabitants (Fig. 10). I have not included presence or absence of the endocarina. A complete endocarina is probably plesiomorphic, but this feature is variably expressed and may be present or absent in Eumolpinae.

49: head normal (0) or head elongate, coronal suture much longer than frontoclypeus (1; Fig. 32).

50: epicranial suture present (0), absent, epicranial halves widely diverging (1; Fig. 36) or absent, epicranial halves proximal (2).

A tuft of hairs on the inner face of the mandible, the mandibular penicillus, is known from Orsodacninae, Hispinae and Galerucinae (Böving and Craighead

1931; Cox 1981; Costa *et al.* 1988), and is also present on the larva of *Geomela* in Chrysomelinae. It may often be overlooked. The mandibles vary considerably in shape but I have tried to reduce this to the two states discussed by Mann and Crowson (1981), either palmate or non-palmate. The palpi and antennae may be reduced in segmentation, although the reduced (basal) segments may also be present as thin rings. In Cryptocephalinae the apical epipharyngeal setae have migrated to the dorsal surface.

51: mandibular penicillus absent (0) or present (1; Fig. 37).

52: mandibles triangular with 1–5 teeth, 1–2 much larger (0; Figs. 32, 38) or mandibles broad, palmate, with 3–4 approximately equal-sized large teeth (1; Fig. 37).

53: labial palp segments 2 (0; Fig. 11), 1 (1) or 0 (2).

54: labrum free (0; Fig. 32) or fused to clypeus (1).

55: apical epipharyngeal setae ventral (0; Fig. 32) or dorsal (1; Fig. 11).

56: antennal segments 3 (0), 2 (1; Fig. 32) or 1 (2).

The number of stemmata varies in some subfamilies and even between instars (Prevett 1971). They may shallow and inconspicuous and may have been overlooked in some descriptions. Often eye spots are present but stemmata are not distinguishable. As the most plesiomorphic state in this loss sequence is preferred I have not distinguished between eye spots and stemmata.

57: stemmata or eye spots 6 (0), 5 (1), 4 (2), 3 (3), 2 (4), 1 (5) or 0 (6; Fig. 32).

Three features included here describe structures on the floor of the head which are absent from all Chrysomelidae.

58: labium and thorax separated by visible gula (0) or contiguous (1).

59: occipital foramen single (0) or divided into two (1). Svachá and Danilevsky (1987) suggest a single origin for the derived state.

60: hypopharyngeal bracon present (0) or absent (1).

BODY. — Most but not all chrysomeloid first-instar larvae have short thoracic and/or abdominal spines which are apparently homologous and usually functional egg bursters, although the sclerites may vary slightly in shape and position (Figs. 12, 33). The distribution of egg bursters in Chrysomeloidea, Cerambycoidea and Curculionoidea has been extensively reviewed (Gardiner 1966; Cox 1988, 1994; May 1994). The egg-burster sclerite appears to be phylogenetically informative (Cox 1988; 1994), but its identification is not always clear therefore I have not used this character. Homology of the egg bursters is not always certain and there is variation in numbers of egg bursters within genera, therefore I have not treated these characters as irreversible.

61: thoracic egg bursters on all segments (0), prothoracic absent (1; Fig. 12) or all absent (2; Fig. 33).

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62: abdominal egg bursters on segments I–VII or VIII (0), I–III (1; Fig. 33), I–II (2), I only (3; Fig. 12) or absent (4).

It is difficult to find other informative characters on the larval body. Particularly problematic is spiracle type, which appears to change with the instar. For example, the probably plesiomorphic biforous spiracle occurs in first-instar *Colasposoma* (Eumolpinae) but later instars have annular spiracles (Reid 1993c) and these are the instars that are usually described in Chrysomelidae.

63: spiracles of first-instar biforous (0), annular (1) or cribriform, including linear-cribriform (2; Fig. 12).

Ambulatory ampullae occur as swellings or outgrowths of the intersclerite membranes. Ventral ampullae are widespread in externally feeding larvae. Ampullae may not be homologous and it may be difficult to determine their presence because of their diaphanous nature. They may be overlooked in descriptions. Dorsal ampullae occur in many non-Chrysomeloidea and two plesiomorphic taxa, all of which are to some extent tunnel inhabiting. At least some of these larvae are able to crawl upside down (Kuschel 1994).

64: dorsal ampullae absent (0; Figs. 8, 33, 35) or present (1).

Some taxa have a pair of projections (urogomphi) on tergite 9 which may be fixed (Galerucinae: Böving and Craighead 1931) or articulated (*Orsodacne*: Mann and Crowson 1981) but may not be homologous.

65: paired urogomphi present on tergite 9 (0), or absent (1).

The shape of the anus has been considered a significant identification feature by some authors, but is not considered here because determination of character states is difficult. Further body characters included here have not been examined in a wide range of material.

66: larva without large EP–DLe sclerite at base of mid and hind legs (0; Figs. 8, 35), or with this sclerite greatly enlarged (1; Fig. 12).

67: abdominal venter with normal short setae (0), or with long stiff setae (1; Fig. 8).

LEGS.— Fully developed legs are retained by almost all Chrysomelidae (Figs. 8–10). Whole leg proportions have not been used, but it should be noted that short fat legs characterize the external leaf-feeding larvae (Figs. 9, 35). These larvae also generally have a soft extruded lobe at the apex of the tibiotarsus, the paronychial appendix.

68: paronychial appendix on tibiotarsus absent (0; Figs. 10, 34) or present, either single (Fig. 9) or bilobed (1).

69: pretarsus elongate, at least 2.5 times basal height (0;), short, 2 or less times basal height (1; Fig. 9) or absent (2).

70: femur of first-instar with normal setae (0) or with one very long median ventral seta (1; Fig. 34).

71: trochanters apparently articulated (0) or fused to femora (1; Fig. 34).

LARVAL DEFENCE

Larval defence is effected in many ways, especially among the external feeders. Greatly increased sclerotisation of the apical abdominal tergites is present in Orsodacninae and some Galerucinae and Chrysomelinae. In some species of *Allocharis* (Chrysomelinae), the apical plate acts a plug for the diurnal burrows of nocturnal larvae (J. Dugdale, *personal communication*; Fig. 35). The apical tergites of the *Syneta* larva are only slightly more sclerotised than the remainder of the body (Lee 1990) and the similarity of this larva to Galerucinae is only slight. Exserted glands are present in some Galerucinae (Takizawa 1972) and some Chrysomelinae (Kimoto 1962). Excrement may be retained, either carried dry over the body (some Hispinae), mixed with secretion as a moist layer on the body (all externally feeding Criocerinae), or mixed with secretion and other materials and carried as a case around the body (an extension of the scatoshell formed by the female parent, characteristic of Lamprosomatinae and Cryptocephalinae; *see* above, under eggs). Larval defences are not universal in subfamilies and have therefore not been used here.

PUPAE

Very few pupal descriptions are available and many of them are poor, therefore pupal characters were not included in the analysis. The exarate chrysomeloid pupa looks like a hybrid of larval and adult characters, therefore ignoring pupal characters could be justified because they repeat features of the other two developmental stages. However, the pupal setal system has little relationship to the larval system and other pupal features are unique, such as lobes or spines on the pronotum, elytral and leg thecae and abdomen. A modification of the setal nomenclature system for Curculionoidea (May 1994) has been applied to Chrysomelinae (Reid 1993a). The pupa of *Palophagus* is similar to that of Belidae (May 1994). The *Palophagus* pupa may represent the plesiomorphic type for Chrysomelidae, with a full complement of cephalic setae, plus setae in single rows on the abdominal segments and apically on the femora (Kuschel and May 1990), although it lacks the urogomphi present widely in Curculionoidea, Cerambycidae, Chrysomelinae and Galerucinae (Duffy 1960; Reid 1991, 1993a; May 1994). It is more similar to a belid pupa than to any cerambycid (May 1994).

Table 2. Character matrix for 29 taxa of Curculionoidea and Chrysomeloidea.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1 Nemonychidae	0	1	0	0	1	1	2	0	1	0	1	0	1	0	1	0	1	1	0	0	0	0	1	0	0
2 Belidae	2	1	1	0	1	1	2	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0
3 Anthribidae	2	1	0	0	1	1	2	0	1	0	1	0	0	0&1	7	0	1	1	1	1	1	1	1	0	0
4 Distenilidae	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
5 Anoplodermatidae	2	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0
6 Parandrinae	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0
7 Prioninae	2	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1
8 Cerambycinae	0	0	7	0	0	0	0	0&1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0
9 Lepturinae	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0&1
10 Vesperidae	2	1	1	0	0	0	0	1	0	0	0	0	0&1	0	0	0	0	0	1	0	1	0	0	1	0
11 Palophaginae	1	1	0	1	0	0	0	0	0	0	0	0	0&1	0	0	0	0	0	0	0	0	0	0	1	0
12 Megalopodinae	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	0	0	1	1	0
13 Zeugophorinae	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	2	1	1	0	1	1	0
14 Orsodacninae	1	0	0	1	0	0	1	3	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0
15 Aulacoscelidinae	1	0	0	1	0	0	1	3	0	0	0	0	0	0	0	0	0	1	2	0	0	2	0	1	0
16 Spilopyrini	1	0	1	0	0	1	0	0	0	0	0	0	0&1	0	0	0	0	0	1	0	0	0	0	1	0
17 Synetini	2	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	2	1	1	2	1	1	0
18 Eumolpini	2	0	1	0	0	1	0	0	0	0	0	0	0&1	1	0	1	0	0	1	0	0	0	0	1	0
19 Megascelidini	2	0	1	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	1	0
20 Lamprosomalinae	2	1	1	0	0	1	0	0	0	0&1	0	0	0	0	0	0&1	0	0	1	0	0	0	0	1	0
21 Cryptoccephalinae	2	1	1	0	0	1	0	0	0	0&1	0	0	0	0	0	0	0	0	2	1	0	2	1	1	0
22 Bruchinae	0	0	0	1	0	0	1	0	0	0&1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
23 Sagraeae	0	0	0	1	0	0	1	2	0	0	0	0	0&1	0	0	0	0	0	0	0	0	0	0	1	0
24 Donacinae	0	0	0	0	1	0	0&1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0
25 Ctiocerinae	0	0	0	0	0	1	0&1	2	0	0	0	1	1	0	0	0	0	1	3	1	1	2	1	1	1
26 Hispinae	2	1	1	0	0	1	0	0	0	0	0	0	0&1	0	0	0	0	0	0	2	0	0	2	0	1
27 Chrysomelini	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	2	0	1	0
28 Timarchini	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	7	7	?	?	?	?	?	0
29 Galerucinae	1	0	1	0	0	1	0	0	0	0	0	1	0&1	0	0	0	0	1	3	0	1	2	0	1	0

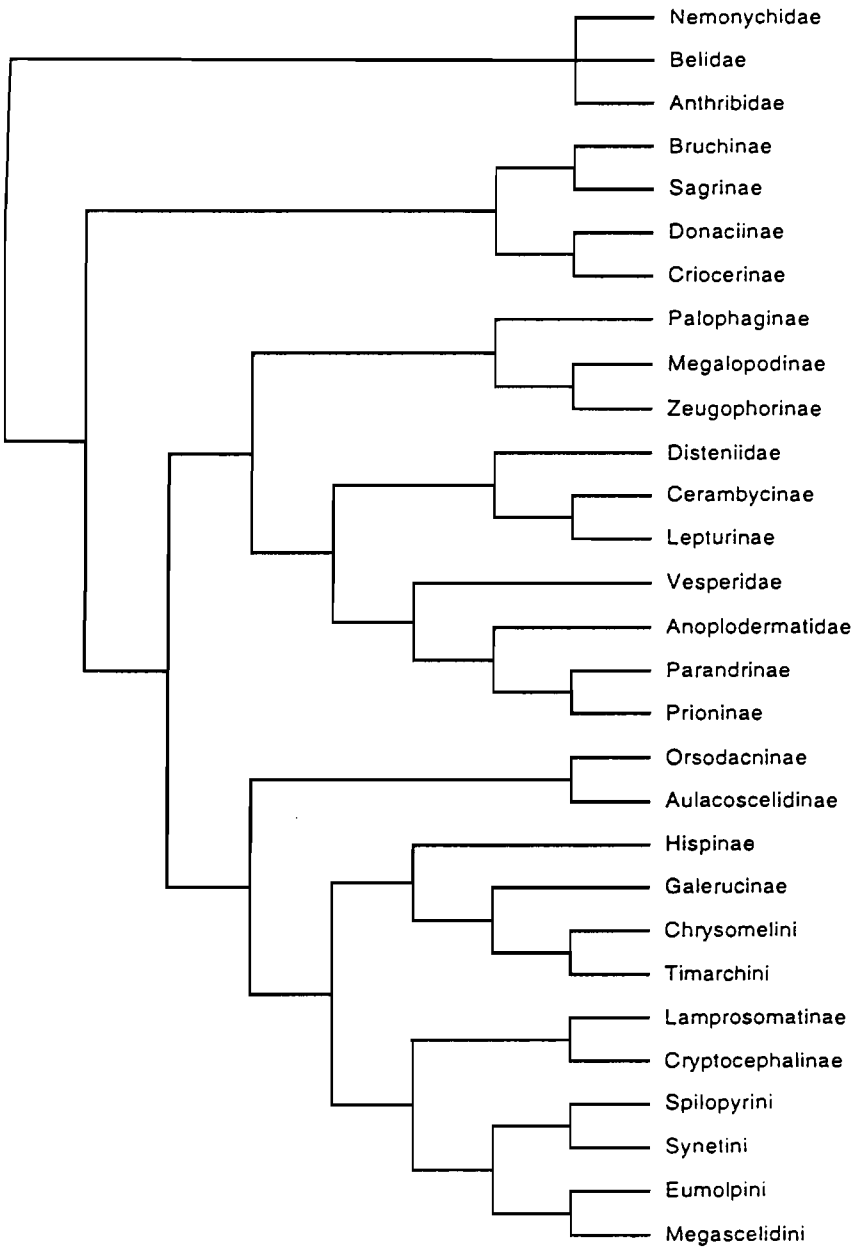


Figure 39. Strict consensus of two trees, 276 steps long, all characters unordered; Character 13 included.

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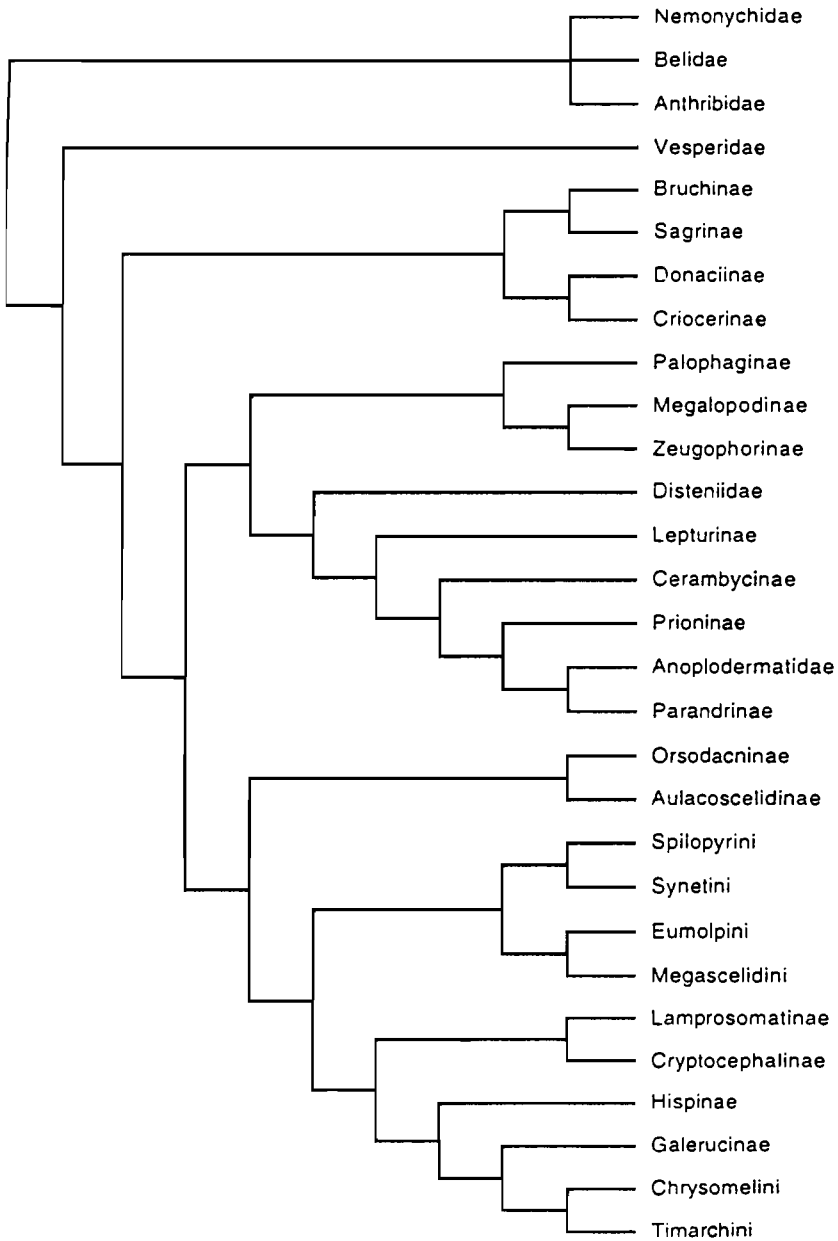


Figure 40. Strict consensus of two trees, 264 steps long, all characters unordered; Character 13 excluded.

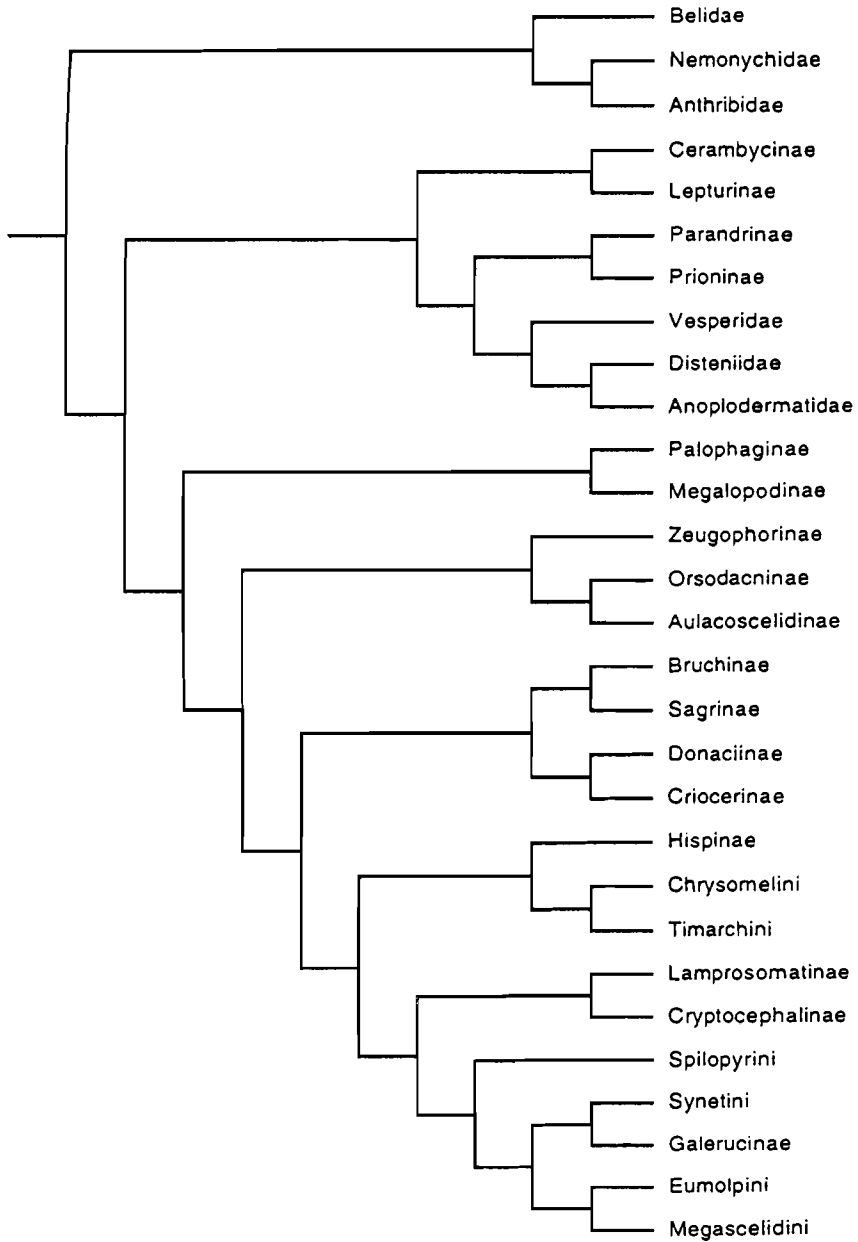


Figure 41. One of 10 trees, 305 steps long, character types as listed in text.

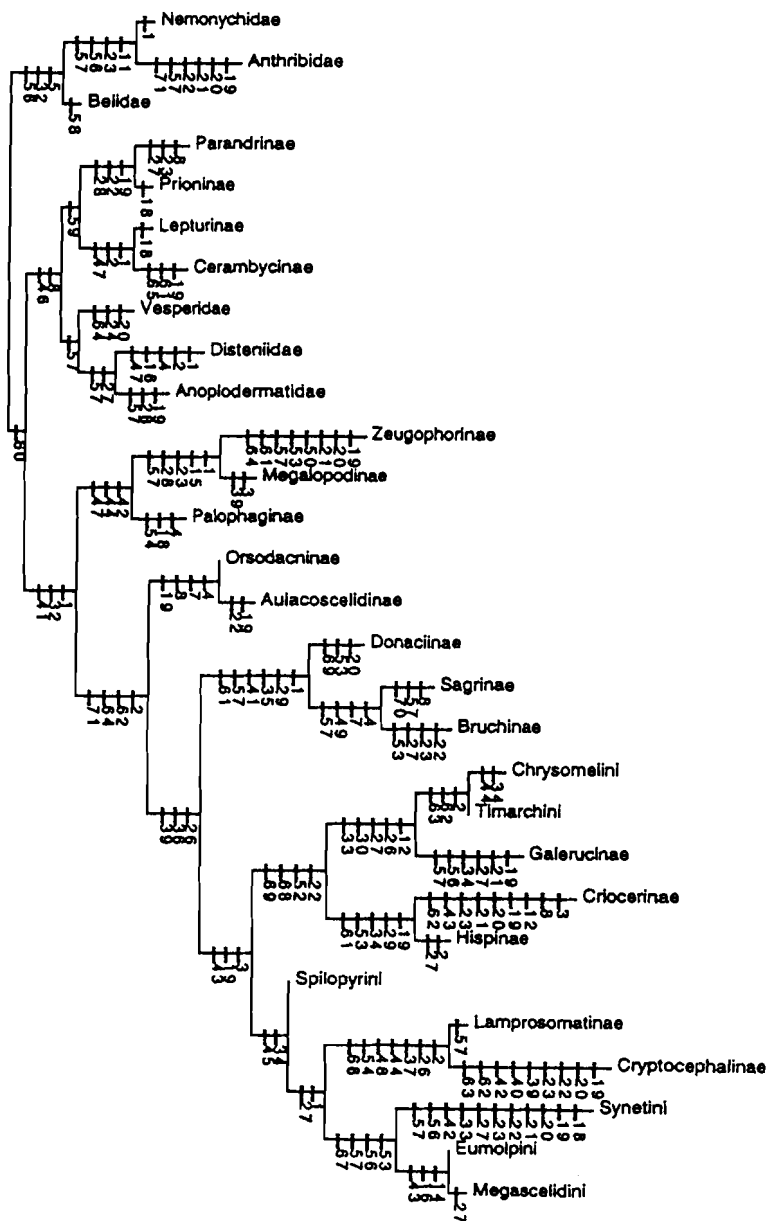


Figure 42. One of 10 trees, 305 steps long, character types as listed in text, weights equal, unequivocal character state changes marked. Taxa with bifid setae and Eumolpinae non-monophyletic.

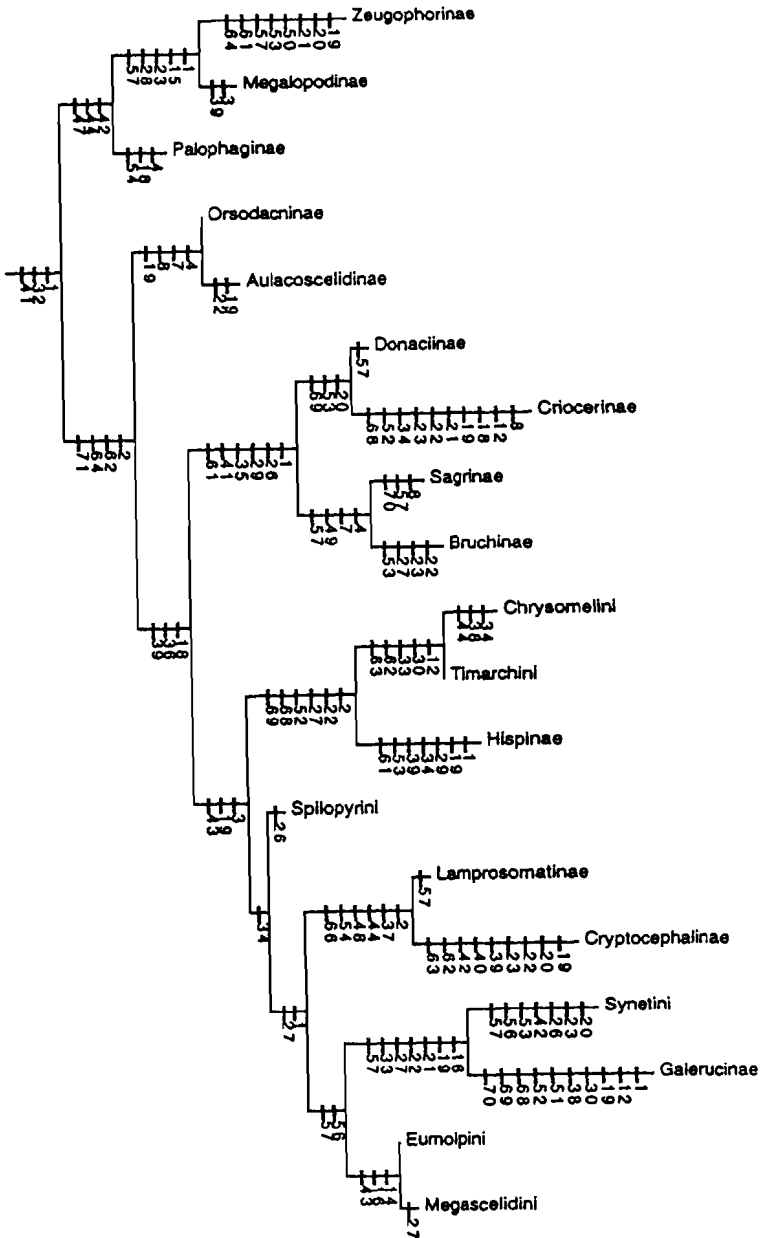


Figure 43. Part of one of 10 trees, 305 steps long, character types as listed in text, weights equal, unequivocal character state changes marked. Taxa with bifid setae and Eumolpinae non-monophyletic.

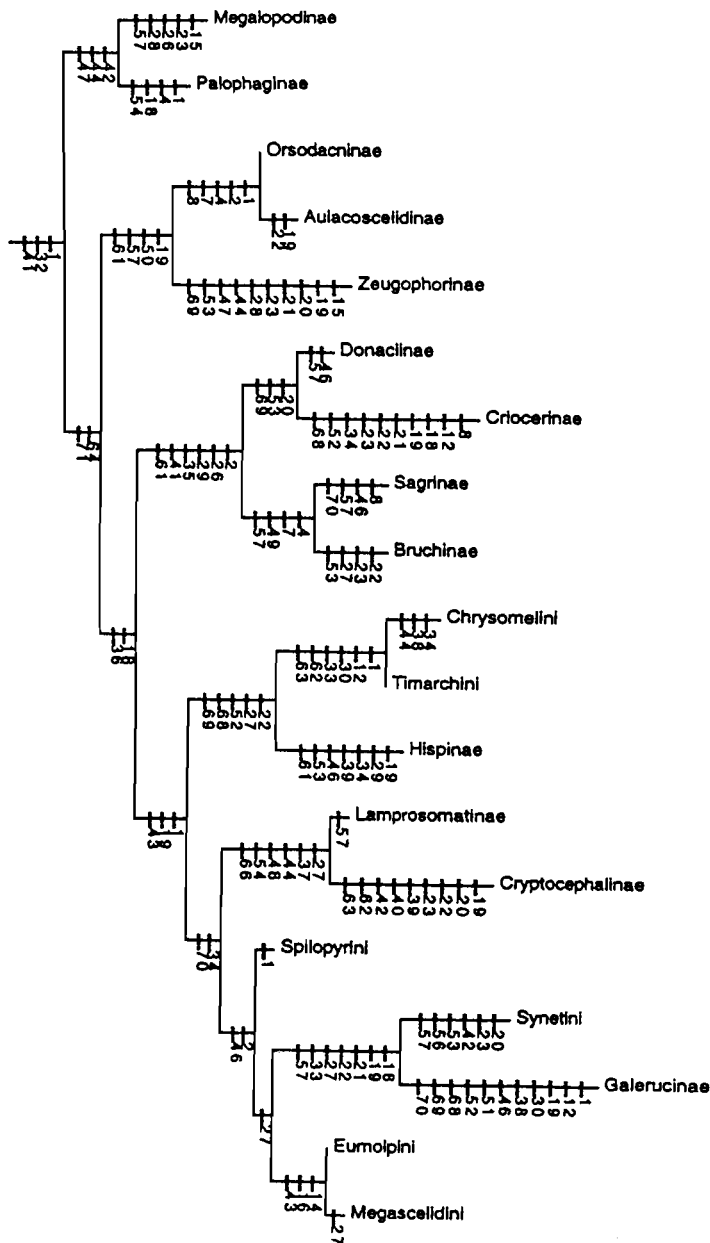


Figure 44. Part of one of 10 trees, 305 steps long, character types as listed in text, weights equal, unequivocal character state changes marked. Taxa with bifid setae, Megalopodidae and Eumolpinae non-monophyletic.

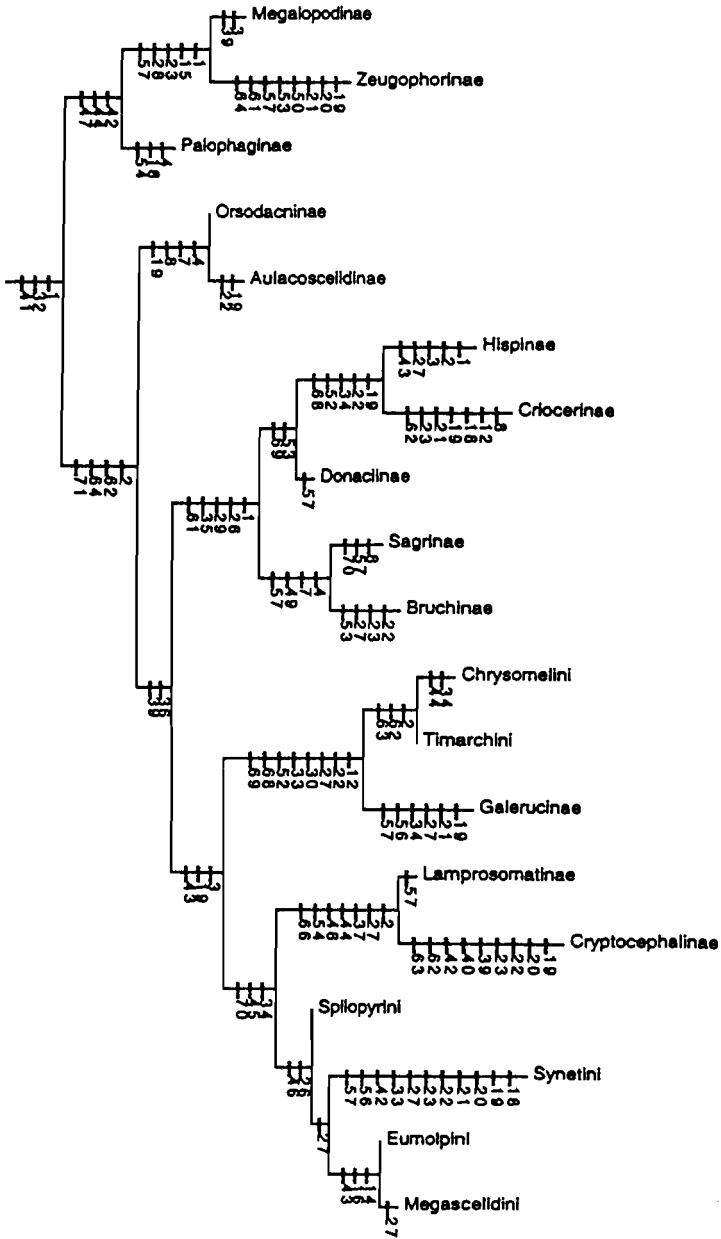


Figure 45. One of several trees, 306 steps long, character types as listed in text, weights equal, unequivocal character state changes marked. Taxa with bifid setae, Megalopodidae and Eumolpinae monophyletic.

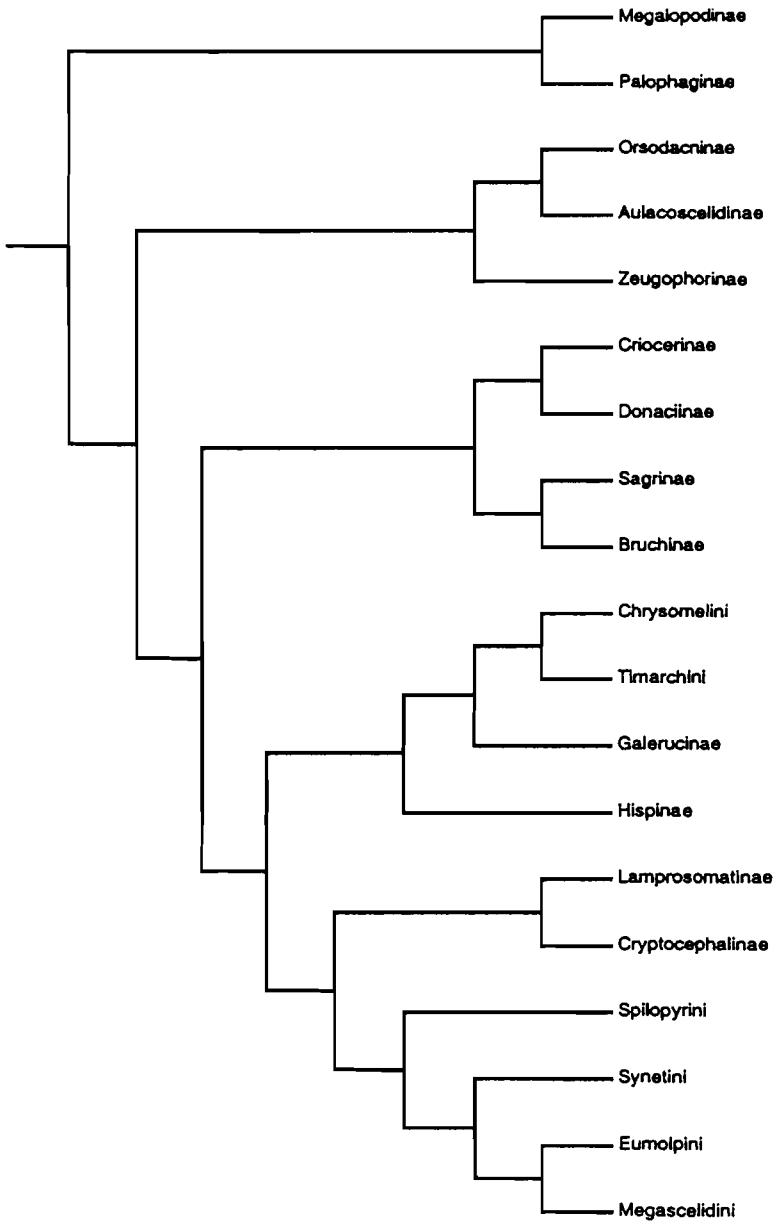


Figure 46. One of 12 trees, 218 steps long, character types as listed in text, weights equal, hypothetical larval data for Aulacoscelidinae, Spilopyrini and Synetini.

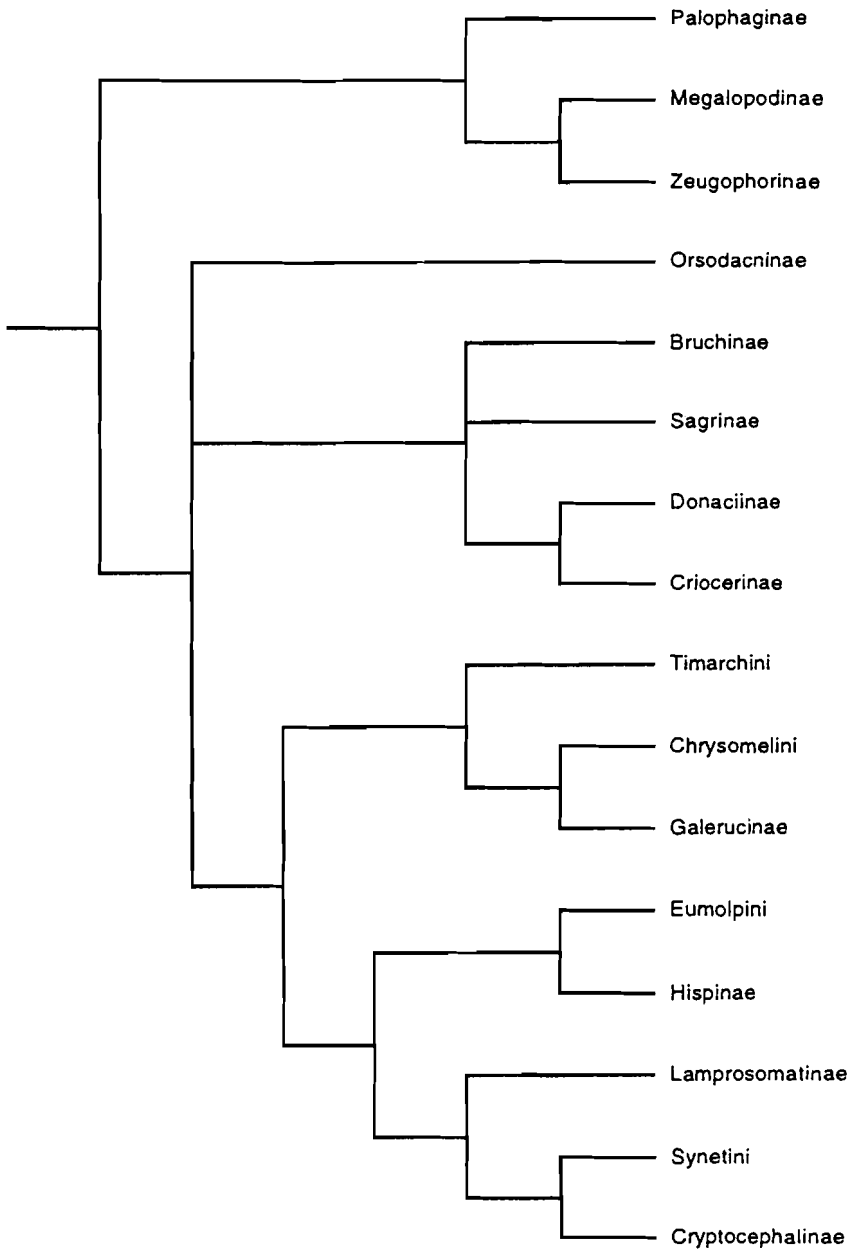


Figure 47. Strict consensus of 23 trees, 135 steps long, character types and weights as listed in text. Adult characters only.

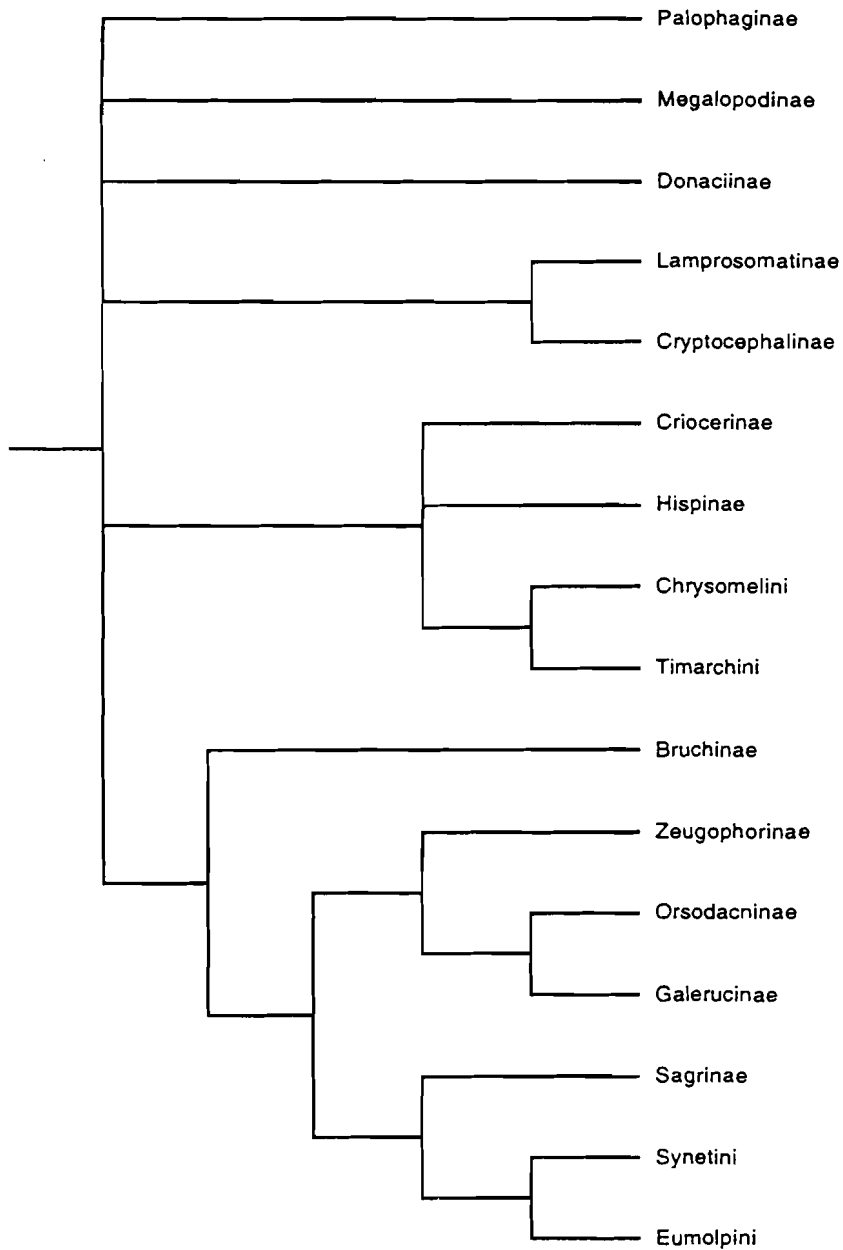


Figure 48. Strict consensus of 9 trees, 68 steps long, character types and weights as listed in text. Larval characters only.

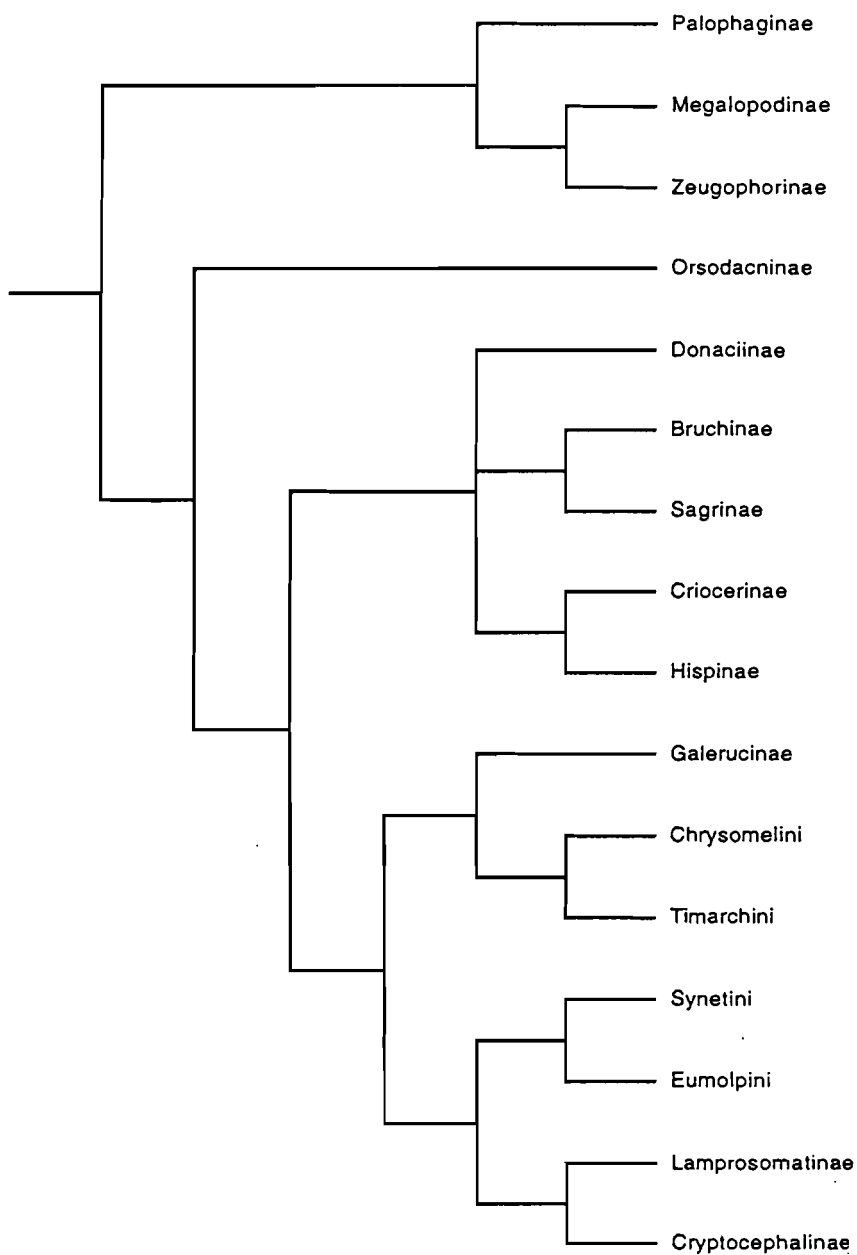


Figure 49. Strict consensus of 2 trees, 224 steps long, character types and weights as listed in text. Adult and larval characters.

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Cladistic analysis

Preliminary analysis of the distribution of the 71 characters on all 29 taxa was performed with PAUP, using the heuristic search routine. All character state changes were weighted equally. None of the taxa were redundant (*i.e.* scored identically for all characters), but character states 10 (1), 25 (1), 31 (1), 53 (2), 55 (1), 56 (3) and 63 (2) were either uninformative because they were only universal in single terminal taxa or were deleted as too difficult to score (Character 10). Characters 10, 25, 31 and 55 were deleted from analyses.

EFFECT OF CURCULIONOIDEA AS OUTGROUP

The data were initially analysed with all characters unordered, using Curculionoidea as outgroup (monophyletic outgroup option). Two minimum length trees of 276 steps were found and a strict consensus of these (Fig. 39) showed non-resolution of both cerambycid and chrysomelid lineages. Character 13 (presence or absence of lateral pronotal margins) had been included because of its historical significance, but both character states were often present in single taxa suggesting that it is of very little use in a study of phylogeny. When Character 13 was deleted, two minimum length trees of 264 steps were found (Fig. 40) with similar structure (polyphyly of chrysomelid lineage, but monophyly of cerambycid lineage). In both sets of trees, the Megalopodidae, Orsodacnidae and Eumolpinae *s.lat.* were each resolved as monophyletic and a clade including Bruchinae, Sagrinae, Donaciinae and Criocerinae was resolved as the sister group of all, or all except Vesperidae, other ingroup taxa. A sample of 10,000 randomly derived trees with Character 13 deleted found no trees shorter than 403 steps, suggesting that there is highly significant hierarchic structure in this data set. Further testing for significance was not considered necessary, especially as these analyses can only be regarded as preliminary. All consistency indices for the following minimum-length trees were greater than 0.4.

Treating all the characters as unordered could be considered naïve. In the second set of analyses, the distribution of characters and taxa was studied with Characters 10, 13, 25, 31 and 55 deleted (therefore a matrix of 29 taxa by 66 characters) and Characters 5, 12, 19, 27, 32, 34, 36, 53, 54, 56, 57, 60 and 71 designated irreversible (from derived to ancestral). These designations of character change make logical sense, because most involve loss or sequential loss of an attribute, for example larval stemmata or antennal segments, or involve fusion of sclerites. The assumption of irreversibility had already been made in the scoring of certain variable taxa, for example by scoring the greatest number of stemmata present in a given subfamily. With these character types, ten minimum-length trees of 305 steps were found in which the cerambycid and chrysomelid lineages formed sister clades, with the Chrysomelidae monophyletic but

with varying positions of the Zeugophorinae, Galerucinae and Spilopyrini (*e.g.*, Fig. 41).

INTERNAL ARRANGEMENTS OF CHRYSOMELID TAXA

With MacClade (Acctran and Deltran settings not used) the taxa were rooted with Curculionoidea as the outgroup and the character type designations as above, and three groups of minimum-length trees of 305 steps were found (in all of these the cerambycid lineage is not fully resolved). One of these sets of trees (*e.g.*, Fig. 42) showed monophyly of each of Megalopodidae and ((Hispininae + Criocerinae) + (Galerucinae + Chrysomelinae)), and paraphyly of Eumolpinae. Another showed polyphyly of Eumolpinae with the inclusion of Galerucinae, and placed Hispininae and Criocerinae with separate groups (*e.g.*, Fig. 43), and the third set showed polyphyly of Megalopodidae (*e.g.*, Fig. 44). There were several trees one step longer (306 steps). One of these (Fig. 45) included monophyly of each of Megalopodidae, the Eumolpinae and the taxa with bifid setae, and another excluded Hispininae from this clade and made Eumolpinae paraphyletic. If the Megalopodidae were placed as sister group to the cerambycid lineage the shortest tree with any of the above taxon configurations was 308 steps long.

If the classification presented here is "correct", the unknown larvae of Aulacoscelidinae, Spilopyrini and Megascalidini should be similar to their sister taxa. Therefore I replaced their missing larval entries with those of the sister taxa (Orsodacninae for Aulacoscelidinae, and Eumolpinae for Spilopyrini and Megascalidini) and ran a PAUP analysis of Chrysomelidae and Orsodacnidae with Megalopodidae as outgroup and the same deleted characters and irreversible characters as above. 12 minimum-length trees resulted, 218 steps long (Fig. 46), in all of which Zeugophorinae joined the Orsodacnidae, the clade ((Bruchinae + Sagraeinae) + (Donaciinae + Criocerinae)) was preserved, the Eumolpinae were forced into monophyly and Hispininae became sister group of (Chrysomelinae + Galerucinae). The configuration illustrated is one of the 305 step trees noted above.

WEIGHTING OF MORPHOLOGICAL NOVELTY

For the final set of analyses I introduced a further assumption; that gain of a new morphological structure was more significant than loss of a structure or presence of one state of a neutrally varying character. The few characters for which this argument could be justified (12, 14, 16, 29, 30, 42, 45, 59 and 68) were therefore weighted, with an arbitrary value of 2. The larval scores for Aulacoscelidinae, Spilopyrini and Megascalidini were restored to unknown. The effect on the lengths of the 305–306 step cladograms was interesting. The three shortest trees were 325 steps long, corresponding to one of the sets of the

305 step trees without weighting of characters (Fig. 42). But the other unweighted minimum-length trees were much longer than this when fitted with weighted characters, with 331 steps. There were only a few 326 step trees, in all of which the Eumolpinae and/or the taxa with bifid setae were monophyletic (e.g., Fig. 45).

COMPARISON OF ADULT AND LARVAL CHARACTER SETS

The contributions of adult and larval characters were compared, using PAUP, with Megalopodidae as outgroup for (Orsodacnidae + Chrysomelidae) and Aulacoscelidini, Spilopyrini, and Megascalidini and non-chrysomelid taxa ignored and the character type settings as described above (including deletion of Characters 10 and 13 and with character weights applied). Twenty-three shortest trees were found for the adult character set (Fig. 47), which produced the curious clades (Hispininae + Eumolpinae) and (Synetini + Cryptocephalinae), and split the Chrysomelinae. A similar analysis of the larval characters produced 9 minimum-length trees (Fig. 48), with the odd combinations of (Zeugophorinae + (Galerucinae + Orsodacninae)) and (Sagrinae + Eumolpinae). Analysis of the combined adult and larva data set for this small set of taxa gave two shortest trees with a third set of taxon combinations (Fig. 49) which agree completely with the arrangement in Fig. 45.

In spite of lack of a clear resolution of these data, support for the arrangement of taxa in Fig. 45 is argued for in the next section.

Discussion

SYSTEMATIC CONCLUSIONS

There were only two minimum-length trees for this set of taxa with 5 characters deleted and all states unordered. However, with character types designated as above, many different arrangements of the taxa led to trees of 305–306 steps. More fudging of the data, by weighting morphological novelty states more highly, gave trees which were a subset of these unweighted minimum-length trees. What conclusions (if any) can be drawn?

(1) Whether the state changes are unordered or not makes a huge change to the result. A naïve analysis of all characters as equal and with unordered states is not adequate: the possible evolutionary changes to each character should be assessed. It is important to consider the most logical character state changes and to incorporate such assumptions in analyses.

(2) The data set is not adequate for resolution of all relationships without considerable massage of the data. Not enough characters and not enough species have been examined. The phylogeny and classificatory system proposed

here can only be tentative (Fig. 45), nevertheless, the following discussion attempts to justify this system.

None of the family-group rank designations suggested here are new, but they may present a slightly different combination from any previous scheme. The nomenclature used here is based on evidence that the Megalopodidae, Orsodacnidae and Chrysomelidae are monophyletic groups of approximately equal rank. Fifteen subfamilies are recognised as monophyletic units within these families, ten of these belonging to Chrysomelidae. I do not consider further division of the Chrysomelidae to be warranted, given that there is no clearly defined hierarchical structure amongst the subfamilies. Whether or not a family-group taxon should be a family, subfamily or tribe is not so important, as long as the classification logically follows the hierarchy of proposed relationships.

CHRYSOMELOIDEA

The Chrysomeloidea are defined as follows. Adult: without rostrum, or prolongation and expansion of fused frontoclypeus anterior to antennal insertions; 3 apical segments of antennae neither in a club nor strongly differentiated; mentum not fused to gula; mesocoxal cavities open; with at least four free abdominal ganglia. Larva: hypopharyngeal bracon absent. The radial cross-vein (r-m) spur, referred to by Crowson (1955) is often difficult to distinguish, but apparently absent in *Vesperus* and *Eurispia*, and present in some Nemonychidae. It is also likely to be a plesiomorphy, being found in several polyphagan groups. At present it seems that the Chrysomeloidea are only defined by absence of the synapomorphies defining Curculionoidea and by the absent larval hypopharyngeal bracon. The sister group of (Chrysomeloidea + Curculionoidea) in the Polyphaga is as yet unknown.

The Chrysomeloidea are resolved as two groups of taxa: the "cerambycid" and "chrysomelid" lineages, both rather weakly defined. Monophyly of the cerambycids is based on the antennal tubercles (lost in Parandrinae and some Cerambycinae) and absence of vaginal pouches or glands (also absent in several chrysomelids). Most have open procoxal cavities (rare in chrysomelids) and plesiomorphic venation with a short apical region. Internal structure of the adults is poorly known. The larva has characteristic form, but first instars, which may be considerably different (*Vesperus*), have not been studied. Pupal morphology is also characteristic and apparently different from all chrysomelids. Suzuki (1988, 1994) suggested that the Megalopodidae and Orsodacnidae belong in the cerambycid lineage, but provided no evidence. Such an arrangement is not supported by this study.

Monophyly of the chrysomelid lineage is supported by fusion of abdominal ganglia 6-8, a character for which only a few taxa have been examined. The other characters supporting this clade are even weaker (mandibular prostheca

and number of male assessor glands). The Chrysomelidae are well defined, so the main problem of separation of this lineage lies with the Megalopodidae and Orsodacnidae.

The Megalopodidae are probably the sister group of (Orsodacnidae + Chrysomelidae). Apart from the rather feeble shared characters from the analysis above (fused abdominal ganglia, one assessor gland), the larval head capsule is not inserted into the prothorax (except the typical leaf-mining larva of Zeugophorinae) and the antennae are not on adjacent frontal tubercles. The megalopodine characters cited by Schmitt (in press) as diagnostic for Cerambycidae are also found in the plesiomorphic weevil family Nemonychidae, or are relatively variable in Chrysomeloidea. Either the larval dorsal ampullae and mesonotal stridulatory file are symplesiomorphic for Curculionoidea, and the two lineages of Chrysomeloidea (Kuschel 1994) or they have evolved independently at least twice. Neither argument justifies placing the Megalopodidae with the Cerambycidae. Leaf-surface larvae generally have ventral ampullae, although there are differences in presence, size and number of these, even within genera. The presence of dorsal ampullae in various burrow inhabiting larvae may also not be significant.

The family Orsodacnidae is probably the sister group of the Chrysomelidae, with shared apomorphies: loss of basal prosthecal lobe on mandible (reversed in Chrysomelinae), reduced abdominal egg bursters, dorsal ampullae absent, larval trochanters fused. All of these are weak but the orsodacnine larva bears no resemblance to any cerambycid and a more rigorous study of larval characters than given here would probably emphasise this difference.

MEGALOPODIDAE

The Megalopodidae are a monophyletic group—(Palophaginae + (Megalopodinae + Zeugophorinae)), defined by: mesonotal stridulatory files present, female sternite 7 with a small shallow apical pit, apodeme of female sternite 8 freely articulated with remainder of sternite. The subfamilies (Zeugophorinae + Megalopodinae) share: expanded antennae from segment 4, pronotal hypomeron lobes overlapping behind prosternal process, tarsal empodium present, reduced wing venation, reduced larval stemmata. A study of the phylogeny of the Zeugophorinae and the Megalopodinae would be useful to test whether recognition of the Zeugophorinae renders the Megalopodinae paraphyletic. At present the two groups are well defined as adults and larvae and the Zeugophorinae retain a few plesiomorphies lost in Megalopodinae, *e.g.*, the prothoracic egg burster (Cox 1994). However, only few taxa have been studied in each subfamily.

ORSODACNIDAE

Orsodacnidae, comprising (Aulacoscelidinae + Orsodacninae) are a monophyletic group, as suggested by Kuschel and May (1990), defined by similar reduced wing venation, shape of clypeus, quadrate depression between antennae and bilobed ligula. The two subfamilies have almost identical head, prosternum, elytra and male and female genitalia. The larva of Aulacoscelidinae is unknown, probably because it has a cryptic life habit like that of *Orsodacne*. These two subfamilies are so similar and so different from Chrysomelinae, that it is difficult to understand why Aulacoscelidinae and Chrysomelinae have been considered sister groups for so long (Monrós 1960; Mann and Crowson 1981; Suzuki 1988).

CHRYSOMELIDAE

The family Chrysomelidae is distinguished by a single autapomorphy (fused basal struts of aedeagus) plus the absence of prothoracic egg bursters (also absent from Megalopodinae). The basal struts are not completely fused in Timarchini and other Chrysomelinae (*Phaedon*: Balsbaugh 1989), but are much shorter and more fused than in Megalopodidae and Orsodacnidae.

Two loosely defined groups can be recognized.

GROUP 1.— Sagrinae, Bruchinae, Donaciinae; probably Criocerinae and Hispinae

Monophyly of the first four subfamilies was suggested by Monrós (1960) and monophyly of all five subfamilies was inferred by Crowson (1955). These five subfamilies share: bifid tarsal setae; raised anterior corner of metepisternum; keeled tegmen (small or reduced in many Hispinae), absence of thoracic egg bursters. Four have 1-segmented or absent larval labial palpi (2-segmented in Sagrinae). Four share presence of mola and setose prosthema on adult mandibles (absent in Hispinae). Most taxa have a well-defined neck and evenly arched prosternal process (usually flat in Hispinae). All of these subfamilies show reduced wing venation, with the most complete in Sagrinae and Bruchinae and a very similar form of reduced venation in the other subfamilies (except some Hispinae with enlarged wedge cell). Lack of a lateral pronotal carina is common in this group and is probably plesiomorphic, although a carina appears to have evolved several times. Enlarged hind femora are also widespread in this group and may be plesiomorphic, with secondary loss in some Criocerinae and almost all Hispinae (in *Promecotheca* the hind femora are a little larger and sometimes toothed). The history of systematic placement of the subfamily Criocerinae (*see* below) epitomises the amount of conflict in the literature concerning phylogeny of the Chrysomelidae. On gross morphology,

the adults are similar to sagrines, but the larvae are similar to chrysomelines. Gall-forming and leaf-mining larvae are supposed to occur in the Criocerinae (Monrós 1960; Schmitt 1988), but are undescribed. Adult features of this subfamily similar to chrysomelines are generally reductions (mouthparts, wing, aedeagus, ovipositor) but they share similar defence glands.

Monophyly of (Sagrinae + Bruchinae) is supported by shape of larval head and number of stemmata, and structure of adult clypeus and ligula (reduced in some Bruchinae). The Bruchinae can be derived from Sagrinae in most adult and larval features and the two have very similar larval and adult body forms.

The Donaciinae are either sister group of (Sagrinae + Bruchinae) or belong with Criocerinae or (Criocerinae + Hispinae) as sister taxon to (Sagrinae + Bruchinae). The first combination of three subfamilies shares more than one male accessory gland and reduced larval stemmata. The second grouping is supported by the form of the tibiotarsus and the reduced wing venation.

There is some evidence for monophyly of (Criocerinae + Hispinae). The Hispinae are so autapomorphic that they are difficult to place, but it is difficult to find strong objections to their sister group status with Criocerinae. The two taxa share reduced tegmen and reduced wing venation, larva with plesiomorphic number of stemmata, paronychial appendix on tibiae and one segmented labial palpi. Furthermore, at least some Hispinae share the unusual metepisternal elytral lock of Criocerinae and both subfamilies include species with tightly fitting overlapping cylindrical antennal segments. *Ovamela*, a Madagascan genus, differs from all other Criocerinae in broad flat prosternal process and broad short tarsi, which appear to be of hispine type (Monrós 1960). The head is similar to other criocerines and the aedeagus is typical of Criocerinae and some Hispinae, but the wing venation is slightly different from either subfamily because it is single celled with four anal region veins (Crowson 1955; Jolivet 1957; Monrós 1960). Further study of *Ovamela* may help to confirm that Criocerinae and Hispinae are sister groups. The hispine *Promecotheca*, which is relatively cylindrical, has a relatively unhyponathous head and a constricted unbordered prothorax. The larva of *Promecotheca* lacks the lateral and apical spines typical of Hispinae, but this may be due to its leaf-mining habit (Gressitt 1960). Criocerinae and Hispinae have different (but unique in Chrysomelidae and therefore not conflicting evidence) stridulation mechanisms and the latter lack the deep X-shaped grooves on the head and the adult mandible structures. It seems very likely that the cassidine body form has arisen several times in Hispinae, as exemplified by *Imatidium*, *Notosacantha* and *Cassida* (see Borowiec 1995).

A recent study (Askevold 1990b) assumed monophyly of the clade—(Sagrinae, Criocerinae, Donaciinae) based on the following supposed synapomorphic character states: elytral suture explanate (but reversed in *Plateumaris* and some sagrines), frontoclypeal grooves present (but intra-ocular groove lost in Donaciinae and all absent from some sagrines and Donaciines); median depres-

sions on basal and apical ventrites in male (only in some sagrines and absent from criocerines); pronotal margins lost (but lateral margins present in some sagrines and possibly a plesiomorphy in Chrysomelids); sclerite MEG of penis present (this may be the same as Karren's ejaculatory duct in Camptosomata, therefore not a synapomorphy for "sagroids"); presence of "basal sac sclerites" (but this not checked in other subfamilies); pubescent scutellum (identified as a symplesiomorphy but absent from Criocerinae, some Sagrines). None of these characters support monophyly of this particular clade.

GROUP 2.— Chrysomelinae, Galerucinae, Eumolpinae, Lamprosomatinae and Cryptocephalinae; probably not Criocerinae and Hispinae

Excluding Criocerinae, these subfamilies share lack of adult mandibular mola, four or less median and anal vein terminal branches and presence of short, heavily sclerotised ovipositor (reversed to telescopic in some Chrysomelinae and Eumolpinae, which are generally characterised by loss of ovipositor sclerites). Inclusion of Hispinae and Criocerinae with Chrysomelinae and Galerucinae requires unlikely retention or independent derivation of several features which become plesiomorphies from the common ancestor of these and the sagrine lineage. It does, however, allow monophyly of adult defence glands (but these are not in all Galerucinae), palmate larval mandibles, larval paronychia appendix and the external leaf-feeding habitus generally. If the Criocerinae and Hispinae are included here they should be paired together (for the reasons discussed above) as sister group of (Chrysomelinae + Galerucinae). The evidence for either classification from the analysed characters is almost equivocal, but I think more general morphological attributes not analysed favour the placement of (Criocerinae + Hispinae) with the sagrine lineage, as discussed above. The larva of *Allocharis* (Chrysomelinae) is superficially similar to hispine larvae (Fig. 35), but has normal palpi and its apical abdominal plate (a plug for the diurnal burrow) appears to be derived from fusion of tergites 8 and 9.

Monophyly of Hispinae + (Lamprosomatinae + Cryptocephalinae) has been suggested because of the commonest form of the male softparts, with short vas deferens and 1 + 1 testes (Suzuki 1988), but neither of these features are constant in Hispinae or Lamprosomatinae. It may also appear to be supported by the production of an ootheca in these groups, but this is produced by pressure between the eighth tergite and sternite in Hispinae, which lack any sensillary apparatus in the rectum.

The pairing of (Chrysomelinae + Galerucinae) is supported by adult defence glands, papillate adhesive setae, loss of lateral lobes of metendosternite, reduced wing venation, male last ventrite rectangularly produced. Larvae of both groups may also have defence glands, but these are probably not homologous, even within the Chrysomelinae.

If this sister group relationship is accepted, it is possible to polarize character states in the Galerucini, using Chrysomelinae as the outgroup. "Alticinae" and "Galerucinae" have always been recognized as sister groups. However, "Galerucinae" have always been seen as more "primitive" than "Alticinae" because they cannot hop, unlike "Alticinae" which are "probably the most advanced subfamily of Chrysomelidae" (Furth 1988: 296). I disagree with the doubtful wisdom of this statement, that life forms are in constant progression from simple to complex. There is some evidence that the Alticini are at least paraphyletic around a monophyletic Galerucini, that is, that the jumping mechanism is plesiomorphic for the Galerucinae as defined here and has been subsequently lost by the Galerucini and perhaps separately by *Microdonacia*, *Orthaltica*, *Cassena* and possibly other genera (Reid 1992c). This evidence includes the fact that for nearly all characters other than the "spring" the more plesiomorphic state is found in the Alticini rather than the Galerucini. Acceptance of monophyly of each group is due to refusal to accept that the alticine metafemoral spring may be secondarily lost and ignorance of the problems with definition of larval characteristics. Attempts to provide an internal classification of the Galerucinae are worthless without use of an outgroup to polarise character states. It is hoped that recognition of the Chrysomelinae as the unequivocal sister group of the Galerucinae will provide impetus for such badly needed studies. *Podontia*, with a relatively complete ovipositor (Kasap and Crowson 1985), may be a relatively plesiomorphic member of the Galerucinae.

Chrysomelini and Timarchini have always been considered monophyletic. They share: basal prosthecal lobe present, loss of tibial spurs, larval first-instar spiracles annular, egg bursters present on abdominal segments 1-2 in some taxa, and some other attributes not included in this study. Within the Chrysomelini, there are several relatively plesiomorphic taxa, including *Geomela* and *Brachyhelops* (Brendell *et al.* 1993).

The Eumolpinae are associated with (Lamprosomatinae + Cryptocephalinae), but are difficult to define as a monophyletic group. These three subfamilies have a reduced tegmen and first instar larva with long ventral femoral seta, and possibly also share presence of a kotpresse (secondarily lost in most Eumolpinae?). The form of the adult head capsule is similar, for example in antennal insertions and shape of anterior margin of fused frontoclypeus (except Synetini). Structurally similar features may occur independently in the two groups, for example the prothoracic antennal grooves and serrate abdominal apex of both *Pachnephorus* and *Lamprosoma*.

The only character state, of those listed above, shared by all Eumolpinae is the presence of vaginal glands which have a characteristic internally frothy appearance (present, but small, in *Syneta* and *Megascelis*). The problem taxa are the Spilopyrini, which are relatively plesiomorphic, and the Synetini, which have an unusual combination of plesiomorphic and derived features. Both tribes also have a rectal kotpresse, a feature present in Lamprosomatinae, Cryptoce-

phalinae and plesiomorphic Eumolpinae (Figs. 26–27), but not in Megascelidini (Reid 1990). The Spilopyrini have plesiomorphic wing venation and ovipositor sclerites, but the head capsule, with basally fused and apically arcuate clypeus, is typical of Eumolpinae. The larva is unfortunately unknown, but may also possess relatively plesiomorphic characters for the—(Eumolpinae + (Lamprosomatinae + Cryptocephalinae)) clade. The adult of *Syneta* has reduced wing venation, reduced procoxal process, reduced metendosternite, reduced tegmen and basal part of penis, reduced ovipositor (including loss of sternite 8 apodeme) and a prominent posterior clypeal margin, but these features are hardly sufficient to place it as sister group of the Galerucinae as some authors have suggested (Mann and Crowson 1981), although they are exceptional in the Eumolpinae. The unusual ovipositor of *Syneta*, with most sclerites fused together, is also found in the otherwise plesiomorphic eumolpine genus *Eupales*, and is more derived than in Lamprosomatinae. The form of the prothorax is also similar in these two genera, but the male genitalia are quite different (that of *Eupales* similar to Spilopyrini). The deep abdominal hollow of the *Syneta* female is undoubtedly independently derived from that of Cryptocephalinae because Lamprosomatinae and plesiomorphic Cryptocephalinae have at most a shallow pit. Synetini is therefore highly unlikely to be the sister group of the (Lamprosomatinae + Cryptocephalinae). The larva of *Syneta* is almost identical to most other eumolpine larvae, with similar chaetotaxy, head capsule, antenna, mandible and leg structure (Kurcheva 1967; Lee 1990; Reid 1990, 1993c). It has slightly sclerotised apical tergites, but these are not similar to the heavily sclerotised ninth tergites of some Galerucinae (suggested by Mann and Crowson 1981). The evidence is strongly in favour of *Syneta* being a plesiomorphic eumolpine with many adult autapomorphies.

Monophyly of (Eumolpini + Megascelidini) is strongly supported by: prosternal process with lateral spurs, mesosternal process with lateral spurs, ovipositor telescopic, kotpresse absent (scattered sensilla are present). *Megascelis* has a typical eumolpine head capsule and a relatively reduced ovipositor which is completely unlike that of Lamprosomatinae or Cryptocephalinae, or the plesiomorphic Eumolpinae. It is probably most appropriate to regard Megascelidini as a monophyletic group within the Eumolpini *s.lat.*, rendering the latter paraphyletic, but this will have to await a study of eumolpine phylogeny. The unknown larva of Megascelidini is undoubtedly soil-dwelling like other Eumolpinae. This probably explains why the larva is unknown despite the adults being agricultural pests (King and Saunders 1984).

Monophyly of (Lamprosomatinae + Cryptocephalinae) is supported by absence of prostheca at base of adult mandible, setae present on penis (rare exceptions), female without apodeme on sternite 8, larva with labrum fused to clypeus, large sclerite at base of legs, and encased in scatoshell. Both subfamilies are well-defined as adults and larvae. The larva of the relatively plesiomorphic genus *Sphaerocharis* will be of great interest.

CHARACTER EVOLUTION AND HOMOLOGY

Mann and Crowson (1981) have already noted the probable independent origin of many apomorphic states in the Chrysomeloidea. Their comments are equally appropriate to this study, although they reach fundamentally different phylogenetic conclusions.

The main problem with my study (based largely on literature) is that it includes many characters with reductions or loss which, while they might not be reversible, are likely to happen many times independently, just as life habits have evolved independently, for example leaf-mining. Very few of the characters involve the gain of novel features and when they do there is often character conflict (the taxa with bifid setae versus the taxa with dorsal adult glands). Clearly, if the ancestral states are as suggested by the morphology of the most plesiomorphic of Curculionoidea and Chrysomeloidea, the evolution of adult leaf-beetles has been characterised by the reduction of a relatively complex organism to a relatively simple one, involving loss of features of the mouthparts, wing venation, metendosternite structure and male and female genitalia. This loss of complexity is a source of frequent homoplasy which is difficult to detect, presumably because of physical restraints—a certain pattern of reduced venation is required for flight, a less complicated metendosternite still has to function as an anchor for the wings. For example, to determine whether the lobes on the two metendosternites illustrated here (Figs. 22–23) are really homologous (as I have assumed) would require a study of the thoracic musculature.

There are several logical arguments for this apparent reduction of structural diversity. Loss of mouthpart complexity is probably due to a switch of pabulum from pollen to leaf tissue (Mann and Crowson 1981; Crowson 1981), but the other features are not obviously related to changes in life habit. In Coleoptera loss of wing veins is probably correlated with small size and it is likely that those groups with reduced veins originated from small-sized ancestors. The reduced wing venation, reduced metendosternite and fused sternites and ovipositor segments of Cryptocephalinae may be due to the morphological “bottle-neck” caused by a small ancestor. The Synetini, with numerous reductions or losses, may also have had a small ancestor. A similar argument could be made for the (Chrysomelinae + Galerucinae) clade. Loss of larval features such as stemmata seems to be associated with stem or leaf mining or soil habitation. Thus external feeding larvae with reduced stemmata should be secondary colonists of that habitat. Therefore, the galerucine ancestor is likely to have been a stem or leaf miner. Another feature of leaf or stem mining larvae is the strongly sclerotised apical tergite(s), and this has also been independently derived, in *Orsodacne*, some Galerucinae and some Chrysomelinae (Fig. 35).

For Chrysomelidae, two associations of the subfamilies Hispinae and Criocerinae were suggested above: (1) with Sagraeinae and allies to give monophy-

letic bifid tarsal setae; (2) with Chrysomelinae and Galerucinae to give monophyletic defence glands and leaf-feeding larvae. The former is favoured here, in which case the external leaf-feeding larva (characterised by six stemmata and short legs, usually with paronychial appendix) may be a synapomorphy for the Chrysomelidae—reversed in Sagrinae–Bruchinae (in woody tissue or seeds), Eumolpinae (stems or soil), most Cryptocephalinae (leaf litter), two Criocerinae (leaf-mining or stem galling), some Hispinae (leaf mining) and probably all Galerucinae (stems or leaf mining, with secondary external feeders). But the actual structures associated with leaf feeding may have evolved independently *e.g.*, the paronychial appendix (present in Chrysomelinae, Galerucinae, Criocerinae and Hispinae).

HOST-PLANT ASSOCIATIONS

If the phylogeny that I have tried to justify is accepted (Fig. 45), an interesting pattern of preferred hosts is revealed. Plesiomorphic taxa in Nemonychidae and Megalopodidae feed on pollen of Araucariaceae (Kuschel and May 1990; Kuschel 1994) as adults and larvae. Adults of some cerambycid taxa, Orsodacnidae, and plesiomorphic Chrysomelidae (Sagrinae) feed on angiosperm pollen, the larvae are found in plant tissues. Aulacoscelidinae feed on both cycad and angiosperm pollen (Monrós 1954). The remaining Chrysomelidae feed on leaves or flowers, but rarely pollen. The Chrysomelidae, as defined here, appear to have originated with the angiosperms and to have radiated as leaf-feeders.

The species of the clade (Donaciinae + (Criocerinae + Hispinae)) predominantly feed on monocotyledonous hosts, which is relatively unusual in the Chrysomeloidea (Gressitt 1960; Jolivet 1988, Schmitt 1988, Askevold 1990b). Species of the plesiomorphic tribe Pachymerini (Bruchini) are also monocot specialists (Borowiec 1987). A pupa of *Mecynoder* (Sagrinae) has been reared from roots of the monocot *Lomandra*. Feeding on monocotyledons may be a synapomorphy for all these subfamilies and the split tarsal setae shared by these taxa may be a significant feature for feeding on these plants. However, most Sagrinae and Bruchinae feed on dicots. In the Sagrinae, *Carpophagus banksiae* is supposed to feed on cycads (Mann and Crowson 1981; Jolivet 1988; Crowson 1994), and this “host” association has been used as evidence for the ancient origin of Sagrinae. Early records of this species from *Banksia* and *Macrozamia* are of specimens sitting on leaves, but the adult of this species has been observed to feed on pollen of *Angophora* (Myrtaceae). I have collected other Australian sagrines feeding on *Melaleuca* pollen (Myrtaceae: *Diaphanops*) and *Acacia* pollen (Mimosaceae: *Mecynoder*). The neotropical genus *Atalasis* occurs on Malvaceae and the palaeotropical genus *Sagra* occurs on various families, predominantly Mimosaceae (Monrós 1960). There is no evidence for a cycad feeding ancestor for this group of subfamilies, as has been

proposed (Schmitt 1988), and although cycads are still extremely common in Australia only two species of *Lilioceris* are recorded feeding on them (Forster and Machin 1994).

Most of the other chrysomelid subfamilies show a very wide range of dicotyledonous hosts, with a few species feeding on other plants, such as Bryophyta (e.g., *Geomela*), Poaceae (e.g., *Rhyparida*) or Pinaceae (e.g., *Cryptocephalus*) (Jolivet 1988). Generalizations about the original host plants for the larger chrysomelid subfamilies are meaningless, as their generic phylogenies have not been determined. It is interesting to note, however, that the predominant subfamilies in the tropical rainforests of Amazonia (Farrell and Erwin 1988), Java (*personal observation*), Borneo (Mohamedsaid *et al.* 1990), Sulawesi (Hammond 1990) and Australia (*personal observation*) are Galerucinae and Eumolpinae. These two subfamilies have very active adults but cryptic larvae, which are usually in soil or plant tissues. The significance of these features in the rainforest environment can only be guessed. The Cryptocephalinae also have active adults and cryptic larvae, but in my experience the latter are highly susceptible to fungal attack in humid conditions. The rectal kotpresse of adult Cryptocephalinae may have been a pre-adaptation for water retention (Schöller *in press*), allowing this group to diversify in the dry woodlands of Africa and Australia, but in Australia, Eumolpinae and Chrysomelinae are equally abundant in such habitats.

BIOGEOGRAPHY

Both the Sagrinae and Spilopyrini have distributions which track the break up of Gondwana towards the end of the Cretaceous. One sagrine genus, *Megamerus*, also has such a distribution (Monrós 1956b). There is a probable Gondwanan distribution of a group of genera in the Chrysomelini, although the characters used to define this particular group are weak (Brendell *et al.* 1993). The sister taxa of the above groups, Bruchinae, and parts of Sagrinae, Eumolpinae and Chrysomelinae, must also have Cretaceous ancestors. Therefore, without reference to fossils, several subfamilies of Chrysomelidae can be dated to at least mid Cretaceous origin (break up of Gondwana). The origin of the family Chrysomelidae must be considerably older than the mid Cretaceous, but the Kara Tau fossils (Upper Jurassic) are too poorly preserved to be helpful (Crowson 1981; Santiago-Blay 1994). The Palophaginae also have a Gondwanan distribution, as might be expected for such a plesiomorphic taxon; the described species occur in north Queensland, but larvae have been collected from *Araucaria* cones in Chile (W. Kuschel, *personal communication*). The fossil history of Donaciinae confirms a pre-Tertiary origin for this group (Askevold 1990a) which has a tropical or northern hemisphere origin.

Considerably more notice needs to be taken of continental drift in studies of chrysomelid systematics. It is still conventional to treat the faunas of modern

continents or archipelagos in isolation (*e.g.*, tribes of Hispinae), ignoring the long period of contact between the tropical zones of West Africa and South America, the relative insignificance of the modern sea between New Guinea and Australia, the scattered fragments of a Gondwanan archipelago throughout south-east Asia and the well-known connections between South America and Australia (Audley-Charles 1987; Struckmeyer and Totterdell 1990). Studies of taxa should be encouraged and regional studies discouraged—the first process discovers synonyms, the second creates them.

Key to subfamilies of Megalopodidae, Orsodacnidae and Chrysomelidae

ADULTS

1. Male: basal apodemes free for at least half length of penis and tegmen usually with deeply bilobed dorsal cap (Fig. 25); dorsum almost always entirely pubescent; elytra non-striate 2
 - Male: basal apodemes of penis fused (Fig. 26), or fused in basal half and free much less than half length of penis (some Chrysomelinae), tegmen rarely with bilobed dorsal cap; dorsum often glabrous; elytra often striate [Chrysomelidae] 6
2. Clypeus quadrate, projecting between base of mandibles (Figs. 16, 18, 19); female: apex of sternite 7 not excavate, apodeme of sternite 8 fused to basal plate, segments of vaginal palpi distinguishable and palpi prominent; head with evenly convex hemispherical eyes separated by a quadrate depression on frons (Fig. 19); mesoscutum without a pars stridens [Orsodacnidae] 3
 - Clypeus usually transverse, not projecting; female: apex of sternite 7 with a small deep excavation, apodeme of sternite 8 loosely articulated to basal plate, vaginal palpi not distinguishable, fused into a weakly sclerotised quadrate plate; internal margin of eyes at least slightly excavate; mesoscutum with a pars stridens [Megalopodidae] 4
3. Lateral margins of pronotum absent, prothorax constricted near base; wing venation relatively plesiomorphic (Holarctic) Orsodacninae
 - Lateral margins of pronotum present, prothorax not constricted; wing venation relatively reduced, $CuA_1 + MP_4/MP_{3+4}$ reduced to a single vein (Central and South America) Aulacoscelidinae
4. Prothoracic hypomerion lobes overlapping behind apex of short prosternal process; tarsal empodium present; ligula not bilobed 5
 - Prothoracic hypomerion lobes separated by prosternal process; tarsal empodium absent; ligula large, bilobed (Australia) Palophaginae

5. Mandibular mola absent; wing venation usually complete, with MP_{3+4} and MP_{1+2} connected or nearly so, AA_{3+4} present and 4–5 post MP_{1+2} branches; testes fused together in common membrane (pantropical) Megalopodinae
- Mandibular mola present; wing venation reduced, MP_{3+4} and MP_{1+2} distant, AA_{3+4} absent and <4 post MP_{1+2} branches; testes not fused together (Holarctic and Palaeotropical) Zeugophorinae
6. Male: tegmen forming a complete ring with sclerotised dorsal cap; head usually constricted posteriorly to a distinct neck; hind femora almost always much larger than other femora and often ventrally dentate . . . 7
- Male: tegmen without sclerotised dorsal cap, or if so (Timarchini) head not constricted posteriorly to a distinct neck and all femora similar sized 10
7. Ventral surface coated in dense short adpressed setae, forming respiratory plastron; antennae set on raised tubercles, separated by deep, elongate, median groove; eyes with simple inner margins (Holarctic and Palaeotropical) Donaciinae
- Ventral surface without plastron of dense adpressed setae; antennae not on raised tubercles; eyes with excavate inner margins 8
8. Head prognathous, usually with X- or H-shaped grooves between antennal insertions (Fig. 18); rarely with lateral pronotal carina; metendosternite with lamellar plate at base of arms (east South America, Palaeotropics, Australia) Sagrinae
- Head usually hypognathous, without X- or H-grooves (Fig. 16); pronotum laterally carinate, at least at base; metendosternite reduced to Y-shape (Cosmopolitan) Bruchinae
10. Bifid tarsal setae present; stridulatory file (pars stridens) on tergite 7, or vertex, or absent but with sternites 3 and 4 fused and mouthparts ventrally deflexed; wing venation reduced, anal area veins not all connected; kotpresse absent 11
- Without bifid tarsal setae; without pars stridens; if sternites 3 and 4 fused, mouthparts not deflexed, wing venation plesiomorphic and kotpresse present 12
11. Pars stridens present on tergite 7; X-groove present between antennal insertions; sternites 3 and 4 not fused; mouthparts not ventrally deflexed; mandibular mola present (Cosmopolitan) Criocerinae
- Tergite 7 without pars stridens; head without X-groove between antennae; sternites 3 and 4 fused; mouthparts deflexed ventrally; mandibular mola absent (Cosmopolitan) Hispinae

12. Female: kotpresse present in rectum, usually as sclerotised plates, and sternite 8 without apodeme; male: apex of penis conspicuously setose (Fig. 6; rare exceptions with sclerotised plates in female rectum) 13
- Female: kotpresse absent or present as patches of spines only (Figs. 28–29) and if so sternite 8 with distinct apodeme; male: penis glabrous or rarely with minute setae 14
13. Procoxal cavity closed by insertion of hypomeron lobes into prosternal process (Fig. 4); sternites 6 and 7 free; kotpresse without sclerotised plates (Holarctic and pantropical) Lamprosomatinae
- Procoxal cavities open or closed by insertion of sides of apex of prosternal process into hypomera; sternites 6 and 7 fused; kotpresse usually with sclerotised plates (Cosmopolitan) Cryptocephalinae
14. Internal face of mandible with a large oval membranous prosthema at least 0.3 times mandible height, arising from an elongate slit on the basal half; male: apex of sternite 7 with a rectangular lobe or invagination; female: vaginal pouches absent; spatulate adhesive setae papillate; wings never with 2 anal cells 15
- Prosthema absent or very small and arising from base of internal edge as one or two short lobes (Fig. 13); male: apex of sternite 7 rarely with rectangular lobe; female: vaginal pouches present (Fig. 28); spatulate adhesive setae simple; wings usually with 2 anal cells (Fig. 20) (Cosmopolitan) Eumolpinae
15. Antennal sockets <2.5 socket diameters apart; female: sternite 8 with apodeme; all testes at least held together in a common membrane, usually compacted into a single sphere; almost all species either with metafemoral spring or tapered apex of mesosternal process (Cosmopolitan) Galerucinae
- Antennal sockets >2.5 socket diameters apart; female: sternite 8 usually without apodeme, if present, tegmen of male with dorsal cap; each set of testes separated; without metafemoral spring or tapered mesosternal process (Cosmopolitan) Chrysomelinae

LARVAE (larvae of Aulacoscelidinae unknown)

1. Spiracles on segment 8 modified as a pair of ventrally directed hook-like siphons; galea and lacinia each with elongate spine-like extensions (antennae 3-segmented; stemmata absent; egg bursters absent; larva attached to submerged vegetation) Donaciinae
- Spiracles on segment 8 similar to other segments; galea without spine, lacinia usually not distinguishable (larva not aquatic) 2

2. C- or U- or J-shaped (*i.e.* hind body tucked under fore body), in life enclosed in conical to balloon shaped transportable case; elongate legs all directed towards anterior and large coxal plates present (Fig. 12); head free, circular (Fig. 10); labrum fused to clypeus; first-instar mandibles with at least 2 teeth (egg bursters present on meso- and metathorax; in leaf litter or on plant surfaces) 3
 - C- shaped (Fig. 33), to gently curved, not in a transportable case; legs variable, often absent; head elongate, deeply inserted into prothorax (Figs. 32-33); labrum free; first-instar mandibles with single tooth (egg bursters confined to basal abdominal segments (Fig. 33); inhabiting woody galls or seeds) 4
 - Not C-shaped (Fig. 8), nor in a transportable case; legs variable; head free; labrum rarely fused to clypeus; first-instar mandibles with at least 2 teeth (Fig. 38) 5
3. Spiracles biforous; setae simple; apical epipharyngeal setae ventral Lamprosomatinae
 - Spiracles cribriform (Fig. 12); at least some cephalic setae apically hispid or clavate (Fig. 10); apical epipharyngeal setae dorsal (Fig. 11) Cryptocephalinae
4. Labial palpi 2-segmented; legs with distinct femur, tibiotarsus and praetarsus (Fig. 34) (no ridge on prothorax, eggbursters on abdominal segments 1-3) Sagrainae
 - Labial palpi 1-segmented or absent; legs usually reduced, often lacking pretarsal claw (median prothoracic ridge present in first-instar, usually X-shaped, egg bursters on abdominal segment 1 only) Bruchinae
5. Legs absent; labial palpi absent (body dorso-ventrally flattened; vertex completely divided, coronal suture absent; prothoracic and abdominal egg bursters present; leaf-mining) Zeugophorinae
 - Legs present; labial palpi present 6
6. Dorsal ambulatory ampullae present (probably with egg bursters on thorax and more than 3 abdominal segments) 7
 - Dorsal ambulatory ampullae absent (at most with egg bursters on meso- and metathorax and abdominal segments 1-2) 8
7. Coronal suture absent, two halves of epicranium not meeting; labrum fused to frontoclypeus (inhabiting male cones of gymnosperms) Palophaginae
 - Coronal suture present; labrum free (stem mining) Megalopodinae

8. 2 short, setose, articulated urogomphi present on tergite 9; tibiotarsus without paronychial appendix and pretarsi long; antennae 3-segmented; (mandibular penicillus present; body dorsoventrally depressed; habit unknown) Orsodacninae
- Urogomphi absent, or if present, minute, rigid and without setae, and tibiotarsus with paronychial appendix, short claws and antennae 2-segmented 9
9. Stemmata 0, although eye spots may be present; femur with median ventral seta as long as or longer than femur; tibiotarsus without paronychial appendix; pretarsus very long, almost tibiotarsus length; mandible triangular, with 1–3 teeth, without penicillus (Fig. 38); labial palp 1-segmented (egg bursters variable; in soil, stems, roots, or tubers) Eumolpinae
- Stemmata 0–1; femoral setae short; lobate paronychial appendix present; pretarsus short; mandible usually broad, with >3 teeth and penicillus; labial palp 2-segmented (egg bursters absent or confined to meso- and metathorax; external or in soil, roots, stems or leaf mining) Galerucinae
- Stemmata >4; femoral setae short; paronychial appendix usually present (Fig. 9); pretarsus short; mandible usually with >3 teeth, rarely with penicillus (Fig. 37); labial palp 1- or 2-segmented 10
10. Labial palpi 2-segmented; egg bursters almost always present on meso- and metathorax (maxillary palpi 3-segmented; abdomen cylindrical or globular; external leaf or flower feeders) Chrysomelinae
- Labial palpi 1-segmented; egg bursters absent from thorax 11
11. Maxillary palpi 1–2 segmented; abdominal segments with lateral spines or flattened extensions, or head with epicranium posteriorly divergent from midline (Fig. 36); without ventral ampullae; paronychial appendix usually bilobed; egg bursters absent (external leaf feeders or leaf miners) Hispinae
- Maxillary palpi 3-segmented; abdomen globular, without lateral prominences; epicranium not split; abdomen with distinct ventral ampullae; paronychial appendix not bilobed; egg bursters present on abdominal segment 1 (external leaf feeders or stem miners) Criocerinae

Summary of classifications of chrysomelid taxa

The format of this section is as follows: name; systematic position preferred in this work; short-hand summary of major historical classifications; discussion of internal classification problems (if necessary); number of genera.

The following abbreviations are used in the indications of relationship: ALT = Alticini; AUL = Aulacoscelidinae; BRU = Bruchinae; CAS = Cassidini; CER = Cerambycidae; CHL = Chlami-

sini; CHR = Chrysomelinae; CLY = Clytrini; CRI = Criocerinae; CRY = Cryptocephalinae; DON = Donaciinae; EUM = Eumolpinae; GAL = Galerucinae; HIS = Hispinae; LAM = Lamprosomatinae; MGL = Megalopodinae; MGS = Megascalidini; ORS = Orsodacninae; PAL = Palophaginae; PRO = Protoscelidinae; SAG = Sagrinae; SPH = Sphaerocharitini; SPI = Spilopyrini; SYN = Synetini; TIM = Timarchini; ZEU = Zeugophorinae.

Superfamily **CHRYSOMELOIDEA** Latreille, 1802: 220, *sensu* Crowson (1955, 1981), Lawrence and Newton (1982), Lawrence and Britton (1991).

= CERAMBYCOIDEA *auct.*

This superfamily has eight families, including all taxa formerly placed in Cerambycoidea, currently five families (Švácha and Danilevsky 1987). The latter are not treated further, but are clearly long overdue for a systematic overhaul.

Family **MEGALOPODIDAE** Latreille, 1802: 227.

I follow Crowson and other authors in giving this group family status (Crowson 1981; Kuschel and May 1990).

Three subfamilies are included.

Megalopodinae Latreille, 1802: 227

REVISED SYSTEMATIC POSITION: - (MGL + ZEU).

HISTORICAL SYSTEMATIC POSITION: - ((MGL + ZEU) + (CLY + (CRY + (LAM + CHL)))) (Monrós 1960); - (SAG + (MGL + ZEU)) (Medvedev 1971); - (ZEU + (MGL + (CLY + CRY + ((CHL + LAM) + (EUM + MGS)))) (Jolivet 1978; 1988); - ((MGL + ZEU) + (MGS + (LAM + CRY))) (Mann and Crowson 1981, 1983b); - (CER + (ORS + MGL + ZEU)) (Chen 1985); - (LAMIINAE + (MGL + ZEU)) (Suzuki 1988); - (MGL + ORS) and - (ZEU + (CRIO + (SYN etc.))) (Lee 1993); - (LAMIINAE + (MGL + (ZEU + PAL))) (Suzuki 1994); - (CER + (PAL + ZEU + MGL)) (Schmitt, in press).

The subfamily includes 25 genera, with no tribal arrangement (Seeno and Wilcox 1982).

Palophaginae Kuschel and May, 1990: 699

REVISED SYSTEMATIC POSITION: - (PAL + (MGL + ZEU))

HISTORICAL SYSTEMATIC POSITION: - (PAL + MGL) (Kuschel and May 1990); - (MGL + (ZEU + PAL)) (Suzuki 1994); - (CER + (PAL + ZEU + MGL)) (Schmitt, in press).

This subfamily was erected to accommodate *Cucujopsis* and *Palophagus* (Kuschel and May 1990).

Zeugophorinae Böving and Craighead, 1931: 63

REVISED SYSTEMATIC POSITION: - (ZEU + MGL)

HISTORICAL SYSTEMATIC POSITION: *see* under Megalopodinae, with which this subfamily has almost always been associated.

There is one genus with two subgenera (Monrós 1959).

Family **ORSODACNIDAE** Thomson, 1859: 154, *sensu* Kuschel and May (1990).

There are two subfamilies.

Aulacoscelidinae Chapuis, 1874: 54

= Aulacoscelinae

REVISED SYSTEMATIC POSITION: – (AUL + ORS), as suggested by Kuschel and May (1990).

HISTORICAL SYSTEMATIC POSITION: – (AUL + CHR) (Monrós 1960; Medvedev 1971); (Mann and Crowson 1981, 1983; Suzuki 1988); – (AUL + (CRI + (CHR + (GAL + ALT)))) (Jolivet 1978, 1988); – (AUL + ORS) (Kuschel and May 1990); – ((AUL) + ?) (Suzuki 1994)

There are two genera (Monrós 1953, 1954).

Orsodacninae Thomson, 1859: 154

REVISED SYSTEMATIC POSITION: – (AUL + ORS)

HISTORICAL SYSTEMATIC POSITION: – (ORS + (MGS + (EUM + (GAL + ALT) (Monrós 1960); – (SAG + ORS) (Medvedev 1971); “stemgroup” for (DON, AUL, etc.) (Jolivet 1978, 1988); – (ORS + (SYN + EUM + (GAL + ALT))) (Mann and Crowson 1981); – (ORS + (EUM + (SYN + (GAL + ALT))) (Mann and Crowson 1983b); – (CER + (ORS + ZEU + MGL)) (Chen 1985); – (LEP-TURINAE + ORS) (Suzuki 1988, 1994)); – (ORS + MGL) (Lee 1993)

There is one genus (*Cucujopsis* belongs in Palophaginae).

Family **CHRYSOMELIDAE** Latreille, 1802: 220, *sensu* Kuschel and May (1990)

There are 10 subfamilies.

Alticinae: *see* under Galerucinae

Bruchinae Latreille, 1802: 192

REVISED SYSTEMATIC POSITION: – (BRU + SAG), as suggested by Monrós (1960).

HISTORICAL SYSTEMATIC POSITION: – (BRU + SAG) (Monrós 1960, Mann and Crowson 1981); excluded from Chrysomelidae (Jolivet 1978, 1988; Suzuki 1988, 1994); – (BRU + (SAG + (DON + SAG + (CRI + (HIS + CAS)))) (Mann and Crowson 1983b); – (SAG + BRU + DON + CRI) (Chen 1985); – (BRU + ((CAS + HIS) + (DON + (SAG + CRI)))) (Schmitt 1989); – (BRU + other Chrysomelidae except Megalopodinae and Orsodacninae) (Kuschel and May 1990; Lee 1993)

There are 58 genera in 6 tribes (Borowiec 1987). First-instar larvae of the most plesiomorphic genus, *Rhaebus*, are unknown.

Cassidinae – *see* under Hispininae

Chlamisinae – *see* under Cryptocephalinae

Chrysomelinae Latreille, 1802: 220

REVISED SYSTEMATIC POSITION: - (CHR + GAL) [= ((CHR + TIM) + (GAL + ALT))]

HISTORICAL SYSTEMATIC POSITION: - (AUL + CHR) (Monrós 1960; Medvedev 1971); (Mann and Crowson 1981, 1983b; Suzuki 1988); - (CHR + (GAL + ALT)) (Jolivet 1978, 1988); - (CHR + GAL + ALT + SYN) (Chen 1985); - (CHR + CAS) (Lee 1993); - ((CHR) + ?) (Suzuki 1994)

Hennig dabbled in the problems of chrysomeline phylogeny by studying the larvae (Hennig 1938), but the most useful work (Kimoto 1962), reviewed the distribution of larval setae and tubercles. Small discrepancies in the nomenclature of the ventral sclerites by subsequent workers have been noted (Reid 1991).

There are 176 genera currently recognised (Seeno and Wilcox 1982) arranged in 2 tribes and 12 poorly delimited subtribes.

Clytrinae - *see* under **Cryptocephalinae****Criocerinae** Latreille, 1807: 43

REVISED SYSTEMATIC POSITION: probably - (CRI + HIS), as suggested by Mann and Crowson (1981).

HISTORICAL SYSTEMATIC POSITION: - (CRI + (DON + (SAG + BRU))) (Monrós 1960); - (CRI + (DON + ((ALT + GAL) + (PRO + (AUL + CHR)))) (Medvedev 1971); - (CRI + (CHR + (GAL + ALT))) (Jolivet 1978, 1988); - (CRI + (CAS + HIS)) (Mann and Crowson 1981, 1983b); - (CRI + DON + BRU + SAG) (Chen 1985); - (DON + (SAG + CRI)) (Schmitt 1985, 1989); - (SAG + (DON + CRI)) (Suzuki 1988, 1994; Askevold 1990b); - (CRI + (SYN + (EUM + (LAM + CRY)))) (Lee 1993).

The generic concepts in this subfamily need to be revised, especially to deal with the profusion of subgenera. Currently there are 20 genera in 3 tribes (Seeno and Wilcox 1982), although the most recent revision lists only 11 genera (Monrós 1960).

Cryptocephalinae Gyllenhal, 1813: 582

= Clytrinae Lacordaire, 1848: 9

= Chlamisinae Gressitt, 1946: 84

REVISED SYSTEMATIC POSITION: - (LAM + CRY) [= (LAM + (CRY + CLY + CHL))]

HISTORICAL SYSTEMATIC POSITION: - (CRY + (LAM + CHL)) (Monrós 1960); - (CRY + (CHL + CLY)) (Medvedev 1971); - (CHL + (CRY + CLY)) (Kasap and Crowson 1976); (Mann and Crowson 1981, 1983b); - (CLY + (CRY + ((CHL + LAM) + (EUM + MGS)))) (Jolivet 1978, 1988); - (CRY + CLY + CHL + LAM + EUM) (Chen 1985); - ((CLY + CRY) + (CHL + LAM)) (Suzuki 1988, Suzuki 1994); - (CHL + (LAM + (CLY + CRY))) (Lee 1993)

There are 122 genera (Seeno and Wilcox 1982) in 3 tribes and 11 subtribes, although the Clytrini are badly oversplit and many Australian genera of Cryptocephalini are also invalid.

Donaciinae Kirby, 1837: 222 (Askevold 1990b)

REVISED SYSTEMATIC POSITION: either - (DON + (CRI + HIS)) or - (DON + (BRU + SAG)), as suggested by Monrós (1960).

HISTORICAL SYSTEMATIC POSITION: - (DON + (SAG + BRU)) (Monrós 1960); - (DON + ((GAL + ALT) + (PRO + (CHR + AUL)))) (Medvedev 1971); - (DON + ORS) (Jolivet 1978, 1988); - (DON + (CRI + (CAS + HIS))) (Mann and Crowson 1981); - (DON + SAG + (CRI + (CAS + HIS))) (Mann and Crowson 1983b); - (DON + (SAG + CRI)) (Schmitt 1985, 1989); - (DON + CRI + SAG + BRU) (Chen 1985); - (DON + CRI) (Suzuki 1988, Suzuki 1994; Askevold 1990b); - (DON + all Chrysomelidae except BRU, MGL, ORS) (Lee 1993)

Currently there are eight genera in three tribes (Askevold 1990b).

Eumolpinae Hope, 1840: 162

= Megascalidinae Chapuis, 1874: 82 (synonymy in Bechyné and Bechyné 1969)

= Synetinae Edwards, 1953: 28

REVISED SYSTEMATIC POSITION: - (EUM + (LAM + CRY)) [EUM = - (SYN, SPI, (EUM + MGS))]

HISTORICAL SYSTEMATIC POSITION: - (MGS + (EUM + (GAL + ALT))) (Monrós 1960); - (MGS + (EUM + (LAM + (CRY + (CHL + CLY)))) (Medvedev 1971); - ((EUM + MGS) + (LAM + CHL)) (Jolivet 1978, 1988); - (EUM + SYN + (GAL + ALT)) and - (MGS + (LAM + CRY)) (Mann and Crowson 1981); - (EUM + (SYN + (GAL + ALT))) and - (MGS + (LAM + CRY)) (Mann and Crowson 1983b); - (EUM + LAM + CRY + CHL + CLY) (Chen 1985); - ((MGS + EUM) + ((HIS + CAS) + (CRY + (LAM + CRY)))) (Suzuki 1988, Suzuki 1994); - (EUM + (CRY + LAM)) (Lee 1993)

Synetinae: HISTORICAL SYSTEMATIC POSITION: - (SAG + SYN) (Medvedev 1971); - (SYN + ?) (Jolivet 1978, 1988; Suzuki 1988, Suzuki 1994); - (SYN + EUM + (GAL + ALT)) (Mann and Crowson 1981); - (SYN + (GAL + ALT)) (Mann and Crowson 1983b); - (SYN + ALT + GAL + CHR) (Chen 1985); - (SYN + (EUM + (LAM + CRY))) (Lee 1993)

The Eumolpinae are in a mess. The current checklist includes 442 genera in 15 highly dubious tribes and many subtribes (Seeno and Wilcox 1982), with the inclusion of Megascalidini and Synetini. I consider one third of the Australian genera to be invalid; a similar figure may be applicable to other faunas.

Galerucinae Latreille, 1802: 228

= Alticinae Spinola, 1844: 5

REVISED SYSTEMATIC POSITION: - (CHR + GAL) [= (CHR + (GAL + ALT))]

HISTORICAL SYSTEMATIC POSITION: - (EUM + (GAL + ALT)) (Monrós 1960); - ((GAL + ALT) + (PRO + (CHR + AUL))) (Medvedev 1971); - (CHR + (GAL + ALT)) (Jolivet 1978, 1988); - (SYN + EUM + (GAL + ALT)) (Mann and Crowson 1981); - (SYN + (GAL + ALT)) (Mann and Crowson 1983b); - (CHR + GAL + ALT + SYN) (Chen 1985); - ((GAL + ALT) + ?) (Suzuki 1988, Suzuki 1994); - ((GAL + ALT) + (CHR + CAS)) (Lee 1993)

There are 992 genera in an indeterminate number of tribes and subtribes which need to be revised (Seeno and Wilcox 1982). The Galerucini, which may be monophyletic if a few genera are excluded (Reid 1992c), are oversplit to the point where new genera are described from sclerites in the bursa copulatrix and regional keys to genera simply do not work for new species. Rather than every new species becoming a new genus, a moratorium should be declared on the

naming of new genera until a workable tribal and subtribal classification is available.

Hispinæ Gyllenhal, 1813: 448

= Cassidinae Gyllenhal, 1813: 434

REVISED SYSTEMATIC POSITION: uncertain, probably - (CRI + HIS)

HISTORICAL SYSTEMATIC POSITION: - ((CAS + HIS) + (AUL + CHR) + (CRI + (DON + (SAG + BRU)))) (Monrós 1960); - (SAG + (CAS + HIS)) (Medvedev 1971); - ((HIS + CAS) + ?) (Jolivet 1978, 1988); - (CRI + (HIS + CAS)) (Mann and Crowson 1981, 1983b); - ((CAS + HIS) + (EUM + LAM + CRY)) (Chen 1985); - ((CAS + HIS) + (CRY + (LAM + CRY))) (Suzuki 1988, Suzuki 1994); - ((CAS + HIS) + (DON + (SAG + CRI))) (Schmitt 1989); - (HIS + (GAL + (CHR + CAS))) (Lee 1993).

This subfamily could be referred to as either the Cassidinae or Hispinæ because both names originate from the same publication. Systematists seem to have preferred Hispinæ (Crowson 1955; Lawrence and Britton 1991).

The subfamily includes 221 genera in a tribal classification which requires revision (Seeno and Wilcox 1982).

Lamprosomatinae Lacordaire, 1848: 559 (Lamprosominae, emended Monrós (1958))

= Sphaerocharitinae Chapuis, 1874: 206 (Sphaerocharinae)

REVISED SYSTEMATIC POSITION: - (LAM + CRY) [= - ((LAM + SPH) + (CRY + CLY + CHL))]

HISTORICAL SYSTEMATIC POSITION: - (LAM + CHL) (Monrós 1960; Jolivet 1978, 1988; Suzuki 1988, 1994); - (LAM + (CRY + (CHL + CLY))) (Medvedev 1971); - (LAM + (SPH + (CHL + (CRY + CLY)))) (Kasap and Crowson 1976); - (LAM + (CHL + (CLY + CRY))) (Mann and Crowson 1981, 1983b); - (LAM + EUM + CHL + CLY + CRY) (Chen 1985); - (LAM + (CRY + CLY)) (Lee 1993)

There are 13 genera in three tribes (Monrós 1956a, 1958).

Megascalidinae (Megascalinae): *see* under Eumolpinae

Sagrinae Leach, 1815: 113

REVISED SYSTEMATIC POSITION: - (SAG + BRU), as suggested by Monrós (1960)

HISTORICAL SYSTEMATIC POSITION: - (SAG + BRU) (Monrós 1960, Mann and Crowson 1981); "stemgroup" for all Chrysomelidae (Medvedev 1971; Jolivet 1978, 1988); - (SAG + (DON + SAG + (CRI + (CAS + HIS)))) (Mann and Crowson 1983b); - (SAG + BRU + DON + CRI) (Chen 1985); - (SAG + CRI) (Schmitt 1985, 1989); - (SAG + (DON + CRI)) (Suzuki 1988, Suzuki 1994; Askevold 1990b);

There are 12 genera in four tribes (Monrós 1960).

Sphaerocharitinae (= Sphaerocharinae); *see* under Lamprosomatinae

Synetinae: *see* under Eumolpinae

Acknowledgments

I am especially grateful to John Lawrence (ANIC) for advice and generous access to the Australian National Insect Collection, and facilities rendered there. Michael Schmitt kindly allowed me a preview of unpublished papers. I thank John Dugdale (New Zealand Arthropod Collection, Auckland) for the loan of interesting larval material and discussion of the behaviour of *Allocharis*. John Lawrence and Penny Gullan (Australian National University) kindly checked early drafts of this MS, but they are certainly not responsible for any errors or omissions. Ingof Askewold comprehensively reviewed this manuscript for which I am grateful, although I have not necessarily accepted all of his ideas. I thank Andy Shepperd (CSIRO Entomology) for information on the use of chrysomelids in Australian weed control. I also thank the editors of this book for their infinite patience.

This paper was undertaken while the author was in receipt of an Australian Biological Resources Study grant, for which he is very grateful. I particularly thank Jean Juste (ABRS) for his support for my work.

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