Observations on the morphology and classification of weevils (Coleoptera, Curculionoidea) with a key to major groups

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A brief account of the present state of weevil taxonomy is followed by a detailed study of certain structures used in their classification, namely the venter, abdominal tergites, sternite 8 of the male, apex of the hind tibia and deciduous mandibular processes. A key to some 50 families and subfamilies of Curculionoidea is followed by a list of family-group taxa. The following changes are made: Brachyceridae, Eriphinae, Cryptolaryngidae and Raymondnymes are promoted to family rank from Curculionidae; Antliarolininae is demoted to a subfamily of Brentidae, and Allocoryninae to a subfamily of Oxyctinae; Coptonotini is demoted to a tribe of Curculionidae–Scolytinae; Carinae, subfam. n. is erected for Car Blackburn (genus incertae sedis) in Belidae; Dinomorphini is demoted to a tribe of Molytinae and Brachyceropsidinae is revived from synonymy with Dinomorphinae (Curculionidae); Brachyderini, Eremnini, Otiorthychinae and Sitonini are demoted to tribes of Entiminae; Desmidophorinae is transferred from Brentidae to Curculionidae; Peries Schönherr is transferred from Curculionidae–Thecesterninae to Cryptolaryngidae and Agriocheta Pascoe from Cryptorhynchinae to Hyperinae (Curculionidae); Schedlarius Wood and Mecopelmus Blackman are transferred from Coptonotidae to Platypodidae.

KEYWORDS: Curculionoidea, morphology, classification, key.

Introduction

In his Systema naturae of 1758, Linnaeus recorded 86 species of Curculionoidea (79 in Curculio, five in Dermestes and two in Attelabus). In only 14 cases does he give references to earlier works by authors other than himself. Less than a century later, Schönherr and his collaborators (Schönherr, 1833–1845) described 6808 species, distributed among 627 genera. After a further century and a half we have approximate totals of 57000 species and 6000 genera (figures based on O'Brien and Wibmer (1978) and other sources). The actual number of curculionoids that exist can only be guessed at but, in view of the recent greatly increased estimates for arthropods in general (Erwin, 1982; Stork, 1988) it would seem that the estimate of 85000 by O'Brien and Wibmer (1979) may have to be multiplied, rather than merely augmented.

Classification of weevils is like a mirage in that their wonderful variety of form and the apparent distinctness of many major groups lead one to suppose that classifying them will be fairly straightforward but, when examined closely, the distinctions disappear in a welter of exceptions and transformation series. As a result, a number of
major groups are currently defined by single characters. This has produced a workable system but the groups so formed are inevitably artificial and the true relationships of their components are obscured. For example, Marshall (1952: 266) erected the genus *Charactopus* in the Tanyrhynchinae for two species whose mandibles fit his (Marshall, 1908: 10) definition of that group, notwithstanding the fact that in all other respects they are typical tanymecines and were described as such by Hustache. The problem is made even worse by the fact that some of the structures used in weevil classification have been incorrectly observed or misinterpreted. The purpose of this paper is to clarify the morphology so that these structures may be used more effectively as sources of characters for defining taxa. They include the venter, the abdominal tergites, the apex of the hind tibia and the deciduous mandibular processes. In addition, the male sternite 8 is introduced as a potent source of characters at family level. Even where groups can be defined satisfactorily, the problem of ranking arises. In the latest comprehensive study of the group, Lacordaire (1863, 1866) recognized as families the Curculionidae, Scolytidae, Brentidae and Anthribidae. Within the first of these he recognized 82 'tribus' which Pascoe (1870) regarded as subfamilies. While most of these would be better regarded as tribes, a few have been given family rank. Thus Crowson (1955), using cogent arguments and the best characters then available, recognized the Nemonychidae (= Rhinomaceridae auctt.), Anthribidae, Belidae, Oxyacridinae, Aglycyderidae (= Proterhinidae), Attelabidae, Brentidae, Apionidae and Curculionidae (including Scolytinae and Platypodinae). These proposals have not been seriously challenged except by those who are reluctant to see the Scolytidae and Platypodidae fall as subfamilies within the Curculionidae (Morimoto, 1976; Wood, 1986). Morimoto (1962a, 1962b, 1978) promoted to family rank the group of the palm and grain weevils (Rhynchophoridae) and (1976) that of the New York weevil (Ithyceridae). Sanborne (1981), in a detailed study of this species, accepted this promotion and, in turn, proposed family status for the cychad weevils (Antiarhinidae). O'Brien and Wibmer (1982) promoted the Allocorynidae from the Oxyacridinae and the Rhynchitidae from the Attelabidae. The latter act was followed by Wood (1986), but in the same year Wibmer and O'Brien (1986) returned the group to subfamily status in the Attelabidae. Crowson (1984) has proposed giving family status to the Urodontidae and (1985) splitting the Nemonychidae into two separate families. The latter proposal has been rejected by Kuschel (1989), who has also (1990) united the Brentidae and Apionidae.

In this paper I propose separating the Brachyceridae, Cryptolaryngidae, Raymondionymidae and Erirhinidae from the Curculionidae in order to make the latter more certainly holophyletic, and have kept the Platypodidae as a separate family. I have, however, been unable to keep the Scolytinae separate from the Curculionidae, nor do I support the proposed family status for the Antiarihini (Brentidae) or Allocoryninae (Oxyacridinae) in spite of Crowson's (1986) strong argument in favour of the latter. I follow Crowson in keeping the Urodontidae separate from the Anthribidae (and give additional characters in the key, p. 870) but have opted to keep *Nemonyx* Redtenbacher with the other nemonychids (though in its own subfamily). To the characters given by Crowson can be added the anthribid-type ovipositor of *Nemonyx* (Fig. 170) which is not found in other nemonychids. Such disparate subfamily pairs occur in other weevil families, e.g. Oxyacridinae and Attelabidae. The number of weevil families here recognized is therefore 16. This contrasts strongly with the Chrysomeloidea where only three families are recognized. Perhaps, when their characters are more firmly established and their relationships are better understood, it will be possible to reduce the number of families by amalgamation.
Morphology and classification of weevils

FIGS 1–8. Figs 1–5, NEMONYCHIDAE. Venter (a) and sternite 8 (b) of male of: 1, *Nemonyx lepturoides* (F.) (Europe); 2, *Rhynchitomacer flavus* Voss (Chile); 3, *Doydirhynchus austriacus* (Olivier) (Europe); 4, *Cimberis attelaboides* (F.) (Europe); 5, *Rhinorhynchus zealandicus* Sharp (New Zealand). Fig. 6, URODONTIDAE. Venter of *Bruchela* sp., male (Europe). Figs 7 and 8, ANTHRIBIDAE. Venter (a) and sternite 8 (b) of male of: 7, *Anthribus albinus* (L.) (Europe); 8, *Brachytarsus nebulosus* (Forster) (Europe). Scale lines: (a) = 1 mm; (b) = 0.1 mm.
Morphology

As a contribution towards the solution of some of the problems mentioned above, I now present detailed studies of some adult weevil structures, followed by a key to major groups based, in part, upon the results of these studies.

Abdomen

Venter. Salient feature of adult weevil evolution has been a progression from small, depressed, soft-bodied forms to large, convex, rigid or armoured ones. Effects of this progression include major changes in the structure of the abdomen. Apex of the abdomen must be able to open to the exterior for the purposes of defaecation, copulation and, in females, oviposition. In most lower weevils (Nemonychidae, Belidae, Oxycorynidae, Aglycyderidae) the elytra are relatively flat and the small amount of apical deflexion of the venter needed to open the abdomen is spread among the five ventrites which are all free and subequal in length (Figs 1a–5a, 9a–18a). During the process of strengthening, however, the elytra have become increasingly convex, clasping the abdomen and metathorax and eventually interlocking (not fusing) with them to form a rigid capsule. In addition, the first two ventrites have become greatly enlarged and fused together. Flexure of the venter has thus been increasingly concentrated on the shortened ventrites 3 and 4 which eventually form a hinge with which ventrite 5 articulates in order to open and close the apex of the abdomen. The

FIGS 9–12. BELIDAE. Venter (a) and sternite 8 (b) of male of: 9, *Agathinus tridens* (F.) (New Zealand); 10, *Homalocerus lyciformis* (Germar) (Brazil); 11, *Belus suturalis* Boisduval (Australia); 12, *Car condensibus* Blackburn (Australia). Scale lines: (a) = 1 mm; (b) = 0.1 mm.
Intersegmental membranes in the lower weevils allow the ventrites to move apart horizontally, rather than articulate vertically. Their joints may therefore be described as 'stretch joints' as opposed to the 'hinge joints' of the higher weevils.

An alternative means of opening the abdomen is by the development of a pygidium. This consists of one or more tergites which are exposed and specially strengthened. It fits tightly against the truncate apex of the venter with which its base articulates in opening and closing the apex of the abdomen. It occurs in various groups but is best developed in the Anthribidae, most Attelabidae and many Rhynchophoridae. When a well-developed pygidium is present, the abdominal ventrites are in some cases more extensively fused than would otherwise be the case (Figs 7a, 8a, 34a, 35a).

The precise nature of the joints between the ventrites cannot be established by casual inspection. In Anthribidae in particular, joints that appear free may prove to be fused. To determine the condition with certainty, it is necessary to place the detached
venter from a well-potashed abdomen in glycerine and manipulate each ventrite in turn. In the lower weevils, adjacent ventrites should be pressed firmly against the bottom of the dish with blunt needles or fine forceps which are then moved to and fro. If no movement (other than fracture) occurs then the ventrites may be considered fused. Similarly, hinge joints may be tested by gripping the base of the venter in forceps and rotating it so that it is viewed from the side, then flexing the joints in turn. Hinge-jointed ventrites have well-developed vertical flanges at the sides which overlap strongly when they articulate. This movement, which is easy to observe, provides an absolute check on the freedom of the joints; if it is absent (and the lateral flanges abut), then the joint is fused or, at any rate, immovable. Figures 1a–78a are based on the foregoing criteria; where movement is possible, the ventrites are shown as detached; when fused, a broken line is used, the degree of fusion (depth of suture) being indicated by the size and spacing of the dashes; when no suture is visible, no line is shown.

Abdominal tergites. Tergites 1–7 are exposed (beneath the elytra) in all Curculionoidea. The exposure of the eighth tergite (the ‘additional anal segment’ of LeConte and Horn, 1876: xii, xv) varies from group to group and often between the sexes of the same group. A ninth tergite is well developed in female Nemonychidae. It is therefore necessary to identify tergite 7 in order to evaluate those that follow it. In actively flying groups (e.g. Anthribidae, many Atelabidae and Rhynchophoridae) the terga are well sclerotized and distinct, and can be identified by association with the corresponding ventrites, but in groups that fly less, or are apterous, the tergites are soft, unpigmented and indistinct. In extreme cases (e.g. Brachycerinae) the metanotum may also be entirely membranous, thus adding to the difficulty. In addition, just as sternites 1 and 2 are compressed within the hind coxal cavities, so tergites 1 and 2 are shorter and less distinct than the others; when the abdomen is broken off for dissection, one or both of them usually remains attached to the metanotum. This problem may be overcome by removing all, or at least the posterior part, of the metanotum together with the tergites. This drastic procedure requires some care to ensure that the metanotum remains attached to the tergites. If the segmentation is still unclear, recourse may be had to the spiracles. The spiracle of the first abdominal segment is often larger than the others (Crowson, 1981, fig. 59c) and may occupy the full length of the segment. Functional spiracles normally occur on segments 1–7, though in some cases (e.g. Sternochetus) the spiracles on segments 6 and 7 are much smaller than the others. Tergite 7 is usually sclerotized, at least posteriorly, and the spiracles lie either within the sclerotized area or in the membrane immediately adjacent to it. Muir (1918: 225–226) correctly reported spiracles on tergite 8 in Ithycerus, Rhynchophorus and the amycterine Acantholophus and Brachycerus, Dinomorphus, Entimus, Trichalophus and several other amycterines can be added to the list. In all these cases the spiracles are very small and probably non-functional.

In several groups the elytra are abbreviated so that one or two tergites are uncovered, forming a pygidium. This occurs independently of the exposure or concealment of tergite 8 so that a large number of combinations is possible. To express these succinctly I propose to use a tergal formula (TF). Tergites that are permanently exposed are shown in bold type; those that are covered by the elytra are in ordinary type; those that are concealed within the genital chamber are also in ordinary type but enclosed in parentheses. Thus Rhynchophorus, with tergite 7 uncovered and 8 concealed in both sexes has the formula  ♂: 1–6, 7 (8) while the majority of Curculionidae have TF  ♂: 1–8, ♀: 1–7 (8).
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Figs 19–25. Figs 19–21, BRENTIDAE. Venter (a) and sternite 8 (b) of male, and venter (c) of female of: 19, Cyphagopus westwoodi Parry (Asia); 20, Brentus anchorago (L.) (Americas); 12, Pseudoceocephalus depressus (Lund) (Africa). Fig. 22, ITHYKERIDAE. Venter (a) and sternite 8 (b) of male, and venter (c) of female of Ithycerus novaboracensis (Forster) (USA). Figs. 23–25, BRENTIDAE. Venter (a) and sternite 8 (b) of male, and venter (c) of female of: 23, Eurhynchus laevior (Kirby) (Australia); 24, Nanophyes marmoratus (Goeze) (Europe); 25, Ctenomerus tesselatus Faust (South Africa). Scale lines: (a,c) = 1 mm; (b) = 0.1 mm.
Male sternite 8. It is well known that the five ventrites of the weevil abdomen are morphologically sternites 3–7, sternites 1 and 2 having been absorbed into the hind coxal cavity. Sternite 8 is the next ventral sclerite after ventrite 5 and is concealed within the genital chamber. Despite Sharp’s (1918a: 211) observation that ‘the [eighth] ventral plate is usually membranous in the middle so as to be two distinct plates, but sometimes it is entire, and this is a character of much taxonomic importance’, scant attention has been paid to this structure by subsequent workers. Sharp himself (1918b: 216, fig. 5) described and figured it in the New York weevil, *Ithycerus novaboracensis* (Forster) and Muir (1918: 225) described it in the same species. Being closely attached to the spiculum gastrale, it is often inadvertently figured with that structure, e.g. Kissinger, 1968 (Apionidae); Morimoto, 1983 (Viticis); Oberprieler, 1988 (*Eremnus*); Ramamurthy and Ghai, 1988 (*Mylocerus*) and Kuschel, 1989 (Nemonychidae). Baker and Thompson (1978, 1980) used it to distinguish between species of Curculionidae–Amycteriinae. In this group it varies greatly in size and shape, and includes the fantastic forceps-like structures found in some *Phalidura* species. It was again described and figured in *Ithycerus* by Sanborne (1981), who mis-identified it as the ninth sternite. It has also been described and figured in 58 species of New Zealand Anthribidae by Holloway (1982).

In preparing the male genitalia sternite 8 usually separates easily from the venter, but in *Ithycerus* it is firmly attached to the truncate edge of ventrite 5 along its entire width. In many cases it can be examined in situ, but for critical study it should be separated, a procedure requiring great care. Small or delicate specimens should be stained with chlorazol black (very dilute, in 70% ethanol) to show up the membranes, while with large tough specimens the plate is best cut free with microscissors. Figures 1b–78b show that sternite 8 varies greatly in shape, relative size, pigmentation, sclerotization and in the presence and disposition of setae. This variation is remarkable, since the only obvious function of the plate is to support the spiculum gastrale during copulation. Nor is the variation random; several major groups have distinctive plates while in others the variation is limited. An interesting feature is the presence in several groups of rudiments of an apodeme which corresponds to the spiculum ventrale of the female. Although Muir (1918: 225) refers to it as ‘the false spiculum or strut’ I propose to call it the *spiculum relictum* (‘left over’). This apodeme may be an integral part of the plate (Fig. 22b) or separated from it by membrane (Figs 4b, 9b). It may be a solid rod (Figs 1b, 2b, 5b), a flat strip (Fig. 12b), or a forked process (Figs 52b, 61b). Whether all these structures are homologous is open to question.

To clarify the terminology, we now have the following:

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<th>Apodeme of:</th>
<th>Male</th>
<th>Female</th>
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<tr>
<td>sternite 8</td>
<td>spiculum relictum</td>
<td>spiculum ventrale</td>
</tr>
<tr>
<td>sternite 9</td>
<td>spiculum gastrale</td>
<td>—</td>
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<tr>
<td>tegmen</td>
<td>manubrium</td>
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It is interesting that sternite 8 of some male Dermestidae (Bostrychoidea) resembles that of some weevils. In the former family it is known as ‘periphallic sternite 1’ and has been used to distinguish species of *Trichelodes* by Peacock (1978). In this genus, and in *Evorinea*, there is an integral apodeme; in fact sternite 8 of *E. iota* Beal (Beal, 1961, fig. 2c) is not unlike that of *Cryptolarynx* (Fig. 50b).

The Nemonychidae present a major paradox. As arguably the most primitive curculionoids, one would expect them to have a large undivided plate with a strong
integral apodeme. Instead, we find a plate which is either divided (Fig. 4b) or entirely membranous (Fig. 5b) and a detached apodeme. A further paradox is provided by the Platypodidae, often regarded as the most derived curculionoids, in which, although there is no apodeme rudiment, the eighth sternite is undivided, large and seta-fringed so that it closely resembles the eighth tergite (Figs 76b–78b). The fully divided condition of the plate is characteristic of the great majority of Curculionidae, but occurs also in some Nemonychidae, Attelabidae and Rhynchophoridae. If Deuve (1988) is correct in his assertion that (my translation), ‘sternites VIII and IX are absent in both sexes of Coleoptera; the sclerites generally considered by authors as sternites are laterotergites’, then the divided condition might be expected in any primitive Coleoptera. I would maintain, however, that the presence of the spiculum relictum in the Nemonychidae suggests that their progenitors had a more or less united ventral plate in the eighth abdominal segment with an integral spiculum (possibly forked, as is the spiculum gastrale of the ninth segment). Support for Deuve is found in Metcalfe (1932: 84), who studied the development of several Coleoptera, including *Anthonomus pomorum* (L.). She writes: ‘Since the spiculum gastrale and the genital pocket are already in existence at a time when the full complement of tergites and sternites is visible, it is impossible that a tergite or sternite should form the whole, or a part of, the structures in question.’

**Tibial apex**

Primitively, the weevil tibia is subcylindrical, with a transversely truncate apex the greater part of which is occupied by the socket into which the condyle of the first tarsal segment fits. Scarcely modified clothing setae project beyond the apex, forming an irregular fringe all round. In more advanced forms the tibial apex expands dorsoventrally and the anterior (outer) edge extends distally, so that the apical area becomes ovate and oblique to the tibial axis, with the tarsal insertion facing posteriad (inwards). A regular comb of enlarged setae forms along the anterior (distal, outer) edge. This comb continues around the ventral end of the apex and ends adjacent to the tarsal insertion leaving a gap on the dorsal edge which allows the tarsus to be reflexed against the tibia. In the higher weevils two further developments may occur:

1. The outer apical edge, adjacent to the fringing setae, becomes swollen and the more or less abruptly truncate apex of this swelling becomes defined by a secondary comb of setae which joins up with that of the true apex to enclose completely a lenticular area on the outer aspect of the tibial apex. The surface of this area, which is more or less oblique to the tibial axis, may be either flat or concave, smooth and bare (Figs 87, 95) or setose or squamose (Fig. 93). The setae of the secondary (proximal) comb are often weaker and less regular than those of the distal comb, and are sometimes difficult to distinguish from the adjacent clothing setae (Thompson, 1988, pl. 1, figs d–i). This modification, which is almost always confined to the hind tibia, is the *enclosed corbel* of recent authors (Figs 86–88, 92–95).

2. The margin of the tarsal socket becomes raised on its distal side, and this elevation develops into a broad flange which shields the tarsal insertion outwardly and extends across the full width of the tibial apex. This flange, which is always smooth and bare, occurs on all three tibiae; groups possessing it are said to have *semi-enclosed corbels* (Figs 82–85). This term was proposed (Emden, 1944) on the incorrect assumption that the edge of the smooth flange is the true tibial apex (having lost its setae) and that the setose edge is not the true
FIGS 26–33. BRENTIDAE. Venter (a) and sternite 8 (b) of male of: 26, Cylas formicarius (F.) (Asia); 27, Antliarhis zamiae (Thunberg) (South Africa); 28, Cybebus dimidiatus (F.) (Madagascar); 29, Myrmacielus formicarius Chevrolat (Australia); 30, Tanaos sanguineus (Thunberg) (South Africa); 31, Aplemonus gibbipennis Boheman (South Africa); 32, Piezotrachelus pullus Boheman (West Africa); 33, Apion frumentarium (L.) (Europe). Scale lines: (a) = 1 mm; (b) = 0.1 mm.
apex (as here interpreted) but corresponds to the proximal comb of the enclosed corbel. Thus, according to van Emden, the tibial apex is setose when the corbel is enclosed and bare when it is semi-enclosed. Under this interpretation it would be impossible for enclosed and semi-enclosed corbels to coexist in the same tibia (since the apex would have to be both bare and setose at the same time), whereas under the present interpretation such coexistence would be possible. Although no unequivocal example of this has been found, Fig. 95 shows a tibia which approaches this condition.†

Where neither of the above developments has taken place, the tibia is said to have open corbels (Figs 79–81).

The various terms that have been used to describe the three principal states of the corbel may best be given as shown in Table 1. In addition, some workers writing in English have used closed instead of enclosed, as Faust and van Emden apparently did when writing in German.

It is unfortunate that the stable nomenclature established by van Emden cannot be maintained (chiefly because of his misinterpretation of the 'semi-enclosed' state). For this reason, and because the term corbel is, in any case, a misnomer (Thompson, 1991) I advocate that it be abandoned. The only descriptive terms required are outer bevel and inner flange; when neither bevel nor flange is present the tibial apex can be described as simple.

The reinterpretation of the tibial 'corbel' has implications for the mucro–uncus problem. Many broad-nosed Curculionidae have a tooth-like process at the inner apical angle of the tibia (the mucro) while many long-nosed Curculionidae have an incurving apical spine which seems to arise from the outer apical angle (the uncus). A study of many examples has led me to believe that the uncus is formed by fusion of the mucro with the inner flange (Figs 82, 98, 108–113). In some advanced groups (Cossoninae, Zygopinae) a further development occurs when the uncus opens out so its axis coincides with that of the tibia. It now genuinely arises from the outer apical angle (Figs 118, 119). During this process the outer seta-comb, previously intact, is displaced,

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<td>Emden, 1944</td>
<td>corbels</td>
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<td>enclosed</td>
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†Since this paper went to press, I have observed that the hind tibiae in some species of Lepriopus (Entiminae, Tanymecini) have a well developed outer bevel, with two rows of setae and a well developed inner flange.
abbreviated and finally eliminated. At the same time the inner apical angle may become acute or produced, forming a secondary mucro or premucro (Kuschel, 1951: 24). The space between the premucro and the extended uncus is usually devoid of both combs and flanges. The distinction between mucro and uncus is therefore one of degree rather than kind. Moreover, well-developed unci and intermediate structures may occur on different tibiae of the same specimen. Thus in both _Anthonomus_ and _Curculio_ the (fore and) middle tibiae (Figs 96–98, 102–104) are clearly uncinate, while the posteriors (Figs 99–101, 105–107) are not. Similarly, in the Cleoninae there is a constriction between the flange and mucro in the posteriors (Fig. 111), and there is also a flexure between them (Fig. 113). A similar partial fusion occurs in some entimines, e.g. _Amystax_ (Figs 82, 85), a group in which unci are not supposed to occur.

Figs. 34–39. _Attelabidae_. Venter (a) and sternite 8 (b) of male, and venter (c) of female of: 34, _AtteLABus nitens_ (Scopoli) (Europe); 35, _Apoderus coryli_ (L.) (Europe); 36, _Auletobius sanguisorbae_ (Schrank) (Europe); 37, _Rhychites hungaricus_ (Herbst) (Europe); 38, _Deporaus betulae_ (L.) (Europe); 39, _Pterocolus ovatus_ (F.) (USA). Scale lines: (a, c) = 1 mm; (b) = 0·1 mm.
Figs 40–49. BRACHYCERIDAE. Venter (a) and sternite 8 (b) of male of: 40, Desmidophorus hebes (F.) (Asia); 41, Microcerus retusus (F.) (South Africa); 42, Episus contractus Fähraeus (southern Africa); 43, Gyllenhalia crinita Marshall (South Africa); 44, Brachycerus barbarus (L.) (Europe, North Africa); 45, Euretus aurivillii Péringuey (South Africa); 46, Brotheus praemorsus (Thunberg) (South Africa); 47, Byrsops sulcicollis Gyllenhali (South Africa); 48, Synthocus truncatus Boheman (South Africa); 49, Hoplitotrachelus spinifer Lacordaire (South Africa). Scale lines: (a) = 1 mm; (b) = 0.1 mm.
Figs 50–57. Figs 50–53, CRYPTOLARYNGIDAE, RAYMONDIONYMIDAE and ERIRHINIDAE. Venter (a) and sternite 8 (b) of male of: 50, Cryptolarynx vitis (Marshall) (South Africa); 51, Raymondionymus marqueti appeninus Dieckmann (Europe); 52, Notaris aethiops (F.) (Europe); 53, Neochetina bruchi Hustache (South America). Figs 54–57, RHYNCHOPHORIDAE. Venter (a) and sternite 8 (b) of male of: 54, Sitophilus glandium (Marshall) (India); 55, Dryophthorus corticalis (Paykull) (Europe); 56, Rhynchophorus palmarum (L.) (South America); 57, Rhinostomus barbirostris (F.) (Central and South America). Scale lines: (a) = 1 mm; (b) = 0.1 mm.
Figs 58–64. Curculionidae. Venter (a) and sternite 8 (b) of male of: 58, Otiorhynchus clavipes (Bonsdorff) (Europe); 59, Brachyderes lusitanicus (F.) (Europe); 60, Entimus nobilis (Olivier) (Brazil); 61, Brachyceropsis verrucosus (F.) (Africa); 62, Curculio nucum L. (Europe); 63, Hylobius abietis (L.) (Europe); 64, Baris davidis (Fairmaire) (China). Scale lines: (a) = 1 mm; (b) = 0·1 mm.
Figs 65–71. Curculionidae. Venter (a) and sternite 8 (b) of male of: 65, Cossonus canarensis Faust (India); 66, Rhyncolus elongatus (Gyllenhal) (Europe); 67, Stenoscelis hylastoides Wollaston (South Africa); 68, Coptonotus cyclopus Chapuis (South America); 69, Hylastes ater (Paykull) (Europe); 70, Scolytus scolytus (F.) (Europe); 71, Ips sexdentatus (Boerner) (Europe). Scale lines: (a) = 1 mm; (b) = 0.1 mm.
Figs 72–78. PLATYPODIDAE. Venter (a), sternite 8 (b) and aedeagus (c) of male of: 72, *Mecopelmus zeteki* Blackman (Panama); 73, *Carphodicticus cristatus* Wood (Venezuela); 74, *Craniodicticus mucronatus* Blandford (Sri Lanka); 75, *Platytarsulus* sp., near *elongatus* Schedl (Borneo); 76, *Schedlarius mexicanus* (Dugès) (Mexico); 77, *Platypus cylindrus* (F.) (Europe); 78, *Crossotarsus mniszechi* Chapuis (Malaysia). Scale lines: (a) = 1 mm; (b, c) = 0.1 mm.
Unci are mainly present in weevils which are associated with wood or woody plants, but they are not a necessary adaptation to walking on bark (otherwise genera such as *Strophosoma*, which regularly climbs trees to reach the flowers, would have developed them). Rather I suspect that they enable the weevil to grip woody stems when boring oviposition holes or feeding on the tough rind of woody shoots. This may be why they are better-developed on the fore and middle tibiae than on the hind.
Deciduous mandibular processes

Large horn- or blade-like processes occur on the mandibles of a variety of Coleoptera, including Leiodidae (*Agathidium mandibulare* Sturm), Lucanidae (*Nigidius*), Tenebrionidae (*Molion*) and Cerambycidae (*Chemsakiellus*). Within the Curculionoidea, similar processes occur, in females only, in Scolytidae (*Pityophthorus abnormalis* Bright) and Platypodidae (*Spathidicerus thomsoni* Chapuis and *Diapus spatulifer* Browne). Extrorse cusp-like processes occur on the mandibles of some Attelabidae–Rhynchitinae, Rhynchophoridae–Rhynchophorinae and Curculionidae (some Cholinae; *Sibinia tanneri* Clark (Tychiinae)). Blunt tubercles have been observed...
on the left mandible of some male *Microcerus* species (Brachyceridae) and on one or both mandibles of some male Curculionidae–Amycterinae. None of these processes is dehiscent (though those of *Diapus spatulifer* are sometimes broken off). The processes we are here concerned with invariably occur in both sexes (though they may be dimorphic) and, except for some Curculionidae–Sitoniini, on both mandibles. In the great majority of species the processes are shed by active dehiscence early in adult life,

Figs 96–107. CURCULIONIDAE–ANTHONOMINAE and CURCULIONINAE, tibiae: 96–101, *Anthonomus grandis* Boheman, apex of left middle tibia (96–98) and hind tibia (99–101) in inner, apical and outer views; 102–107, *Curculio glandium* Marsham, ditto (note that, in both species, the middle tibiae are imperfectly uncinate, while the hind tibiae are not uncinate at all).
although some individuals may retain one or both into maturity. Only in a few cases, listed below, has the dehiscence mechanism been totally lost so that the processes are invariably retained throughout adult life. The site where the process was attached is usually marked by a distinct well-defined rough area, or scar. When the processes are small the scar may be hard to see. Thus Marshall (1908: 10) commented (on Tanyrhynchus): ‘owing to their ill-defined character and outwardly oblique position, it seems improbable that they can really serve as supports for temporary false mandibles’. I have confirmed, however, that processes are present in this genus, though they are very small and slender. Another problematic group is the Ottistiriini. F. van Emden (1936: 77) placed them in his key with groups which lack processes but conceded that ‘Manche Ottistiriini mit Narbe nahe der Basis der Unterseite der Mandibeln’. In fact, Heller (1925: 55; fig. 27) figured processes in Eutinophaea maculicollis Heller, so it is likely that they occur throughout the group. In cases where the mandible is flattened and the process arises from a narrow edge, the scar is rapidly worn away completely. Thus Sharp (1896: 86) commented on his new genus Meotiorhynchus: ‘This genus could be placed quite satisfactorily in the Otiorhynchidae were it not that no mandibular scar exists’. In fact the type-series includes a teneral specimen with small but distinct scars. In all the other specimens they have been worn away. (This error was perpetuated by van Emden (1936: 222; 1944: 570).) A similar situation exists in some Alophini, e.g. Triglyphulus and in Otiorhynchus chrysocomus Germar. Two other Otiorhynchus species (truncatus Stierlin and vastus Apfelbeck) have flattened mandibles, but in these
the process arises on the lower surface, away from the edge. A similar condition has been observed in an unnamed Australian entimine. Normal processes vary greatly in shape, being either straight (Fig. 122), incurved (Figs 120, 124–126) or extrorse (Figs 127, 129); sometimes there is a tooth on the inner aspect, near the base (Figs 122, 125). Extrorse processes occur only in the Entiminae–Promecopini and some Neotropical Polydrusus species.

Early authors, including Schönherr, regarded such processes as the very mandibles themselves ("mandibulae exsertae"); Müller (1818: 424) noted that they were present in a small minority of specimens of three different species. Their true nature was described by Lacordaire (1863: 5, note). He suggested that they might be used by the weevil to dig its way out of the soil in which it had pupated. He confirmed their presence in the pupa and, perhaps because of this, and their rapid dehiscence after emergence, some authors have mistakenly referred to them as 'pupal mandibles'. They have also been called

Figs 120–129. CURCULIONIDAE-ENTIMINAE, deciduous mandibular processes (various types): 120, 121, Naupactus sp. in dorsal and left lateral views; 122, 123, Heterostylus sp., ditto; 124, Exophthalmus sp.; 125, Astycus lateralis (F.); 126, Polycelaes krokisii Dohrn; 127, 128, Colecerus variegatus Boheman, in dorsal and left lateral views; 129, Promecops sp. (left process missing). For drawing conventions, see text (p. 870). Scale lines, 0.5 mm.
mandibular appendages' and 'deciduous pieces' (Le Conte, 1874), 'false mandibles' (Marshall, 1908: 10), 'provisional mandibles' (Imms, 1925: 458) and 'Supplementzähne' (Scherf, 1964). Jeannel (1949: 790) has identified these processes with the terebra (elongated terminal cusp) of the mandible, and this may well be true in the Entiminae–Sitoniini (Figs 154–157) and possibly also in the Brachycerinae (Figs 158–165), but the processes in other Curculionidae (Figs 120–152) and Attelabidae (Fig. 153), are far removed from the cutting edge of the mandible and no intermediates are known that would support Jeannel's opinion. Their correct interpretation was given by Ting (1936: 98): 'the deciduous cusp is a part of the mandible itself and is not an appendage, modified seta, or additional articulated structure'. Nonetheless, dehiscence usually takes place at a precise point which is marked, on the intact mandible, by a constriction or fine groove. Often this is at the base of the process, flush with the surface of the mandible proper (Figs 120–130), but in many cases it is above the base so that, after dehiscence, a truncate stump or pedicel is left. In the Tanymeclini a transformation series can be traced in which the pedicel increases in size at the expense of the process until it replaces the latter almost completely (Figs 130–135). In several other cases (see below) a similar enlargement of the pedicel has occurred, and all have hitherto been misinterpreted as 'persistent appendages'. Only Marshall (1945: 433) realized what had

Figs 130–135. CURCULIONIDAE–ENTIMINAE–TANYMECINI, deciduous mandibular processes, showing development of pedicel (p): 130, Cycloides sp.; 131, Tanymeles discolor Gyllenhal; 132, Leptoscapus sp.; 133, genus indet., near Ischnotachelia; 134, Iphisomus falciger (Gerstäcker); 135, I. mandibularis Hustache. Scale lines, 0·5 mm.
FIGS 136–143. CURCULIONIDAE–ENTIMINAE–PRYPNINI, deciduous mandibular processes, showing sexual dimorphism and permanent retention: 136–138, *Prostomus scutellaris* (F.), male in dorsal and ventral views (with long pedicels but processes shed) and female in dorsal view (with short pedicels, processes shed); 139–141, *Prostomus murinus* (Lea), male in dorsal, left lateral and ventral views (with long pedicels and base of left process present); 142, *Prypnus squalidus* (Gyllenhal), male (pedicels absent, left process present); 143, *Prypnus trituberculatus* Germar, female (with short pedicels and permanently retained processes). Scale lines, 0.5 mm; s, scar.
Fig. 144–150. Curculionidae—Entiminae, deciduous mandibular processes, showing unusual types of pedicel: 144, *Psallidium concinnum* Faust, female, with very long blade-like pedicels and deciduous processes attached to their outer aspect; 145, *idem*, male, with short (normal) pedicels; 146, 147, *Psallidium aurigerum* Desbrochers, male and female without pedicels; 148, *Nothognathus schoutedeni* Marshall, male, with falciform pedicels and deciduous process attached along inner aspect (cf. Fig. 144); 149, *Mesostylus hauseri* Faust, with falciform pedicels and deciduous processes arising from inner aspect near base; 150, *Parastylus* sp., ditto. Scale lines, 0.5 mm.
happened: ‘each mandible [in *Iphisomus*] bears a long stout curved process which has hitherto been regarded as the temporary deciduous piece that is characteristic of the vast majority of adelognathous weevils. But this structure differs from all known types of deciduous mandibles in that it is coarsely punctate and bears numerous long erect setae; moreover it is present in every specimen... [it] is not a false mandible but a solid process of the mandible itself, the deciduous piece being attached to its apex’. In other examples the enlarged pedicels are, like those of *Iphisomus* (Figs 134, 135), punctate and setose, whereas all the deciduous processes so far examined are bare and smooth. On the basis of this distinction it is possible to recognize those cases in which the dehiscence mechanism has been lost and the formerly deciduous processes are always retained throughout adult life. The six examples so far noted are *Leptomias waltoni* Marshall (both sexes), *Chlorophanus excisus* (F.), *Prynus trituberculatus* Germar, *Stereogaster globosa* Van Dyke, *Bletonius hustachei* Hoffmann (all in female only) and *Anomonychus henoni* Faust (female certainly, male doubtful). The last three belong to monotypic genera but the first three are each congeneric with species with normal, deciduous processes. All six belong to the Curculionidae–Brachyderinae (auctt.) but are not closely related to each other. Enlarged pedicels occur in the following genera:

*Prostomus.* Elongate pedicels are present only in the male; in the female they are short (Fig. 138). In the common species, *P. scutellaris* (F.), they are smoothly rounded apically

Figs 151–157. Fig. 151, ATTELABIDAE–RHYNCHITINAE, mandibles of *Byctiscus venustus* (Pascoe) with deciduous mandibular process. Figs 152, 153, CURCULIONIDAE–ENTIMINAE, miniaturized deciduous processes: 152, *Leptostethus aureus* Thompson; 153, *Trigonoscuta rothi* Pierce. Figs 154–157, CURCULIONIDAE–ENTIMINAE–SITONINI, abnormal deciduous mandibular processes: 154, 155, *Cecractes* sp. in dorsal and apical views (deciduous cusps on both mandibles); 156, 157, *Eugnathus curvus* Faust, ditto (deciduous cusp on left mandible only). Scale lines, 0.5 mm.
and the deciduous process (which has not yet been observed) is attached beneath the apex (note scars in Fig. 137). In a specimen of *P. murinus* (Lea) a broken process is attached to the apex of a shorter pedicel (Figs 139–141).

**Cherrus.** The male of one (undescribed) species had pedicels very similar to those of *Prostomus scutellaris*.

**Prypnus.** Short pedicels are present in the males of some species (cf. Fig. 138) but not in others (Fig. 142). A complicating factor here is that *P. trituberculatus* Germar has persistent mandibular processes in the female (Fig. 143).

**Psallidium.** Only the females of some of the species have pedicels (Fig. 144). Hence in some species very few individuals have processes (these being deciduous but not yet shed), in others a high proportion of specimens have them (females with pedicels, males without (Figs 145, 146)) while in some, e.g. *P. maxillosum* (F.), every specimen has them (females with pedicels, males absent).

**Nothognathus.** Two males of *N. schoutedeni* Marshall have falciform pedicels, each with a deciduous process on its mesoventral aspect (Fig. 148). Two females of *N. varius* Marshall lack pedicels, as does a third, unsexed, specimen (the holotype). The state of the mandibles in the female of the former species and in the male of the latter is therefore unknown.

**Mesostylus and Parastylus.** Here the pedicels are similar to those of *Nothognathus schoutedeni*, but the deciduous processes are slender and arise from near the base of the pedicel and are at right angles to it, forming a remarkable V-shaped structure (Figs 149, 150). The pedicels in the Mesostylini are largely bare and smooth (contradicting the distinction made above between pedicels and processes) except for a few setiferous punctures near the base on the underside. The tapering apical part could easily be misinterpreted as a fixed process if the scar on its mesoventral aspect were overlooked.

**Iphisomus.** (See above.)

Two further kinds of variation in mandibular processes occur:

1. Miniaturization. Here the process is reduced in relative size (but not proportions) until it is patently vestigial (Figs 152, 153). Examples are *Leptostethus speciosus* Thompson (and some of its relatives) and *Bothynorhynchus lascivus* Boheman (both Entimini) and *Caneorhinus biangulatus* Champion (Cylindrorhini). Whereas the lengths of normal processes are 8–14% of total body length, those of *Leptostethus aureus* Thompson (Fig. 152) are only 3% of it.

2. Transformation. The process becomes converted into (or is derived from) an accessory mandibular cusp. Two instances of this are known, one in *Brachycerus* (Brachyceridae) the other in the Sitonini (Curculionidae–Entiminae).

Marshall (1916: 28) noted the presence of deciduous processes in some species of *Brachycerus*. I have observed scars in over 50 species and processes in a further 30. The processes can be arranged in a transformation series passing from stout discrete processes to thin ill-defined blade-like structures (Figs 158–165). In a few species the blade-like mandibles have themselves become elongated (Figs 167, 168) but these elongations are not deciduous (though they are sometimes broken off (Fig. 169)) and
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FXGS 158-168. BRACHYCERIDAE, mandibles: 158-165, Brachycerus spp., series showing development (or loss) of deciduous processes; the species figured are (158) B. foedus Boheman, (159) B. rudolphi Aurivillius, (160) B. oblongus Fåhraeus, (161) B. emeritus (L.), (162) B. congestus Gerstäcker, (163) B. duplicatus Gyllenhal, (164) B. intermedius Péringuey, (165) B. verrucosus (Olivier); 166, Desmidophorus sp. with deciduous flange; 167-169, Brachycerus spp. with non-deciduous flanges; the species figured are (167) B. apicatus Gyllenhal, (168, 169) B. impendens Fåhraeus. Scale lines, 0.5 mm.
are not accompanied by deciduous processes of any kind. In the Sitonini, cusp-like deciduous processes have been reported in *Eugnathus* by van Emden (1936: 68, fig. 1) and Voss (1940: 17, fig. 1). They occur on the left mandible only (Figs 156, 157) of both sexes, and leave a distinct scar in the angle between the small apical cusp and the cutting edge. The genus *Catachenus* has similar scars on the left mandible. In *Ceceractes* there is a smaller, less well-defined process on both mandibles (Figs 154, 155). These are certainly deciduous though the scars they leave are indistinct. In *Sitona*, as described by van Emden (1936: 236), fresh adults have elongate mandibular cusps but these are not deciduous, being worn away during adult life, and their relationship to the deciduous cusps is problematic.

From the foregoing it will be apparent that recognizing the presence (or proving the absence) of deciduous mandibular processes is far from straightforward. Certainly they are characteristic of the adelognathous Curculionidae, being present in 76 of the 78 nominal tribes so far examined. The two exceptions are the Brachyceropsidinae, based on a single African species, and the Entiminae–Pachyrhynchini, an important Southeast Asian group. A strong case has been made out by May (1978: 359) for regarding the lack of processes in the latter group as a secondary loss. Among the
Figs 175–180. CURCULIONOIDEA, tegmina: 175, 176, BELIDAE, (175) Rhinotia hae-moptera Kirby, (176) Car condensatus Blackburn; 177–180, BRENTIDAE, (177) Brentus anchorago (L.), BRENTIDAE (178) Antliarhis zamiæ (Thunberg), (179) Eurhyn-chus laevior (Kirby), (180) Apion frumentarium (L.). Scale lines, 0·2 mm.
Figs 188–196. Curculionidae, tegmina: 188–193, Entiminae, (188) Lordops schonherri (Dalman), (189) Entimus nobilis (Olivier), (190) Artipus calceatus Marshall, dorsal view, (191) idem, lateral view (stippling shows 'ghost' of ring), (192) Metacinops rhinomacer Kraatz; 194, 195, Molytinae, (194) Hylobius abietis (L.), (195) Lepyrus capucus (Schaller); 196, Brachyceropsidinae, Brachyceropsis sp. (the asymmetrical pigmentation is normal and is sometimes even more marked). Scale lines, 0.5 mm.
Figs 197–201. Figs 197–200, BRACHYCERIDAE: 197, 198, DESMIDOPHORINAE, (197) Tetracyphus aequatorialis Faust, (198) Ocladius ziczac Marshall; 199, 200, BRACHYCYRINAE, (199) Brachycerus cylindripes Bedel, (200) Euretus aurivillii Péringuey. Compare the marked difference of form between Brachycerus and Euretus with the similarity of their male eighth sternites (Figs 44, 45). Fig. 201, CURCULIONIDAE–BRACHYCROPSIDINAE, Brachyceropsis sp. Scale lines, 5 mm.
phanerognathous Curculionidae there are at least 15 nominal tribes which have mandibular processes and which are currently associated with the Adelognathi to form the Entiminae. One further group which may be included in it is the Ectemnorhinini, which have the general appearance of broad-nosed weevils but are both phanerognathous and devoid of mandibular processes. In addition to Brachycerus (see above) deciduous processes occur in most, if not all, of the other genera of Brachycerinae, though not in the three genera of Brachyceridae—Microcerinae. Thin, deciduous flanges do, however, occur in Desmidophorus (Fig. 166) and its allies, as noted by Marshall (in van Emden, 1936: 68, note) though not (apparently) in Ocladius (Brachyceridae—Desmidophorinae). But they are not confined to the Curculionidae and Brachyceridae: Buck (1952: 162; figs 11, 12) described and figured them in Attelabidae (Deporaus and Byctiscus) (see also Daanje, 1964: 9; fig. 2). Although Buck was the first to record them in print, the specimen of Byctiscus here figured (Fig. 151) bears a label, 'Vide mandibular process!' in the hand of its former owner, Dr David Sharp (died 1922). Whether these processes and those of the Brachyceridae are strictly homologous with those of the Curculionidae is open to question, but their existence inevitably devalues the processes as a taxonomic character.

Authors are agreed that the function of the processes is to assist the adult weevil to escape from its pupal cell in the soil and make its way to the surface. Unfortunately there is only one published observation of this (Lesne, 1899). In this often-quoted account (reproduced in full by Donisthorpe, 1942) Lesne describes the adult of Barypeithes pellucidus (Boheman), confined under soil in a glass tube, using the processes to seize grains of sand which it then passed between its front legs repeatedly, thereby clearing a passage through the soil. The processes in this species are strongly curved so it would be perfectly possible for the weevil to grasp sand grains (bracing them against the front of the mandibles), but in many species the processes are straight or even divergent (Curculionidae—Promecopini, Figs 127–129) and would be unable to function in the manner described by Lesne. Perhaps in these cases the processes are used for scraping, the head moving vertically in those cases where the processes are straight and transversely where they are divergent. Certainly there is a strong correlation between miniaturization of the processes and sandy habitats where digging would not be so necessary; in Leptostethus (Curculionidae—Entiminae) there is a correlated transition series in both factors (Thompson, 1988: 9). Similarly, Attelabidae—Rhynchitinae which have processes pupate in the soil, whereas those that lack them do not (Daanje, 1964: 11). The Curculionidae—Sitoniini are, however, an exception to this rule; Sitona species pupate in soil at a depth of 5 cm (Anon, 1983: 3) but, as stated above, lack mandibular processes.

Dehiscence normally takes place very soon after emergence. Occasionally the mechanism fails in an individual, and one or both processes are retained throughout adult life, when they are subject to abrasion or fracture. Dehiscence is aided by feeding; the interposition of a leaf-blade between the processes causes one to break the other off when the weevil closes its jaws, which is why so many specimens retain one process longer than the other (Kolbe, 1927: 2).

Regular process-retention and pedicel-formation, as described earlier, seem to be two ways of providing the weevil with a permanent digging or scraping tool. The use of such a tool is not immediately apparent. It is unlikely to be used for burying the eggs, since it may occur in either or both sexes and one species which is known to bury its eggs, Leptostethus speciosus Thompson, digs a pit for the purpose with its hind legs (Thompson, 1988: 50).
In preparing the figures of mandibular processes, the following conventions have been employed: all setae and punctures are omitted; rostrum, persistent appendages and scars are drawn with thin lines; mandibles, including pedicels, with thick lines; deciduous processes solid black (with highlights).

Tentative key to the families and some subfamilies of adult Curculionoidea

Although many of the characters used in the key are difficult to observe, it is nevertheless intended to be usable. To facilitate this I have appended a series of notes, qualifications, etc., to which the superscript numbers in the key refer.

As this paper was originally intended to be an introduction to a projected reclassification of the broad-nosed weevils, the treatment of the families in the key is somewhat uneven; the Anthribidae are left undivided and the long-nosed weevil subfamilies are merely sorted into informal groups.

   - Maxillary palpi compact, not projecting. Labrum indistinct.

2. Pygidium present. Tibiae without spurs.
   - Pygidium absent. Tibiae with spurs. (Abdominal ventrites all free. TF3: 1–8 (9); ☵: 1–7(8,9)).

3. Prothorax with lateral carinae, at least near base; these carinae continuous with transverse pre-basal carina.
   - Ventrites 1–3 (–5) fused (Figs 7a, 8a). Pygidium 1-segmented (tergite 7) in both sexes. Male with pedon of aedeagus and manubrium of tegmen both distinct and sternite 8 present. Female with small spiculum ventrale; ovipositor stout, with small pre-apical styli and extrorse apical teeth (Fig. 172).

   ANTHRIBIDAE–ANTHRIBINAE and CHORAGINAE
   - Prothorax without lateral or pre-basal carinae. Ventrites all free (Fig. 6). Pygidium 2-segmented in male. TF3: 1–6, 7, 8; ☵: 1–6, 7 (8). Male with pedon of aedeagus indistinct, manubrium of tegmen vestigial and sternite 8 absent. Female without a spiculum ventrale; ovipositor delicate, with apical styli and no teeth.

   URODONTIDAE

4. Ovipositor (Fig. 170) distally narrow, compressed, valves near apex with extrorse teeth and small styli (as in Anthribidae).
   - Ovipositor (Fig. 171) broader, depressed, with large styli and no teeth.

   DOYDIRYNCHINAE (including RHINORHYNCHINI)

5. Ventrites 1–5 all free or, if 1 and 2 are fused, then antenna without terminal club; 2–5 usually subequal in length. (Antennae not geniculate).
   - Ventrites 1–2 (–4) fused; either 2 or 5 distinctly longer than 3 and 4 (taken separately).

6. Tarsi pseudotrimerous. All coxae relatively small; each pair separated by a distance exceeding the width of one of them. (Spirogyra 8 of male (Figs 16b–18b) a broad plate with setae on either side).
   - Tarsi pseudotetramerous. Coxaes larger, separated by less than width of one of them.

7. Segment 2 of all tarsi transverse, often bilobed. Antennae inserted at extreme base of rostrum but, if not at extreme base, then antenna with compact club. Tergite 8 concealed in both sexes. Sternite 8 of male (Figs 13b–15b) a broad, weakly sclerotized plate with strong and continuous seta-fringe and no trace of apodeme. Spermatheca a simple straight or arcuate vesicle, or absent.

   OXYCORYNIDAE
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Segment 2 of all tarsi quadrate or elongate, apex often emarginate but not bilobed (cf. segment 3). Antennae inserted some distance from base of rostrum but, if very near base, then antenna without any club. Tergite 8 exposed in male (beneath the elytra). Sternite 8 of male a narrow transverse seleritized strip with a distinct apodeme. Spermatheca complex. BELIDAE 9

Antenna with compact 1–3-segmented club. Prothorax with side margins carinate. Base of head with separate, very short gular sutures (often indistinct)

OXYCORYNINAE

Antenna with loose 3-segmented club. Prothorax somewhat depressed but without lateral carinae. Base of head with a single, distinct gular suture

ALLOCORYNINAE

Antennae inserted on underside of rostrum. Elytra punctate–striate (10 complete striae). Ventrites all free but movement very limited. Sternite 8 of male (Fig. 12b) broadly U-shaped, with weakly seleritized apodeme. Tegmen (Fig. 176) with apex of dorsal plate bilobed and setose. CARINAE subfam. n.

Antennae inserted on sides of rostrum. Elytra confusedly punctured. Ventrites either all quite free or 1 and 2 fused. Sternite 8 of male (Figs 9b–11b) narrowly W-shaped, with strongly seleritized apodeme. Tegmen (Fig. 175) with apex of dorsal plate undivided and asetose. CARINAE

BELINAE

Maxillary palpi 4-segmented but if only 3-segmented then elytra confusedly punctured. (Antennae non-geniculate. Tergite 8 concealed in both sexes. Elytra separately and broadly rounded at apex, exposing tergite (6 and) 7 which forms a + distinct pygidium. TF 3: 1–6, 7 (8). Body setose or pilose but without any broad scales; cuticle often metallic or otherwise brightly coloured. Elytra often with a scutellary striae).

Maxillary palpi 2- or 3-segmented (Elytra punctate-striate).

ATELABLE (including APIDERINI)

Prothorax sharply carinate at sides. Pygidium composed of 3 or 4 tergites. Mesepimera clearly visible in dorsal view. PTEROCOLINAE

Prothorax smoothly rounded at sides. Pygidium composed of 1 tergite. Mesepimera not visible in dorsal view. RHYNCHITINAE

Antennae composed of 11 free segments which may be simple or variously modified but never form a compact club; scape sometimes enlarged but antennae never truly geniculate. Antennae composed of <9 free segments and a compact club; geniculate or not

BRENTIDAE (part)

Fore coxae separated by prosternal processes. Ventrites 4 and 5 of male ± fused (Figs 19a–21a) so that no articulation can take place between them. Surface of eyes smooth, glassy (several exceptions). Form slender, often very markedly so. Colour usually dark red or red-brown, without any covering of recumbent scales

BRENTINAE (less ULOCERINI)

Fore coxae contiguous. Ventrites 4 and 5 free in both sexes. Surface of eyes very finely faceted. Form at most moderately slender. Colour variable, including metallic, often with spots or areas of recumbent scales. EURHYNCHINAE

Surface of eyes smooth, glassy. (Antennae non-geniculate). BRENTIDAE (part)

Surface of eyes faceted

BRENTINAE–ULOCERINI

Antennae with 9 segments and a compact 2-segmented club (segmentation of club obscure). Claws fused. Body devoid of scales. CYLADINAE

Antennae with 8 segments and a compact 3-segmented club (segmentation of club obscure or indistinct). Claws free. Body covered with imbricate scales
17(15) Trochanters of all legs enlarged or elongated, separating bases of femora from coxae.
(Mostly small or very small, body globose or pyriform, prothorax subcylindrical or subconical; rostrum slender). BRENTIDAE (part) 18
- Trochanters small, not separating femora from coxae (but if so, then form different) 19

18(17) Antennae geniculate. Ventrites 4 and 5 + fused in both sexes (Figs 24a, c, 25a). Sternite 8 of male \-\-\- shaped (Figs 24b, 25b). (Body globose or rhomboidal, widest near elytral humeri; prothorax broadly conical, rostrum deflexed)
- Antennae straight (scaope sometimes elongate but antenna not functionally geniculate). Ventrites 4 and 5 free in both sexes. Sternite 8 of male U- or W-shaped (Figs 28b-33b). (Body pyriform, widest about middle of elytra, prothorax narrowly conical or subcylindrical, rostrum usually porrect). NANOPHYINAE

19(17) Antennae straight or curved; scape sometimes elongate but antennae not functionally geniculate.
- Antennae functionally geniculate, with \+ elongate scape on which funicle is inserted ventrally so that it can move freely in horizontal plane 16

20(19) Antennal club elongate, linear or fusiform. Body depressed; prothorax broad, subcircular or cordiform. Sternite 8 of female forming a tapering tube surrounding ovipositor and rectum; tergite 8 absent. (Fore coxae separated by prosternal processes). BRENTIDAE-ANTLIARHININAE
- Antennal club stout. Body not depressed, prothorax variable but not subcircular or cordiform. Sternite 8 of female normal, tergite 8 present 21

21(20) Rostrum slender, deflexed. Prementum concealed. Sternite 8 of male divided to form paired hemi sternites (cf. Fig. 54b). (Antennae straight; club compact and without sutures; funicle 6-segmented) RYNCHOPHORIDAE (part)
- Rostrum stout. Prementum exposed. Sternite 8 of male not divided 22

22(21) Wings fully developed. Prementum with 2 or 4 principal setae. (Antennae straight) 23
- Wings absent (metanotum membranous). Prementum multisetose 17. (Antennae \+ curved or, if straight, then inserted near apex of rostrum)

23(22) Maxillary palpi 3-segmented but basal segments retracted into palpifer; labial palpi 3-segmented. Scrobes entirely lateral. Ventrite 5 of male (Fig. 22a) strongly truncate, clearly exposing pouch-shaped tergite 8 from below; latter with deep, sharply defined longitudinal groove into which sutural edges of elytra fit. Ventrites 1 and 2 each shorter than 3 + 4. Sternite 8 of male (Fig. 22b) closely attached to sternite 7 along its entire width and with integral apodeme; tergite 8 with spiracles

- Maxillary palpi 2-segmented (exposed); labial palpi 1-segmented. Scrobes lateral but connivent beneath rostrum. Ventrite 5 of male (Fig. 30a) weakly truncate, only narrowly exposing tergite 8 from below; latter with strong pre-apical transverse carina. Ventrites 1 and 2 each much longer than 3 + 4. Sternite 8 of male (Fig. 30b) of the apionid type, without any apodeme, only loosely attached to posterior edge of ventrite 5. Tergite 8 without spiracles

BRENTIDAE-TANAINAE

24(22) Ventrite 2 longer than 3 + 4 (Figs 41a-43a). Labial palpi small or minute and set in pits or grooves; basal segment asetose. Tergite 8 of male entirely, or almost entirely, covered by tergite 7. Sternite 8 of male (Figs 41b-43b) without any apodeme

- Ventrite 2 shorter than 3 + 4 (Figs 44a-49a). Labial palpi larger, free; basal segment with two or more setae. Tergite 8 of male not covered by 7. Sternite 8 of male (Figs 44b-49b) with apodeme vestige BRACHYCYRINAE (including BROTHERINI)
Morphology and classification of weevils

25(19) Rostrum lying between fore coxae in repose and tegmen with finely setose dorsal plate (Fig. 182). (Form globose (Figs 186, 187). Tibiae not, or imperfectly, uncinate, often finely denticulate or crenulate along outer edge. Mandibles sometimes with deciduous flanges (Fig. 166))

**BRACHYCERIDAE—DESMIDOPHORINAE**
- Rostrum either not lying between fore coxae in repose or, if so, then tibiae uncinate and tegmen without a dorsal plate .

26(25) Male with manubrium larger than spiculum gastrale (which is sometimes absent).
- Rostrum present, almost always elongate .
- Male with manubrium smaller than spiculum gastrale; if latter absent, then rostrum absent. (Rostrum very variable)

27(26) Antennal club shiny, with spongy apex and no sutures; scape not fitting closely into scrobe when retracted. Abdominal tergite 8 concealed in both sexes. Tegmen without a dorsal plate. (Antennal funicle with never more than 6 segments. Abdominal tergite 7 often forming a pygidium) RHYNCHOPHORIDAE (bulk)
- Antennal club pubescent, with sutures; scape fitting into linear scrobe when retracted. Abdominal tergite 8 exposed in male (sometimes only very narrowly). Tegmen with dorsal plate

28(27) Tarsi composed of 4 subequal segments. Eyes absent. Manubrium only slightly larger than spiculum gastrale .
- Tarsi pseudotetramerous (segment 4 very small). Eyes present. Manubrium much larger than spiculum gastrale .

29(28) Rostrum transverse, retractable, with antennae, into cavity in front of fore coxae.
- Maxilla with galea and lacinia almost separate . CRYPTOLARYNGIDAE
- Rostrum elongate, antennae free. Maxilla with galea and lacinia fused ERIRHINIDAE

30(26) At least one pair of tibiae with emergent denticles or stout socketed setae along or near their dorsal (outer) edge. (Rostrum very short or absent).
- Tibiae without such denticles or setae; sometimes with a single tooth in middle of middle tibia .

31(30) Posterior coxal cavities strongly encroaching on abdominal ventrite 1 (Figs 76a–78a); ventricle 2 shorter than 3. Sternite 8 of male (Figs 77b, 78b) a delicate quadrate plate with fringe of fine setae on its free edge. Galea of maxilla distinct. (Tarsal segment 1 = or > 2-5 together. Form linear, rostrum absent, head as wide as prothorax which is laterally constricted; spiculum gastrale of male and ovipositor of female usually absent). PLATYPODIDAE—PLATYPODINAE
- Posterior coxal cavities not strongly encroaching on abdominal ventricle 1; ventrites 2 and 3 subequal in length. Sternite 8 of male otherwise. Galea of maxilla indistinct .

32(31) Sternite 8 of male (Figs 68b–70b) divided to form a pair of hemisternites, or absent. Manubrium I-shaped. (Head narrower than prothorax which is not laterally constricted). Spiculum gastrale present; aedeagal apodemes present)
- Sternite 8 of male not divided (Figs 72b–75b). Manubrium V-, Y-, or H-shaped (Figs 72c, 75c), or absent .

33(32) Abdominal ventrites 1 and 2 firmly fused (suture very fine), 2 much longer than 3 (Fig. 72a).
- Abdominal ventrites less firmly fused (suture well marked), 2 and 3 subequal or 2 shorter than 3 (Figs 73a–75a).

34(33) Head narrower than prothorax and with a very short rostrum. Tarsi linear, segment 1 longer than 2 + 3. Posterior edge of tergite 7 produced as a free lobe which covers tergite 8 in both sexes. Sternite 8 of male (Fig. 75b) delicate, quadrate, partly divided. Spiculum gastrale absent; manubrium present PLATYTARSULINAE
Head as wide as prothorax and without any rostrum. Tarsi normal, segments 1 and 2 subequal. Posterior edge of tergite 7 not abnormally produced. Sternite 8 of male (Figs 73b, 74b) strongly transverse. Spiculum gastrale sometimes present; manubrium absent. CARPHODICTICINAE

35(30) Legs with well developed (but not necessarily identical27) unci on all three tibiae. Rostrum usually elongate. Size medium (mostly 10–25 mm) Curculiones medirostres28

- Legs without, or with imperfect unci on at least one pair of tibiae (see above, p. 845). Rostrum variable. Size variable. 

36(35) Head relatively small, subspherical. Eyes relatively large, ovate, forwardly placed, contiguous with base of slender rostrum and separated dorsally by its basal width, or less. (Antennal scape not passing anterior margin of eye. Tibiae without spurs. Phanerognathous. Length seldom exceeding 10 mm) Curculiones longirostres29, 30

- Head larger, not subspherical. Eyes variable in size and position, usually facing outwards. Rostrum usually stout. Size variable. Curculiones brevirostres 37

37(36) Each mandible, at emergence, with an elongate, porrect, blade-like process which is usually soon shed, leaving a scar on the surface of the mandible, or this process is mounted on a secondary process, or pedicel, which persists (see above, p. 858) Entiminae (bulk)31

- Mandibles without such process. 

38(37) Mouthparts adelognathous (maxillae covered by enlarged prementum)32. (Scrobes strongly decurrent) 

- Mouthparts phanerognathous (maxillae more or less exposed at sides of prementum) 

39(38) Male with tegminal ring complex (Fig. 196). Female with tergite 8 exposed (as in male) and bearing spiracles. Antennal club compressed into seventh funicular segment (sutures visible) which is not wider than preceding funicular segments; scrobes connivent ventrally. Ovipositor reduced to pair of well separated tubular processes, without styli; spiculum ventrale much shorter than venter. Eyes flat, vertically elongate. Fore and middle coxae contiguous. Body with sharp tubercles (Fig. 201) Brachyceropsidinae

- Male with tegminal ring simple. Female with tergite 8 concealed and without spiracles. Antennal club free, wider than funicule; scrobes not at all connivent ventrally. Ovipositor well developed, with styli; spiculum ventrale about as long as venter. Eyes convex, subcircular. Fore and middle coxae separated. Body smooth or with rounded tubercles. Entiminae–Pachyrhynchini

40(39) Tergite 8 of female fully exposed, non-retractable, sometimes forming a pygidium. Body ± depressed, finely pubescent but devoid of scales. Fore femora often inflated but also flattened; fore coxae widely separated. Uolomascinae

- Tergite 8 of female at least partly retractable beneath 7. 

41(40) Styli of ovipositor strongly sclerotized, divergent, usually claw-like33 (Figs 173, 174) 

- Styli of ovipositor subcylindrical or absent 

42(41) Prosternal furrow present, in front of fore coxae, in which rostrum can be laid 

Rhytirhinhinae

- Prosternal furrow absent 

43(41) Tergite 8 of female partly exposed beyond 7 but, if not, then ovipositor styli subterminal. Entiminae (part) 

- Tergite 8 of female concealed beneath 8. Ovipositor styli terminal or absent (Other subfamilies)35
44(43) Ovipositor reduced to a pair of transverse lunulate sclerites. 'Accessory claws' present. Mandibles densely squamose or at least with dense recumbent pigmented setae. Scrobes lateral, strongly decurrent .... SITONINI

- Ovipositor well developed, with subterminal styli. 'Accessory claws' absent. Mandibles with fine unpigmented setae only. Scrobes subdorsal, foveiform .... ECTEMNORHININI

Notes on the key

1. Some Meriphus species (Curculionidae–Eugnominae) appear to have projecting palps, but this results from elongation of the basal part of the maxilla; the palp itself is normal (compact).

2. In some anthribids, especially small globose ones, the pre-basal carina may be truly basal (Scirtetinus) or completely absent (some Xenorchestes). In these cases faint traces of the lateral carinae remain. In Cisanthribus, on the contrary, the basal carina is well marked and complete.

3. The sutures appear free until tested (see p. 839 above).

4. In Brachyceridae–Desmidophorinae (Fig. 40a) and some Platypodidae (Figs 77a, 78a) ventrites 1 and 2 are free but their lateral flanges are fused, so that they cannot articulate.

5. In the minute Afrocorynus and Hispodes (Oxycornidae) the distance between the coxae approaches their width; otherwise it is much less.

6. Only in Afrocorynus, where it is covered by a flange, is the antennal insertion distinctly pre-basal.

7. Tergite 8 is only very narrowly exposed in male Car.

8. In fact the antennal club in Oxycoryninae is always composed of two segments. Sometimes these segments are fused (Afrocorynus, Hispodes) or the distal one is contained within the penultimate (Metrioxena) so that, in both cases, the club appears to be 1-segmented. In other cases the two apical segments are only partially fused and the distal one has dense pubescence in the basal part which is sharply marked off from the apical part by a sinuous groove, creating an illusion of an extra segment (3 in all) (Oxycorynus). Finally, in Oxycraspedus, the club is clearly 2-segmented but the eighth funicle segment has enlarged to form part of an apparently 3-segmented club (as in Allocorynus).

9. Usually the lateral carinae of the prothorax are well developed and complete, but in Afrocorynus they are ill-defined and incomplete anteriorly. In Hispodes they are quite obsolete, though their position is indicated by a row of erect setae.

10. The apex of the dorsal plate is covered with soft, translucent trichia, similar to those on the dorsal lobes of the tegmen in many Curculionidae.

11. Owing to the strong convexity of many species their pygidium is only visible in posterior view. In a few Rhynchites, notably R. castaneus Jekel (West Africa), however, tergite 7 seems to be genuinely covered by the elytra, at least in dried specimens.

12. The junction of the scape and first funicle segment is often oblique and the condyle of the latter asymmetrical but only in Gynandrorhynchus bocandei Lacordaire (West Africa) is the scape so elongated as to simulate a geniculate antenna. Even so, it is unlikely to function as one.

13. Some Brentidae–Nanophyinae appear to have a loose 3-segmented antennal club, but this has resulted from enlargement of the two penultimate funicle segments. The elongate club of some Antliarhis species (Brentidae–Antliarhinae) is genuinely rather loose. Another exception is Trichodocerus (Curculionidae–Cryptorhynchinae), which has a club consisting of 3 (apparently 4) very slender pilose segments.

14. The fusion of these segments is scarcely apparent to external observation; indeed in some cases the joint itself is free but the lateral flanges are fused (see note 4).

15. Ulocerus longicornis Senna (Brazil) has an elongate scape very similar to that of Gynandrorhynchus bocandei (see note 12).

16. The antennal scape is secondarily reduced in many Curculionidae, with some loss of geniculation. In a few cases, e.g. Rhamphus (Rhamphinae) and Onycholips (Onycholipinae) the geniculate function has been entirely lost. In all these cases the lack of a dorsal plate on the tegmen will serve to distinguish them from the truly orthocerous groups.

17. Euryxena (Brachyceridae–Brachycerinae) has only 4 setae on the prementum.
18. The curvature of the antenna results from asymmetry of the individual funicle segments.
19. This character will serve to distinguish the Desmidophorinae from the Curculionidae–Cryptorhynchinae which they otherwise resemble (Figs 96–113 and p. 845).
20. It seems clear (though I am not aware that it has been demonstrated) that the antennal club in Rhynchophoridae is the enlarged seventh funicle segment into which the true club has been compressed. Certainly, there are only 6 funicle segments in this family (not 7) and the basal part of the club is shiny and bare like the funicle segments. The spongy apical part usually forms a wedge-shaped projection but sometimes, as in Trochorhopalus, it does not project at all, so that the apex of the club is abruptly truncate, while in Rhinostomus (the bottle-brush weevil) it is greatly attenuated, with the shiny part occupying only its extreme base.
21. This plate is very delicate in some Raymondionymidae.
22. This segment can be seen only in a cleared preparation in the case of Cryptolarynx.
23. Some Curculionidae–Cossoninae, e.g. Coptocorynus have denticulate tibiae but they also have a distinct rostrum.
24. A small relict spiculum gastrale is present in the male of the problematic genus Schedlarius and a small ovipositor is present in the female.
25. Ventrite 2 is shorter than 3 in some Platytarsulinae.
26. The prothorax is laterally constricted in Coptonotus.
27. Some Cleoninae have less well-developed unci on the hind tibiae (see above, p. 846).
28. This informal group includes the Molytinae, sensu Kuschel, 1987 less Onycholipini, plus Dinomorphini, and the Baridinae, Cleoninae, Cossoninae, Cryptorhynchinae, Magdalininae, and Zygoptinae (including Campylococci and Phaenomerina). It also includes the Bagoinae, hitherto included in the Erirhinidae.
29. This informal group includes the Anthonominae, Ceutorhynchinae, Cioninae, Curculioninae, Derelominae, Gymnetrinae, Hyperinae, Rhamphinae, Tychinae and Xiphaspidinae. It also includes the Smicronychinae and Storeinae, hitherto included in the Erirhinidae.
30. Tanyrhynehus and its allies (Entiminae) would run out here except that the antennal scape passes part, or all, of the eye and the mouth parts are not fully panerognathous. Lixellus (Listroderinae) would also run out here but it has a minute spur on each tibia.
31. This group includes the Brachyderini, Otiorhynchini, Eremnini and Entimini (= Leptopiini) which have hitherto been regarded as subfamilies (see below p. 883).
32. The extent to which the prementum covers the maxillae varies from completely to not at all. The peduncle which forms below the prementum when the latter is small is similarly variable. Nor is the relative size of the prementum of any use; it is very small in some Naupactus species but so also is the gap it covers. I have regarded as adelognathous the many cases where the stipites are visible at the hind angles of the prementum. Only when the maxilla is exposed continuously at the sides of the prementum is the condition regarded as panerognathous. While panerognathy is clearly plesiomorphous, it seems likely that most of the examples of it in the Entiminae are reversions from the adelognathous state.
33. In Stramia the styli are blunt, with a few subterminal setae, and thus represent an early stage in the transition from normal styli to the claw-like state.
34. This applies only when the ovipositor is fully retracted; when it is even slightly extended the eighth tergite is drawn out with it. Hence this character can be checked only when the abdomen is removed or the elytra parted.
35. These include the Amyeterinae, Aterpinae, Diabathrariinae, Eugnominae, Gonipterinae, Listroderinae, Onycholipinae (including Emphyastini), Rhadinosominae, Somatodinae and Rhyparosominae.
36. These are modified (narrowly spatulate) setae which arise from the base of the claw on its outer aspect. Normal setae occur in this position in many Curculionidae. See below, p. 885.

List of family group taxa referred to in the key and notes

This list includes all subfamilies in current use except those now included as tribes within the Molytinae (sensu Kuschel, 1987). Where a long-accepted name is known to be a junior synonym, the senior name(s) are listed at the end of the entry. The numbers of genera and species (in parentheses) are mostly taken from, or are based on, O'Brien
and Wibmer (1978). I have given what appear to be the original references as these are not readily available (Watt, 1975). Where appropriate I have added recent or crucial references. A full list of available key works will be found in Hollis (1980).

AGLYCYDERIDAE Wollaston, 1864 (2: 130) Pacific (mainly Hawaii); Canary Is (1); North Africa (1); New Zealand (2). See Zimmerman and Perrault, 1989.

ALLOCORYNINAE Sharp, 1890 (1: 4) Mexico (2), Cuba (1), Florida (1). (Oxy.).

AMYCTERINAE Waterhouse, 1854 (41: 451) Australia. (Curc.).

ANTHONOMINAE Thomson, 1859 (68: 605) Cosmopolitan. Includes the cotton boll weevil (*Anthonomus grandis* Boheman) and a number of orchard pests. (Curc.).

ANTHRIBIDAE Billberg, 1820 (350: 3000) Cosmopolitan. Commonly known as fungus weevils but includes the coffee bean beetle (*Araecerus fasciculatus* (De Geer)). [The name is threatened by Choragidae Kirby, 1819.]

ANTLIARHININAE Schrnherr, 1823 (4: 14) South Africa. Cycad weevils. (Brent.).


ATERPINAE Lacordaire, 1863 (15: 93) Mainly Australia and Chile. (Curc.).

ATTELABIDAE Billberg, 1820 (96: 1908) Cosmopolitan. Includes the leaf-rolling weevils. (Curc.).

BAGOINAE Thomson, 1859 (c. 10: 160) Cosmopolitan. Aquatic. (Many aquatic genera, currently in the Bagoinae, belong in the Erirhinidae (G. Kuschel, unpublished data)). (Curc.).

BARIDINAE Sch0nherr, 1836 (547: 4234) Cosmopolitan. (Curc.-Ent.).

BRENTIDAE Billberg, 1820 (c. 340: 3600) Cosmopolitan. (Curc.-Onych.).


BRACHYCEROPSIDINAE Aurivillus, 1926 (1: 1) Africa. (Curc.).

BRACHYDERINI Sch0nherr, 1826 (384: 4365) Cosmopolitan. (Curc.-Zyg.).

BROTHEINI Marshall, 1907 (3: 40) Africa. (Brach.).

CAMPYLOSCELINI Sch0nherr, 1845 (20: 95) Africa and Madagascar. (Curc.-Zyg.).

CARINAE subfam, n. (Kuschel, MS) (1: 3) Australia. (Curc.).


CEUTORHYNCHINAE Thomson, 1859 (72: 1041) Cosmopolitan (but very few in the Australian region). Some European species are pests of cruciferous crops. (Curc.).

CHORAGINAE Kirby, 1819 (50: 350) Mostly Old World. (Anth.).

CIONINAE Schöngherr, 1825 (5: 95) Old World (except the Australian region). Larvae ectophytic. (Curc.).

CLEONINAE Schöngherr, 1826 (23: 1445) Cosmopolitan. [The name is threatened by Lixinae (emend.) and Geomorinae (emend.) both Schöngherr, 1823.] (Curc.).

COSSONINAE Schöngherr, 1825 (301: 1666) Cosmopolitan. Wood-boring weevils. (Curc.).


CRYPTORHYNCHINAE Schöngherr, 1825 (667: 4200) Cosmopolitan. Larvae mostly in dead wood but some in seeds and fruit, e.g. the mango weevils (*Sternochetus* spp). (Curc.).

CURCULIONIDAE Latreille, 1802 (4100: 42000) Cosmopolitan. Weevils in the (increasingly) strict sense.

CYLADINAE Schöngherr, 1823 (4?: 38) Old World tropics. *Cylas formicarius* (F.), the sweet potato weevil, more widely distributed. See Kissinger, 1968. (Brent.).

DERELOMINAE Lacordaire, 1866 (17: 107) Cosmopolitan. Some species pollinate palms. (Curc.).

DESMDOPHORINAE Morimoto, 1962b (2: 69) Old World tropics. (Brach.).

DIABATHRARIINAE Lacordaire, 1863 (10: 63) Africa, Madagascar, Australia and New Zealand. An artificial group united by the lack of tarsal claw segments. (Curc.).

DINOMORPHINI Lacordaire, 1863 (2: 4) Brazil. (Curc.-Molyt.).


ECTEMNORHININI Lacordaire, 1863 (6: 13) Subantarctic islands of the Indian Ocean. See Jeannel, 1940. This group has not yet been included in *Coleopterorum Catalogus*. (Curc.-Ent.).

EMPHYASTINI Lacordaire, 1863 (1: 1) North America. Littoral. (Curc.-Onych.).
ENTIMINAE Schönherr, 1823 (1150: 12200) Cosmopolitan. Broad-nosed weevils (bulk). (Curc.).

ENTIMINI Schönherr, 1823 (= LEPTOPIINI Oke, 1951) (150: 1350) Cosmopolitan. (Curc.-Ent.).

EREMNINI Lacordaire, 1863 (90: 750) Old World. (Curc.–Ent.).

ERIRHINIDAE Schönherr, 1825 (50: 180) Cosmopolitan. Some species are pests of rice. (Curc.).

EUGNOMINAE Lacordaire, 1863 (22: 130) Australian region and South America. See Cawthra, 1966. (Curc.).

EURHYNCHINAE Lacordaire, 1863 (2: 30) Australian region. (Brent.).

GONIPTERINAE Lacordaire, 1863 (8: 132) Australian region. Larvae ectophytic on eucalyptus and other Myrtaceae. (Curc.).

GYMNETRINAE Thomson, 1859 (4: 158) Palaearctic region (several introduced into North America). (Curc.).

HIPPORHININAE Lacordaire, 1863 (6: 188) South Africa. [The name is threatened by Cyclominae (emend.) Schönherr, 1826.]

HYPERINAE Lacordaire, 1863 (31: 393) Cosmopolitan (mainly Palaearctic region). Larvae ectophytic. [The name is threatened by Phytonominae (emend.) Thomson, 1859.] (Curc.).

ITHYCERIDAE Schönherr, 1823 (1: 1) North America. The New York weevil. (Curc.).

LISTRODERINAE LeConte and Horn, 1876 (10: 280) New World, including Falkland Is; pest species (Listroderes costirostris Schönherr and Listronotus bonariensis Kuschel) more widely distributed by introduction. (Curc.).

MAGDALININAE Thomson, 1859 (14: 246) Cosmopolitan (except Ethiopian region). (Curc.).

MECOPELMINAE Wood, 1973 (1: 1) Panama. (Plat.).

MICROERINAE Lacordaire, 1863 (3: 67) Ethiopian region. See Louw, 1986. (Brach.).

MOLYTINAE Schönherr, 1823 (280: 3000) Cosmopolitan. This group is an amalgamation of some 30 tribes and subfamilies which are listed, with original references, in Kuschel, 1987. It includes a number of forest pests including the pine shoot weevil (Hylobius abietis L.). (Curc.).

NANOPHYINAE Seidlitz, 1891 (8: 266) Mainly Palaearctic, Oriental and Ethiopian regions. See Kissinger, 1968; Alonso-Zarazaga, 1989. (Brent.).

NEMONYCHIDAE Bedel, 1882 (> 13: 70) Holarctic, Neotropical and Australian regions. See Kuschel, 1989. (Curc.).

NERTHOPINAE Lacordaire, 1866 (3?: 4) Old World. (Curc.).

ONYCHOPINAE Wollaston, 1873 (5: 7) West Palaearctic region, Australia, the Americas. Littoral. (Curc.).

OTIORHYNCHINI Schönherr, 1826 (452: 5000) Cosmopolitan. Includes the vine and strawberry weevils (Otiorhynchus spp). (Curc.–Ent.).

OXYCORYNIDAE Schönherr, 1840 (7: 27) Neotropical, Oriental and Ethiopian regions.

PACHYRHYNCHINI Schönherr, 1826 (10: 375) Eastern Oriental and Australian regions. (Curc.–Ent.).

PACHYRHYNCHINI Schönherr, 1826 (10: 375) Eastern Oriental and Australian regions. (Curc.–Ent.).

PHTHINAE Thomson, 1859 (145: 1460) Cosmopolitan. Leaf-miners (larvae). (Curc.).

PHTHINAE Thomson, 1859 (145: 1460) Cosmopolitan. Leaf-miners (larvae). [The synonym Rhynchaeninae Thomson, 1859 is a junior homonym of Rhynchaeninae (emend.) Thomson, 1859.] (Curc.).

RHINORHYNCHINI Voss, 1922 (15: 50) Mainly Australian and Neotropical regions, also Nearctic (3). See Kuschel, 1989. (Nem.–Doyd.).

RHYNCHITINAE Thomson, 1859 (48: 1080) Cosmopolitan. (Att.).

RHYNCHOPHORIDAE Schönherr, 1833 (140: 1070) Cosmopolitan (few in Palaearctic region). Associated with palms and other monocotyledonous plants. Pests include the grain weevils (Sitophilus spp) and the banana weevil (Cosmopolites sordidus Germar). [The name is threatened by Dryopithoridae (emend.) Schönherr, 1825.]

RHYPAROSOMINAE Lacordaire, 1863. A small group of uncertain rank and composition; the type genus is South African. (Curc.).
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RHYTIRHININAE Lacordaire, 1863 (30: 270) Old World (except Oriental region). [The valid name of the type genus is Rhythirrinus Schönherr, 1823.] (Curc.).


SITONINI LeConte, 1874 (8: 125) Cosmopolitan (mainly Palaeartic region, not Australian region (except by introduction)). Pests include the pea and bean weevils (Sitona spp). (Curc.–Ent.).

SMICRONYCHINAE Seidlitz, 1891 (6: 160) Cosmopolitan but mainly in the Palaeartic and Neartic regions. Associated with dodders (Cuscuta spp.) and other parasitic plants. [The name is threatened by ‘Desmorhines’ LeConte and Horn, 1876.] (Curc.).

SOMATODINAE Lacordaire, 1863 (2: 8) South Africa. [Schrnherr’s use of the name in 1823 is invalid because the type genus is a nomen nudum; if valid it would be a senior synonym of Pachyrhynchus Germar, 1824.] (Curc.).

STOREINAE Lacordaire, 1863. A small group of uncertain composition. The type genus is Australian. (Curc.).

TANAINAE Schönherr, 1839 (1: 6) South Africa. (Brent.).

THECESTERNINAE Lacordaire, 1863 (2: 9) New World. (Curc.).

TYCHIIINAE Thomson, 1859 (32: 747) Cosmopolitan. (Curc.).

ULOCERINI Schönherr, 1823 (2: 22) Central and South America; Madagascar (1). (Brent.).

ULOMASCINAE Lacordaire, 1866 (3: 14) Ethiopian region. (Curc.).


XIPHASPIDINAE Marshall, 1920 (1: 1) Africa. (Curc.).

ZYGOPINAE Lacordaire, 1866 (210: 2108) Cosmopolitan. [The name is threatened by Conoderinae (emend.) Schönherr, 1833, Conophorinae (emend.) Schönherr, 1838 and Coryssomerinae Thomson, 1859. (Curc.).

Discussion

It has long been recognized (LeConte, 1874; Marshall, 1916; Crowson, 1955) that the classification of the Curculionoidea, the largest and one of the most important groups of insects, is confused and unsatisfactory. The first characters used in the classification of weevils were based on the variable development of the rostrum and whether the antennae are straight or have the basal segment elongated, with the remainder flexed at an angle to it (geniculate). Variation in the rostrum is more or less continuous, but the two states of the antenna are reasonably distinct, with few anomalies or exceptions (see note 16, p. 875). Accordingly, Schönherr (1823) divided the weevils into two groups—the Orthoceri, with straight antennae, and the Gonatoceri with geniculate antennae. Recent studies (Kuschel, 1971: 246) have shown that the male genitalia in the Orthoceri, and some Gonatoceri, differ from those in the bulk of the Gonatoceri, and this difference provides a firm basis for the primary division of the Curculionoidea. As a result, a number of groups with geniculate antennae, previously included in the Curculionidae, have been separated from it. These are the Nanophyinae, which have long been recognized as being related to the Brentidae—Apioninae, the Antliarhininae, here also placed near the Apioninae, and the Rynchophoridae, another distinct group (see key). This process is here extended to its logical conclusion so that in the Curculionidae, as here recognized, the male genitalia are entirely and exclusively of the gonatocerous type. The groups here separated are the Brachyceridae, Cryptolaryngidae, Raymondionymidae and Erirhinidae.

Recognition of the orthocerous type of genitalia is sometimes difficult. Primitively the median lobe consists of two plates—the pedon (below) and the tectum (above)—rather loosely connected to one another by membrane, and the tegmen has a well-developed dorsal plate, the apex of which is usually setose (Figs 176–183). In the
gonatocerous type the tectum is obsolete or absent, the pedon forms a stout cylinder (though often membranous dorsally) and the dorsal plate of the tegmen is either entirely absent or, more often, reduced to a pair of delicate asetose lobes (Figs 184–185). Difficulty arises because the trend towards a rigid tubular median lobe has been followed independently by several orthocerous groups. In *Apion* the median lobe is not very different from that of the Curculionidae, although the tegmen (Fig. 180) is typically orthocerous. In the Rhynchophoridae the pedon and tectum together form a stout tube (their junction being marked by a fine suture) and the dorsal lobe of the tegmen is absent, having been replaced by the membranes of segment 9 which envelop the median lobe tightly at the point where the dorsal plate would have been. In addition, the apodeme of sternite 9 (spiculum gastrale) is much smaller than the manubrium (and is often absent), whereas in Curculionidae the reverse is the case. Although the gonatocerous type of male genitalia could have arisen more than once, it seems reasonable to assume that it has not, and that it is an apomorphic state defining the Curculionidae.

Division of the Curculionoidea on the characters of the male genitalia is to some extent supported by the structure of sternite 8 of the male (see above, p. 842). In most orthocerous groups this is not, or only partially, divided and often has a distinct apodeme associated with it (Figs 1b–5b). In Curculionidae, as here defined, it is almost always divided to form a pair of hemisternites and the apodeme is obsolete or absent (Figs 58b–71b). It is, however, divided in most Nemonychidae (Figs 3b, 4b), Rhynchophoridae (Figs 54b, 57b) and some Attelabidae (Figs 35b, 38b), while it is undivided in *Curculio* (Fig. 62b) and the Platypodidae (Figs 72b–78b).

Changes in the rank and/or composition of individual groups are discussed in detail below. The groups are taken in alphabetical order.

**ALLOCORYNINAE**

Crowson (1986) raised this group to family rank from the Oxycorynidae on the basis of its lack of prothoracic lateral carinae and single gular suture, but the carinae are reduced or absent in African oxycorynids (e.g. *Hisodes* Marshall) and the paired gular sutures are indistinct in some cases. The Allocoryninae have a very loose, 3-segmented antennal club (Crowson, 1986: fig. 1) which has no exact counterpart in other oxycorynids (though *Oxycraspedus* Kuschel comes close—see note 8, above) but they do share with them a very similar, delicate, transverse male sternite 8, with a continuous seta-fringe (Figs 13b–15b) and have tergite 8 concealed in both sexes. These characters serve as adequate apomorphies for the combined groups. The separation of the Allocoryninae as a distinct family is therefore not justified.

**BRACHYCERIDAE**

*Brachycerus* Olivier and its allies have long been regarded as distinct from other curculionoids (Billberg, 1820). Both Jekel, 1864 and Pape, 1910 (*Coleopterorum Catalogus*) regarded them as constituting a distinct family in which they included another apterous group, the Microcerinae. To these is now added the alate Desmidophorinae, formerly placed in the Cryptorhynchinae and later transferred to the Brentidae by Morimoto (1962b) on account of their orthocerous male genitalia. The Desmidophorinae now includes the apterous genus *Ocladius* Schönherr, here transferred from the Cryptorhynchinae–Ithyporini. These groups differ markedly from each other in external characters (see key) but all have a characteristic crescent-shaped male sternite 8 (Figs 40b–49b). The only similar sternite outside the group is that of...
Cryptolarynx (Fig. 50b) but the Cryptolaryngidae have a strongly divided maxillary mala and so are unlikely to be closely related to the Brachyceridae, in which the mala is entire. The dorsal plate of the tegmen is very similar in Brachycerus (Fig. 181), Desmidophorus (Fig. 182) and Ocladius, being broadly rounded at the apex, with a median notch or division and covered with dense, fine setae. The dorsal plate of Microcerus (Fig. 183) is clearly derived from this type but that of Episus (Fig. 184) is different. However, Episus, Microcerus and Gyllenhalia are externally similar and all have their labial palpi sunk in grooves, a good apomorphy for the Microcerinae.

Kuschel (1987) transferred both the Desmidophorinae and Ocladius to the Curculionidae-Erirhininae, and in 1990 he combined the Brachycerinae and Entiminae; both these proposals run counter to the logic of the arguments presented here.

Although Agriochaeta Pascoe (Australia), the other genus included in the Ocliadiina in Coleopterorum Catalogus (Hustache, 1936), has a prosternal furrow (a character which has been independently developed many times in Curculionoidea), it closely resembles in every other detail some species of Hypera (Europe) and is covered in loose, oblong scales with truncate, bifid or multifid apices, a type characteristic of the Hyperinae and of no other group. Agriochaeta is therefore transferred to the Hyperinae.

BRACHYCEROPSIDINAE

As explained below, Brachyceropsis (Fig. 201) is not related to Dinomorphus and must be removed from the Dinomorphini. Although it superficially resembles some Brachyceridae it does not belong there either, since it has gonatocerous male genitalia. Within the Curculionidae it might be regarded as a molytine, but it is unequivocally adelognathous and has imperfectly uncinate tibiae (with poorly developed inner flange). The tegmen (Fig. 196) has a very strange, asymmetrically sclerotized ring. Since its affinities are at present unclear, it must remain in a separate subfamily pending further studies.

BRENTIDAE

Notwithstanding the presence of legs in their larvae, brentids have many features in common with apionids (Morimoto, 1976) and these groups have been united by Kuschel (1990). The structure of the male sternite 8 is variable in both groups, as is the tegminal dorsal plate in apionids (Figs 178–180). However, some apionids (Alonso-Zarazaga, 1990: figs 222, 239) have a dorsal plate resembling that of most brentids (Fig. 177). Antliarhis Billberg has the same porrect rostrum as the rest of this family, and its male sternite 8 (Fig. 27b) is clearly of the apionine type (cf. Figs 28b–31b). Sanborne (1981) regarded the Antliarhininae as a distinct family but very close to the Apionidae, and stated that if the two were united it would probably be necessary to include the Brentidae as well. Accordingly, the concept of the Brentidae is widened to include the Eurhynchinae, Cyladinae, Apioninae, Nanophyinae, Tanainae and Antliarhininae.

CAMPYLOSCELINI

In Coleopterorum Catalogus (Csiki, 1936) the Campyloscelini (including the Phaenomerina) stand at the head of the Rhynchophoridae. The male genitalia show them to be Curculionidae, however, and their antennae have a 7-segmented funicle and a pubescent, segmented club, whereas rhynchophorids have a 6-segmented funicle and a bare, un segmented club. This group is here transferred to the Zygopinae because they
have large eyes and tibiae of the zygopine type (cf. Figs 118, 119). A possible apomorphy for the group is that the aedeagal apodemes are connected to the median lobe only by membrane.

CARINAE, subfam. nov.

The genus Car Blackburn, comprising three Australian species, possesses a unique combination of characters which demand a new family-group taxon for its reception. It was regarded as an attelabid by Crowson (1955) in spite of the fact that, as he himself states, its abdominal ventrites are all free (though only just). The male sternite 8 (Fig. 12b) is quite different from those of the Attelabidae (Figs 34b–39b) but similar to those of the Belidae (Figs 9b–11b) which also have free ventrites. Although the tegmen of Car (Fig. 176) is quite different from those of other Belidae (Fig. 175), its tarsi are very similar, with segment 1 enlarged and emarginate, segment 2 smaller and (usually) more strongly emarginate and segment 3 strongly bilobed. This tarsal conformation is characteristic of the Belidae and provides an apomorphy for the entire family. Carinae are readily distinguished from other belids by characters of the tegmen and by their short, punctate–striate elytra.

COPTONOTINI

The Coptonotidae, as conceived by Schedl (1962), is an artificial group. Its three component genera were associated by him on the basis of their constricted prothorax and 'hylesinartenigen Habitus'. He regarded the group as being intermediate between the Curculionidae–Cossoninae and the Scolytidae (which he held as a separate family) and this may well be true of Coptonotus Chapuis itself, judging by the structure of its male sternite 8 (Fig. 68b) which has the same sclerotized anterior edge as have those of the Cossoninae (Figs 65b–67b) and Scolytinae–Hylastini (Figs 69b, 70b). The aedeagus is well developed, with a complex transfer apparatus and short apodemes, and there is a large spiculum gastrale. The Coptonotini, with a single genus and two species (South America) can therefore stand next to the Hylastini in the Curculionidae–Scolytinae.

Schedlarius Wood (= Chapuisia Dugès) (Mexico), though somewhat similar to Coptonotus superficially, has a male sternite 8 (Fig. 76b) of the same type as the typical Platypodidae (Figs 77b, 78b) and a venter (Fig. 76a) with segment 1 similarly reduced (cf. Figs 77a, 78a). Although, unlike them, it has a small ovipositor in the female and a very small spiculum gastrale in the male, it is best placed with the typical Platypodidae for the present.

The minute Mecopelmus Blackman (Panama) differs from both the preceding genera in having a curculionid-type venter (Fig. 72a) and a reduced male sternite 8 (Fig. 72b). It belongs, therefore, with the atypical Platypodidae (cf. Figs 73–75).

CRYPTOLARYNGIDAE

Although Thecesternus Say (North America) and Perieges Schönherr (Turkestan) have in common a transverse rostrum capable of being retracted, with the antennae, into a prosternal furrow (and for this reason were placed together as Curculionidae–Thecesterninae in Coleopterorum Catalogus (Schenkling and Marshall, 1929)), they are not closely related since the former has gonatocerous, and the latter orthocerous male genitalia. Perieges is, in fact, related to Cryptolarynx van Schalkwyk (South Africa). These two genera have in common a broad prosternal furrow which is open behind (closed in Thecesternus), a globose form, dense scales and a tendency to lose the elytral strial punctures. The male sternite 8 is crescentic, with a distinct spiculum rudiment,
and differs from all others except those of some Brachyceridae (see above). The ovipositor is, remarkably in such globose species, very elongate and contained in a leathery sheath; that of Cryptolarynx is delicate, with large subapical styli, while that of Perieges is stouter, with extrorse apical teeth, as in the Anthribidae (cf. Fig. 172). The galea and lacinia of the maxilla are almost completely separate in both genera. The above unique combination of characters, and the lack of any obvious affinity with any other group, necessitates promoting the Cryptolarynginae to family rank.

DINQMORPHINI

Dinomorphus Perty (Brazil) and Brachyceropsis Aurivillus (Africa) resemble each other superficially and stand together as the Curculionidae–Dinomorphinae in Coleopterorum Catalogus (Schenkling and Marshall, 1931), notwithstanding that Aurivillus (1926) had separated them because the former is phanerognathous while the latter is adelognathous (see above, under Brachyceropsidinae). Dinomorphus also resembles Rhytidophloeus Schönherr (Madagascar) of the Molytinae–Lithinini, and may be related to it. Both genera have vertically elongate eyes, a reduced antennal club and uncinate tibiae. Their tegmina are of the molytine type, with a sclerotized ring (sometimes incomplete) and well-developed dorsal lobes (cf. Figs 194, 195). Dinomorphus, however, has a well-developed scutellum (absent in Rhytidophloeus) and an outgrowth from the submentum which covers and conceals the very small prementum. Dinomorphini, with a single genus and species, is therefore added to the 30 tribes of Molytinae listed by Kuschel (1987).

ENTIMINAE

This name necessarily replaces Leptopiinae (Thompson, 1988: 55). In an unpublished document dated 19 April, 1988, G. Kuschel expands this subfamily of Curculionidae to include the Brachyderini, Otiorhynchini and Eremnini, all previously regarded as subfamilies. The vast majority of this enormous assemblage possess well-developed deciduous mandibular processes, and those that do not (Pachyrhynchini, Ectemnorhinini) are likely to have lost them secondarily. The other groups of Curculionoidea with similar processes all have orthocerous male genitalia so are not closely related to the Entiminae. The presence of these processes is therefore a possible apomorphy for the group (see detailed account above, p. 853).

ERIRHINIDAE

This family is restricted to some 50 (G. Kuschel, unpublished manuscript dated 29 June 1987) of the more than 200 genera of Erirhininae listed in Coleopterorum Catalogus (Klima, 1934). They have orthocerous male genitalia, with a well developed tegmental dorsal plate (Figs 185–187). The tectum of the median lobe is either membranous or reduced to a narrow strip. Neither the dorsal plate nor the male sternite 8 (Figs 52b, 53b) seem likely to provide apomorphies for the entire family. Externally, they are the only orthocerous weevils in which the rostrum is strongly deflexed ventrad from its base, so that, in profile view, it makes a continuous curve with the frons dorsally and a strong angle with the gula ventrally, thus resembling exactly the condition found in the Tychiinae and many other long-nosed Curculionidae with which the Erirhinidae have hitherto been associated. A similar conformation of the rostrum is approached by some Rynchophoridae (which also have geniculate antennae) but they have a pygidium and concealed prementum, whereas the Erirhinidae have no pygidium and the prementum is exposed.
PLATYPODIDA

The status and position of the Platypodidae is the major unresolved problem of weevil systematics. Traditionally the Scolytidae and Platypodidae have been regarded as related to, but distinct from, the Curculionidae. Crowson (1955), supported by Kuschel (unpublished data), have argued for including them, as subfamilies, within the Curculionidae, while Wood (1973) has argued equally strongly in favour of keeping them separate. He claims that Scolytidae differ from Curculionidae - Cossoninae in several cephalic characters (the significance of which is contested by Lyal, 1992) but has difficulty in separating them from the Platypodidae. Later, Wood (1986) gives a series of characters for distinguishing Scolytidae from Platypodidae and claims that neither group is closely related to Curculionidae. My studies have led me to retain the Scolytinae within the Curculionidae but to re-establish the Platypodidae as a separate family. Although the eighth sternite of the male is membranous in many scolytids (Fig. 71) those in which it is not (Figs 68b–70b) show a clear relationship to the Curculionidae - Cossoninae (Figs 65b–67b) in that they are all more or less divided (as in other Curculionidae) and the anterior margins of the hemisternites are, in varying degrees, sclerotized and pigmented. The typical Platypodidae have a quite different type of eighth sternite (Figs 76b–78b) which closely resembles the corresponding tergite, and ventrites 1 and 2 are free (except at the sides). In addition, the male genitalia are greatly reduced in size and complexity (Figs 72c–75c), the spiculum gastrale has disappeared (except in Schedlarius and Carphodicticus) and the females have neither ovipositor nor spiculum ventrale (except Schedlarius). These characters, together with the total loss of the rostrum, seem sufficient to justify family status for the group. Although the atypical platypodids (Mecopelminae, Platytarsulinae and Carphodictinae) have retained the curculionid type of venter (Figs 72a–75a) and are, to that extent, primitive, they do not show any clear relationship to any scolytine known to me. The male genitalia in all these Platypodidae are so reduced and simplified that it is not even possible to determine whether they are of the orthocerous or gonatocerus type. The almost total lack of the spiculum gastrale, which is usually smaller than the manubrium in the Orthoceri, suggests the former rather than the latter. The minute Protoplatypus (Wood, 1973) has both a curculionid type of venter and non-attenuated tarsi, but I am unable to place it for want of a male.

RAYMONDIONYMIDAE

This blind, hypogean group have othocerous male genitalia (Osella, 1977) and therefore have no place in the Curculionidae. Their lack of eyes is not unique, but their genuinely 4-segmented tarsi almost certainly are. Many Curculionoidea appear to have 4-segmented tarsi but close examination always reveals a small fourth segment at the base of segment 5. It is even present in the Rhynchophoridae - Stromboscerinae, where it is difficult to distinguish from the condyle of segment 5, over which it closely fits. The Aglycyderidae have 4-segmented tarsi but they are pseudotrimerous, one of the basal segments having been lost; in the Raymondionymidae the four tarsal segments are subequal. Apart from the tarsi, the Raymondionymidae have a fairly distinctive \( \lambda \)-shaped male sternite 8 (Fig. 51b) and the palaearctic majority have greatly expanded tibiae, with a prominent fringe of setae on the outer edge, a less than 7-segmented antennal funicle and the maxilla with a 2-segmented palp and obsolete galea. Alaocybites Gilbert (North America), although rejected as a raymondionymid by Osella (1977), really does belong to that group. It has similar male genitalia and sternite
8, and 4-segmented tarsi. It differs from other raymondionymids in having slender, mucronate tibiae, with a modest fringe, a 3-segmented maxillary palp (although the basal segment is very short) and a 7-segmented antennal funicle. Nevertheless, it seems clear that O’Brien and Wibmer’s (1982) tentative placement of *Alaocybites* in the Raymondionymidae was justified. Another non-palaearctic genus, *Myrtonymus* Kuschel, 1990 (New Zealand) also has a 7-segmented funicle and slender tibiae.

**SITONINI**

The Sitonini were separated from other broad-nosed weevils by LeConte (1874: 460) because they lack deciduous mandibular processes and are phanerognathous (both characters typical of long-nosed weevils). Morimoto (1962b) promoted them to subfamily rank because the galea and lacinia of the maxilla are separate (see also Ting, 1936: 101, 111) and the ovipositor is vestigial. To these characters may be added the ‘accessory claws’ (Nebenklaue) described by van Emden (1936: 70, 71). Nevertheless, I prefer to retain the Sitonini as a tribe of the (enlarged) Entiminae (see above, p. 883) because:

1. Modified deciduous mandibular processes occur in some sitonine genera (see above, p. 864) while they are absent from the Pachyrhynchini and Ectemnorhinini.


3. Although the galea and lacinia appear, at first sight, to be separate in *Eugnathus* Schönherr, they are in fact broadly connate, and the same is even more true of the other sitonine genera. A similar partly divided condition exists in *Alophus* Schönherr, *Cylydrorhinus* Guérin and *Naupactus* Schönherr.

4. A similarly reduced ovipositor occurs in *Lepidophorus* Kirby (Cylydrorhinini) and in *Seidlitzia* Desbrochers (Alophini), while in some *Trigonoscuta* Motschulsky (Brachyderini) an ovipositor is totally lacking.

5. The ‘accessory claws’ are modified setae, inserted near the base of the claw on its outer aspect. They are expanded apically and curve in sympathy with the claw. When the expanded apex is pigmented, as in *Eugnathus*, they are clearly visible but when, as in some *Sitona* Germar species, they are translucent and lie against the claw, they are very difficult to see. Unmodified setae occur in this position in many Curculionidae, so their significance is not great. Nevertheless, they provide a useful apomorphy for the group.

As regards anatomy, the degree of fusion of the abdominal ventrites provides useful characters but needs to be checked with care. Abdominal tergite 7 is always exposed, and is usually the last with functional spiracles; tergite 8 is often exposed in males; tergite 7 often forms a pygidium. Male sternite 8 provides useful family-group characters, especially in the orthocerous groups. The interpretation and terminology of the tibial corbel is confused and new terminology is proposed above (p. 845) which recognizes an outer bevel (squamose, setose or bare and defined or not by a proximal comb of setae) and an inner flange (which is always bare). The uncus is produced by fusion of the mucro with the inner flange. The distribution of deciduous mandibular processes is such that they cannot be used to define any natural group. Many (but not all) instances of apparently non-deciduous processes result from the development of a pedicel beneath the process, which remains after the true process has been shed.
Transfers, etc., made in the present paper.

*Agriochaeta* Pascoe, 1872 to HYPERINAE from CRYPTORHYNCHINAE (CURCULIONIDAE).

ANTLIARHININAE demoted from family to subfamily of BRENTIDAE.

BRACHYCYPERIDINAE promoted to family from CURCULIONIDAE.

BRACHYCYROPSSIDINAE *subfam. rev.* (not syn. of DINOMORPHINAE) (CURCULIONIDAE).

BRACHYDERINI demoted to tribe of ENTIMINAE (CURCULIONIDAE).

CAMPYLOSCELINI to CURCULIONIDAE-ZYGOPINAE from RHYNCHOPHORIDAE.

*Car* Blackburn, 1897 (*incertae sedis*: ATTELABIDAE-RHYNCHITINAE (Col. Cat.: 1927), APIONIDAE (Crowson, 1955 but not mentioned by Kissinger, 1968)) to BELIDAE.

CARINAE *subfam. n.* (Kuschel MS, BRENTIDAE) (BELIDAE).

CARPHODICTICINAE promoted to subfamily of PLATYPODIDAE from CURCULIONIDAE-SCOLYTINAE.

COPTONOTINI demoted from family to tribe of CURCULIONIDAE-SCOLYTINAE (near HYLASTINI).

CRYPTOLARYNGIDAE promoted to family from CURCULIONIDAE.

DESMIDOPHORINAE to BRACHYCYPERIDAE from BRENTIDAE.

DINOMORPHINAE demoted from subfamily to tribe of MOLYTINAE (near LITHININI) (CURCULIONIDAE).

EREMNINI demoted to tribe of ENTIMINAE (CURCULIONIDAE).

ERRIRHINIDAE promoted to family from CURCULIONIDAE.

*Mecopelminus* Blackman from COPTONOTIDAE to PLATYPODIDAE.

OCLADIINI promoted to tribe of BRACHYCYPERIDAE-DESMIDOPHORINAE from CURCULIONIDAE-CRYPTORHYNCHINAE-ITHYPORINI.

OTIORHYNCHINI demoted to tribe of ENTIMINAE (CURCULIONIDAE).

*Periages* Schönerr, 1842 to CRYPTOLARYNGIDAE from CURCULIONIDAE-

THECESTERNINAE.

RAYMONDIONYMIDAE promoted to family from CURCULIONIDAE.

*Schledarius* Wood from COPTONOTIDAE to PLATYPODIDAE.

SITONINI demoted to tribe of ENTIMINAE (CURCULIONIDAE).

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References


Kirby, W., 1819 [dated 1818], A century of insects, including several new genera described from his cabinet, *Transactions of the Linnean Society of London*, 12, 375–482.


Kuschel, G., 1951, Revision de *Lissorohtpusr LeConte y generos vecinos de America*, *Revista Chilena de Entomologia*, 1, 23–74.


Morphology and classification of weevils


Louw, S., 1986, Revision of the Microcerinae (Coleoptera: Curculionidae) and an analysis of their phylogeny and zoogeography, *Memoirs van die Nasionale Museum Bloemfontein*, 21, 1–331.


Marshall, G. A. K., 1908, A synoptic revision of the Tanyrhythchinae (Curculionidae), *Annals and Magazine of Natural History* (8), 1, 9–33.


Morimoto, K., 1962a, Comparative morphology and phylogeny of the superfamily Curculionoidea of Japan. (Comparative morphology, phylogeny and systematics of the superfamily Curculionoidea of Japan I), *Journal of the Faculty of Agriculture, Kyushu University*, 11, 331–373.

Morimoto, K., 1962b, Key to families, subfamilies, tribes and genera of the superfamily Curculionoidea of Japan excluding Scolytidae, Platypodidae and Cossoninae. (Comparative morphology, phylogeny and systematics of the superfamily Curculionoidea of Japan III), *Journal of the Faculty of Agriculture of Kyushu University*, 12, 21–66.

Morimoto, K., 1976, Notes on the family characters of Apionidae and Brentidae (Coleoptera), with key to the related families, *Kontyû, Tokyo*, 44, 469–476.

Morimoto, K., 1978, Check-list of the family Rhynchophoridae (Coleoptera) of Japan, with descriptions of a new genus and five new species, *Esakia*, 12, 103–118.


Sanborne, M., 1981, Biology of Ithycerus novaboracensis (Forster) (Coleoptera) and weevil phylogeny, *Evolutionary Monographs*, 4, 80 pp, University of Chicago.


Schönheit, C. J., 1826, *Curculionidum dispositio methodicus cum generum characteribus, descriptionibus atque observationibus variis* (Lipsiae), s + 338 pp.


Morphology and classification of weevils


THOMPSON, R. T., 1991, Terminology of the tibial apex—or, when is a corbel not a corbel?, Curculio, 31, 4.


TING, P. C., 1936, The mouth parts of the Coleopterous group Rhynchophora, Microentomology, 1, 93–114.


WEBBER, G. T. and O'BRIEN, C. W., 1986, Annotated checklist of the weevils (Curculionidae sensu lato) of South America, Memoirs of the American Entomological Institute, 39, xvi + 563 pp.


