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Weevils, weevils, weevils everywhere*

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Table of contents

Abstract

An overview is presented of the progress made on the taxonomy, classification and phylogeny of weevils in the 250 years since the first taxonomic descriptions of weevils by Carolus Linnaeus. The number of described weevils species is calculated to be about 62 000 and the likely total number of existing species 220 000, indicating that we have described just over a quarter of the diversity of this important group of beetles and that, at current rates of discovery and description, it will take another 650 years or so to describe the rest. Within the framework of the current concept of weevil phylogeny, a brief account is given of the seven main weevil lineages (families), and of the subfamilies of the largest of them, the Curculionidae, summarising their diversity, distribution and biology and identifying the major classificatory problems remaining in each. In conjunction with the phylogenetic hypothesis of weevil relationships and their fossil record, which is briefly summarised, the evolutionary history of weevils is mapped as a sequence of key evolutionary innovations that together have led to the phenomenal diversification and success of weevils.

Key words: Curculionoidea, diversity, classification, phylogeny, evolutionary history

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Carolus Linnaeus — the humble beginnings

As in most groups of animals, the taxonomic foundation of weevils (superfamily Curculionoidea) and their names was laid by Carolus Linnaeus at the start of our system of binomial nomenclature. In volume 1 of the 10th edition of his epic *Systema Naturae*, Linnaeus (1758) described the nominate genus *Curculio* and pertinently diagnosed it as "*Antennae subclavatae, rostro insidentes. Rostrum corneum prominens*.". Then, 250 years ago, he knew and included in the genus already 80 species, making *Curculio* the largest of the 22 genera of Coleoptera[1] described in that volume, and if the 12 species of *Attelabus*, which he recognised as a separate genus, and the three bark beetles (Scolytinae) described under *Dermestes* are added, weevils comprise 15.8% of the 600 beetle species described by him in 1758. These weevil species span a number of subfamilies and tribes as we classify them today, and they also include several pest species (e.g., *Rhynchophorus palmarum*, *Sitophilus granarius*) that still plague our agricultural enterprises. In fact, *curculio* is the Latin name for the grain-parasitic "corn-worm" or "corn-bug", although this may have been derived from its other meaning of penis (as "little penis"). The name is also immortalised in the classical comedy *Curculio* by the ancient Roman playwright Plautus (254–184 BCE), in which the character of the same name is a social parasite interested only in food and love and running errands for others. It is thus likely that Linnaeus had specifically the grain-infesting *Curculio granarius* in mind when proposing the generic name, but he did not designate a type species for the genus and Latreille (1810) later selected *Curculio nucum*, the European Hazelnut Weevil, as the type species of *Curculio*. This Linnaean species therefore is the archetypal weevil of them all.

With the inherently masculine concept of *Curculio*, Linnaeus also set a trend of establishing weevil generic names masculine in gender, so much so that the "father of weevil taxonomy", Carl Johan Schoenherr (1772–1848), later adapted the endings of all non-masculine generic weevil names and advocated that all weevil genera be given names of masculine gender, so as to prevent adjectival species names having to change their ending when transferred between genera (Schoenherr 1823: 1133). He could not have foreseen the advantages of this practice in the modern world of electronic databases and global name searches, and though of course non-masculine names are valid under the present International Code of Zoological Nomenclature (and Schoenherr's emendations generally invalid), his advice often goes unheeded today as well, and many a modern scholar of weevils without a background in Latin struggles to apply the article of the Code that mandates agreement in gender between genus- and species-group names.

In the 250 years since Linnaeus' first descriptions of weevils, the number known to us has swelled nearly a 1000-fold, and many more undoubtedly await discovery. We have learnt an inordinate amount not only about their diversity but also about their lives. In the preface to his monumental monograph series on the Australian weevils, Elwood C. Zimmerman (1912–2004) paid tribute to their ubiquity: "Weevils, Weevils, Weevils Everywhere — Weevils inhabit all the earth where there is terrestrial vegetation. They are among the most successful and multitudinous forms of terrestrial life. They constitute the largest family group of the animal kingdom. They may be found from the Arctic to the subantarctic, and no habitable island, no matter how remote, escapes their colonisation. No desert that supports vegetation is too dry for them, but it is in the humid tropics where they reach their greatest diversity, and there great numbers of species and individuals occur. … Probably no flowering plant escapes their notice, and many species of higher plants have many species obligately attached to them. Many higher plants depend upon weevils for pollination. All parts of plants are eaten by weevils from roots, bark, sapwood, heartwood, stems, twigs, buds, flowers, pollen, fruits, seeds and sick, dying, dead and decaying plant material." (Zimmerman 1994a: xxiii–xxiv).

As encapsulated by Zimmerman's words, we have come a long way since Linnaeus in our knowledge of weevils. We have studied their anatomy and biology, their diversity and distribution and, more recently, their phylogeny and evolutionary history. We still have a long way to go in all these fields, but the tercentenary of

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[1] Linnaeus additionally also included the orthopteroid genera *Forficula, Blatta* and *Gryllus s. lat.* in Coleoptera

Linnaeus' starting point of the study of weevils is a good time to take stock of where we currently are in what we know about their diversity, their higher classification and their evolutionary history.

Weevil numbers — a most inordinate fondness

Haldane's famous epigram that the Creator has an inordinate fondness for beetles because there are so many of them (Hutchinson 1959, Gould 1993) has become a catchphrase for various expositions of the phenomenal number of species in this insect order (Evans & Bellamy 1996, Farrell 1998, Barraclough *et al*. 1998, Grove & Stork 2000, New 2005). Under the assumption that plant-feeding beetles comprise half the number of described beetle species, Farrell (1998) sought to explain this 'Inordinate Fondness' by expounding the diversity of the largest group of herbivorous beetles, the Phytophaga (superfamilies Chrysomeloidea and Curculionoidea) and he inferred the diversification of the flowering plants (angiosperms) in the Cretaceous to be the principal factor accounting for the species richness of this group, and hence of all beetles. However, highly diverse families also exist among non-phytophagous beetles, notably the predominantly predaceous families Carabidae and Staphylinidae, (about 40 000 and 48 000 respectively, after Beutel & Leschen 2005), and other factors (besides their older age) require consideration to explain their diversity. The largest families of herbivorous beetles besides weevils are Chrysomelidae and Cerambycidae (ca. 35 000 and 20 000, respectively), while other major phytophagous beetle families are less than half as species-rich, Buprestidae numbering only about 14 000 and phytophagous Scarabaeidae (Melolonthinae and relatives, 15 610) barely more than their copro- or saprophagous confamilials (13 453, numbers after Scholtz & Chown 1995). In weevils also, it is only one family, the Curculionidae, with about 51 000 species described, that is so hyperdiverse, whereas its sister group, the Brentidae, numbers only about 4 000 despite being also nearly exclusively associated with angiosperms (below). Phytophagy is evidently not so easy a lifestyle to master for a beetle and in itself not a sure ticket to diversification and evolutionary success. The Curculionoidea, with about 62 000 species described and likely four times as many in existence (below), seem to have excelled in this to a much greater degree than any other beetle group. Why? Did Haldane's Creator have a 'most inordinate fondness' for weevils? Has the angiosperm radiation favoured weevils more than other beetle groups, and is it the sole or even singularly most important factor determining their diversity and species richness? Or was the characteristic elongation of the weevil head into a rostrum the key adaptation that allowed them to uniquely exploit the angiosperm diversity, as inferred by Anderson (1995)?

The most recent comprehensive tally of the number of Curculionoidea (Kuschel 1995) yielded a total of 5 087 described genera and 56 920 species (status at about 1988). Adding the genera and species newly described in the last 20 years[2] raises these numbers to 5 604 and 61 868, an increase of 10% and 8.7%, respectively. The recent comprehensive world catalogue of weevil genera (Alonso-Zarazaga & Lyal 1999, 2002; Lyal & Alonso-Zarazaga 2006) recognises 5 464 valid weevil genera (status at 1999), including fossils but excluding Scolytinae and Platypodinae, which number 225 genera (5 837 species) and 41 genera (1 463 species), respectively, after Wood & Bright (1992) and Bright & Skidmore (1997). Excluding fossils (about 100 genera) and including the latter two groups yields a total of 5 630 genera of weevils, slightly more than the number extrapolated from Kuschel's count but more accurate (though excluding genera described after 1999). A figure of 5 800 genera and 62 000 species is therefore a best estimate of the described diversity of Curculionoidea, comparable with Lawrence's (1982) and Watt's (1982) respective earlier estimates of 60 000 and 65 000.

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[2] as extracted by an electronic search from the taxonomic literature 1988–2008 abstracted in Zoological Record, except numbers for Anthribidae taken from Rheinheimer (2004) and for Brentidae from Sforzi & Bartolozzi (2004) as relevant, and the number of new attelabid genera reduced from 125 to 53 in accord with Riedel (in prep.)

Extrapolation of the likely total species richness of speciose groups such as insects (and weevils) from figures as above is notoriously difficult and beset with many untestable assumptions (Hammond 1992, 1994). For example, in calculations based on area sampling such as forest canopies, varying suppositions of host specificity of insects associated with selected trees can lead to strongly diverging estimates of species richness (Stork 1988). In recent years a number of taxa of mostly small and generally host-specific weevils in the southern hemisphere have been fairly intensively sampled and studied or revised, resulting in an increase in their species numbers by a factor of about 5 (Table 1). In poorly known taxa or where hostplants or habitats have been specifically targeted in the collecting efforts, as with *Bagous*, Nemonychidae, *Tychiodes* and *Cryptolarynx,* the factor of increase is twice as high, indicating that we may know as little as 10% of the real species numbers of such groups, and if their host specificity is very high and if weevil and plant species concepts are broadly congruent, this percentage could be even lower. For example, *Aspalathus* in southern Africa numbers about 260 species and *Moraea* 180 (Germishuizen & Meyer 2003), *Cycas* about 60 in South-East Asia and *Macrozamia* 38 in Australia (Hill & Osborne 2001) and *Callitris* 17 in Australia (K. D. Hill 1998), and while not all such plant species may host a different species of the relevant weevil taxon, some may actually host more than one (e.g. *Callitris* and *Car*). Species accumulation rates in larger, more conspicuous and mostly terrestrial (hence better sampled) weevil taxa are certainly lower and may even be slightly negative after comprehensive revision, e.g., 79 to 67 species (-0.8) in the African Microcerinae (Louw 1986) and 433 to 408 (-0.94) in the Australian Amycterini (Zimmerman 1993). On the other hand, even indiscriminate collecting with light-traps, such as the long-term sampling of the deadwood-boring weevil fauna of Panamanian tropical forests by Wolda *et al*. (1998), can yield a staggering ratio of 1 described to 20 undescribed species in some genera (the derelomine *Phyllotrox* and the conoderine *Eulechriops*), and a survey of the leaf-litter fauna in cloud forests of Honduras and El Salvador (Anderson & Ashe 2000) produced a even more perplexing number of 61 species of the cryptorhynchine genus *Eurhoptus* where none had been known from the area before. Similarly, the Meso-American molytine genus *Theognete*, originally containing a single species from Guatemala and Mexico (O'Brien & Wibmer 1986), was known to comprise more than 75 species a decade later (Anderson & O'Brien 1996) and now approaches 100 as new localities are sampled. These numbers, when considered in concert with high levels of regional endemism (58.7% of weevil species were restricted to a single site in the survey of Anderson & Ashe (2000)), the topographic complexity of Central America (and indeed of most of the tropical regions of the world) and the extent of remaining unsampled or inaccessible habitat, suggest that we are only scraping the surface as far as knowing the diversity of litter weevils is concerned. Numerous species of previously unknown litter-inhabiting weevils have also been collected in other parts of the world, and it appears that regional endemism may have a similar effect on the diversity of such faunas as host specificity does in arboreal taxa.

Across a number of taxa, Basset *et al*. (1994) collected 4.6 times as many unidentifiable (probably undescribed) as identifiable weevil species in a New Guinean case study, and especially in tropical and subtropical regions, where large and poorly studied groups such as Rhynchitinae, Apioninae, Entiminae, Molytinae, Cryptorhynchini and Curculioninae *s. lat.* abound and numerous undescribed species are already sorted in collections, we can estimate at least 5 times as many weevil species as are currently described. Applying this multiplier to the species numbers for Africa (7 516) and the Oriental region (8 579, both after O'Brien & Wibmer 1978), South America (9 046, Wibmer & O'Brien 1986) and Australia (4 118, a comprehensive count), and rounding up the figures to account for Anthribidae, Brentidae, Scolytinae and Platypodinae, which were not included in the O'Brien & Wibmer numbers but together account for ca. 20% of weevil diversity in Kuschel's (1995) counts, the combined species richness for these regions may be estimated at 185 000. Adding 5 000 species for New Zealand (after Watt 1982) and 15 000 (a 2x multiplier) each for the Palaearctic region (8 255, O'Brien & Wibmer 1978) and North America (7 068, O'Brien & Wibmer 1982 and additions), whose faunas are much better known, these estimates combine to a total of 220 000 existing species, or 3.5 times the size of the currently described fauna.

TABLE 1. Increase in species numbers of some weevil taxa after recent sampling and study.

Taxon	Reference	Region	Species before	Species after	Factor of increase	Host
Tychius (Curculioninae)	Caldara 1986, 1989a, 1996	southern Africa	7	35	5.0	*Aspalathus*, *Indigofera* (Fabaceae)
Sibinia (Curculioninae)	Caldara 1989b, 1993	southern Africa	14	59	4.2	several genera of Aizoaceae
Bagous (Curculioninae)	O'Brien & Askevold 1992	Australia	3	27	9.0	aquatics (monocotyledons, also ferns and dicotyledons)
Urodontinae (Anthribidae)	Louw 1993	southern Africa	13	31	2.4	Mesembryanthemaceae, Aizoaceae, Iridaceae
Nemonychidae	Kuschel 1994	Australia	2	20	10.0	*Araucara, Agathis* (Araucariaceae)
Allocorynina (Belidae)	Oberprieler 1995b, 1996, unpubl.	Central America	4	20	5.0	*Zamia, Dioon* (Zamiaceae)
Tychiodes (Curculioninae)	Oberprieler 1995b, 1996, unpubl., Tang *et al.* 1999	South-East Asia	3	33	11.0	*Cycas* (Cycadaceae)
Amorphocerini (Curculioninae)	Oberprieler 1995b, 1996, Downie *et al.* in prep.	southern Africa	7	25	3.6	*Encephalartos* (Zamiaceae)
Tranes (Curculioninae)	Oberprieler 1995b, 1996, unpubl.	Australia	3	9	3.0	*Macrozamia, Lepidozamia* (Zamiaceae)
Phaenomerus (Curculioninae)	Thompson 1996	Australia	3	25	8.3	Curculionidae: Platypodinae
Euops (Attelabidae)	Riedel 1999, 2001a,b,c, 2006	New Guinea	12	84	7.0	mainly *Eucalyptus* (Myrtaceae)
Ceutorhynchus (Curculioninae)	Colonnelli 2006	Africa	2	9	4.5	*Heliophylla* (Brassicaceae)
Metrioxena (Oxycoryninae)	Marvaldi *et al.* 2006	South-East Asia	12	29	2.4	*Arenga* (Arecaceae)
Cryptolarynx (Brachycerinae)	Oberprieler unpubl.	southern Africa	2	18	9.0	*Moraea* (Iridaceae)
Caridae	Oberprieler, Riedel, unpubl.	Australia & New Guinea	3	19	6.3	*Callitris* (Cupressaceae), *Podocarpus* (Podocarpaceae)
Total			90	443	4.9	

The number of described beetle species is about 400 000 (Spangler 1982, Hammond 1992), with weevils (62 000) comprising 15.5% of this number. Interestingly, this is about the same proportion encountered by Linnaeus 250 years ago, when barely 100 weevil species were known. However, this proportion is higher in Australia (18.5%, or 4 118 out of 22 298), and it seems fair to assume that the world's weevil fauna contains a higher share of undescribed species than most other beetle families (but compare Uhlig's (1991) estimates for Staphylinidae), and that their total proportion of the beetle fauna is closer to, if not higher than, the current Australian figure. At 20% of all beetle species, the total species richness of Coleoptera thus calculates to 1 100 000, a figure close to Hammond's (1994) estimate of 870 000 and that of Nielsen & Mound (2000) of 850 000. At this same proportion, higher estimates of beetle species numbers (between 2.4 and 4.7 million; Simon 1996, Grove & Stork 2000) yield a significantly higher number of weevil species (0.5–0.94 million), implying that only between 6% and 12.5% of the world's weevil fauna is currently described. While such a low percentage may apply to some extremely poorly studied taxa, it is unlikely to hold true for weevils overall. However, we can reasonably expect to know barely more than 25% of the world's weevils, and if we maintain the rate of taxonomic exploration and description of the past 250 years, it will take us another 650 years or so to discover and describe the remaining weevils in the world. This rate appears to be quite constant

— taking Kuschel's 1988 species number of 56 920, the annual rate of weevil species descriptions since Linnaeus is 248, whereas the 4800-odd species described over the last 20 years translate to about 240 per annum.

But weevils are not only very speciose and diverse, they can also be extremely abundant. M. P. Hill (1999) provides a pertinent example of their phenomenal reproductive capacity. On 5 December 1997 he released 900 adult *Stenopelmus rufinasus*, a little South American weevil successfully employed around the world to control the invasive aquatic fern *Azolla filiculoides*, in Pretoria, South Africa, on a 1 ha dam completely covered with the fern. Sixty days later, on 1 February 1998, a 2 m^2 mat of decaying fern yielded 30 000 adult weevils, which translates to 150 million weevils for the entire dam. And this spectacular increase in numbers presupposes a significant rate of mortality, for, at the weevil's average fecundity of 325 eggs per female (range 128–474), an average life cycle of 20 days from egg to eclosion (range 16–23) and a 1:1 sex ratio, under zero mortality the 450 females of the original batch would have produced 146 250 weevils after one generation, 23 765 625 after two generations and a staggering 3.862 billion (on the short numerical scale; milliard on the long) after three generations, two months later. The potential population growth of this little weevil is therefore still 25 times higher than the number observed by Hill after 60 days, and under optimal conditions (average fecundity and length of life cycle, zero mortality) he would have needed a mere 36 weevils originally to achieve the same number of adults after two months (18 females producing 154 476 563 progeny after three generations) and the same effect on the population of water fern. No wonder weed biocontrol researchers have an inordinate fondness for weevils in their attempts to control invasive plants around the world (see O'Brien (1995) for an overview).

Weevil classification — progress since Linnaeus

Sixty-two years after Linnaeus, Billberg (1820) proposed a first classification of the Rhynchophora (weevils) by dividing them into seven *nationes* (equivalent to modern families). Schoenherr (1826) shortly afterwards presented a first proper *dispositio methodica* (orderly arrangement) of the group, recognising the difference between those species with straight antennae (Ordo Orthoceri) and those with geniculate ones (Ordo Gonatoceri) and dividing each *ordo* into 16 *divisiones*. These groupings still form the backbone of the modern classification system, although a large number of others were added in the ensuing years — see Alonso-Zarazaga & Lyal (1999) for a full list — and their concepts and ranking varied widely. Crowson (1955) started a modernisation and consolidation of weevil family concepts (to nine) that was extended and refined notably by Morimoto (1962), Thompson (1992), Zimmerman (1993, 1994a, b) and Zherikhin & Gratshev (1995), though in the process again expanded to between 22 and 11 families. In contrast, application of phylogenetic principles and methodology, first by Kuschel (1995) and subsequently by Marvaldi & Morrone (2000) and Marvaldi *et al.* (2002), resulted in the identification of only 6–7 major lineages, treated as families. Support for these lineages rests largely on morphological characters, although molecular data to date provide tacit support for at least the basal ones (Marvaldi *et al.* 2002) and more recent analysis combining two molecular markers (fragments of 18S and 28S rDNA) recovers the same seven lineages (Marvaldi *et al.* in prep.). The non-phylogenetic classification systems by and large recognise the same relationships between their families (Urodontidae with Anthribidae; Oxycorynidae, Allocorynidae and Aglycyderidae with Belidae; Rhynchitidae with Attelabidae; Eurhynchidae, Apionidae and Nanophyidae with Brentidae; Brachyceridae, Dryophthoridae, Erirhinidae, Raymondionymidae, Cryptolaryngidae, Barididae, Scolytidae and Platypodidae with Curculionidae) as are apparent in the subfamilial sequence of the phylogenetic systems, and the differences between the two approaches largely reflect divergent views about family boundaries and translation of phylogenetic relationships into classification systems. With the exception of the large and phylogenetically complex family Curculionidae, the major groups of weevils on family and subfamily level are therefore relatively well established (Table 2). Taking the latest phylogenetic classification as a framework, the following paragraphs outline the current concepts of the seven major weevil lineages (families) as they have developed since Linnaeus, identifying also the principal taxonomic and phylogenetic challenges that face the higher classification and systematics of weevils in the coming decades.

TABLE 2. Classification of Curculionoidea according to current phylogenetic concepts.

- **Family NEMONYCHIDAE**
  - Subfamily Nemonychinae
  - Subfamily Rhinorhynchinae
  - Subfamily Cimberidinae

- **Family ANTHRIBIDAE**
  - Subfamily Urodontinae
  - Subfamily Anthribinae
  - Subfamily Choraginae

- **Family BELIDAE**
  - Subfamily Belinae
  - Subfamily Oxycoryninae

- **Family ATTELABIDAE**
  - Subfamily Rhynchitinae
  - Subfamily Attelabinae

- **Family CARIDAE**

- **Family BRENTIDAE**
  - Subfamily Ithycerinae
  - Subfamily Microcerinae
  - Subfamily Eurhynchinae
  - Subfamily Brentinae
  - Subfamily Apioninae
  - Subfamily Nanophyinae

- **Family CURCULIONIDAE**
  - Subfamily Dryophthorinae
  - Subfamily Platypodinae
  - Subfamily Brachycerinae
  - Subfamily Cyclominae
  - Subfamily Entiminae
  - Subfamily Molytinae
  - Subfamily Cossoninae
  - Subfamily Scolytinae
  - Subfamily Baridinae
  - Subfamily Curculioninae

Nemonychidae

This family of weevils (fig. 1) retains numerous primitive traits, both in structure and in habits. It is a relict group of the ancient past, today comprising only about 76 known species (71 described) in 21 genera but with a rich fossil record of about 60 species from Upper Jurassic and Lower Cretaceous deposits largely in the northern hemisphere. The extant fauna shows a highly disjunct distribution mainly in temperate northern and southern regions but with some species also in the tropics. It is most diverse in the Australian and Neotropical regions, which harbour about 70% of the fauna, fewer species occurring in the Nearctic and Palaearctic regions. Nemonychidae are predominantly associated with conifers, especially the family Araucariaceae, which hosts half of all the species, while Pinaceae provide the common hosts in the northern hemisphere. Only two genera live on angiosperm hosts, *Rhynchitomacer* on *Nothofagus* (Nothofagaceae) in South America and *Nemonyx* on *Consolida* and *Delphinium* (Ranunculaceae) in the western Palaearctic. The association with conifers (especially Araucariaceae) is likely the ancestral one and the angiosperm associations to represent secondary host shifts. The Nemonychidae are presumed to retain the ancestral life style of weevils, their mobile larvae living freely (ectophytically) among the sporophylls inside dehiscing male conifer strobili (cones), feeding on pollen in the open sporangia (pollen sacs) and moving between cones. Eggs are laid openly between the sporangia by means of the ovipositor (Howden 1995), but the females of some species may use their elongated rostrum to separate sporophylls before the cope ripens, allowing them to lay their eggs inside the cone against the sporangia. A few forms, however, such as *Bunyaeus* and *Eutactobius* in Australia and *Brarus* in South America, have a short to very short rostrum, and *Nemonyx* females use their hard, piercing ovipositor to drill holes into the follicles of the host fruits, in which their larvae feed on the developing seeds. Adult nemonychids also feed mainly on pollen.

FIGURES 1–8. 1—*Mecomacer scambus* (Nemonychidae: Rhinorhynchinae), developing in male cones of *Araucaria* (Araucariaceae) in southern South America (Chile and Argentina). 2—*Mecocerinopis* sp. (Anthribidae: Anthribinae) from northern Australia. 3—*Cyrotyphus vestitus* (Belidae: Belinae), a rare Australian agnesiotidine from *Callitris* (Cupressaceae). 4—*Hydnorobius hydnorae* (Belidae: Oxycoryninae), an Argentine oxycorynine associated with the root-parasitic *Prosopanche* (Hydnoraceae). 5—a female of the Australian *Euops falcatus* (Attelabidae: Attelabinae) showing abdominal brushes used for inoculating her leaf rolls with fungal spores 6—the Australian *Car pini* (Caridae) on its hostplant, *Callitris endlicheri* (Cupressaceae). 7—*Orapaeus cretaceus* (Brentidae: Eurhynchinae), an early Upper Cretaceous brentid fossil from Botswana. 8—the Australian *Aporhina australis* (Brentidae: Eurhynchinae), whose larva develops in stem galls of *Litsea leefiana* (Lauraceae). (all photos R. Oberprieler except 1, 4 (A. Marvaldi) and 8 (J. Hasenpusch))

The Nemonychidae are classified into three subfamilies, Nemonychinae (for *Nemonyx* only), Rhinorhynchinae and Cimberidinae. *Nemonyx* differs from all other genera in a number of characters, many of them plesiomorphic (Kuschel 1995), which prompted Crowson (1985) to argue for placing it in a family of its own. However, Kuschel (1994, 1995) and May (1994) identified pertinent imaginal and preimaginal synapomorphic characters that hold all nemonychids together as a single family. *Nemonyx* nonetheless shows the greatest number of plesiomorphic traits of all extant weevils.

Anthribidae

This is a much larger family of weevils, with 371 genera and 3860 species described (Rheinheimer 2004) and occurring throughout the world, mostly in tropical regions. Anthribid success in diversity is seemingly linked to mycetophagy, their adults and larvae developing predominantly on wood-decaying ascomycete fungi (Holloway 1982). Some species, however, feed on pollen, lichens, wood, seeds and even scale insects. The anthribid rostrum is short and broad (fig. 2), seemingly adapted to grazing fungal mycelia and not used in preparing oviposition sites (Howden 1995), but the larvae lead a truly endophytic life inside fungus-infested wood of mainly angiosperms, the eggs being inserted into the plant tissues by means of a specialised, dentate ovipositor. Mycetophagy appears to be the ancestral life style of anthribids and the development in angiosperm seeds and stems by the specialised Choraginae and Urodontinae a derived trait, although the latter group was thought to have retained the phytophagous habits of ancestral weevils (Crowson 1984). The cycad-associated genus *Apinotropis* in southern Africa suggests that mycetophagy may have evolved from a phytophagous larval development in decaying gymnosperm sporophylls (Oberprieler 1999).

Several questions remain about the classification of the Anthribidae. The weevil phylogeny of Kuschel (1995) shows them as the sister-group of all other weevil families except Nemonychidae, but subsequent analyses of expanded character sets (Marvaldi & Morrone 2000, Marvaldi *et al.* 2002) indicate them as being adelphic to Nemonychidae. Although most character agreements between these two families are based on plesiomorphic conditions and few synapomorphies are in evidence in support of this relationship, it is also readily recovered in recent molecular analyses (Marvaldi *et al.* in prep.). Within Anthribidae, uncertainties exist about the status of the three subfamilies Anthribinae, Choraginae and Urodontinae, in that the monophyly of Anthribinae with respect to Choraginae is not established and in that Urodontinae differ from the other two groups in numerous features, prompting several authors (e.g., Crowson 1984, Thompson 1992, Louw 1993) to treat them as a distinct family. They share a few apomorphic features with Anthribinae/Choraginae, notably the long but faint, transverse notosternal sutures, a grooved pygidium (tergites 6/7) and the absence of tibial spurs, but their male genitalia are quite different (Lyal & Barclay 2001, Wanat 2007) and their larvae have dorsal ambulatory papillae and purple Malpighian tubules (May 1993) like those of Nemonychidae. The tubules may be involved in silk production, as at least some urodontine larvae spin cocoons for pupation in the soil (Scott 1930, Oberprieler pers. obs.). Further studies and especially analyses of molecular characters are needed to establish the true relationships and taxonomic status of the urodontines. Relationships within Anthribinae are still unclear, no phylogeny being available yet and no proper concepts existing for the 28 tribes generally recognised.

Belidae

Another small and evidently relict family, the Belidae number only about 375 species classified in 38 genera and occur predominantly in the southern hemisphere. They are divided into two subfamilies, Belinae and Oxycoryninae, with rather different distributions and habits. The Belinae, with about 155 species in 25 genera, are restricted to the southern hemisphere, occurring mainly in the Australian region (140 species in 21 genera) but a few also in South America. The Oxycoryninae, with 13 genera and about 200 species, have a worldwide but highly fragmented distribution (Marvaldi *et al.* 2006). The larvae of Belinae are woodborers in stems and logs, the more primitive Pachyurini and Agnesiotidini (fig. 3) mostly in conifers (Araucariaceae, Podocarpaceae and Cupressaceae) but the Belini in angiosperms, especially acacias in Australia. Oxycoryninae (fig. 4) develop mostly in reproductive plant organs, of gymnosperms (araucarias and cycads) as well as of angiosperms, but also in stems or under bark (see Marvaldi *et al.* 2006). In Belidae and remaining weevil families, the female rostrum is transformed into a proper oviposition tool by the fusion of labrum and clypeus and the development of more advanced mandibles with long pharyngeal processes, enabling their eggs to be deposited inside firm plant tissues and their larvae to develop truly endophytically.

The unification of Belinae and Oxycoryninae into a single family is not universally adopted (e.g., Crowson 1955, Thompson 1992, Zimmerman 1994a, Zherikhin & Gratshev 1995), although the close relationship of these two groups has long been recognised and is well supported in phylogenetic analyses (Kuschel 1995, Marvaldi & Morrone 2000, Marvaldi *et al.* 2002). The Aglycyderini, too, are sometimes treated as a separate subfamily (e.g., May 1993, Kuschel 1995, 2003) or even family (e.g., Thompson 1992, Zimmerman 1994a), but recent phylogenetic analyses (Marvaldi 2005a, Marvaldi *et al.* 2006) place them firmly inside Oxycoryninae. With phylogenetic analyses recently conducted on all the genera of both Belinae (Kuschel & Leschen 2003) and Oxycoryninae (Marvaldi *et al.* 2006), the Belidae are the only weevil family for which comprehensive generic phylogenies are available.

Attelabidae

With approximately 2 500 described species in 150 genera and a cosmopolitan distribution, the Attelabidae are another successful group of weevils. Like Anthribidae, they seem to have achieved their success in diversity also through association with fungi, their larvae developing on withering plant tissues that may be indirectly or directly infected with fungi. In contrast to anthribids, however, female attelabids prepare their oviposition site with their rostrum, which is further modified from the belid condition by the fusion of the gular sutures and the reduction of the ligula. The rostrum is used to variously sever the sap flow in a living plant organ (stem, leaf, bud, fruit) and cause it to wilt or drop off, with the larva feeding on the decaying tissues. In advanced Attelabinae, females roll leaves into elaborate, cigar-like nidi (nests) in which they lay their eggs and which they can inoculate with fungal spores carried in special mycetangia next to their hind coxae (fig. 5). Attelabidae are predominantly associated with angiosperms, only a few primitive ones living on conifers (Cupressaceae, Pinaceae) but indicating these to probably constitute the ancestral hosts of the family.

The Attelabidae generally comprise two subfamilies, Rhynchitinae and Attelabinae, with about equal numbers of described species. Though treated as separate families by some authors (e.g., Zimmerman 1994a, Legalov 2004, 2005), the two groups share several synapomorphic characters (Thompson 1992, Kuschel 1995, Marvaldi & Morrone 2000) and together evidently constitute a monophyletic group. The Attelabinae are strongly indicated to be monophyletic as well, but the same cannot be said for the Rhynchitinae (defined only by the phylogenetically weak characters of appendiculate claws and exodont mandibles) and it remains to be demonstrated that they are not paraphyletic with respect to Attelabinae. Phylogenetic analyses of tribal relationships in both subfamilies were recently published by Legalov (2004, 2005), but they are based on numerous spurious characters of doubtful phylogenetic value and an unproven cladistic algorithm and require critical assessment. Presently therefore, phylogenetic relationships within Attelabidae remain unresolved.

Caridae

With only 4 genera and 6 species described (but about a dozen more known from Australia and New Guinea), this is the smallest of weevil families and evidently another relict group. It is restricted to the southern hemisphere, two species known from South America, about 12 from Australia and about half that number from New Guinea. Host associations are predominantly with cupressaceous conifers, but the New Guinean species have been found on podocarps and probably also the Australian *Carodes* is associated with a different conifer. The known larvae (of the Australian *Car condensatus*) develop on young seeds in closed female cones of *Callitris*, into which the females drill oviposition holes with their rostrum. This rostrum differs from that of the previous groups by having a compacted maxilla, and the antennae are inserted far back on the rostrum with the basal segment (the scape) elongated to reach the front eye margin when folded back. The Caridae evidently also preserve the ancestral association of weevils with conifers (fig. 6), and the larva, which uses its clawed legs to crawl around in the chambers of the female cone over the developing seeds, may represent the first stage in the evolution of endophytic life in weevil larvae.

Controversy surrounds the name of the family, in that, following the placement of the fragmented Karatau fossil *Eccoptarthrus crassipes* in Caridae by Zherikhin & Gratshev (1995), its name is superseded by the older family-group name Eccoptarthridae. However, there is nothing tangible that relates *Eccoptarthrus* to Caridae, and the broadened basal tarsites, which Zherikhin & Gratshev (1995) regarded as a defining feature of the family, are neither restricted to this family nor in fact universal in extant carids. *Eccoptarthrus* evidently is a nemonychid like the other Karatau fossils (Kuschel 2003) and probably just the dorsal impression of another species described as *Archaeorrhynchus* or similar genus (Oberprieler & Kuschel, in prep.). The affinities and classificatory position of Caridae have also been controversial, the group (generally based on *Car* only) having earlier been assigned to Nemonychidae, Rhynchitinae and Apioninae (see Zimmerman 1994a for full account) and more recently to Belidae (Thompson 1992) and Brentidae (May 1993, Kuschel 1995). However, following the discovery of the larva (May 1994) and the inclusion of its characters in phylogenetic analyses, a position as a distinct family adelphic to Brentidae + Curculionidae is strongly indicated (Marvaldi & Morrone 2000, Oberprieler 2000, Marvaldi *et al.* 2002).

Brentidae

In the wide sense as adopted here, the family Brentidae is about as diverse as the Anthribidae, with approximately 400 genera and 4 000 species described, and it also has a cosmopolitan distribution. About 90% of the species belong to the derived subfamilies Brentinae and Apioninae, which are about equal in size (ca. 1 700 and 1 900 species, respectively), while the Nanophyinae (ca. 270), Microcerinae (67), Eurhynchinae (31) and Ithycerinae (1) are much poorer in species and also geographically more restricted. Brentidae are almost exclusively associated with angiosperms, only very few and unrelated apionines occurring on conifers, and since nearly all the putatively basal groups (Ithycerinae, Microcerinae, Eurhynchinae, Nanophyinae, Brentinae: Cyladini, Apioninae: Tanaini, Mecolenini) live on angiosperms, it appears that the family was ancestrally associated with this group of plants. Conspicuous in Brentidae is also the absence of associations with monocotyledons, and although the family is indicated to be at least as old as Curculionidae (extending back to the mid-Cretaceous in the fossil record), it species richness reaches not even 8% of that of the latter. The larvae of Ithycerinae and Microcerinae (fig. 10) feed on roots in the soil, those of Eurhynchinae (fig. 8) and Brentinae (fig. 11) tunnel in living or dead branches and trunks (where some Brentinae may be predaceous on other xylophagous beetles) and those of Apioninae (fig. 12) and Nanophyinae develop mostly in young stems and inflorescences, fruits or seed pods.

FIGURES 9–16. 9—the South African *Microcerus latipennis,* a member of the enigmatic African Microcerinae (Brentidae). 10—larva of *Microcerus latipennis* feeding on the taproot of *Sida rhombifolia* (Malvaceae). 11—the ant-associated *Cordus ganglbaueri* (Brentidae: Brentinae) from Australia. 12—the South African *Tanaos interstitialis* (Brentidae: Apioninae), a primitive apionine developing in flower heads of *Protea caffra* (Proteaceae). 13—a pair of the South African *Antliarhinus zamiae* (Brentidae: Apioninae) on a cut cycad seed hollowed out by their larvae. 14—dead female *Antliarhinus zamiae* with her rostrum stuck in a cycad seed. 15—the large Australian Grasstree Weevil, *Trigonotarsus rugosus* (Curculionidae: Dryophthorinae), on dead trunk of its grasstree host, *Xanthorrhoea* (Xanthorrhoeaceae). 16—the large, colourful Elephant Weevil, *Brachycerus ornatus* (Curculionidae: Brachycerinae), from southern Africa on leaves of *Ammocharis coranica* (Alliaceae or Amaryllidaceae), its larval host.

The family concept of the Brentidae remains in dispute, some authors (e.g., Crowson 1955, Zimmerman 1994b, Wanat 2001) treating some or all of the subfamilies recognised here as distinct families. The case for amalgamating them (except for the African Microcerinae) into a single family was first made by Morimoto (1962, 1976) and consolidated by later studies (Thompson 1992, May 1993) and phylogenetic analyses (Kuschel 1995, Marvaldi & Morrone 2000, Oberprieler 2000, Marvaldi *et al.* 2002). The Microcerinae (fig. 9), which had previously been included in the curculionid subfamily Brachycerinae (e.g. Thompson 1992, Kuschel 1995), were included in Brentidae by Oberprieler (2000) on the basis of mainly larval characters. A number of characteristic morphological features occur in Brentidae in this expanded concept, such as stepped abdominal ventrites (3–5 on a higher level than 1–2), eyes covered by a corneal lens, labial palps sunk into grooves on the ental surface of the prementum and with a reduced number of segments (2 or 1), male tergite 8 pouch-like with medially inflexed posterior margin, aedeagus with frenal sclerities, tegminal ring laterally constricted or articulated; however, none of these conditions are present in all taxa and can be regarded as synapomorphies defining the family Brentidae as a monophyletic group. Only two characters have been identified so far as shared by all of them. One is the single median sensillum on the larval labrum, which is otherwise only known in Ocladiini (Curculionidae: Brachycerinae) but does not occur in the more primitive families (which have a median pair) or in other Curculionidae (which have a median sensillum plus a lateral pair). The other is the reduced number of Malpighian tubules (four), a condition that almost never occurs in Curculionidae (only a few isolated cases reported in Cossoninae and Rhamphini, see Calder 1989). It does, however, also occur in some Nemonychidae and Anthribidae (Calder 1989, May 1993), and although such a reduction is likely to have evolved independently in various groups, its consistent occurrence in all Brentidae suggests that it may indeed be a synapomorphic feature in this family. Further morphological and molecular studies are needed to test this hypothesis and to establish the relationships among the subfamilies as recognised here. Phylogenetic relationships within the subfamilies have been addressed in Microcerinae (Louw 1986) and Apioninae (Wanat 1995, 2001) but remain to be extended and especially studied in the other large subfamily, Brentinae.

Curculionidae

With about 4 600 genera and 51 000 described species, the family Curculionidae is an order of magnitude larger than any other in weevils and comprises in excess of 80% of all weevil species. Its stupendous species richness is a principal factor in the large size of the Phytophaga and in fact of all Coleoptera, thus in Haldane's Inordinate Fondness for beetles. Curculionidae occur all over the world, from the arctic zone in the north to the subantarctic islands in the south, from beaches to mountain tops, from deserts to rainforests. They feed on virtually all plants, mainly angiosperms but also gymnosperms, pteridophytes, bryophytes and lichens and occasionally they even browse on algae and cyanobacteria. Unlike all other weevil families, curculionids also make extensive use of monocotyledons as hosts, the basal subfamilies Dryophthorinae and Brachycerinae being predominantly associated with them and several taxa of other subfamilies as well. It is therefore likely that monocotyledons constitute the ancestral hosts of Curculionidae and that they may have played a pivotal role in the diversification of the family (Marvaldi *et al.* 2002, Oberprieler 2004b). Curculionid larvae predominantly live an endophytic life inside all parts of plants, from underground roots to buds, flowers and seeds high in the canopy. However, several groups have also adopted a more ectophytic life, the larvae feeding exposed on leaves or in the soil on roots, and a few have evolved specialised life styles such as coprophagy (dung-feeding), myrmecophily and even predation.

The classification of Curculionidae into natural subfamilies and tribes probably remains the largest outstanding problem in the higher classification of Coleoptera even half a century after Crowson (1955) wrote these words. A significant first step in addressing this problem was the identification of those taxa with plesiomorphic, pedotectal[3] (Alonso-Zarazaga 2007) male genitalia by, mainly, Morimoto (1962), Kuschel (1971), Thompson (1992) and Zimmerman (1993, 1994a). Thompson (1992) excluded all of these groups from Curculionidae, as separate families Dryophthoridae (as Rhynchophoridae), Brachyceridae, Raymondionymidae, Cryptolaryngidae, Erirhinidae and also Platypodidae, leaving in Curculionidae only those taxa with the derived, pedal type of genitalia. In phylogenetic analyses (Kuschel 1995, Marvaldi & Morrone 2000, Marvaldi *et al.* 2002, Morimoto & Kojima 2006), however, they are included as basal lineages in Curculionidae, and Kuschel's concept of the subfamilies Brachycerinae and Curculioninae includes both types of genitalia. Indeed, it remains to be demonstrated that the derived, pedal type of male genitalia, with no tectum remaining, has evolved only once in Curculionidae. In the expanded phylogenetic concept, the family Curculionidae is delimited by the autapomorphic characters of, in the adult, geniculate antennae (apparently independently evolved also in Brentidae: Nanophyinae) and compact antennal club and, in the larva, 3–4 dorsal folds in the abdominal segments, a prothoracic position of the thoracic spiracle and the frontal sutures of the head blocked by a frontoepicranial bracon (bridge). A condition similar to the last also occurs in the brentid *Ithycerus* and is the principal reason why this genus is often placed in Curculionidae; however, it differs from that in Curculionidae in that the frons almost completely encloses the antenna and the frontal sutures are not properly separated from the mandibular membranes (see also Sanborne 1981) and it is probably not homologous. Other features typical of Curculionidae (although perhaps not autapomorphic) are, in the larva, the postoccipital condyles and, in the adult, the dorsoventral flexion of the head (retractable onto the prosternum), a metendosternite with well separated anterior tendons and a spermatheca with well separated duct and gland.

The number and concepts of subfamilies in Curculionidae remain chaotic and controversial, many of the 16[4] recognised in the recent generic catalogue (Alonso-Zarazaga & Lyal 1999) suffering from poor definitions, amalgamation of not evidently closely related genera and an over-inflated status in the broader picture of curculionid diversity. It will take considerable efforts of painstaking character analysis, both morphological and molecular, to identify and properly delimit the main lineages of particularly the higher Curculionidae (with the pedal type of male genitalia). The smaller number of subfamilies here outlined is meant as an indication of such possible major lineages, as yet mostly without firm concepts but grouping together traditional subfamilies that are difficult to separate as smaller units.

The **Dryophthorinae** (fig. 15) are one of the few well-defined and evidently monophyletic curculionid subfamilies, identified by several clear synapomorphies (Kuschel 1995, Marvaldi & Morrone 2000). It occurs throughout the world and includes the largest weevils known, and the majority of its approximately 1 200 species is associated with woody monocotyledons, especially palms and pandans. It is nowadays usually divided into five tribes, Dryophthorini, Stromboscerini, Orthognathini, Cryptodermatini and Rhynchophorini, and their phylogenetic relationships are under study (Kojima & Lyal 2000).

The **Platypodinae**, counting about 1 500 species world-wide, are specialised woodborers whose larvae develop on ambrosia fungi cultivated in galleries in the wood. Usually related to bark beetles, Scolytinae, and often treated as a distinct family, their phylogenetic position is still unclear but recent evidence from larval characters (Marvaldi 1997) and, more tentatively, also from molecular sequences places them at the base of Curculionidae close to Dryophthorinae.

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[3] the aedeagus featuring a distinct dorsal tectum and ventral pedon, also referred to as "orthocerous type" of genitalia as they typically occur in the families with orthocerous (non-geniculate) antennae; in the pedal ("gonatocerous") type the tectum is absent

[4] exluding those placed in the separate families Brachyceridae, Dryophthoridae, Erirhinidae, Raymondionymidae and Cryptolaryngidae


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FIGURES 17–24. 17—an undescribed species of the southern-African endemic *Cryptolarynx* (Curculionidae: Brachycerinae) on leaf of its hostplant *Moraea* (Iridaceae). 18—the localized South African *Somatodes misumenus* (Curculionidae: Cyclominae) on a spathe of its larval hostplant, *Bobartia* (Iridaceae). 19 – the Australian aterpine *Aesiotes leucurus* (Curculionidae: Cyclominae) on a branch of its hostplant, *Callitris* (Cupressaceae). 20 – *Afroleptops coetzeei* (Curculionidae: Entiminae), a relict South African relative of the Australian leptopiines, feeding on a leaf of its *Protea* hostplant (Proteaceae). 21—the Australian *Tranes lyterioides* (Curculionidae: Molytinae) on a male cone of the cycad *Macrozamia communis* (Zamiaceae), which it pollinates. 22—the long-snouted *Ludovix fasciatus* (Curculionidae: Curculioninae) from South America, which lays its eggs inside the stems of the water hyacinth *Eichhornia* (Pontederiaceae), where its larvae feed on *Cornops* grasshopper eggs. 23—an undescribed *Tychius* species (Curculionidae: Curculioninae) from South Africa feeding on a shoot of Rooibos Tea (*Aspalathus linearis,* Fabaceae), in whose flower buds its larvae develop. 24—the South African hyperine *Frontodes brevicornis* (Curculionidae: Curculioninae) on its host, *Chaetacme aristata* (Ulmaceae), on whose leaves its exposed larvae feed and spin mesh-like silken cocoons for pupation

The **Brachycerinae**, here treated in a wider sense that includes Erirhinini, Ocladiini, Cryptolaryngini (fig. 17) and Raymondionymini (Oberprieler 2004b), combine more typical curculionid taxa with pedotectal male genitalia and number about 1 200 species. The difficulty of separating the flightless African Brachycerini (fig. 16) from traditional Erirhinini is exemplified foremost by the Ocladiini (*Ocladius, Tetracyphus*, *Desmidophorus*), which agree with the former group in genital and larval characters (Thompson 1992, Kuschel 1995, Marvaldi 2000, Morimoto & Kojima 2006) but with many genera of traditional Erirhininae (e.g., *Afghanocryptus, Aonychus, Arthrostenus, Hypselus, Tadius*) in having a setose groove below the antennal insertion and a swollen or raised, basal elytral locking mechanism. In fact, a preliminary phylogenetic analysis of Brachycerinae in this sense on morphological characters (Oberprieler 2004b) suggests that the deepest split may lie between the New-World Tanysphyrini (= Stenopelmini) and Erirhinini + Ocladiini + Cryptolaryngini + Byrsopini + Brachycerini (Raymondionymini not included). Brachycerinae are also predominantly associated with monocotyledons, the Tanysphyrini with aquatic Alismatales and Commelinales (some also with aquatic grasses and ferns), the Erirhinini and Ocladiini with Poales (a few with dicotyledons or mosses) and the Cryptolaryngini, Byrsopini and Brachycerini with geophytic Asparagales and Liliales. Further studies, especially of molecular characters, are required to elucidate the precise composition of Brachycerinae and the relationships among its subgroups. The subfamily may be paraphyletic in that some groups of higher Curculionidae (with a pedal type of genitalia) may have derived from it, such as Bagoini and also Entiminae. The latter were included in Kuschel's (1995) concept of Brachycerinae and share conspicuous characters such as deciduous mandibular cusps and metatibial corbels, although other phylogenetic studies (Marvaldi 1997, Marvaldi *et al.* 2002) place them in a clade with Cyclominae.

The **Cyclominae** are a 'subfamily of convenience' for now, sharing no obvious synapomorphic characters. It combines several southern-hemisphere taxa of mostly large weevils, namely the African Cyclomini (fig. 18), Hipporhinini and Gronopini, the Australian Amycterini and Aterpini and the more widespread Rhythirrinini and Listroderini, together numbering more than 1 000 species. The Diabathrariini[5] and Gonipterini, included in Cyclominae by Morrone (1997a, b) and the latter placed close to some of these groups in the phylogenetic analyses of Marvaldi (1997) and Marvaldi *et al.* (2002), probably do not belong here but rather in Curculioninae, judging by the endophytic habits of the former and the long rostrum (and also likely endophytic larvae) of several gonipterines. Features of the ovipositor group Hipporhinini, Gronopini and Amycterini together, and possibly Cyclomini, Rhythirrinini and Listroderini are also related, while Aterpini in their current composition are a mixed group and may include elements of other subfamilies, such as Molytinae. Host associations are poorly known in Cyclominae, but the larvae generally develop in the soil feeding on or in roots and underground stems. Amycterini and Cyclomini appear to be largely associated with monocotyledons but the other groups with dicotyledons. The larvae of Aterpini mostly tunnel in roots, trunks, stems, shoots and inflorescences of Myrtaceae and Proteaceae but some (*Aesiotes,* fig. 19) also in conifers, and, unlike the other tribes, the females of at least some genera use their rostrum for preparing oviposition sites. Detailed studies, especially of the larvae, are required to properly define both the subfamily and its constituent tribes and to establish monophyletic groupings.

The **Entiminae** (fig. 20), with more than 12 000 species described, are the largest group of weevils and spectacularly successful not only in diversity but also in distribution and abundance, including many serious agricultural pests. They are characterised by a short, broad rostrum with adelognathous mouthparts (the prementum closing the buccal cavity from beneath), mandibles bearing deciduous cusps that assist the teneral weevil to escape form its earthen pupal cell but then break off, and, in the larva, a cushion-like antennal sensorium. The last character appears to constitute a good synapomorphy for Entiminae, whereas the other two also

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[5] limited to the African genera *Aphanonyx, Diabathrarius* and *Onychogymnus* (which develop in seed pods of legumes such as *Schotia*), and to exclude the unrelated, wood-boring Australian *Aromagis, Atelicus, Kershawcis* and *Strongylorhinus*, whose affinities are unclear (see also Zimmerman 1994a: 677)

occur in other groups. The similar deciduous mandibular cusps in Brachycerinae are interpreted as a parallel development by Thompson (1992) and Marvaldi (1997), but their homology or not with those of Entiminae remains to be convincingly established. Many genera also bear corbels on the hind tibiae like they occur in a number of Brachycerinae; again the homology of this feature remains to be elucidated. Adult Entiminae mostly feed on leaves and young shoots and their larvae on roots in the soil, but host associations tend to be very broad and loose. The classification of the Entiminae into natural tribes and subtribes is chaotic, as many as 55 recognised in the generic catalogue of Alonso-Zarazaga & Lyal (1999) and many based on Palaearctic genera with no clear relationships to southern-hemisphere forms. The recognition of a smaller number of more distinct groups as tribes by Thompson (1992) and Marvaldi (1997, 1998) — Alophini, Pachyrhynchini, Ectemnorhinini, Sitonini and Entimini — seems a more meaningful approach but needs to be expanded to cover the entire diversity of the subfamily.

The subfamily **Molytinae** (fig. 21) as treated here combines the majority of the wood-boring taxa in Curculionidae. Its traditional, narrow concept was first expanded by Kuschel (1987), who also commented on the difficulty of separating the group from especially the traditional Cryptorhynchinae and Cossoninae. Indeed, the "Cryptorhynchinae" are a mixture of taxa that have in common only a pronounced prosternal canal into which the rostrum folds in repose, but such a canal also occurs in other groups (e.g., Brachycerinae) and is in fact quite differently constructed in different groups of "Cryptorhynchinae". Kuschel (1987) moved the Ithyporini from Cryptorhynchinae to Molytinae, and Zimmerman (1994a) afforded subfamily rank to Camptorhinini and Aedemonini (as Mechistocerinae), pointing out the affinity of the latter with Molytinae, and transferred several other genera from Cryptorhynchinae to Molytinae. Other features, such as sclerolepidia (Lyal *et al.* 2006), are also useful in distinguishing the disparate elements of "Cryptorhynchinae". Cryptorhynchini in the narrow sense may be identified by a particular type of rostral canal (ending in a mesosternal receptacle) and, like the others, appear to be just another specialised group of Molytinae. Also Psepholacini are distinct from Cryptorhynchini and approach Scolytinae in their adaptations to boring into wood with the entire body, hence reducing the rostrum and developing stout denticles on the tibiae. The boundary is also hazy between Molytinae and traditional Lixinae (Marshall 1932, Aslam 1963), and additional problems are posed by a large and poorly studied fauna of microphthalmic or eyeless species in leaf litter that are difficult to assign to any of the traditional subfamilies (e.g., Nesiobiini). Also Mesoptiliini appear to belong here, although their larvae display significant agreements with those of Scolytinae (Lekander 1967, May 1993). In the widened sense as used here, Molytinae comprise around 10 000 species worldwide. Their larvae predominantly develop in dying wood, but several also attack living stems, trunks and roots. The adults nearly always have a stout uncus (spine) at the end of their tibiae, evidently an adaptation for clinging onto wood and also aiding the female in drilling oviposition holes with her rostrum. Host associations are mainly with dicotyledons, but several taxa are also associated with monocotyledons (especially palms) and gymnosperms (conifers and cycads).

The **Cossoninae,** here treated as a separate subfamily, are nonetheless difficult to distinguish from Molytinae. Groups such as Trypetidini, Amorphocerini, Phoenicobatini and Nesiobiini, traditionally included in Cossoninae, combine features of both and are more suitably treated as belonging in Molytinae, leaving the concept of Cossoninae more or less restricted to forms with deep mandibular sockets (limited below by a prominent hypostomal tooth), large proventricular grinding plates, a short, broad aedeagus and a strongly asymmetrical male sternite 9. Kuschel (1995) and Kuschel *et al.* (2000) listed some other apomorphic characters for the group, but their phylogenetic significance is not clear and many appear to be adaptations to a life in tight spaces under bark or deep in moist wood. The precise composition of Cossoninae is therefore still unclear. Alonso-Zarazaga & Lyal (1999) listed 18 tribes but Kuschel (1992) recognised only five, Onycholipini, Rhyncolini, Cossonini, Dryotribini (as Cotasterini) and Pentarthrini; however, their concepts remain to be confirmed and clarified. Others are even more obscure, such as the Araucariini, which are often regarded as close relatives of Scolytinae or the "link" between Cossoninae and Scolytinae but most likely an artificial concept. The six included genera (Kuschel 1966) are held together only by the feature of stout, socketed tibial spines but display numerous differences and also similarities with other genera (e.g., *Amorphocerus* with *Porthetes*, together placed in Molytinae as Amorphocerini), and the Australian / New Zealand genera (*Coptocorynus*, *Inosomus, Mastersinella* and *Xenocnema,*) cannot be regarded as close relatives of the South American *Araucarius* nor exclusively of each other. *Araucarius* has a more molytine type of tibial apex rather than the typically cossonine condition, and the other genera differ from each other again in mainly the tibial apex (typically cossonine in *Inosomus* but shovel-like expanded in the others) but also i.a. in the number of funicular segments (5 in *Coptocorynus*, 7 in all others), the shape of the rostrum (very short and broad in *Xenocnema*, long in *Mastersinella*) and the shape of the antennal club (various). The proper cossonines generally develop in dying or dead wood, the adults tunnelling into stems and trunks in advanced stages of decay. Most develop in dicotyledons but without any great degree of host specificity; however, some have more or less strict associations with monocotyledons, conifers and ferns. About 1 700 species are classified in Cossoninae, many of them widely distributed or even cosmopolitan.

The **Scolytinae** or bark beetles are a large (ca. 6 000 species) and highly adapted group of weevils of considerable economic significance because of their impact on trees and the forestry industry. Their classificatory position remains controversial, specialists and sylviculturists usually treating them as a distinct family but recent morphological and phylogenetic studies of weevils generally including them as a subfamily in Curculionidae (but see Morimoto & Kojima 2003, 2004). In Curculionidae they are usually closely affiliated with Platypodinae and/or Cossoninae (e.g., Kuschel *et al*. 2000), but a close relationship to Platypodinae is unlikely (see above) and in regards to Cossoninae it is unclear whether they might be adelphic to all Cossoninae or to just a subset of genera (for the link to “Araucariini” see above). Considerable character agreements also exist with the Psepholacini, to the extent that *Psepholax latirostris* was redescribed as *Protohylastes annosus* and interpreted as the most primitive scolytine (Wood 1973, for details see Zimmerman 1994a), and the genus *Dactylipalpus*, embedded in the tribe Hylesinini of the subfamily Hylesininae in Wood’s (1986) classification, is in fact also a psepholacine, taking the reduction of the rostrum in this group to a similar extent as it occurs in Scolytinae. Further, Lekander (1967) and May (1993) identified several similarities between scolytine larvae (especially *Scolytus*) and those of Mesoptiliini. In view of these extreme character convergences and misinterpretations of genera, it remains to be demonstrated that Scolytinae as currently composed are in fact a monophyletic group, and doubts have to be cast on the reliability of many of the morphological characters used in phylogenetic analyses to establish the relationships of the group. It appears that comprehensive molecular analyses, spanning a large selection of curculionid groups, are required to properly elucidate the relationships and taxonomic status of this group. Within Scolytinae, two groups are traditionally recognised, subfamilies Hylesininae and Scolytinae in Wood’s (1986) classification, but the former has already been shown to be paraphyletic (Sequeira *et al.* 2000), as have some tribes in either group (Tomicini, Sequeira & Farrell 2001; Dryocoetini, Jordal 2002). The current system of 26 tribes is therefore likely to undergo significant changes in future.

The **Baridinae** are here used in the sense of Zherikhin & Egorov (1990) and Zherikhin & Gratshev (1995), who included Conoderinae, Ceutorhynchinae, Trigonocolinae and Orobitinae in it, the former study as tribes in a subfamily but the latter as subfamilies in a separate family, Barididae. Several characters are given in support of this grouping: a transverse carina at the hind margin of the pronotum, a strongly curved submarginal fold at the interior surface of the elytra, a total fusion of metepisternum and metepimeron, a strong median carina on the inside of the metathorax (an apparently unique feature in Curculionoidea) and a number of agreements in wing venation. This relationship and the characters supporting it have not been tested and confirmed, and while there are at least some species in this grouping that have a separate metepisternum and metepimeron, the taxa in this group also share some other notable features, such as large ascending mesepimera and a similar pygidium, so that there appears to be some merit in pulling them together. A more detailed evaluation of this indicated relationship is, however, direly needed. Baridinae in this concept comprise about

8 000 species, over half of them in Baridini, which are especially diverse in the American tropics. Their larvae develop mostly in fruits but also in stems of various angiosperms, but those of Conoderini are often woodborers. Associations with monocotyledons and gymnosperms (including Gnetales) also occur. Ceutorhynchini are predominantly associated with Brassicaceae and Polygonaceae and include important biological control agents of invasive weeds.

The **Curculioninae** include the remaining tribes of the family, such as Acalyptini, Anthonomini, Cionini, Cryptoplini, Curculionini, Derelomini, Erodiscini (fig. 22), Eugnomini, Mecinini, Ochyromerini, Otidocephalini, Rhamphini, Smicronychini, Storeini, Tychiini (fig. 23), Viticiini and likely also Diabathrariini, Gonipterini, Omophorini and others. Often referred to as “flower weevils”, their larvae develop predominantly in reproductive plant organs such as flowers, fruits and seeds. Hyperini appear to belong here as well but are rather different in their biology, their larvae feeding ectophytically on leaves and spinning net-like silken cocoons (fig. 24). The concepts of many of these tribes are yet unclear, and phylogenetic relationships among them even more so, but a few promising advances have recently been made, e.g. in the delimitation of Acalyptini and Derelomini (Kojima & Morimoto 2005, Franz 2005). Whether Curculioninae in this or a similar concept constitute a natural group remains to be seen; Kuschel (1995) advocated an even large one that includes also the Molytinae and Baridinae as outlined here as well as Erirhinini and Raymondionymini.

Weevil fossils — a record of the past

Weevils have a comparatively rich fossil record, in part owing to the ease of distinguishing them in compression fossils by means of their rostrum. However, many palaeontologists who described fossil weevils had little knowledge of the extant fauna and its characters, with the result that many weevil fossils were misidentified and, in the worst cases, are not weevils at all. A pertinent example is *Antliarhinites gracilis*, described by Heer (1864) as a relative of the African cycad weevil *Antliarhinus* but, on re-examination, proving to be a heteropteran bug (Oberprieler 2004a). Several other fossils described early by Heer, Dunstan, Handlirsch, Scudder and others are also not readily identifiable as weevils and represent other types of beetles instead. This, too, applies to the Triassic Obrieniidae, small rostrate beetles resembling weevils and often treated as such (e.g., Zherikhin & Gratshev 1994, Farrell 1998, Gratshev & Zherikhin 2003, Soriano *et al*. 2006) but evidently representing a primitive archostematan group (Zherikhin 2002, Kuschel 2003). The greatest contribution to the knowledge of fossil weevils was undoubtedly made by the late Russians Lev Arnoldi (1903–1980), Vladimir Zherikhin (1945–2001) and Vadim Gratshev (1963–2006), who described numerous forms especially from the important Mesozoic fossil sites in central Asia.

The majority of weevil fossils described is from Europe and North America and mostly of Caenozoic age. More informative for weevil evolutionary history, however, are the Mesozoic forms described over the last 30 years. The oldest and richest assemblage of these is that of Karatau in Kazakhstan, dated to the Upper Jurassic (Oxfordian–Kimmeridgian, 161–151 million years old) and described by Arnoldi (1977) as a separate family, Eobelidae. Subsequently mostly treated as a mixture of Nemonychidae, Belidae and Caridae (e.g., Zherikhin & Gratshev 1995, Gratshev & Zherikhin 2003), the fauna was ultimately divided into 18 genera and 47 species. However, a critical appraisal of the fauna (Kuschel 2003, Oberprieler & Kuschel, in prep.) indicates that all eobelids are extinct nemonychids and that their described diversity is grossly exaggerated, largely due to dorsoventral and lateral impressions of very similar forms being described as different species and even assigned to different families (mainly following Gratshev & Zherikhin 1996), compression artefacts and missing or poorly preserved features being misinterpreted and sexual differences being ignored. The majority of the Lower Cretaceous fossils (from Sierra del Montsec in Spain, Yixian in China, Bon-Tsagan in Mongolia, Khetana in Russia, Santana in Brazil) likewise represents Nemonychidae, and again fewer genera and species than described. Anthribidae are known since the late Lower Cretaceous (*Anthribidites*, from Khetana; mid-

Albian, 112–99.6 my) but very scarce in the Mesozoic record (the recently described, older *Cretochoragus* from Montsec requiring reassessment). The enigmatic Ulyanidae (*Ulyana*, *Ulyanisca*) evidently belong to the nemonychid-anthribid lineage as well but show little evidence of constituting a coherent taxon, only the large *Ulyana nobilis* from Khetana possibly representing a group distinct from other fossil Nemonychidae. Surprisingly and in spite of the various assertions to such effect, fossils unequivocally assignable to Belidae are absent from the Mesozoic weevil record to date. Attelabidae, too, are not definitely known from this era, *Martinsnetoa* from Santana (Upper Aptian, 125–112 my) and *Sayrevilleus* from the Upper Cretaceous New Jersey amber (Turonian, 94–89 my) possibly representing the family. Caridae are more definitely known from the Mesozoic, both from the Lower Cretaceous in Russia (*Cretonanophyes, Baissorhynchus, Auletomacer, Emanrhynchus, Cretulio*, but only representing 1–2 genera) and the Upper Cretaceous in the USA (*Cretocar*, from New Jersey amber). Other forms attributed to this family, in particular *Eccoptarthrus* from Karatau, on which the older family name Eccoptarthridae is based, represent Nemonychidae instead. Brentidae appear in the fossil record in the late Lower to early Upper Cretaceous in Brazil (*Axelrodius*, from Santana) and Botswana (*Orapaeus*, fig. 7, from Orapa; Turonian), both representing the primitive subfamily Eurhynchinae, while the recently described *Mesophyletis* from Burmese amber (dated as Upper Albian, 112–100 my) evidently belongs to Nanophyinae. The earliest true Curculionidae have been reported from the Upper Cretaceous (Turonian) sites of Orapa (Kuschel *et al*. 1994) and Kzyl-Zhar in Kazakhstan (Gratshev & Zherikhin 2003), but none of them have so far been described. Later but very fragmentary curculionid fossils have been described from Canada (*Hylobiites*), USA (*Curculionites*) and Chile (*Dorotheus*) but generally need reassessment.

Weevil evolutionary history — a sequence of key innovations

Anderson (1995) identified the key role of the "oviposition rostrum" in the phenomenal diversity of weevils, and Farrell (1998) that of the mid-Cretaceous angiosperm radiation. But when comparing weevil numbers more closely in conjunction with the weevil phylogenetic tree, it becomes clear that there can be no single and simple explanation for the huge diversity of weevils but rather that a cascade of evolutionary innovations is responsible for their success. These putative key innovations are hypothesized to enhance weevil speciation rates by allowing colonisation of various new evolutionary niches and promoting high lineage survival rates, thus sustained diversification. Testing these features as key innovations is difficult but may be approached by contrasting the diversity of relevant sister taxa (Farrell 1998, Brooks & McLennan 2002), although great care has to be taken to properly delimit both the groups and the innovation.

The Curculionoidea belong in the series Cucujiformia of the suborder Polyphaga (Lawrence & Newton 1995) and are usually placed at the end of the series behind the other great superfamily of herbivorous beetles, the Chrysomeloidea. Together referred to as Phytophaga, these two superfamilies have intrinsically been treated as sister-groups (e.g., Crowson 1981), but morphological support for this relationship is scant and in essence restricted to the common possession of pseudotetramerous tarsi (which also occur outside the Phytophaga). Recent studies based on aligned sequences of ribosomal genes, however, provide evidence for the monophyly of Chrysomeloidea and Curculionoidea as well as of Phytophaga and suggest a subgroup of Cucujoidea to be their closest relatives (Marvaldi 2005b, Marvaldi *et al*. in prep.). Vogler (2005) also recovered a monophyletic Phytophaga from molecular (18S) data, and Wanat (2007) reached a similar conclusion from his study of the sclerites and membranes of the male terminalia, in that Curculionoidea and Chrysomeloidea share a particular kind of genital alignment (the phytophagan type) with only some families currently included in Cucujoidea. It is therefore apparent that the Phytophaga are rooted within Cucujoidea and that Curculionoidea and Chrysomeloidea share a common ancestor and also age of origin.

Since the oldest unequivocally curculionoid and chrysomeloid fossils are Upper Jurassic in age (from the Karatau deposits) and both (Eobelinae and Protoscelinae, respectively) are primitive types, and no weevils are known from extensive fossil beetle assemblages of Middle and Lower Jurassic sites (Gratshev & Zherikhin 2003), current evidence suggests that the diversification of the Phytophaga and its two major lineages commenced somewhere in the Middle Jurassic (ca. 160–175 mya). The weevil fossil record is broadly congruent with the diversification of the major groups of plants in the Mesozoic (Anderson & van Wyk 1999). The first weevils, Nemonychidae, appeared in the late Jurassic, when their hosts, the conifers, had diversified and become the dominant floristic element. Their larvae probably were mobile (possessing legs) and developed in male conifer strobili, feeding openly on pollen as those of the extant nemonychids by and large still do, and also those of the most primitive living chrysomeloids, the Palophaginae (Megalopodidae). In contrast to the latter, however, which lay their eggs on the outside of the cones (Kuschel & May 1996) from where the larvae have to enter the cones to feed in the pollen sacs, nemonychids typically lay their eggs inside the cone directly against the sporangia, the females likely using their rostrum to force open the sporophylls of the cone before it ripens (Kuschel 1994). The development of a rostrum in the earliest weevils would therefore have presented not only an effective way of circumventing the sporophyll defence of the cone but also an advantage over other herbivorous beetles. Indeed, the diversity of extant Nemonychidae (76 species in 21 genera) against that of extant Palophaginae (only 4 species in 3 genera) seems to bear testament to this early "evolutionary edge" that the rostrum bestowed on weevils. The evolution of a rostrum evidently was the first key innovation on the road of weevil success.

Essentially two ways of life appear to have opened up for weevils from this original type of larval development. One involves the development in dying vegetative tissues, originally of the cones but later also of other plant organs, and is broadly represented by Anthribidae, Belidae and Attelabidae. The other is the development in living reproductive tissues, again originally cones but later all other parts of the plant, and is represented by Caridae, Brentidae and Curculionidae. In both categories there are taxa that show how these life styles may have evolved and led to the phenomenal success of weevils.

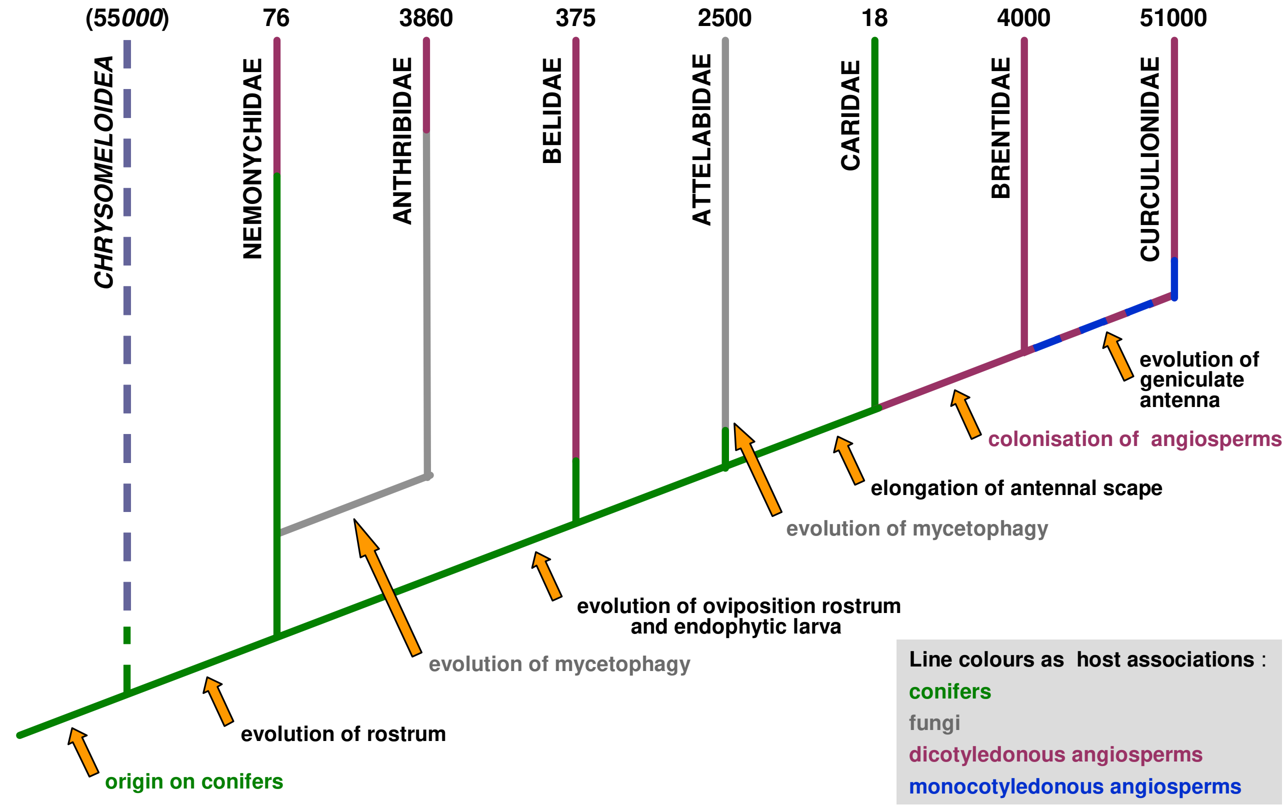
Anthribidae owe their modest diversity seemingly largely to mycetophagy, and genera like *Apinotropis* indicate how this may have evolved from larval development in mouldy cones (but probably of conifers rather than cycads) and then spread to other decaying, fungus-infested plant structures. Anthribid larvae are properly endophytic but the females generally use a specialized ovipositor rather than their rostrum to insert their eggs into plant tissues. In Belidae, too, primitive genera in both subfamilies (*Apagobelus, Basiliobelus*; *Oxycraspedus*) develop in conifer cones, whereas other Belinae live in stems and logs of conifers and, especially in the derived Belini, also of angiosperms, and other Oxycoryninae develop predominantly also in rotten stems but, in Oxycorynini, also in fleshy inflorescences and decaying cycad cones. In belids the female rostrum is transformed into a proper oviposition tool by the fusion of labrum and clypeus and the development of more advanced mandibles. Attelabidae again largely develop in decaying plant tissues, except that the females attack living structures and induce the decay by severing the sap flow with their rostrum. As inferred by Anderson (1995), the evolution of the "oviposition rostrum" is indicated to be the next key innovation that enabled weevils to become truly endophytic in the larval stage and to master phytophagy to an even greater extent. Due to the absence of authentic belids and attelabids in the early Mesozoic fossil record, it is unclear when the oviposition rostrum may have evolved, but anthribids were present by the late Lower Cretaceous (Albian) and carids even earlier (Valanginian-Hauterivian), so that the first diversification of weevils, into the main lineages other than Brentidae and Curculionidae, is likely to have occurred in the very late Jurassic to early Cretaceous.

The Caridae are a vital link in the evolutionary history of weevils, both structurally and biologically. On the one hand, the carid larva retains clawed legs and crawls around in living female *Callitris* cones, feeding on the developing seeds just like nemonychid larvae do on pollen in male conifer cones; on the other hand, the female rostrum is more advanced in having compacted maxillae and the antennae inserted far back on the rostrum, with the scape elongated, allowing it to be inserted deep into the seed chambers of the closed cone. The carids thus demonstrate how the ancestral larval habit of feeding freely on pollen in dehiscing male cones may have been adapted to feeding on developing seeds in closed female cones. This switch to larval development in living reproductive structures may have been another important evolutionary stage in the advancement of weevil associations with plants, although in extant carids this appears to be limited to conifers.

Brentidae and Curculionidae appear in the fossil record between the late Lower Cretaceous (Aptian) and early Upper Cretaceous (Turonian), about 100 mya and at the time when the angiosperms began to rapidly diversify, and since the primitive groups of both these families are exclusively associated with these plants, it is apparent that their evolution and diversification is closely linked to that of the angiosperms. The larvae of the basal groups (Eurhynchinae, Microcerinae, Ithycerinae, Brachycerinae, Dryophthorinae) generally tunnel in living stems or live in close association with living roots, but those of the more advanced groups develop in just about any plant organ, alive, dying or decaying. The colonisation of angiosperms on its own, however, evidently did not lead to a major diversification in these weevils, as the number of brentid species has remained at a modest level of about 4 000 whereas that of curculionids has reached a order of magnitude more. In an evolutionary context, the main difference apparent between these two families is the form of the antenna, which is orthocerous in brentids (except Nanophyinae) as in the more basal families but gonatocerous (geniculate) in curculionids. Since the antennal insertions on the rostrum determine the depth to which the rostrum can be pushed into plant tissues, orthocerous antennae have to be inserted far back on the rostrum for the latter to be able to reach deep-lying plant tissues. This requires the antennae to become longer as well, as the club plays an important role in selecting the exact location on the hostplant where the tip of the rostrum is to begin the drilling of the oviposition hole. In Brentidae this dilemma and the extreme form of rostrum necessary to reach deep-lying tissues is deftly illustrated by the cycad-associated *Antliarhinus zamiae*, the female of which requires a rostrum twice the length of her body to pierce the thick sporophylls and reach the deeply hidden ovules in which the larvae develop (fig. 13). To commence drilling, and also when withdrawing the rostrum from the finished hole, she has to lift her forequarters off the plant surface and bend down her head and flexible rostrum to the limit — a clumsy and very hazardous process, as apparent from not infrequently encountered specimens stuck in cycad seeds and sporophylls (fig. 14). It appears that these limitations of the brentid rostrum may have played a crucial role in preventing the full exploitation of the potential for endophytic life on the radiating angiosperms by this weevil family. In Curculionidae, this obstacle was apparently overcome by the development of a new kind of antenna, which allows penetration by the rostrum beyond the antennal insertions through elongating only the basal antennal segment, the scape, and folding it back into a furrow, or scrobe, along the sides of the rostrum (figs. 21, 22). This rostrum can be inserted into plant tissues up to the eyes of the weevil, while maintaining the forward reach of the antennal clubs and their role in determining the precise point of oviposition (fig. 23). An incipient form of this antenna already occurs in some Belinae and Eurhynchinae and also in Caridae, the scape being elongated and compressed and folding back into a slight furrow on the rostrum, and the brentid Nanophyinae have evolved such an antenna as well. However, the full potential of this more efficient antenna was realised only by the Curculionidae and seemingly played a major role in catapulting their species diversity into another order of magnitude. Their ultimate success in diversity is, however, likely to have been more complex and involved also other contributing factors. In contrast to the Brentidae, which are not associated with monocotyledons at all, the Curculionidae have radiated on this group of plants extensively and seemingly early, as their basal groups (Brachycerinae, Dryophthorinae) live more or less exclusively on them. The Curculionidae may thus have colonised dicotyledons only subsequently and independently from brentids but achieved a singularly spectacular success when they did. Another evidently very successful adaptation in higher Curculionidae was the reduction of the rostrum in both the root-feeding Entiminae and the wood-boring Platypodinae and Scolytinae (together accounting for about 40% of the diversity of Curculionidae), allowing them to exploit two other evolutionary niches to a far greater extent than other phytophagous beetles.

Weevils diversity — a tale of success

The evolutionary success of weevils evidently lies in their specialised endophytophagy, their larvae developing inside a great variety of plant structures. This unique life style appears to have evolved along a cascade or ‘stepping stones’ of key innovations and invasions of new adaptive zones (fig. 25), of which the evolution of the oviposition rostrum and the rise of the angiosperms in the Cretaceous were crucial and major evolutionary events but clearly not the only ones. The diversification of the conifers in the Jurassic, and their evolution of protective strobili, must be ranked as an equally significant (if not as the *sine qua non*) event in the evolutionary history of the weevils, and the evolution of the geniculate antenna in higher weevils stands out as the adaptation that perhaps had the greatest impact on their success in exploiting the angiosperm diversity, and thus on their own diversification. Important specialised ways of life, such as different and repeated utilisation of fungi (mycetophagy) and an ectophytic larval development on roots in the soil also contributed significantly to the enormous species diversity of this lineage.



25

R. Oberprieler, CSIRO Entomology, 2007

FIGURE 25—key evolutionary events in the diversification of the Curculionoidea mapped onto their phylogeny, with numbers of described species for each family

The combined morphological, biological, phylogenetic and palaeontological evidence indicates that the Curculionoidea evolved on conifers in the Jurassic, diversified on early angiosperms (and probably also on fungi) in the Cretaceous and explosively radiated on eudicotyledons in the Tertiary. As they perfected their endophytic way of life, they also colonised most groups of more primitive plants. Subantarctic Ectemnorhinini (Entiminae) feed extensively on cryptogams, a diet seemingly evolved through ecological constraints of glaciation and large-scale reduction of vascular plants in limited areas (islands) (Chown 1994). Pteridophytes are used as hosts mainly by Brachycerinae (horsetails and aquatic ferns, apparently representing host shifts from aquatic monocotyledons) and some Molytinae (terrestrial ferns, seemingly shifts from angiosperms, especially palms). Among gymnosperms other than Coniferales, only Gnetales (*Ephedra*) and Cycadales harbour weevils, but all of these have close relatives living on angiosperms and evidently shifted onto these gymnosperms secondarily, seemingly mediated by co-occurrence in the same habitat (Anderson 1993, Oberprieler 2004c, Marvaldi *et al*. 2006), and the early evolution of weevils is clearly linked to conifers rather than gymnosperms as a whole. Anderson (1995) suggested that their origin and evolution may have occurred on an extinct plant group such as the Bennettitales, but while these and also the Pentoxylales were also diverse in the Jurassic (Anderson & van Wyk 1999) and may well have harboured weevils, there is no direct evidence for this and the early weevils could have been associated only with conifers. The families that largely retain this habit, Nemonychidae, Belidae and Caridae, are today only very small, apparently mere remnants of a previously larger fauna and in decline, although some Australian Belidae have successfully colonised angiosperms and the group appears to be diversifying again (Richardson & Oberprieler 2007). Overall, the diversification of weevils appears to reflect the evolution of host resources and their ability to utilise these resources, rather than the evolution of host taxa themselves (Brooks & McLennan 2002).

There is uncertainty about the precise words of Haldane's famous quip, as to whether he used 'inordinate fondness' or 'special preference' (Gould 1993). Gould compromised with 'special fondness'. However, 'inordinate fondness' has entered the realm of fame and history by now and is best left there, regardless of whether Haldane really used these words or not. In light of the evolutionary success of weevils, we may adopt a more appropriate conciliation by concluding that the Creator, if he exists, has *an inordinate fondness for beetles with a special preference for weevils*. This suitably accounts not only for the fact that every 20th species of organism on earth is a weevil and that almost every single plant species harbours at least one species of weevil, but also that these specialised phytophages have played a major role in the evolution of plants and thus our natural world.

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