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### 3.7.13 Platypodinae Shuckhard, 1840

Bjarte H. Jordal

**Distribution.** More than 1400 species in 34 genera and four tribes are currently included in Platypodinae (Wood & Bright 1993), excluding *Protoplatypus* Wood, *Protohylastes* Wood, *Coptonotus* Chapuis, *Scolytotarsus* Schedl, *Phylloplatypus* Kato (see, e.g., Kuschel 2000), and Carphodicticini (contrary to Thompson 1992), but adding the recently described *Pereioplatypus* Beaver (2007). Virtually all species are found in tropical or subtropical regions, with only a handful of species reaching the temperate zone in each of the hemispheres. There are only eight species present in southern USA and only two in southern Europe; a few more are present in Argentina-Chile and South Africa (Wood & Bright 1992). Genera and species have a generally restricted distribution, with only 8 of the 34 genera found on more than one continent. Most of these are distributed on closely separated land masses such as Madagascar and tropical Africa or Oceania and tropical Asia. The high degree of endemism in this subfamily is also reflected by many groups of closely related genera that have taxonomic counterparts on different continents. Only

two species, *Euplatypus parallelus* (Fabricius) and *Crossotarsus externedentatus* (Fairmaire), are widespread in tropical forest around the globe (Wood & Bright 1992).

**Biology and Ecology.** Nearly all species of Platypodinae are ambrosia beetles that cultivate fungi for food in tunnels excavated deep into the sapwood or heartwood of a dead tree. Only the two most basal lineages in Platypodinae – the wood feeding *Schedlarius* Wood and the phloem-feeding *Mecopelmus* Blackman – feed on cambium of dead wood. All other species of Platypodinae are entirely dependent on the fungus they grow in the tunnels and larval development is possibly reliant on steroid components in their fungal diet (e.g., Kok *et al.* 1970). The symbiotic fungi carried by an individual beetle is usually one or two ascomycete taxa, termed collectively ambrosia fungi due to the rich growth of erect conidial hyphae on the tunnel walls. Transmission of fungal spores or hyphae between host plants is facilitated by highly specialized structures in the beetle integument, forming glandular, invaginated mycangia in the pronotum or in coxal cavities (Beaver 1989). Mycangia are often found only in the females, and they may take very different shapes in different taxa and can sometimes be used as a taxonomic character.

Because of the ambrosia habit, platypodines can usually utilize a wide range of host tree families for breeding and fungus inoculation. It is not uncommon that species of this subfamily utilize more than 10–20 different plant families (Browne 1958). However, some interesting exceptions to this pattern occur in the oriental region, where several unrelated lineages restrict their host choice to dipterocarp trees (some species of *Platypus* Herbst and all species of *Genyocerus* Motschulsky, see, e.g., Browne 1958; Beaver & Liu 2007). Relatively few species are able to attack living trees on a regular basis, but if they do, some of these (e.g., several *Platypus* species, *Notoplatypus elongates* Lea, *Trachyostus ghanaensis* Schedl) may breed over multiple generations without apparent damage to the tree (Kirkendall *et al.* 1997). Tree killing is a relatively rare phenomenon in Platypodinae and only a few species of *Platypus* and *Euplatypus* Wood may be capable of injuring trees that are stressed or unhealthy.

Species of Platypodinae are typically monogamous, and the male is staying with the female during all stages of larval development (Kirkendall 1983). The entrance tunnel into a new gallery system is always made by the male, which admits only a single female into the new tunnel. Mating occurs at, or close to, the entrance opening; the female will then excavate a longer tunnel system and lay eggs in clusters in the terminal end. Females produce on average from as few as 10–15 eggs for a low fecund species to more than 50 eggs for species with the highest fecundity (Browne 1961). Larvae may move and feed freely on the fungi but move near to the hatching site and excavate vertical cradles before

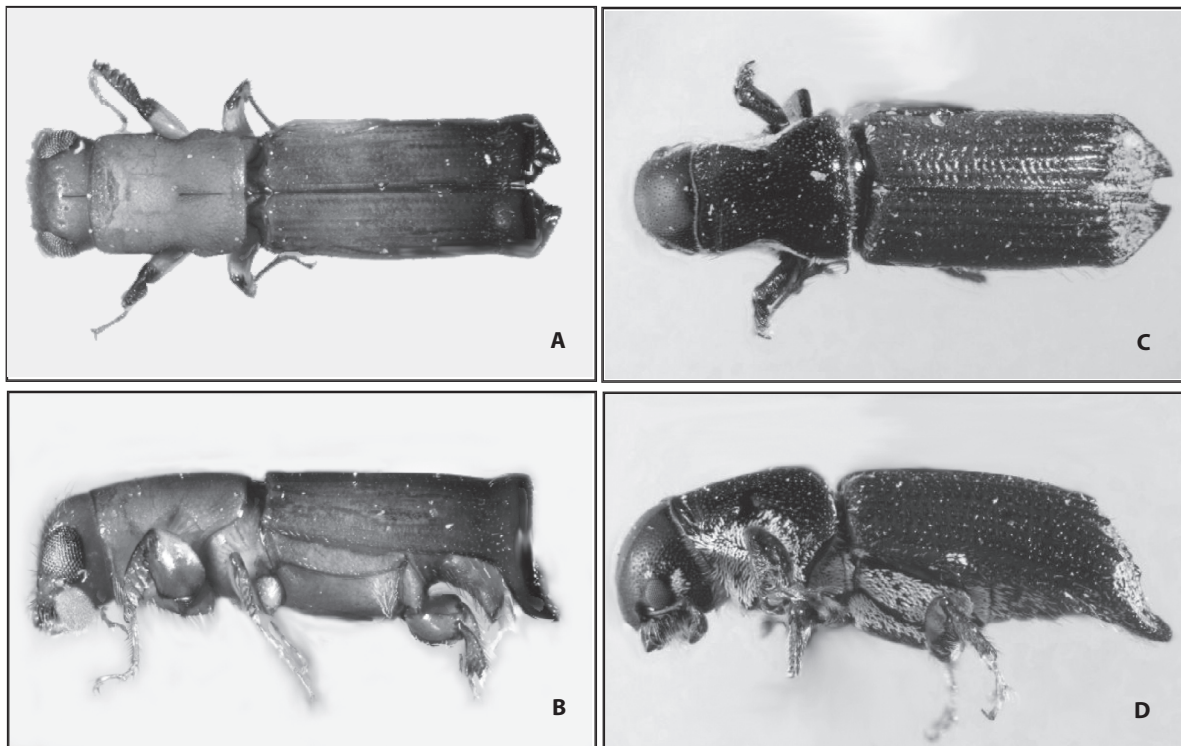
pupation. During brood development, the male is helping the female with removing frass from the tunnel system and block the entrance against predatory insects and parasitoids. Highly specialized nest parasites in Brentinae and Conoderini frequently occur at the entrance opening where they try to pull out the male. When they succeed, the female will also usually be expelled or eventually killed by the intruder.

The prolonged duration of nests (that may last for months to several years), and the frequent overlap of generations in some species, creates an ideal condition for evolving complex social behavior. Many platypodine species thus actively care for their offspring by moving eggs and larvae toward food resources (Kirkendall *et al.* 1997). In some species, the females show pronounced morphological modifications to facilitate the protection and transportation of eggs that are held in place by prolonged appendices of the antennal scape in front of a concavely shaped frons (Browne 1961, see also Fig. 3.7.13.2). Social behavior is most pronounced in the putatively eusocial *Platypus incompertus* Schedl in Australia where unseminated daughters stay to help their reproducing mother (Kent & Simpson 1992). The helping daughters cannot leave their nest because they have lost the tarsi that are necessary for external foothold. This species is also the only known species where the male is not staying to help the reproducing female, as this function has been taken over by the daughters.

**Morphology, Adults** (Fig. 3.7.13.1–3.7.13.3). Length 1.5–12.0 mm. Body narrowly elongate, 2.8–8.0 times longer than wide, cylinder-shaped, glabrous, or sparsely clothed with setae, rarely with scales on declivity.

Head with rostrum entirely absent, moderately declined, visible from above, not constricted posteriorly. Dorsal occipital area truncated. Frontal region usually abruptly declined. Compound eyes usually circular, sometimes slightly to strongly elongated (*Platytarsulus* Schedl and *Periommatius* Chapuis), entire, flat to moderately protuberant, finely to coarsely faceted, without setae between facets. Clypeus fused or merged with frons, rarely visible as epistomal lobe (*Chaetastus* Nunberg). Labrum absent. Antennal insertions exposed and widely separated, usually attached close to mandibles, sometimes closer to upper level of the eyes (female *Genyocerus*). Subantennal groove absent. Antennae geniculate; scape usually longer than funiculus, about as long as club, sometimes strongly inflated or extended into an appendix, sparsely or densely setose; funiculus usually four-segmented (five in *Schedlarius*, three in *Mecopelmus*, and *Notoplatypus* Lea, two in *Platytarsulus*); club large and strongly flattened, never with sutures. Mandibular sockets shallow; hypostomal spine absent. Mandibles short and broad, with one or two rows of setae, gradually curved mesally, ending in an acute point; mesal edge weakly bidentate or tridentate; dehiscent mandibular appendages in females sometimes present (Diapodini); pharyngeal

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Fig. 3.7.13.1 A, B, *Dinoplatypus pseudocupulatus* Schedl (male, length 3.5 mm); C, D, *Schedlarius mexicanus* (Chapuis) (length 5.6 mm).

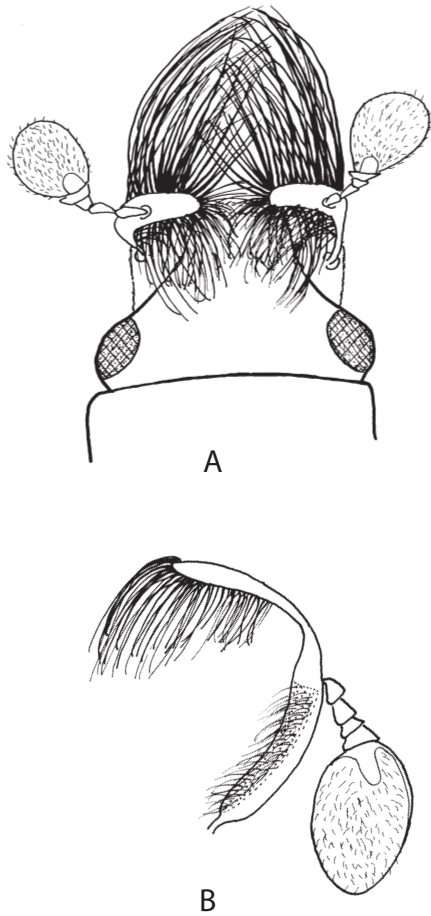


Fig. 3.7.13.2 A, *Tesserocerus* sp. near *spinax* Blandford, ♀ head; B, *Tesserocerus insignis* (Saunders), ♀ antenna. Note the long extension of the scape in both species, with a long tuft of hair-like setae.

process of mandible absent (short process present in *Schedlarius*). Maxillae with galea and lacinia distinct (*Tesserocerini*) or fused; inner lacinial fringe usually with long hair-like setae; palpus three-segmented, fusiform, frequently asymmetrical. Labium undivided, broad, not inserted into a socket; palpus fusiform, three-segmented. Segment 1 of labial palpi

fused in some species (e.g., *Crossotarsus* Chapuis, *Triozastus* Schedl). Gular sutures fused; gula not inflexed, vestigial; V-shaped subgenal (pregular) sutures present.

Anterior margin of prothorax nearly vertical; posterior margin strongly procurved (nearly vertical in *Schedlarius*, and *Mecopelmus*). Pronotum about 1.2–2.2 times longer than wide, widest anteriorly or posteriorly; sides straight, usually with lateral notch for reception of profemur; lateral pronotal carinae absent; posterodorsal margin weakly bisinuate (except *Schedlarius* and *Mecopelmus*), with or without weakly raised line; disc flat; cuticle smooth, posteriorly often with pores or transverse cuticular invaginations housing fungal spores. Prosternum in front of coxae convex, much shorter than coxal width; prosternal process usually flat, complete, and broad (*Diapodina*), or interrupted with its apex acute; surface usually flat; posterior process overlapping mesoventrite. Procoxae circular or moderately to strongly elongate, projecting well below prosternum. Trochantin partly exposed, visible externally as narrow strip. Mesonotum with longitudinal carina (“anti-twist device”, sensu Kuschel *et al.* 2000) usually present (absent in *Diapodina*, *Tesserocerus* Saunders, *Tesserocranulus* Schedl, *Platyarsulus*, and *Schedlarius*). Scutellar shield usually narrowly elongated and sunken. Mesepisternum inflated in most cases (not in *Schedlarius* and *Mecopelmus*); mesepisternal suture absent. Mesoventrite flat, never with discri-  
men. Mesocoxae circular, usually distinctly separated but sometimes nearly contiguous, slightly projecting ventrally. Mesoventral process usually horizontal, sometimes acutely interrupted. Elytra about 1.5–4.5 times longer than wide, 1.5–4.2 times longer than pronotum; basal margin straight, with a finely raised line; punctures usually arranged in 8–9 rows, frequently deeply impressed into continuous furrows; declivity usually sexually dimorphic, armed in males with carinae, granules, or spines, very short to long; epipleura absent; wing guides on ventral side of

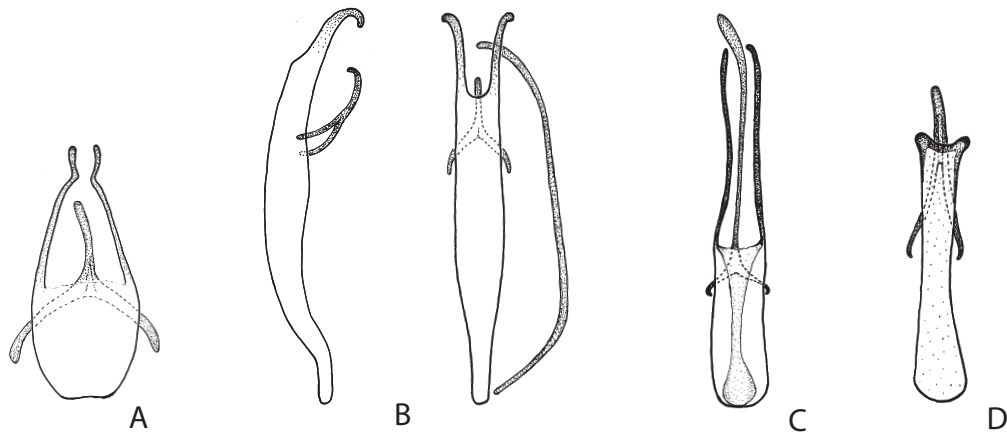


Fig. 3.7.13.3 A–D, Male genitalia, dorsal view, with tegmen. A, *Mecopelmus zeteki* Blackman; B, *Schedlarius mexicanus* (Chapuis) lateral and dorsal view, with speculum gastrale; C, *Tesserocerus spinax* Blandford; D, *Teloplatypus excisus* (Chapuis).



apical flange usually present (absent in *Mecopelmus*, *Periommatius*); width of apical sutural flanges usually equal (unequal in *Mecopelmus*). Metaventrite flat to convex, with very short to long and complete discrimen. Metacoxae contiguous, strongly transverse, almost reaching elytral margin; sometimes strongly enlarged posteriorly into shovel-like blades (many Platypodini). Metepisternum strongly elongated; posterior end of metepisternum and metaventrite slightly impressed for reception of metafemur, often marked anteriorly by vertical row of spines or carina; sclerolepidia on metepisternal suture absent. Pleural suture forms zigzag pattern. Scutoscuteellar suture runs for most of its length straight and parallel to the scutellar groove. Metapostnotum separated from remaining segment by a membrane. Metendosternite with long anterior furcal arms; lateral arms absent, stalk vestigial. Hind wings about three times longer than wide; costa and subcosta fused; R fused with subcosta before basal one-sixth; C-SC-R ending in an expanded stigmal patch ("radial cell");  $RP_1$  vestigial;  $RP_2$  well marked, reaching wing margin;  $MP_{1+2}$  and CuA usually well marked; anal field without veins; costal margin with few setae; apical portion of stigma without setae. Ventral side of femora sharply impressed for the reception of tibia. Protibiae with outer edge carinate or serrate, without socketed teeth or spines; outer proximal angle gently rounded and extended into a latero-posteriorly curved process; inner edge slightly curved mesally to meet the process; posterior face granulate, with transverse ridges (absent in *Mecopelmus*); tarsal insertion before (above) proximal end. Mesotibiae and metatibiae usually flat, outer edges smooth or carinate, gently rounded, without socketed teeth; median apical area transverse, inner and outer apical edge extended into a blunt process or spine, never with distal comb of setae. Tarsi 5–5–5, segment 1 much longer than segments 2–5 combined, all segments cylindrical (segment 3 bilobed in *Schedlarius*), segment 4 clearly visible. Proventriculus located in prothoracic lumen, with vestigial blades. Hind gut rarely with rectal loop (*Mecopelmus*), usually with a ring.

Abdomen with five ventrites; basal two ventrites usually free (except *Schedlarius*, *Mecopelmus*, *Platytarsulus*); ventrite 1 usually shorter than ventrite 3 (except *Mecopelmus*, *Platytarsulus*); ventrite 2 shorter than ventrites 3 and 4 combined (except *Mecopelmus*); ventrites 2, 3, or 4 in males sometimes armed posteriorly by spines or processes or variously excavated and subvertical; intercoxal process acute. Terminal tergites never forming pygidium; tergite VIII concealed in all females and nearly all males (partly exposed in *Schedlarius*). Male sternite VIII without pigmentation, usually large and undivided (short in *Mecopelmus*). Male sternite IX (spiculum gastrale) absent (except long and curved in *Schedlarius*). Aedeagus very simple; apodemes usually vestigial, but longer in some Tesserocerini, *Mecopelmus* and *Schedlarius*; apodemal

bridge absent; tegmen Y-shaped, with long to very long manubrium. Spermathecal duct slightly shorter than spermatheca; spermathecal apex usually broadly rounded (Morimoto 1962; Schedl 1972; Wood 1973, 1993; Thompson 1992; Kuschel 1995; Lyal 1995; Zherikhin & Gratshev 1995; Kuschel *et al.* 2000; Morimoto & Kojima 2003, 2004; terminology following Kukulova-Peck & Lawrence 1993).

**Morphology, Larvae (Last Instar, Fig. 3.7.13.4).** Body cylindrical, soft, white or pallid. Legs absent. Vestiture consisting of scattered hair-like and bristle-like setae only.

Head free, hypognathous, subcircular; head capsule 1.0–1.2 times longer than wide. Postoccipital condyles absent; dorsal occipital margin usually with a pair of apodemes well developed. Stemmata absent. Frontal sutures weakly to clearly indicated. Epicranium usually with five pairs of short to very long dorsal setae; frontal plate with three to five pairs of setae. Epistoma without median tubercle. Clypeus reduced to a narrow membrane, narrowly visible in *Schedlarius*. Labrum slightly triangular, frequently trilobed, with one or two pairs of dorsal setae; epipharynx with setae branched and displaced anteriorly; tormae usually U-shaped and fused posteriorly. Antennae one-segmented, conical; antennal field with few setae and papillae. Mandibles with chisel-like cutting edge; dorsal side usually with a series of small transverse ridges and two transversely placed setae. Maxilla with galea and lacinia fused, lacinial setae bristle-like or with bundles of fine hair-like setae; palpus usually one-segmented (two-segmented in *Periommatius*). Labium broad; postlabium with three pairs of setae; posterior postlabial seta 1 usually placed inside longitudinal line from postlabial seta 2; palpus usually one-segmented (two-segmented in *Periommatius*). Hypopharyngeal bracon absent.

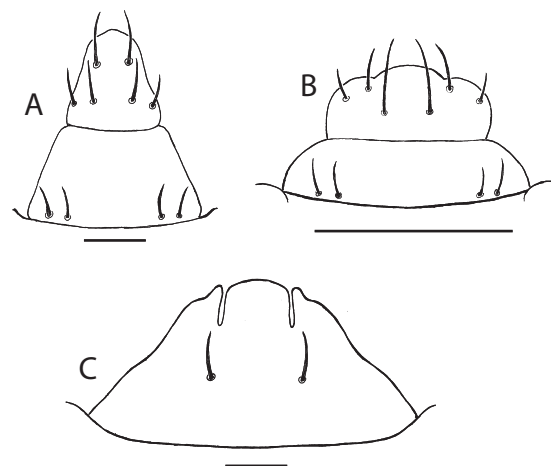
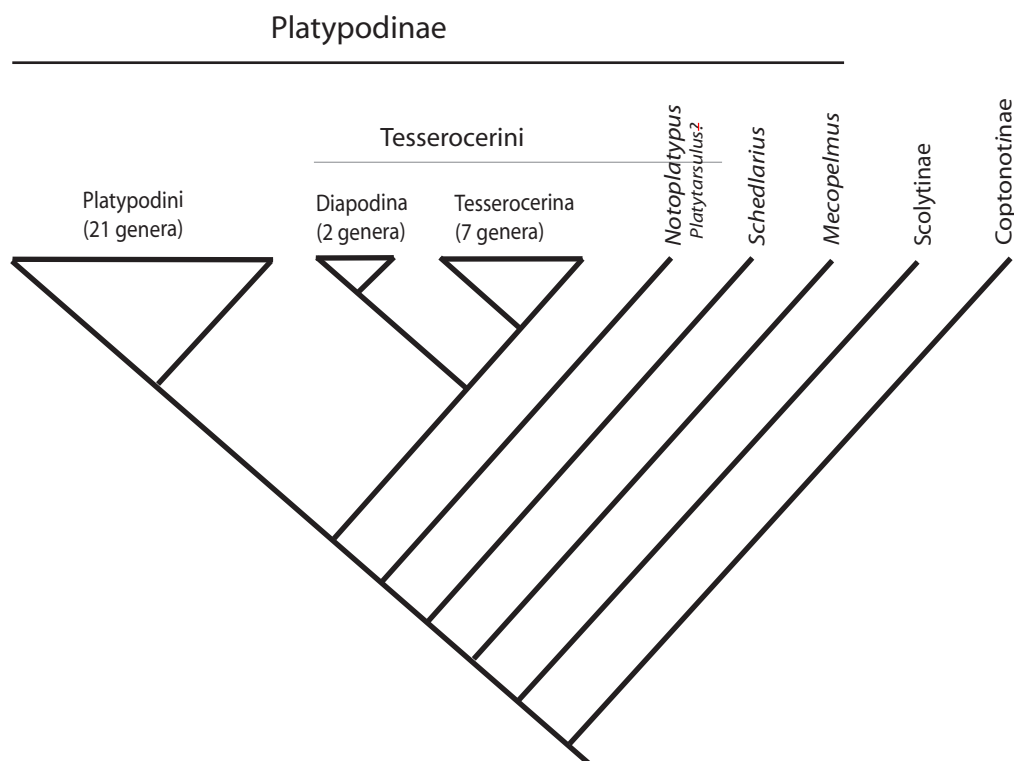


Fig. 3.7.13.4 A–C, Labrum of weevil larvae (redrawn from May 1993). A, Cossoninae, *Mesites pallidipennis* Boheman; B, Scolytinae, *Coccotrypes carpophagus* (Hornung); C, Platypodinae, *Euplatypus parallelus* (F.). Line = 0.2 mm.



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Fig. 3.7.13.5 Summary cladogram of Platypodinae and close relatives based on phylogenetic analyses of 128 morphological characters and 3801 nucleotides/amino acids from five gene fragments (Jordal *et al.* 2011). Platypodini includes all genera listed under Platypodinae by Wood (1993); Tesserocerini includes all genera listed under Tesserocerinae.

Thorax generally not sclerotized. Prothorax usually slightly enlarged, sometimes with slightly raised patterns of lines and rings. Spiracle present on prothorax, **invariably** larger than those on abdomen.

Abdomen composed of ten segments. Segment X usually with apical tubercle. Abdominal pleura subdivided into two or more superimposed lobes. Spiracles present on abdominal segments I–VIII; usually with a single finger-like, non-annulated air sac (Browne 1972; May 1993; Marvaldi 1997).

**Pupa.** Last pair of legs exposed. Pseudocerci vestigial or absent (Browne 1972; May 1993; Marvaldi 1997).

**Phylogeny and classification.** The phylogenetic position and taxonomic rank of Platypodinae represents one of the major recurrent controversies in weevil taxonomy. Platypodinae has been given either the rank of a family (Schedl 1972; Wood 1973; Thompson 1992; Alonso-Zarazaga & Lyal 1999; Morimoto & Kojima 2003) or a subfamily (Crowson 1955; May 1993; Kuschel 1995; Lawrence & Newton 1995; Zherikin & Gratshev 1995; Marvaldi 1997; Marvaldi & Morrone 2000; Marvaldi *et al.* 2002) and has recently been reduced to tribal rank within Scolytinae (Kuschel *et al.* 2000). Platypodinae has often been placed as the sister group to Scolytinae within Curculionidae (Crowson 1955; May 1993; Kuschel 1995; Lawrence & Newton 1995; Zherikin & Gratshev 1995; Marvaldi & Morrone 2000; Marvaldi *et al.* 2002) or outside

all other Curculionidae (Wood 1973; Morimoto & Kojima 2003) or as an independent family (Thompson 1992; Alonso-Zarazaga & Lyal 1999) close to the origin of Curculionidae, e.g., close to Dryophthorinae (Marvaldi 1997; McKenna *et al.* 2009). A complete treatment of the historical changes in classification is given by Wood (1993) and by Kuschel *et al.* (2000).

The core Platypodinae *sensu* Schedl (1972) or Wood (1993) includes all Tesserocerini (Diapodina, Tesserocerina) and Platypodini. This is a rather uniform group ecologically as well as morphologically, and its monophyly is not debated. Adults of these taxa are most readily diagnosed by the lack of a pharyngeal process, by their cylindrical tarsi with a very long first tarsomere, the transverse rugae on the protibiae, the strongly procurved posterior pleural margin of the pronotum, the absence of sclerolepidia, the equal width of the apical sutural flanges of the elytra, and the large and undivided male sternite VIII (hemisternites). Larvae are characterized by the more or less triangular shape of the labrum, which bears one to two pairs of dorsal setae, by the vestigial clypeus (Fig. 3.7.13.4), and by the subdivided abdominal pleura. *Schedlarius* and *Mecopelmus* most likely form the two most basal lineages within the Platypodinae, as they both share some, but not all character states with the other Platypodinae. However, species of both genera have a very long first tarsomere, which represents the most evident autapomorphy for Platypodinae as defined here.

Table 3.7.13.1 Taxonomic status for several contentious taxa currently or previously classified as Platypodinae (Platypodidae *sensu* Wood 1993).

Taxon	Previous status	Current status	Supporting reference
<i>Schedlarius</i>	Platypodinae	Platypodinae	Wood 1993; Kuschel <i>et al.</i> 2000
<i>Mecopelmus</i>	Platypodinae	Platypodinae	Wood 1993; Kuschel <i>et al.</i> 2000
<i>Coptonotus</i>	Platypodinae	Scolytinae	Thompson 1992; Kuschel <i>et al.</i> 2000
Carphodicticini	Platypodinae	Scolytinae	Wood 1986
<i>Protoplatypus</i>	Platypodinae	Cossoninae	Zimmerman 1994; Kuschel <i>et al.</i> 2000
<i>Phylloplatypus</i>	Platypodinae	Cossoninae	Kuschel <i>et al.</i> 2000
<i>Scolytotarsus</i>	Platypodinae	Baridinae-Conoderini	Alonso-Zarazaga & Lyal 1999
<i>Protohylastes</i> (= <i>Psepholax</i> )	Platypodinae	Molytinae-Cryptorrhynchini	Zimmerman 1994; Kuschel <i>et al.</i> 2000

They differ from the core Platypodinae by having a near vertical posterior pleural margin of the prothorax and, in the larvae, by the exposed clypeus (Wood 1973). *Schedlarius* deviates further from all other Platypodinae (including *Mecopelmus*) by having a bilobed third tarsomer, a long and curved spiculum gastrale, and a short pharyngeal process at the mandibular base. *Mecopelmus* differ from all other Platypodinae (including *Schedlarius*) by having a broader sutural apical flange of the left elytra, by the lack of transverse rugae of the protibiae, and by the short male sternite VIII.

In addition to *Schedlarius* and *Mecopelmus*, four additional contentious genera were previously classified in a separate subfamily Coptonotinae in "Platypodidae" (Wood 1993; also see Kato 1998). However, these four taxa lack nearly all of the defining character states of Platypodinae, and they have therefore recently been placed in other weevil subfamilies by various authors (see Table 3.7.13.1). The type genus for "Coptonotinae", *Coptonotus*, is currently placed in, or close to, Scolytinae, based on a range of morphological characters (Thompson 1992; Kuschel *et al.* 2000; Jordal *et al.* 2011; see Chapter 3.7.12 (Scolytinae). *Protohylastes* has a definite rostral canal and lacks sclerolepidia, which confidently places this taxon in Molytinae-Cryptorrhynchini (Psepholacina), in or near *Psepholax* (Zimmerman 1994; Kuschel 1995; see Chapter 3.7.12 (Scolytinae). *Scolytotarsus* is currently placed in Conoderini (Alonso-Zarazaga & Lyal 1999). *Protoplatypus*, together with the recently described *Phylloplatypus* (Kato 1998), was moved to Cossoninae, close to *Dissotomus* and close allies, based on phylogenetic analyses of morphological characters (Kuschel *et al.* 2000). These two cossonine taxa are readily distinguished from Platypodinae and Scolytinae by the narrow and ciliated flight wings, the long pharyngeal process of the mandible, and the placement of the proventriculus in the metathoracic lumen. Yet other authors have placed *Phylloplatypus* in a separate subfamily, Phylloplatypodinae, close to Cossoninae, based on unusual larval characters (Morimoto & Kojima 2004). Finally, the transfer of Carphodicticini from Scolytinae to Platypodinae made by Thompson (1992) is here refuted for reasons given in the Scolytinae chapter.

The first phylogenetic analyses of morphological and molecular data suggested a position close

to Scolytinae, or nested within Scolytinae, usually with Cossoninae as the sister group to these two lineages combined (Kuschel 1995; Kuschel *et al.* 2000; Farrell *et al.* 2001; Marvaldi *et al.* 2002). However, these studies either included a limited number of outgroups or the results were supported by morphological data only. Recent and more comprehensive analyses indicate strongly (McKenna *et al.* 2009), or partly (Jordal *et al.* 2011), that the genetic divergence between Platypodinae and Scolytinae is very large and may support a closer relationship with Dryophthorinae and Brachycerinae than with Scolytinae and Cossoninae. A closer relationship to Dryophthorinae is also supported by larval characters, particularly by the subdivided abdominal pleura and by the branched setae on the apical portion of the epipharynx (Marvaldi 1997). The exact position of Platypodinae is therefore by no means firmly established. However, the latest phylogenetic study (Jordal *et al.* 2011), which was based on a broad sample of intergrading taxa, and data from morphology as well as five genetic loci, indicated a sister relationship between Platypodinae and Scolytinae as the most likely result.

The fossil record of Platypodinae is scarce compared with Scolytinae, with the oldest known fossil dating back only some 33 Myr (Bright & Poinar 1994). The various fossils belong to genera affiliated with the modern Platypodini (most likely *Platypus*) and to the extant tesserocerine genus *Cenocephalus*. The abundance of recognized extant genera, particularly in Dominican amber (Eocene-Miocene), suggest that Platypodinae evolved long before the Eocene and thus may support an origin relatively early in the evolutionary history of weevil (Bright & Poinar 1994; McKenna *et al.* 2009; Jordal *et al.* 2011).

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