3.7.5 Entiminae Schoenherr, 1823

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Distribution. The Entiminae include about 1370 genera and more than 12,000 species worldwide, occurring in all biogeographical regions (Nearctic, Palaearctic, Afrotropical, Oriental, Australasian, Neotropical and Chile/southern Argentina). Among the 55 tribes recognized in the catalogue by Alonso-Zarazaga & Lyal (1999), about 40 are represented mainly in a restricted region, about ten occur in two biogeographical regions [e.g., Nearctic and Palaearctic, Palaearctic and Oriental, Afrotropical and Oriental, Afrotropical and Palaearctic, Australasian and Patagonian (Chile/southern Argentina)], and the remaining occur in more than three regions. As an example, Agraphini, Hormorini and Ophryastini are typically Nearctic; Holcorhinini, Otiorhynchini, Phyllobiini and Sciaphilini are Palaearctic; Anypotactini, Entimini, Eudiagogini, Eustylini and Lordopini are Neotropical; Embrithini, Oosomini and Tanyrhynchini are Afrotropical; Mesostylini, Nastini and Omiini are Oriental; Celeuthetini and Ottistirini are Australasian; and Anomophthalmini are endemic to Patagonia. Some tribes have more restricted ranges, such as Nothognathini, which only occur in India, Ophtalmorrhynchini in Central Africa, Premnotrypini in the high Andes of northern South America, Typhlorhinini in Madagascar, Ectemnorhinini on small islands in the southern Ocean (from Marion and Prince Edward Islands to Heard Island), Elytrurini in Polynesia, Laparocerini on the Macaronesian islands (Azores, Madeira and Canary Islands), Polycatini in the Philippines and Rhyncogonini on various islands of the eastern Pacific (Marquesas, Hawaii and Tahiti). One extinct tribe is described from the Upper Miocene of Germany. [O'Brien & Wibmer 1978; Alonso-Zarazaga & Lyal 1999; Yunakov & Nadein 2006.]

Biology and Ecology (Fig. 3.7.5.1 A–D). Larvae (Fig. 3.7.5.1 A) of most species of Entiminae live freely in the soil, feeding externally on the roots of their host plants. Pupation (Fig. 3.7.5.1 B) also occurs in the soil, in an earthen cell lined with a larval secretion. Adults (Fig. 3.7.5.1 C) feed on the aerial green parts of the plants, especially fresh leaves or flowers, cutting their edges in a characteristic "notching" pattern. Life cycles usually last about a year but in some cases are completed in two or three years (Young *et al*. 1938; May 1994). Larvae overwinter underground (usually as prepupae) and pupate in warmer months, and the teneral adults emerge from the soil during spring and summer. The longest part of the cycle is spent in the larval stage, which is the more injurious for the plants. The number of instars varies among species, for intance, four occur in *Premnotrypes latithorax* Pierce (Tisoc-Dueñas 1989), seven in *Ectemnorhinus* spp. (Chown & Scholtz 1989 a) and up to 11 in *Naupactus leucoloma* Boheman (Matthiessen 1991).

Females of Entiminae (as well as those of other broadnosed weevils classified in Cyclominae) do not use their rostrum for preparing an oviposition site. Two main oviposition types occur in Entiminae: eggs deposited loosely and at random (the "*Sitona* type") and eggs deposited in batches between adjoining surfaces (the "*Brachyderes* type") (van Emden 1950, 1952; Marvaldi 1999). Eggs laid randomly are usually placed on plants, surface litter or soil, and they darken as they develop, whereas eggs laid in batches are covered with an adhesive glutinous substance secreted during oviposition, hidden between adjoining surfaces (leaves, cracks in the soil, crevices, litter or various niches near the soil) and remain pale (Marvaldi 1999). Eggs of Ectemnorhinini are laid individually or in small groups in ground litter below the host plant or among plant parts, and they darken as they develop (Chown & Scholtz 1989 a). In Pachyrhynchini (e.g., *Pantorhytes* Faust) they are laid singly in the bark (van Emden 1952; May 1978). When laid in batches, each batch (Fig. 3.7.5.1 D) consists on an agglutinated cluster of 20–80 eggs, a number that can vary depending on the food resources available to the female, time after its eclosion and other environmental conditions. The fecundity of entimines is very high compared with that of other weevil subfamilies. Eggs hatch after 5–20 days, with the length of the egg stage being affected mainly by temperature and humidity.

Soil-dwelling larvae and polyphagy are characteristic features of the Entiminae, most of them feeding on a variety of plants (spanning different angiosperm families) in the adult and larval stages. However, larvae of Ectemnorhinini and Pachyrhynchini do not feed on roots in the soil. Larval development in the Ectemnorhinini occurs on or near the soil surface, usually among plant mats or detritus (Chown & Scholtz 1989 a), whereas pachyrhynchine larvae feed arboreally, tunneling in branches, where they also pupate in a chamber lined with plant fibers and frass (May 1978). The large pupal cases of *Leptopius duponti* (Boisduval) (Leptopiini) formed in calcareous sands along the South Australian coast can become calcified after eclosion of the weevil and preserved for a long time (Lea 1925; Tilley *et al*. 1997). Similar bauxitic pisoliths from northern Queensland have been suggested to represent entimine pupal cases as well (Tilley *et al*. 1997; Eggleton & Taylor 2008), although without direct evidence of any weevil constructing them.

Entiminae are primarily and ancestrally associated with angiosperm plant taxa (Marvaldi *et al*. 2002). Associations with gymnosperms or cryptogams most likely constitute secondary host shifts and/or, in polyphagous species, expansions of the original host range. Ectemnorhinini mostly feed on cryptogams, both as adults and larvae, but some also

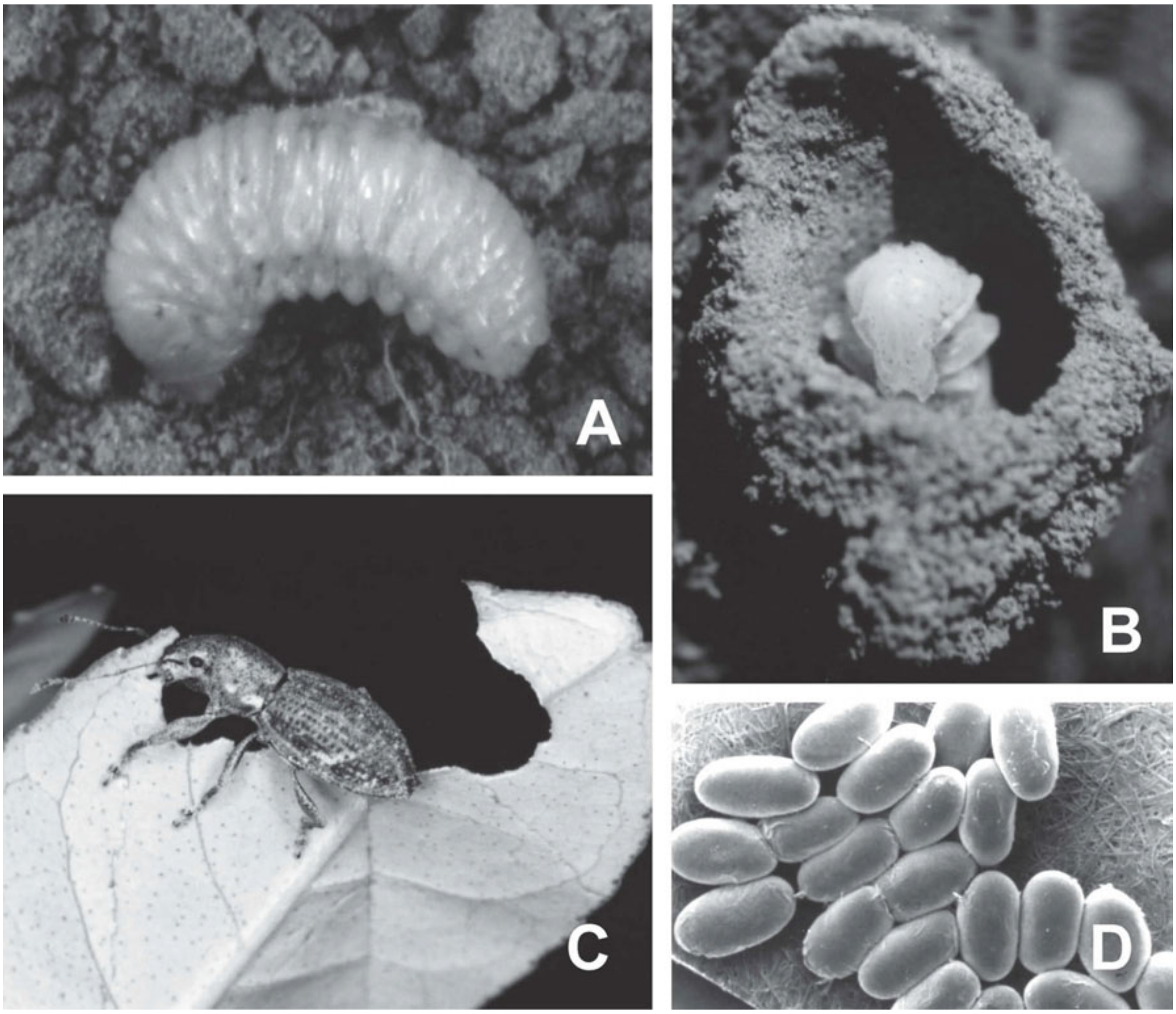

Fig. 3.7.5.1 Life cycle of Entiminae. A, *Naupactus leucoloma* Boheman, mature larva in soil; B, *N. leucoloma*, pupa in earth cell; C, *N. cervinus* Boheman, adult feeding; D, *Atrichonotus taeniatulus* Berg, posture.

feed on bryophytes, lichens, algae and cyanobacteria (Chown 1989, 1994; Chown & Scholtz 1989 a). Members of the genera *Canonopsis* C. O. Waterhouse, *Christensenia* Brink and *Ectemnorhinus* G. R. Waterhouse are the only Ectemnorhinini that feed on angiosperms, but they also incorporate bryophytes and other cryptogams in their diet (Chown 1989). The only exception is *Palirhoeus eatoni* (C. O. Waterhouse) which is oligophagous, restricted to feeding on three species of marine algae (Chown 1994). A different association with cryptogams occurs in some species of *Gymnopholus* Heller (Leptopiini) and *Pantorhytes* (Pachyrhynchini) inhabiting humid forests at high elevations in New Guinea. These weevils live in an epizoic symbiosis with cryptogamic plants and microfauna, the lichens, algae and mosses growing on their pronotum and elytra providing camouflage and protection for the weevils and food and shelter for the rotifers, nematodes and mites that live among them (Gressit 1966).

Entiminae feed on monocotyledons (e.g., Poaceae) and a great variety of dicotyledonous families, including Fabaceae, Fagaceae, Malvaceae, Rosaceae, Rutaceae, Solanaceae and many others. Legumes are among their main hosts. It is common among polyphagous species that adult and larval stages feed on different plant taxa, i.e., adults on leaves of various dicotyledons and larvae on roots of monocotyledons (pastures) (Marvaldi 1998 b). The frequency of the host shifts depends not only on the physiology of plants and weevils but also on the availability (plant apparency) of these plants. For instance, adults of *Pantomorus ruizi* (Brèthes) (Naupactini), known to feed on various dicotyledons, have recently been found consuming pine needles in Patagonia, whereas the larvae probably feed on roots of grasses growing around the trees (Gómez & Lanteri 2006), and adults of the Palaearctic *Otiorhynchus kollari* Gyllenhal were found feeding on ferns (Muñiz 1970).

Even when polyphagous, entimines can show definite host preferences (oligophagy). South American species of *Pandeleteius* Schoenherr (Tanymecini) are predominantly associated with trees and shrubs of the families Anacardiaceae (*Schinopsis* and *Schinus*), Asclepiadaceae (*Baccharis*) and Fabaceae

(*Prosopis*), and those of *Enoplopactus* Heller (Naupactini) with shrubs of the subfamily Zygophyllaceae (*Larrea*) (Lanteri *et al.* 2002). *Phyllobius oblongus* Linnaeus (Phyllobiini) is much more common on elms (*Ulmus*, Ulmaceae) and blackthorn (*Prunus spinosa*, Rosaceae) than on other trees (Morris 1976). Species of *Sitona* Germar are much more stenophagous than most Entiminae, being mainly associated with legumes (Fabaceae), the adults feeding on leaves and the larvae on roots and nitrogen-fixing root nodules (Manglitz *et al.* 1963; Velázquez de Castro 2004; Velázquez de Castro *et al.* 2007). *Barynotus moerens* Fabricius (Geonemini) is a rare example of a monophagous species of Entiminae, feeding only on the roots of a European herb that is toxic to vertebrates (*Mercurialis perennis*, Euphorbiaceae) (Morris 1976). The capacity to deal with a variety of plant toxins may be more widespread in Entiminae and at least in part responsible for their common polyphagy. At least some entimines can also feed on plants rich in heavy metals. In South Africa, for instance, *Brachytrachelus pseudopatrinus* Oberprieler (Tanyrhynchini) and species of *Holcolaccus* Marshall (Oosomini) have been recorded feeding on *Berkheya coddii* (Asteraceae), a plant that hyperaccumulates nickel in its leaves (Mesjasz-Przybylowicz & Przybylowicz 2001).

Some cosmopolitan entimine pest species are extremely polyphagous, with hundreds of host plants recorded, most of them cultivated. Adults generally do not injure plants seriously, except when they are very numerous, but larval damage to roots can be very harmful. Among the most serious pests are Fuller's rose weevil – *Naupactus cervinus* Boheman, Naupactini; the white-fringed weevils – *Naupactus leucoloma*, *N. peregrinus* (Buchanan), and *N. minor* (Buchanan), Naupactini; the two-banded Japanese weevil – *Pseudocneorhinus bifasciatus* Roelofs, Trachyphloeini, the black vine weevil – *Otiorhynchus sulcatus* Fabricius, Otiorhynchini; the banded fruit weevil or garden weevil – *Phlyctinus callosus* Schoenherr, Oosomini; and the Andean potato weevils – several species of *Premnotrypes* Pierce, Premnotrypini. Fuller's rose weevil and the white-fringed weevils are native to southern South America but have been introduced in many parts of the world, particularly the cooler or more seasonal agricultural areas of the southern USA, Australia, New Zealand and South Africa (Lanteri & Marvaldi 1995). Adults feed on at least 385 species of plants, preferring species with large broad leaves, including peanut, soybean and many other leguminous crops (Young *et al.* 1938). The two-banded Japanese weevil was first recorded in the USA at the beginning of the 20th century, and it is now firmly established in its eastern states, where it feeds on several ornamental plants and strawberry (Maier 1983; Wheeler & Boyd 2005). The European black vine weevil has become a serious pest in the horticultural and nursery industries in many parts of the world during the past two decades, damaging a large number of annual and perennial herbaceous plants, shrubs and climbers. A broad host range and the ability to develop on most gymnosperms and broad-leaved plants have enabled this beetle to establish itself in nurseries, greenhouses and landscapes around the world (Moorhouse *et al.* 1992; van Tol *et al.* 2004). In Australia it has been introduced over a decade ago and, together with the cribrate weevil – *O. cribricollis* Gyllenhal, and the Rough Strawberry Weevil – *O. rugosostriatus* (Goeze), is considered a pest of various berries, vegetables and fruit trees. *Phlyctinus callosus* is native in South Africa, where it is known as the banded fruit weevil and a major pest of apples and nectarines (Barnes 1989). It was introduced to New Zealand, Australia, the Norfolk and Kermadec Islands over a century ago, where it attacks a wide variety of garden flowers and other plants. The Andean potato weevils are the most important pests of *Solanum* spp. (Solanaceae), sometimes causing 70% to complete destruction of unsprayed potato crops (Alcázar & Cisneros 1999). They occur only in northern South America, Bolivia, Chile, Colombia, Ecuador, Peru and Venezuela), particularly in the high-altitude potato-growing areas about 3000 m above sea level. Larvae tunnel in the tubers, causing damage usually not detected by external inspection, and adults feed on leaves of potato and other plants. The most harmful species are *Premnotrypes latithorax* (in Peru) and *P. vorax* Hustache (in Venezuela). Some species of *Pantorhytes* (Pachyrhynchini) have attained pest status on cultivated cocoa plants in New Guinea (Smith 1981 a, b).

Most Entiminae show habitat or substrate preferences rather than plant specializations. Flightless species of *Atrichonotus* Buchanan and *Eurymetopus* Schoenherr (Naupactini) are prairie adapted, feeding on herbs and grasses (Lanteri *et al.* 2002), whereas the fully winged species of *Entimus* Germar and *Phaedropus* Schoenherr (Entimini) are rainforest adapted, living and feeding on trees (Morrone 2002). However, also flightless species of *Pantorhytes* (Pachyrhynchini) are arboreal feeders in rainforests of the Papuan region (May 1978, 1994). Other entimines are terricolous, living under stones or low, prostrate plants in xeric environments. Examples are species of the subgenus *Troglorhynchus* Schmidt of *Otiorhynchus* Germar (Otiorhynchini), which live on the ground under stones, *Cylydrorhinus* Guérin-Méneville (Cylydrorhinini), which occurs under stones and plant cushions on the steppes of Patagonia (Muñiz 1970; Lanteri *et al.* 2002), and *Spartecerus* Schoenherr (Leptopiini), which lives under geophytes and stones in the semi-deserts of southern Africa. A few entimines are adapted to extremely arid habitats. In southwestern Africa, the genus *Leptostethus* G. R. Waterhouse (Leptopiini) is confined to a narrow region ranging from the stony, semidesert Karroo in the south to the sand dunes of the Namib desert, where the showy blue *L. speciosus* Thompson emerges in large numbers in the dunes only after rare rains (Thompson 1988). Its larvae apparently feed on roots of *Stipagrostis* grasses deep under the sand. In the Holarctic region, the small tribe

Ophryastini exhibits even stronger adaptations to a psammophilous way of life. Several species, especially of *Deracanthus* Schoenherr but also of *Ophryastes* Germar and *Sapotes* Casey, have broadened, fossorial legs, long body hairs and smooth, agglutinated scales that enable them to dig into loose sand. Their larvae feed on the roots of xerophilic species of Asteraceae and Zygophyllaceae. Some species of *Leptostethus* live in halophytic habitats along the Namibian coast in Africa, species of *Galapaganus* Lanteri (Naupactini) inhabiting coastal deserts along the Pacific coast of South America (Ecuador and Peru) and the Galápagos islands have a high salt tolerance (Lanteri 1992; Sequeira *et al.* 2000), and *Otiorhynchus ligneus* Schoenherr also inhabits halophytic environments, feeding on unicellular and filamentous terrestrial algae (Muñiz 1970). Ectemnorhinini mostly live in epilithic biotopes of subantarctic islands in the Indian Ocean, feeding on cryptogams (Chown 1989).

Parthenogenesis. Most entimine species reproduce sexually, but there are some species that are parthenogenetic, a rare phenomenon in beetles and occurring in only two other subfamilies of Curculionidae: Scolytinae (bark beetles) and Cyclominae (Suomalainen *et al.* 1987). About 75 parthenogenetic weevil species have been recorded (Saura *et al.* 1993), over 50 in Entiminae (Smith & Virkki 1978; Lokki & Saura 1980; Bell 1982; Takenouchi 1986; Suomalainen *et al.* 1987). They belong to 13 tribes (following Alonso-Zarazaga & Lyal 1999): Blosyrini – *Blosyrus japonicus* Sharp; Brachyderini – *Strophosoma melanogrammum* (Forster); Cneorhinini – *Catapionus gracilicornis* Roelofs; Cyphicerini – *Myllocerus nipponicus* Zumpt, *M. fumosus* Faust, *M. griseoides* Zumpt, *Myosides seriehispidus* Roelofs, *M. pyrus* Sharp, *Cyrtepistomus castaneus* (Roelofs); Geonemini – *Barynotus moerens*, *B. obscurus* (Fabricius), *B. squamosus* Germar; Naupactini – *Aramigus tessellatus* (Say), *Naupactus cervinus* Boheman, *N. leucoloma*, *N. peregrinus*; Otiorhynchini – *Otiorhynchus scaber* Linnaeus, *O. sulcatus*, another 15 *Otiorhynchus* spp., *Sciopithes obscurus* (Horn); Peritelini – *Peritelus hirticornis* Seidlitz; Polydrusini – *Polydrusus mollis* Dejean, *Liophloeus tessulatus* (Mueller); Sciaphilini – *Eusomus ovulum* Germar, *Fourcartia squamulata* (Herbst); Tanymecini – *Scepticus insularis* Roelofs; Trachyphloeini – *Pseudocneorhinus bifasciatus* Roelofs, *P. minimus* Roelofs, *P. obesus* Roelofs, *P. setosus* Roelofs, *Trachyphloeus aristatus* (Gyllenhal), *T. bifoveolatus* (Beck), *T. scabriculus* (Linnaeus), *Trachyrhinus* sp; Tropiphorini – *Tropiphorus carinatus* (Mueller), *T. cucullatus* Fauvel, *T. terricola* (Newman). A particularly high frequency of parthenogenetic lineages has been found in *Otiorhynchus*, a diverse genus native to the Palaearctic region and including some of the most serious insect pests in agriculture (Tomiuk & Loeschke 1992). *Otiorhynchus scaber* has been studied in detail by geneticists and molecular biologists and is frequently cited as model of a bisexual-parthenogenetic system in ecology and evolutionary studies (Stenberg *et al.* 2000, 2003). Most parthenogenetic weevils have been reported from central and northern Europe and Japan, and fewer in North and South America, but this is probably an artifact due to lack of surveys. Lanteri & Normark (1995) published a list of 34 South American species of Naupactini known (by rearing experiments and cytological studies) or suspected (no males known) to be parthenogenetic.

Parthenogenetic weevils are thelytokous, with unfertilized eggs producing only females. Cytological studies revealed that females reproduce by apomixis, and because no meiosis is involved, the offspring is genetically identical unless mutations occur (Smith & Virkki 1978; Vepsäläinen & Järvinen 1979; Suomalainen *et al.* 1987). The morphological characters most strikingly correlated with parthenogenesis in weevils are the reduction or absence of wings and elytral humeri (Lanteri & Normark 1995; Scataglini *et al.* 2005). The only known exceptions are *Polydrusus mollis* Stroem (Polydrusini) and also *Listroderes costirostris* Schoenherr (Cyclominae, Listroderini) (Takenouchi 1970; Lokki *et al.* 1976) with normal body shapes. Flightlessness seems to evolve when the energy cost of flight is high, e.g., in cold and/or windy habitats (Roff 1990; Wagner & Liebherr 1992; Lanteri & Normark 1995). Reduced vagility (loss of flight) accompanies, or apparently antedates, the origin of apomixis because all parthenogenetic weevils are flightless, although the reverse is not the case. Apomictic weevils are frequently polyploid, triploidy being the most common (Takenouchi 1976). Another morphological feature associated with parthenogenesis is the larger body size of polyploids compared with diploids (Suomalainen 1969; Suomalainen *et al.* 1987). The origin of polyploidy in weevils has been related to the impact of sudden temperature drops in high latitudes and/or altitudes on freshly laid eggs, which may disrupt meiosis, leading to polyploidy in the embryo (Takenouchi 1980, 1983; Takenouchi *et al.* 1986).

There are two main hypotheses to explain the origin of parthenogenesis and polyploidy in weevils, the first positing that triploidy is associated with the origin of parthenogenesis and the second that asexuality predates polyploidy (Suomalainen 1969; White 1973; Lokki 1976; Saura *et al.* 1993). Both hypotheses assume the transition from sexual to asexual reproduction to be an irreversible change. A third hypothesis suggests that endosymbiotic bacteria of the genus *Wolbachia* may play a role in the origin of apomixis (Rodriguero *et al.* 2010). These maternally transmitted organisms are responsible for several reproductive alterations in insects, such as feminization, cytoplasmic incompatibility, male death, and automictic parthenogenesis in wasps (Werren *et al.* 1995; Werren 1997), but they have so far not been shown to induce apomictic parthenogenesis (Normark 2003). The discovery of *Wolbachia* strains in *Otiorhynchus scaber* (Stenberg *et al.* 2003; Stenberg & Lundmark 2004), *Aramigus tessellatus*

(Braig *et al.* 2002), *Naupactus cervinus* and other South American Naupactini (Rodriguero *et al.* 2010) may indicate a role that these bacteria play in the origin of parthenogenesis in Entiminae.

Whichever hypothesis holds true, parthenogenetic reproduction coupled with polyploidy may be widespread in broad-nosed weevils because it arises repeatedly and/or creates novel capacity for adaptation and diversification. According to Comai (2005), there are three main advantages of becoming polyploid: (1) heterosis causes polyploids to be more vigorous than their diploid progenitors; (2) gene redundancy shields polyploids from deleterious effects of mutations (these first two advantages result from gene duplication); (3) asexual reproduction enables polyploids to reproduce in the absence of sexual mates.

Parthenogenetic weevils often occur at high altitudes, on islands or in island-like habitats, in xeric environments or in disturbed habitats (Kearney 2005). If there is a bisexual and a parthenogenetic form of a single species or two closely related such species, as a rule they have different geographical ranges (Vandel 1928), the parthenogenetic one usually a much broader range than the respective bisexual one. Such cases of geographical parthenogenesis (Suomalainen 1969; Suomalainen & Saura 1973; Takenouchi 1976), as in *Otiorhynchus scaber*, support the notion that polyploidy is an important factor explaining the broad distribution of parthenogenetic races (Stenberg *et al.* 2000) and that polyploid clones are superior colonizers compared with sexual and diploid clones (Stenberg & Lundmark 2004). An exception to this pattern is seen in *Liophloeus tessulatus* (Polydrusini), in which a parthenogenetic race is restricted to mountains of central Europe and a bisexual race is widespread at lower altitudes on the continent. There are also cases in which the bisexual and parthenogenetic forms coexist (Suomalainen & Saura 1973). Although geographical parthenogenesis has been reported for European weevils, it also occurs in South American Naupactini, such as *Aramigus tessellatus*, *Naupactus cervinus*, *N. leucoloma* and *N. peregrinus* (Lanteri 1984, 1993; Lanteri & Normark 1995). The introduction, establishment and subsequent dispersal of parthenogenetic clones far from their original distributions are testimonies to their ability to colonize new environments. Lastly, in some areas of Argentina bisexual forms of *Aramigus tessellatus* coexist with polyphyletic triploid and tetraploid lineages of probable hybrid origin (Normark 1996 a, b; Normark & Lanteri 1998).

Color Mechanisms. Entimines display a remarkable diversity of color patterns, including iridescent hues and ultraviolet reflectance. The iridescence of some Leptopiini, Naupactini, Pachyrhynchini and other brightly colored species is unique among beetles: whereas other groups derive their color from pigments (e.g., aposematic reds and yellows of Coccinellidae and Erotylidae) or two-dimensional multilayer reflectors (e.g., metallic blues and greens of certain Buprestidae), the colors of entimine weevils are produced almost entirely by three-dimensional photonic crystals analogous to those found in opal (Parker *et al.* 2003; Galusha *et al.* 2008; Seago *et al.* 2009). In this complex iridescence mechanism, a nanoscale three-dimensional lattice of chitin reflects certain wavelengths of light with constructive interference, producing vivid structural colors (Seago *et al.* 2009; Saranathan *et al.* 2010). In entimines, this lattice forms within the lumen of the scales during pupation, as an aggregation of small, variously orientated crystalline domains (e.g., Galusha *et al.* 2008). As an added benefit, the heterogeneous orientation of these domains results in direction-independent reflectance at the macroscale; therefore, the structural colors of entimine weevils are the same from all viewing angles. This chromatic uniformity may have played a role in the evolution of entimine photonic crystals: smaller and less-ordered chitin lattices produce matte, white reflectance, which could aid crypsis in ancestral, bark- or soil-dwelling lineages. Omnidirectional green reflectance (as in *Briarius augustus* (Illiger), Naupactini; Lanteri & del Río 2003) could function also in crypsis to produce aposematic, disruptive or mimetic coloration.

Some entimine species also display strong reflectance of ultraviolet light. In a preliminary survey of UV patterns in beetles, Pope & Hinton (1977) found distinct patches of UV-reflective scales in the entimine genera *Compsus* Schoenherr, *Eupholus* Boisduval, *Exophthalmus* Schoenherr, *Leptopius* Oke, *Pachyrhynchus* Germar and *Rhinosphathe* Chevrolat. Recently Riedel (2010) demonstrated that waxy exudates that may function in visible wavelengths might be involved with interspecies mimicry in *Eupholus*; their colors can be distinguished from those of photonic crystals through differential UV reflectance (as well as microscopic inspection). Although the precise mechanism of UV reflectance in entimines is poorly studied, it is likely that UV and other short wavelengths are scattered or constructively reflected by nanoscale particle arrays (lattices or colloidal suspensions) within the setae and/or cuticular waxes.

Morphology, Adults (Fig. 3.7.5.2–3.7.5.6). Length about 4–30 mm. Body slightly flattened to moderately convex or strongly convex. Cuticle dark, testaceous, rarely glabrous or subglabrous, usually with vestiture including hair-like and/or scale-like setae, ranging from sparsely setose to densely squamose. Species from rainforests usually colorful, covered with dense vestiture of greenish, bluish, golden, bright scales, in some cases with aposematic coloration. Species from deserts and high mountains usually dull-colored, black or dark brown, covered with setae of various lengths but usually lacking scales; some of them brightly colored by a waxy secretion and densely covered with agglutinated scales.

Head (Fig. 3.7.5.3 A, B) relatively large, not subspherical. Eyes slightly to strongly protuberant,

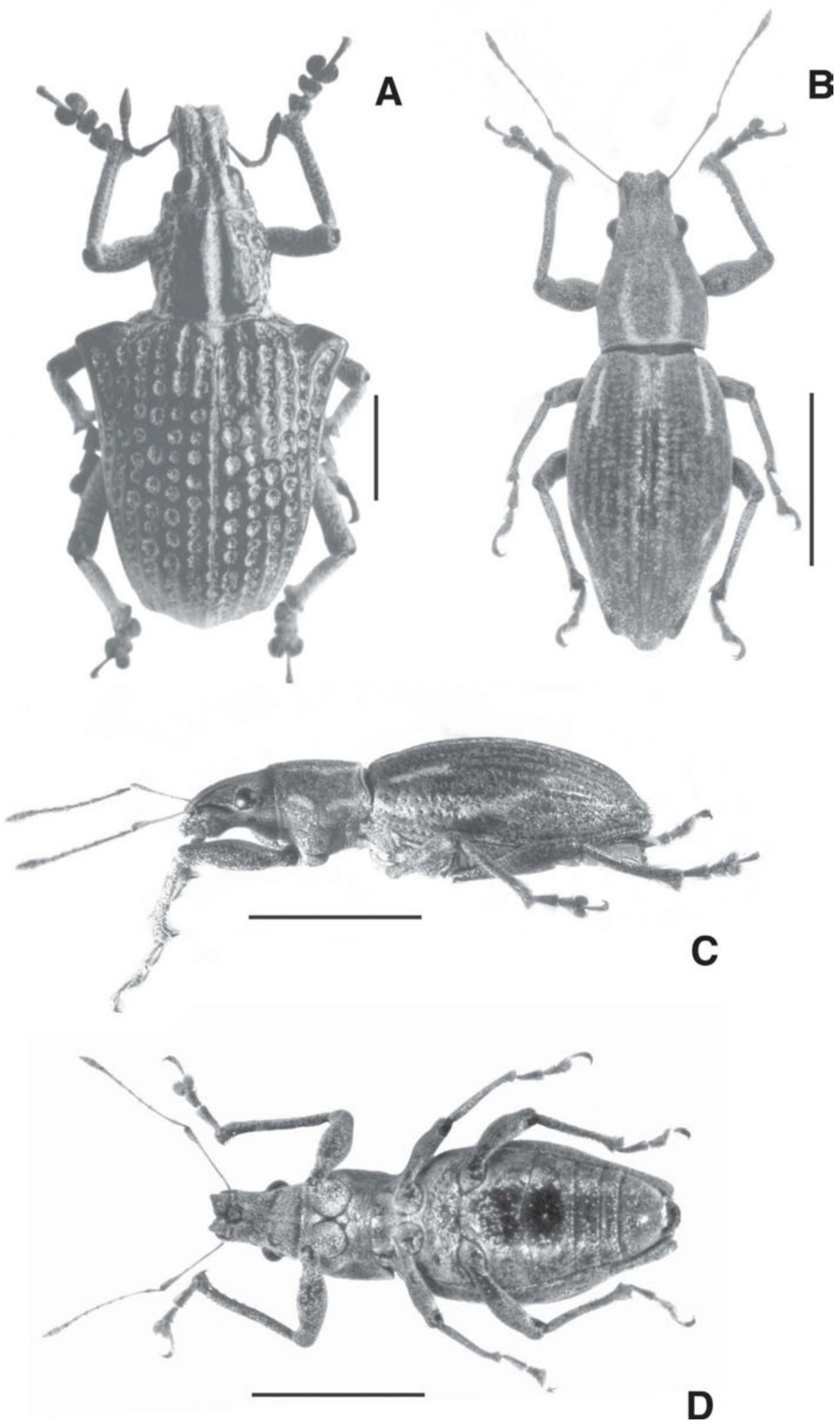

Fig. 3.7.5.2 A, B, Adults, general habitus. A, *Entimus sastrei* Viana; B–D, *Naupactus xanthographus* (Germar). B, Dorsal; C, lateral; D, ventral. Scale bar 5 mm.

variable in size and shape (ovate to subcircular), separated by about width of rostrum, usually facing outward on head. Rostrum broad, stout, short, rarely more than twice longer than wide, usually about as long as to shorter than head, extended forward or directed slightly downward (Fig. 3.7.5.2 C), subcircular to subquadrate in cross section. Antennal insertions (Fig. 3.7.5.3 B) lateral, mostly concealed from above but sometimes dorsal. Scrobes well developed, exposed or partially

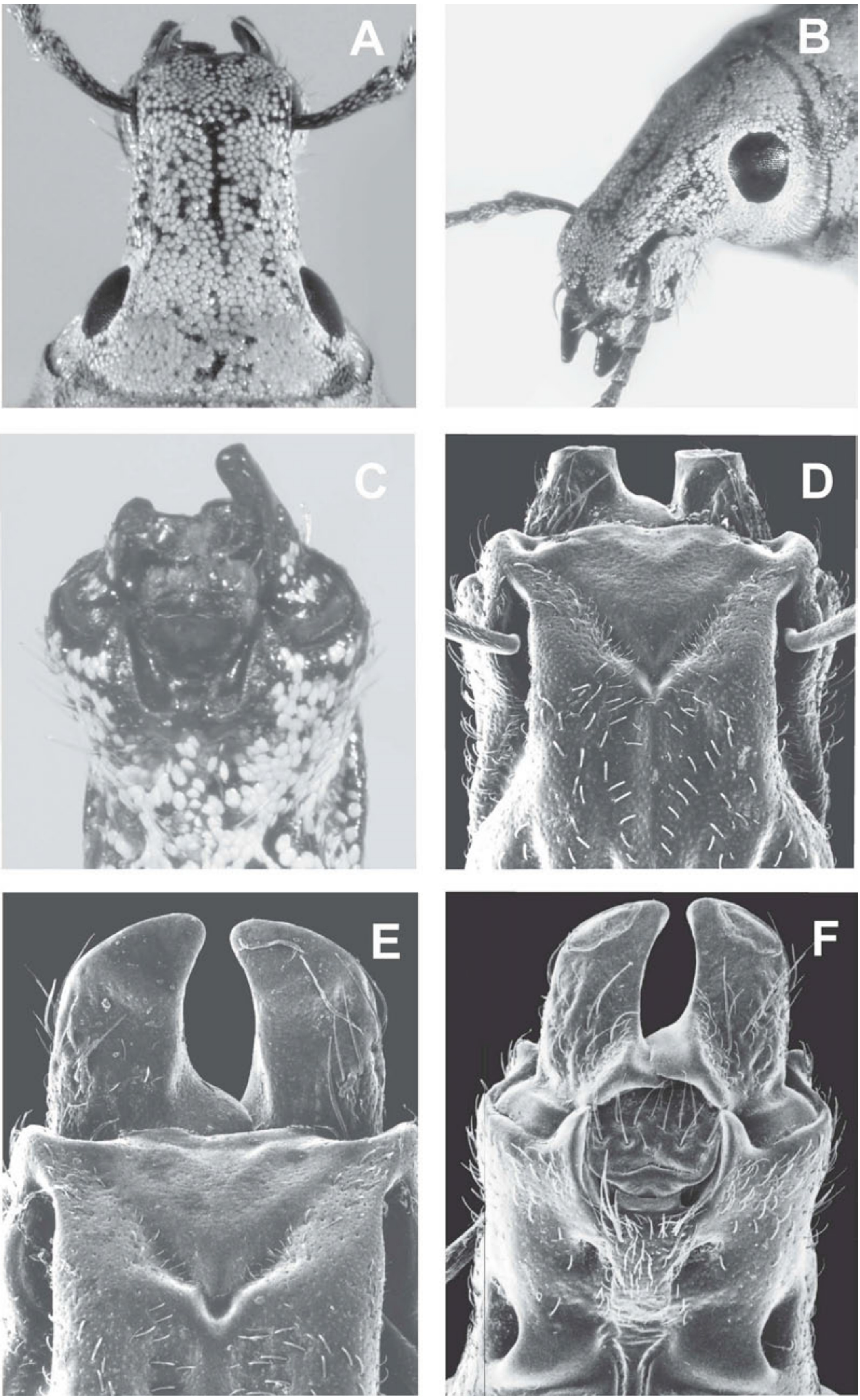

Fig. 3.7.5.3 A–F, Adult morphology, head and mouthparts. A–C, *Platyaspistes argentinensis* Kuschel. A, head, dorsal; B, head and antenna, lateral; C, rostrum and mouthparts, ventral, with scar and process; D–F, *Prostomus scutellaris* Schoenherr, mandibles. D, female, dorsal; E, male, dorsal; F, male, ventral.

concealed in dorsal view of head. Gular sutures confluent. Clypeolabral suture absent. Labrum indistinct. Epistome often raised or impressed. Antennae (Fig. 3.7.5.2 B and 3.7.5.3 B) mostly with 11 segments, geniculate; scape usually more than three times longer than first funicle segment, almost reaching to exceeding anterior margin of eyes; funicle seven-segmented; club compact and three-segmented (sometimes appearing four-segmented, with apical cone). Mandibles (Fig. 3.7.5.3 A–F) short and broad, mostly plurisetose and/or squamose or trisetose to bisetose, without mola, often with concavity in middle of ventral face; partially visible from above and in lateral view; moving in a near horizontal plane, inserted within distinct socket (pleurostomal sinus) (Fig. 3.7.5.3 C, F); with pharyngeal process (Fig. 3.7.5.4 A) about as long as to shorter than mandible; in teneral adults, each mandible usually with a deciduous, blade- to peg-like process (Fig. 3.7.5.3 A, B); processes smooth, bare, greatly variable in shape, being straight – e.g., *Heterostylus* Faust, incurved – e.g., *Naupactus* Dejean or extrorse – e.g., Promecopini, sometimes with a tooth near base of inner edge – e.g., *Lepropus lateralis* (Fabricius); usually well developed and present on both mandibles, sometimes on left mandible only – e.g., some Sitonini: *Catachaenus* Schoenherr and *Eugnathus* Schoenherr, or minute to vestigial – some Cylydrorhinini and Leptopiini, e.g., *Caneorhinus biangulatus* (Champion) and *Leptostethus speciosus* Thompson, absent in Pachyrhynchini, most Sitonini and most Ectemnorhinini; sometimes mounted on a pedicel – e.g., some species of Brachyderini, Entimini, Otiorhynchini, Tanymecini, punctate and setose – e.g., *Iphisomus* Faust, or sexually dimorphic – e.g., *Prostomus scutellaris* (Fabricius) (Fig. 3.7.5.3 D–F); mandibular processes generally lost in young adults by active dehiscence, leaving a distinct rough area or scar (Fig. 3.7.5.3 C, D, F), sometimes very small – e.g., *Tanyrhynchus* Schoenherr or worn away completely – e.g., some Tropiphorini and *Otiorhynchus* spp.; a few species – *Leptomias waltoni* Marshall, *Chlorophanus excisus* (Fabricius), *Stereogaster globosa* Van Dyke, *Bletonius hustachei* Hoffmann, *Anomonychus henoni* Faust – retaining the deciduous processes throughout adult life (dehiscence mechanism lost). [The presence of mandibular processes is associated with pupation in soil, although the reverse is not always the case, and their function is apparently to aid the teneral adult in emerging from its subterranean pupal cell to the surface (Thompson 1992, and references (therein).] Maxillae (Fig. 3.7.5.4 B) usually with single apical lobe or mala, galea and lacinia fused, although often differentiated by sclerotization and arrangement of setae or spines, or galea and lacinia broadly connate, partially divided (in Sitonini and some genera of Naupactini and Tropiphorini); stipes fused with lacinia along its mesal margin; palp three-segmented; apical segment cylindrical to fusiform. Labium (Fig. 3.7.5.4 C) with palps usually three-segmented – two-segmented in *Amystax* Roelofs, Tanymecini; *Episomus* Schoenherr, Episomini; and *Blosyrus* Schoenherr, Blosyrini – and attached to ental surface, usually near apex of prementum; ligula indistinct or represented by membranous area between palps; prementum generally enlarged, covering maxillae (adelognathous condition) (Fig. 3.7.5.3 C, F), but leaving them laterally exposed (phanerognathous condition) in Ectemnorhinini, Cylydrorhinini, Sitonini, Tropiphorini (= Alophini), and some genera of other tribes.

Prothorax (Fig. 3.7.5.2 A–D) with anterior margin and sides curved or straight; base usually

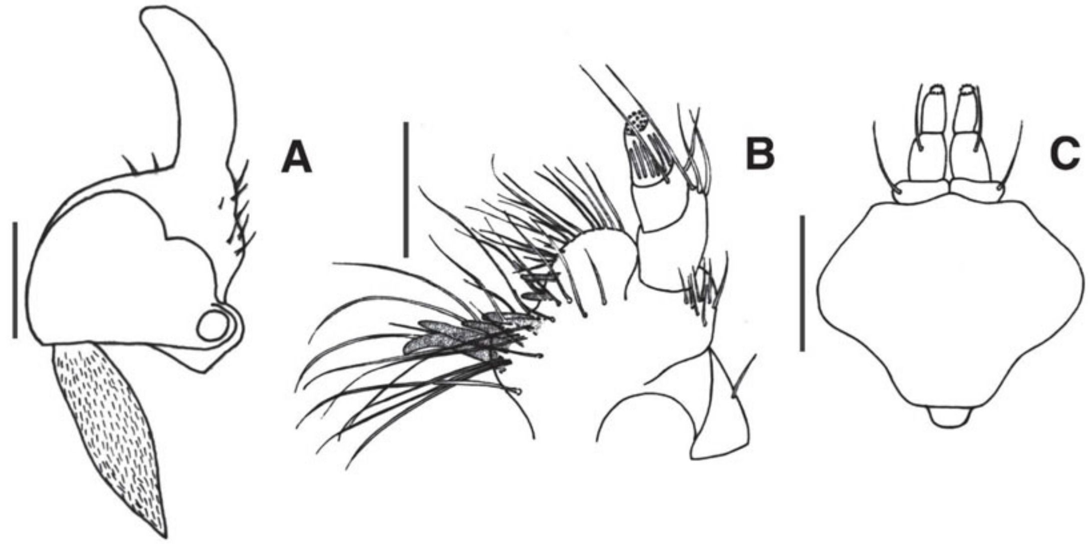

Fig. 3.7.5.4 Adult morphology, mouthparts, *Naupactus leucoloma* Boheman. A, right mandible, with pharyngeal process, ventral, scale bar 0.5 mm; B, right maxilla, dorsal, scale bar 0.25 mm; C, labium, inner face, scale bar 0.25 mm.

distinctly narrower than elytral base (few exceptions, for instance some species of *Protostrophus* Jekel), more or less straight, evenly rounded or bisinuate; maximum prothoracic width usually less than maximum elytral width; sides anteriorly with ocular lobes (e.g., Cylydrorhinini, Entimini, Leptopiini, Premnotrypini, Tanyrhynchini), sometimes carrying stiff vibrissae (Fig. 3.7.5.3 B) (Tanymecini), or straight and without ocular lobes (most other tribes). Prosternal process extending to behind coxae or ending before middle of coxae, often externally interrupted (Fig. 3. 7. 5. 2 D); apex of prosternal process acute or broadly rounded, angulate or truncate. Procoxal cavities externally and internally closed, circular or longer than wide, contiguous or separated. Scutellum well developed, visible as scutellar shield between elytral bases (Fig. 3.7.5.2 B) or not visible. Elytra covering all abdominal tergites; usually with ten rows of punctate striae (Fig. 3.7.5.2 A–C), sometimes apunctate, rarely with supernumerary striae; scutellary striole absent; sutural flanges of about equal width. Mesocoxal cavities circular to slightly transverse, narrowly to widely separated. Metaventrite flat to convex, longer to slightly shorter than first abdominal ventrite; metanepisternal sutures or lateral edge of metaventrite without sclerolepidia; metacoxal cavities slightly to widely separate. Metendosternite with lateral arms moderately to very long; laminae reduced or absent; anterior tendons widely separated; apical portion not or only slightly emarginate. Hind wings well developed, reduced, or absent; flightlessness recorded in Holcorhinini, Omiini, Sciaphilini and several genera or species of other tribes, e.g., *Catasarcus* Schoenherr and *Leptopius* (Leptopiini), *Eurymetopus* and *Amitrus* Schoenherr (Naupactini), *Otiorhynchus* (Otiorhynchini), *Sitona* (Sitonini); two radial sclerites present; point of origin of r3 (Rr) not on radial cell but placed at anterior portion of r4 (r-m); medial field with three or fewer free veins. Procoxae (Fig. 3.7.5.2 D) contiguous to separate; anterior face without trace of either suture or pit with trochanteral projection; profemora usually stouter than meso- and metafemora; inner margin with one or more denticles in some genera (e.g., *Brachystylodes* Hustache, *Hoplopactus* Jekel, Naupactini; *Maleuterpes* Blackburn, Ottistirini); tibiae with apex generally mucronate, rarely amucronate or mucro flattened, laminate and displaced proximad (*Meteremnus* Marshall), spurs usually absent but retained in Cylydrorhinini and Tanyrhynchini (sometimes fused at base), inner margin of tibiae simple, crenulate or denticulate (denticles present in protibiae, protibiae and mesotibiae, or in all tibiae), apex of metatibiae and sometimes mesotibiae obliquely truncate, either simple (outside with only apical fringe of setae) (Fig. 3.7.5.5 A) or with narrow to broad, bare, setose or squamose corbel, whose outside is formed by a secondary, proximal comb of setae (Fig. 3.7.5.5 B–D), rarely with false corbel (a bare flange adjacent to tarsal socket inside of apical fringe of setae) (Fig. 3.7.5.5 E, F). [These conditions were previously often referred to as "open", "closed/enclosed", and "semi-enclosed corbel", respectively (van Emden 1944), but Thompson (1992) showed that the "semi-enclosed" corbel (his "inner flange") is different in origin from the "enclosed" corbel ("outer bevel"), and Oberprieler (2010) restricted the term (true) corbel to only the latter basket-like structure, referring to the former as a false corbel (after Faust 1883); a true corbel occurs only in some genera of the subfamilies Entiminae and Brachycerinae, whereas false corbels are found in various subfamilies.] tarsi pseudotetramerous, with bilobed tarsomere 3; empodium absent or concealed, or with two or fewer setae; tarsal claws usually free, rarely connate or a single claw; without setae near base except in Sitonini (each claw on outside at base with a long, flat, distally expanded seta flanking the claw to its apex).

Abdomen with ventrites 1 and 2 connate (Fig. 3.7.5.2 D), with suture distinct, ventrites 3 to 5 free, articulated; ventrite 1 at middle of metacoxae about as long as to longer than ventrite 2, ventrites 1 and 2 longer than ventrites 3 and 4; ventrite 5 variable in shape, usually sexually dimorphic (apex broadly rounded in males, narrower to triangular in females). Tergites I–VII with different degrees of pigmentation, represented by median sclerites, without lateral or spiracular sclerites; terminal tergite (VII in females, VIII in males) covered by elytra in both sexes, tergite VIII in females concealed under tergite VII (partly exposed in Sitonini), in males exposed beyond tergite VII. Spiracles present on tergites I–VII, absent on tergite VIII except vestigial in few cases (e.g., some species of *Entimus*). Male terminalia with sternite VIII (Fig. 3.7.5.6 A) consisting of a divided plate (variable in shape, pigmentation and number and disposition of setae), in some cases with vestigial apodeme (spiculum relictum); sternite IX (Fig. 3.7.5.6 A) symmetrical, with its basal part largely sclerotized, arms broad and usually discontinuous with apodeme (= spiculum gastrale). Aedeagus (Fig. 3.7.5.6 B) of pedal type (penis without dorsal plate, or tectum); tegmen consisting of a complete, narrow ring with parameres absent or reduced to a pair of asetose lobes fused to it; apodeme (manubrium) well developed but smaller than spiculum gastrale; penis trough-shaped or tubular, mostly curved or sinuate, often dorsally membranous, with pair of proximal apodemes (temones) deflexed at distinct angle in lateral view; endophallus membranous, with or without sclerites; flagellum usually absent. Testes bilobed, both lobes enclosed in common sheath, number of follicles varying from few (six to eight) large ones to many (20–22) relatively small ones; vasa deferentia distinct and usually enclosed within testicular sheath; anterior sections of vasa deferentia free of testicular sheath or enclosed within it; seminal vesicle multilobed (usually eight lobes); accessory gland usually two-branched (one branch larger than other), entering vas deferens anteriorly or on anterior face of seminal vesicle; ejaculatory duct

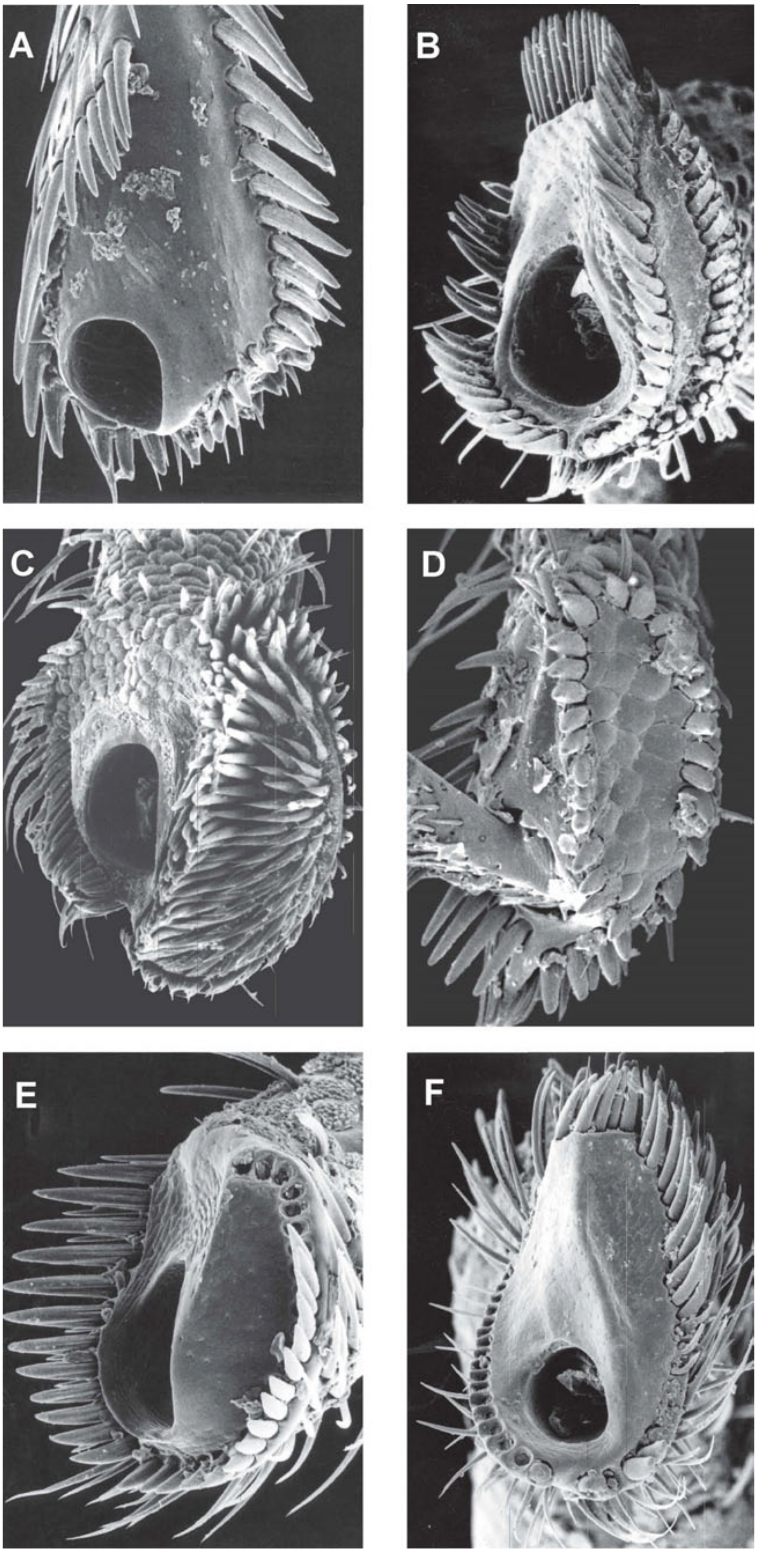

Fig. 3.7.5.5 Adult morphology, metatibial apex. A, *Naupactus cervinus* Boheman, simple, no corbel; B–D, true corbels. B, *Prypnus quinquenodosus* Schoenherr, bare corbel; C, *Leptopius robustus* (Olivier), setose corbel; D, *Polyphrades* sp., squamose corbel. E–F, false corbels. E, *Celeuthetes echinatus* Schoenherr; F, *Mandalotus crudus* Erichson.

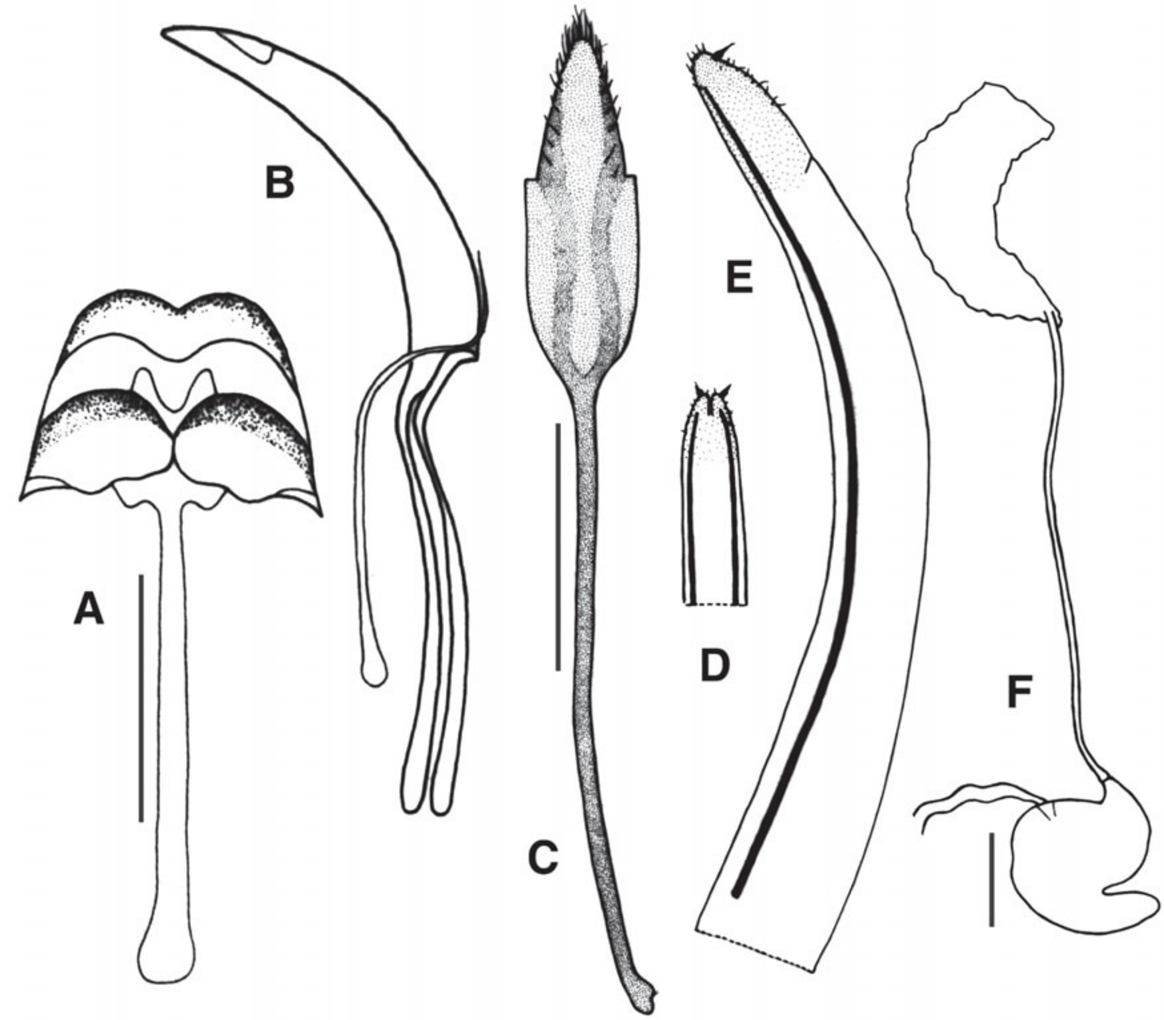

Fig. 3.7.5.6 Adult morphology, terminalia. A, B, *Galapagonotus cuneiformis* (G. R. Waterhouse), male. A, sternite VIII (divided plate), sternite IX and tergite VIII, scale bar 1 mm; B, aedeagus (penis and tegmen), lateral view, scale bar 1 mm. C–F, *Phacepholis elegans* Horn, female. C, sternite VIII, scale bar 1 mm; D, apex of ovipositor, ventral view, scale bar 1 mm; E, ovipositor (gonocoxites and gonostyli), lateral view, scale bar 1 mm; F, spermatheca, spermathecal duct and bursa copulatrix, scale bar 0.25 mm.

of variable length, from very short to very long. Female terminalia with sternite VIII (Fig. 3.7.5.6 C) variable in shape, sclerotization and distribution of setae; apodeme (spiculum ventrale) very long to short or vestigial (e.g., Sitonini). Ovipositor (gonocoxites plus gonostyli) (Fig. 3.7.5.6 D, E) usually well developed, reduced in Sitonini and some species of Cylydrorhinini and Tropiphorini, absent in some species of *Trigonoscuta* Motschulsky (Brachyderini); gonocoxites of variable length, undivided with a dorsal incision or divided into proximal and distal lobes (proximal and distal coxites); proximal coxite (or valvifer) sclerotized or membranous, smooth or wrinkled, with or without baculi; distal coxite entire or divided into two sclerites – e.g., *Arrhapogaster* Roelofs, *Trachyphilus* Faust; styli well developed, reduced or absent, apically or subapically inserted (e.g., Ectemnorhinini). Spermatheca (Fig. 3.7.5.6 F) variable in shape; gland tubular, rarely ovoid (e.g., Sitonini); duct usually long, membranous to sclerotized, entering ventral face of genital tract near entry of common oviduct. Ovaries each with two ovarioles bearing terminal filaments, rarely more ovarioles (e.g., six in some species of *Leptopius*); lateral oviducts uniting in common oviduct entering ventral face of vagina-bursa copulatrix complex (genital tract), anteriorly sometimes with pouch-like structures (*Sitona*). Vagina tubular and sclerotized, rarely unsclerotized (Sitonini); bursa copulatrix strongly developed to completely absent.

Foregut short to moderately long, 5%–15% of total length of tract. Crop well developed to indistinct. Proventriculus bulbous, internally usually with eight well-developed, sclerotized, basal plates, each bearing two longitudinal brushes, usually with retaining bristles. Esophagus usually covered with setae in anterior half. Midgut usually shorter than hind gut, 30%–50% of total length of tract, divided into two sections: (a) a distended anterior ventriculus usually lacking pouches, with several pouches (e.g., *Naupactus cervinus*, *N. leucoloma*) or strongly lobed (e.g., *Leptopius*, *Stenocorynus* Schoenherr, Leptopiini; *Leptomias* Faust, Tanymecini), with the exterior surface mostly smooth or densely papillose (e.g., *Catasarcus*, *Essolithna* Pascoe, Leptopiini; some *Otiorhynchus*, Otiorhynchini); (b) a longer, tubular posterior section having papillae variable in size, distribution and density. Malpighian tubules six in number, cryptonephric; usually located on anterior end of hind gut, anteriorly arranged in one group of four (entering a common chamber in some species, e.g., *Eurymetopus birabeni* Kuschel, Naupactini) and another group of two shorter tubules; posteriorly arranged in two groups of three each, usually in ventrolateral position (dorsal in, e.g., some *Leptopius*, *Perperus* Schoenherr, *Stenocorynus*, Leptopiini).

Prothoracic ganglion separate, mesothoracic and metathoracic ganglia usually fused; abdominal ganglionic chain strongly condensed, with two discrete complexes or only one compound ganglion; some groups with compound meso-metathoracic-abdominal ganglion (some genera of Sitonini and Naupactini). [Muir 1918; Heller 1925; Ting 1936; van Emden 1936, 1944; Marshall 1945; Morimoto 1962 a; Oberprieler 1988; Thompson 1992; Howden 1995; Kuschel 1995; Zherikhin & Gratshev 1995; Morimoto & Kojima 2003; Velázquez de Castro *et al.* 2007; Lanteri & del Río 2008; internal anatomy: Aslam 1961; Calder 1989, 1990.]

Morphology, Larvae (Fig. 3.7.5.7 A–G, 3.7.5.8 A–I, and 3.7.5.9 A–F). The numbers of setae refer to one side of bilateral or paired structures.

Body (Fig. 3.7.5.1 A and 3.7.5.7 A) comma-shaped, apodous, slightly sclerotized. Cuticle smooth or with fine asperities; vestiture consisting of sparsely distributed setae.

Head (Fig. 3.7.5.7 B–G and 3.7.5.8 A, B) usually exposed, but in some cases partially retracted into thorax (e.g., Naupactini). Frontal sutures distinct, vestigial or absent; endocarina (Fig. 3.7.5.7 F) usually absent or vestigial but distinct in Sitonini and Tropiphorini. Stemmata usually present as two dark, pigmented spots (Fig. 3.7.5.7 B, F); large, under convex cornea in Ectemnorhinini and Pachyrhynchini. Five dorsal epicranial setae (*des*) present on each side (Fig. 3.7.5.7 C, E–G and 3.7.5.8 A, B), *des3* and *des5* longest, *des3* on frontal line, sometimes touching frons or epicranium; four frontal setae (*fs*) present, *fs4* longest, *fs5* also usually well developed but reduced or vestigial in Ectemnorhinini and Pachyrhynchini; sensillum next to *des2* absent; four minute posterior epicranial setae (*pes*); two ventral cranial setae (*vcs*) usually unequal in size, *vcs2* much smaller. Labrum (Fig. 3.7.5.8 C) usually pigmented in two subtriangular areas, but uniformly pigmented in Ectemnorhinini and Pachyrhynchini; epipharynx (Fig. 3.7.5.8 D–F) with clusters of sensilla between median epipharyngeal setae (*mes*); labrum-epipharynx with labral rods usually subparallel, sometimes divergent in distal half (e.g., Brachyderini, Otiorhynchini, Polydrusini, Tanyrhynchini), U-shaped in Naupactini. Antennae one-segmented, with sensorium (Fig. 3.7.5.7 D) wider than long, cushion-like, usually truncate or widely rounded at apex (shortly ogival in Tropiphorini), symmetrical in mature larvae but mostly projected outward in earlier instars (Fig. 3.7.5.7 G), asymmetry persistent in entire larval stage in Sitonini; antennae usually in transverse position on anterior margin of head (Fig. 3.7.5.7 C, G) and sensorium ellipsoidal in apical view, in oblique position (Fig. 3.7.5.7 F) and sensorium circular in apical view in Ectemnorhinini, Pachyrhynchini and Tropiphorini. Mandibles without mola or prostheca, usually bidentate at apex but unidentate in Pachyrhynchini and tridentate in Sitonini; accessory teeth usually absent on cutting edge but present in Ectemnorhinini and Pachyrhynchini; mandibular scrobe usually weakly sclerotized and pale but sclerotized in Ectemnorhinini, Pachyrhynchini, Sitonini and Tropiphorini, usually including both mandibular setae. Maxillae with mala holding four ventral setae (*vms*) and frequently eight dorsal setae (*dms*) in a row. Labium with posterior extension of premental sclerite usually subparallel at sides and truncate or expanded at apex, but subtriangular and with convergent sides and acute apex (Fig. 3.7.5.8 H) in Ectemnorhinini, Pachyrhynchini, Sitonini and Tropiphorini.

Pronotum simple, usually pigmented. Legs absent; pedal areas with discrete number of setae. Thoracic spiracles placed on prothorax (Fig. 3.7.5.7 A).

Typical abdominal segments (AII–AVII) with three or four dorsal folds and bearing five postdorsal setae (*pds*) (Fig. 3.7.5.7 A). Segment VIII sometimes with one or more postdorsal setae (*pds*) lost, but bearing the homologous *pds5* of preceding segments. Abdominal apex frequently with modifications, including sclerotizations, particularly in soil-dwelling larvae; anal region terminal or subterminal, usually four-lobed but six-lobed in Pachyrhynchini. Thoracic and abdominal spiracles (Fig. 3.7.5.9 A–F) with two annulated airtubes distinct in early instars but often reduced or absent in last, distinct in all instars in Ectemnorhinini, Pachyrhynchini, Sitonini and Tropiphorini; airtubes usually directed posterad or dorsoposterad, but dorsad in Ectemnorhinini and Pachyrhynchini; spiracle of AVIII (Fig. 3.7.5.7 A) usually lateral but dorsal in Pachyrhynchini. [van Emden 1952; May 1978, 1993, 1994; Chown & Scholtz 1989 b, 1990; Marvaldi & Loiácono 1994; Marvaldi 1997, 1998 a, b.]

Morphology, Pupae (Fig. 3.7.5.9 G, H). Integument creamy white, usually changing to brown

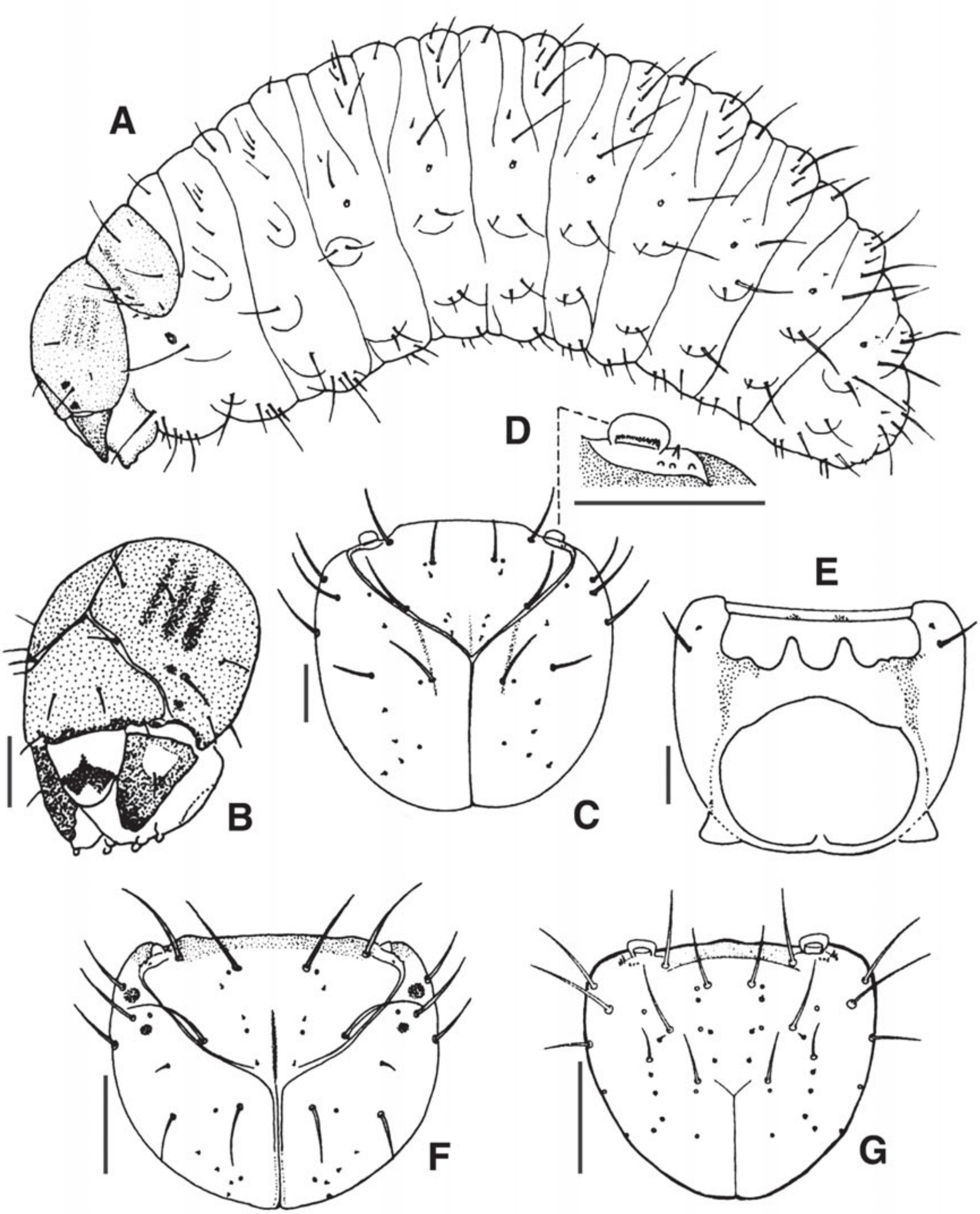

Fig. 3.7.5.7 A–F, Larval morphology. A, *Otiorhynchus sulcatus* (Fabricius), larva in lateral view, length 10 mm; B, *O. sulcatus*, head and mouthparts, general aspect in anterolateral view, scale bar 0.5 mm; C–E, *Cylydrorhinus* sp., first instar. C, head, dorsal, scale bar 0.1 mm; D, antenna, scale bar 0.05 mm; E, head, ventral, scale bar 0.1 mm; F, *Alophus triguttatus* (Fabricius), first instar, head, dorsal, scale bar 0.1 mm; G, *Naupactus leucoloma* Boheman, first instar, head, dorsal, scale bar 0.1 mm.

before eclosion. Setae varying in shape, number and disposition in different taxa; placed on tubercles on frons, rostrum, pronotum, femoral apex and dorsum of abdominal segments. Mandibular thecae large in comparison with other weevils, with setae (one to two) on dorsal surface. Apex of femora with two or fewer setae. Primary pterothecae (elytra) well developed; secondary pterothecae ranging from well developed to strongly reduced, depending on hind wing development in adult. Terminal abdominal segment with paired posterior processes ("pupal urogomphi"), usually sclerotized and with apical spine (May 1978, 1994; Marvaldi 1997).

Phylogeny and Taxonomy. The subfamily Entiminae includes most weevils traditionally

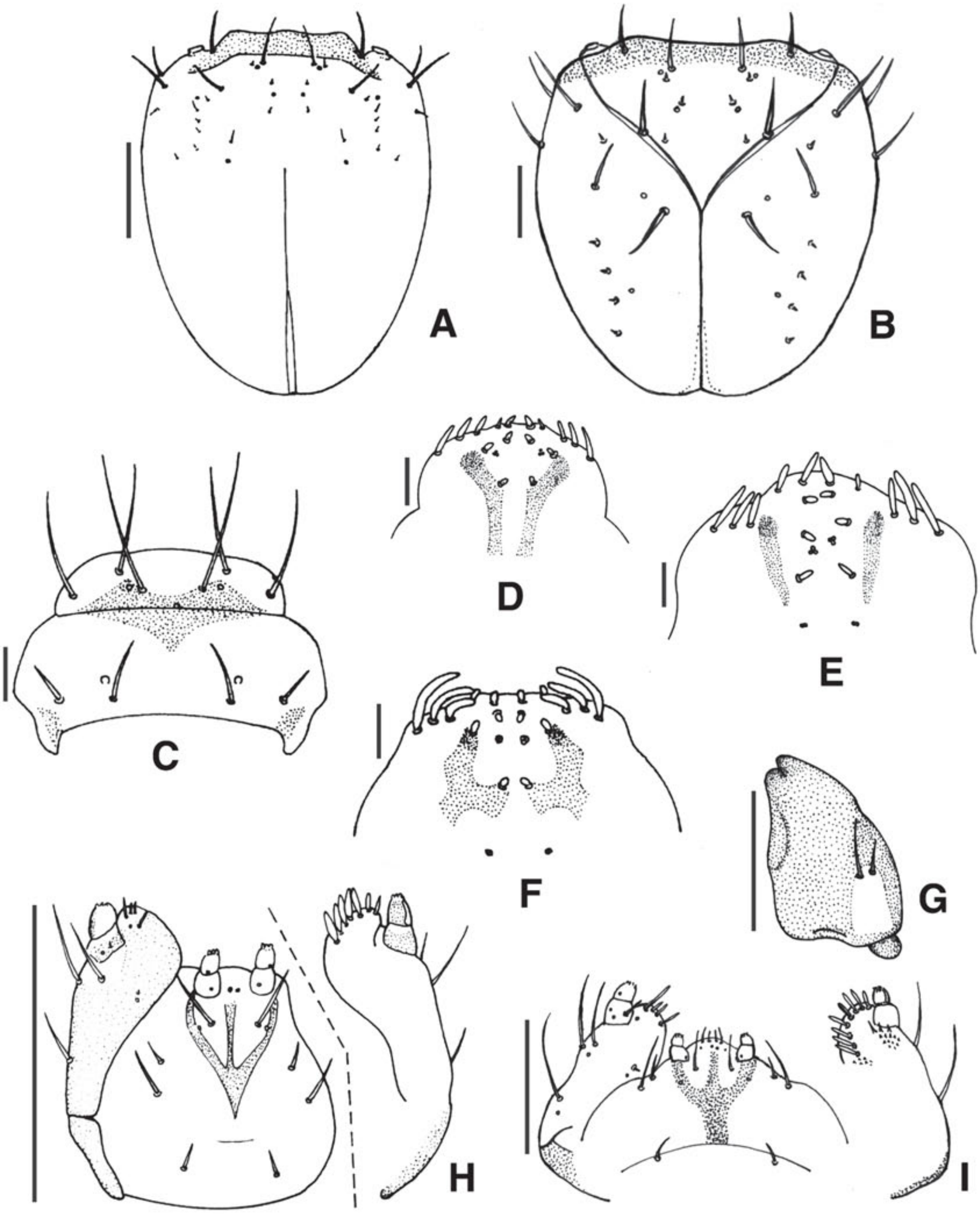

Fig. 3.7.5.8 Larval morphology, head and mouthparts. A, *Naupactus leucoloma* Boheman, head, dorsal, scale bar 0.5 mm; B, *Diaprepes abbreviatus* (L.), head, dorsal, scale bar 0.5 mm; C, *N. leucoloma*, clypeus and labrum, scale bar 0.1 mm; D, *Otiorhynchus sulcatus* (Fabricius), epipharynx, scale bar 0.1 mm; E, *Entimus sastrei* Viana, epipharynx, scale bar 0.1 mm; F, *N. leucoloma*, epipharynx, scale bar 0.1 mm; G, *O. sulcatus*, mandible, scale bar 0.5 mm; H, *Charagmus gressorius* (Fabricius), maxilla and labium, ventral, and maxilla, dorsal, scale bar 0.1 mm; I, *N. leucoloma*, maxilla and labium, ventral, and maxilla, dorsal, scale bar 0.1 mm.

assigned to the informal category Adelognatha (including the subfamilies Brachyderinae, Eremninae, Leptopiinae, Otiorhynchinae, Tanymecinae and Tanyrhynchinae of older classifications). Several different classifications of this group have been proposed in recent decades. Based on studies of the structure of the metendosternite, ovipositor and other characters, Morimoto (1962 b) was the first to combine many of these traditional adelognathous subfamilies into one, which he called Otiorhynchinae, recognizing Alophinae, Pachyrhynchinae and Sitoninae as separate subfamilies. Wibmer &

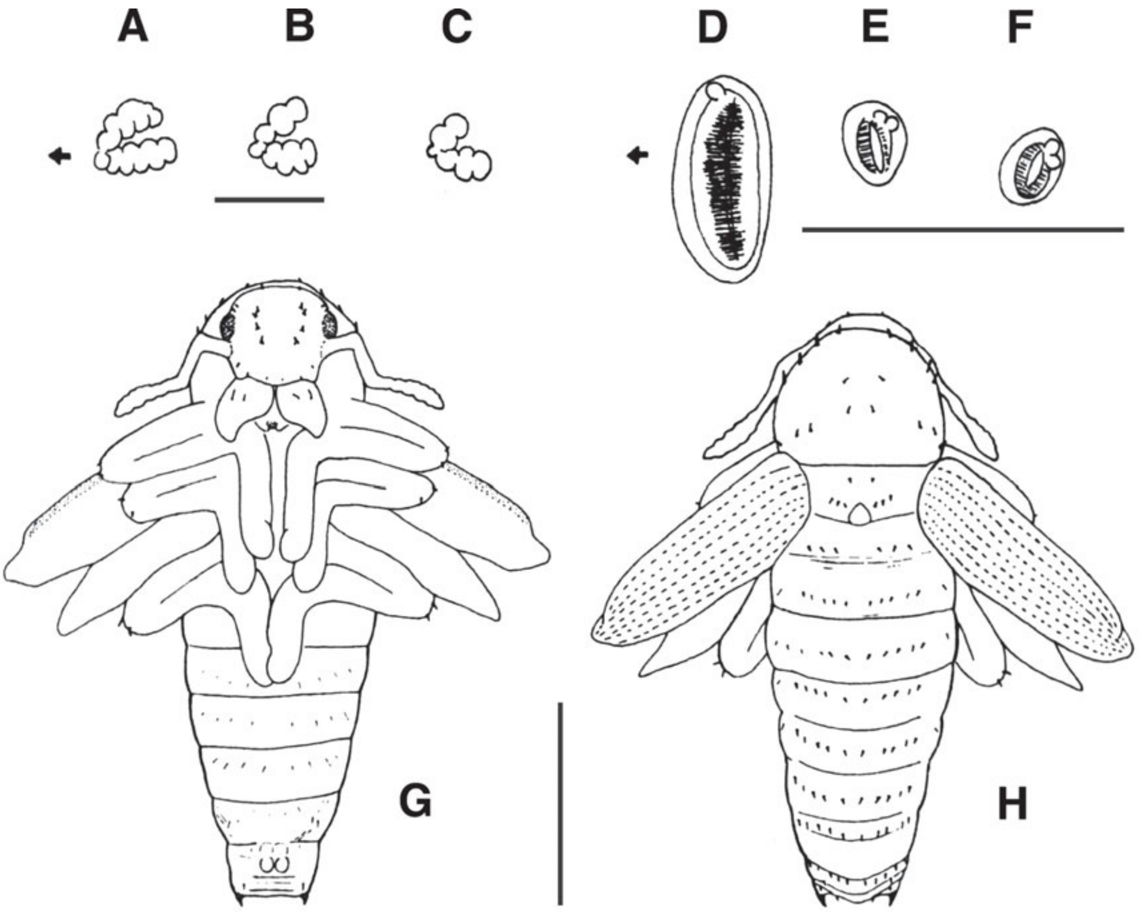

Fig. 3.7.5.9 Larval spiracles and pupal morphology. A–F, *Naupactus leucoloma* Boheman, larval spiracles. A–C, first instar larva, scale bar 0.1 mm. A, thorax; B, AIV; C, AVIII. D – F, mature larva, scale bar 0.1 mm. D, thorax; E, AIV; F, AVIII. G–H, *Naupactus xanthographus* (Germar), pupa. G, ventral; B, dorsal, scale bar 5 mm.

O'Brien (1986: 44, 81), in their checklist of weevils of South America, classified the broadnosed weevils (Adelognatha) into two subfamilies, Polydrusinae and Entiminae. The former subfamily resulted from combining the "otiorhynchine" and "brachyderine" groups, following an unpublished scheme by G. Kuschel, whereas the latter subfamily combined all "leptopiine" groups. Zherikhin & Egorov (1991) were the first authors to include most traditional adelognathous groups in a single subfamily, which they named Polydrusinae, and which included, among other groups, the tribes Entimini and Otiorhynchini. This First Reviser action also determined the relative priority of the simultaneously published family-group names Entiminae Schoenherr, 1823, and Polydrusinae Schoenherr, 1823, not the later opposite one by Alonso-Zarazaga & Lyal (1999), as stated by Bouchard *et al.* (2011). The widely used name Entiminae is nonetheless used here until the issue is settled by the Commission on Zoological Nomenclature. Zherikhin & Egorov (1991) treated Tropiphorinae (Alophinae) as a separate subfamily and as including Sitonini. Thompson (1992), in agreement with an unpublished work by G. Kuschel (see Thompson 1992: 883), included all Adelognatha in a single subfamily, named Entiminae – evidently unaware that the name Polydrusinae had been given preference over Entiminae by Zherikhin & Egorov (1991) – and he suggested that it probably is a monophyletic group based on the presence of deciduous mandibular processes (secondarily lost in a few cases), together with the derived, pedal type of the male genitalia. Like Morimoto (1962 b) and Zherikhin & Egorov (1991), Thompson (1992) also distinguished Pachyrhynchini and Sitonini as well as Ectemnorhinini from all the other tribes of this subfamily. Kuschel (1995) included the Entiminae in a larger subfamily Brachycerinae, but Marvaldi (1997, 1998 a) supported Thompson's (1992) concept of Entiminae as separate from Brachycerinae, adding evidence from larval characters. She recognized only five tribes in Entiminae: Tropiphorini (as Alophini), Pachyrhynchini, Ectemnorhinini, Sitonini and Entimini, the last one including the majority of species in the subfamily. Alonso-Zarazaga & Lyal (1999) divided Entiminae into 55 tribes, but this division and the arrangements of the genera are, in most cases, artificial. For example, Phyllobiini and Polydrusini are probably paraphyletic as their current concepts are based on symplesiomorphies, whereas Brachyderini, Holcorhinini and Sciaphilini are probably polyphyletic (Yunakov & Nadein 2006). The Thecesternini, despite their short rostrum and subterranean larvae, do not belong in Entiminae because they lack the apomorphies defining the subfamily, having instead a number of features that place them in the "curculionine-molytine" clade. In addition, the concept of Tropiphorini is controversial. We follow Zherikhin and Egorov (1991), who treated Alophini as a synonym of Tropiphorini, and use Leptopiini as the name of this large tribe (*contra* Alonso-Zarazaga & Lyal 1999). On the basis of recent and ongoing systematic studies, the concepts of a few tribes are becoming clearer and more likely monophyletic, such as Tanyrhynchini (Oberprieler 1988, 1995), Ectemnorhinini (Kuschel & Chown 1995), Omiini (Borovec 2006, 2010), Sitonini (Velázquez de Castro *et al.* 2007) and Trachyphloeini (Borovec 2009).

The subfamily Entiminae constitutes a monophyletic taxon mainly on the basis of two larval autapomorphies: maxillary mala with four *vms* (other curculionids have five; with an additional seta inserted near the malar sensillum), and antennal sensorium wider than long and cushion-like (Marvaldi 1997). The pupa of Entiminae is characterized by having one or two setae on the mandibular theca, a feature that is even present in taxa lacking mandibular processes in the adult (e.g., Pachyrhynchini, some Ectemnorhinini), thus indicating this absence to be a secondary loss (May 1978, 1994). There are only few known examples of entimines with mandibular processes present but lacking setae in the mandibular theca of the pupa (i.e., *Maleuterpes spinipes* Blackburn, Ottistirini; *Laparocerus undatus* Wollaston, Laparocerini; May 1994; Machado 2010).

Entimine adults are generally diagnosed by having a relatively short and broad rostrum (Fig. 3.7.5.2 A–D), with a deciduous process on each mandible (Fig. 3.7.5.3 A, B) that leaves a scar (Fig. 3.7.5.3 C, D, F) on the mandibular surface after dehiscence. Their mouthparts are usually adelognathous, with the prementum covering the maxillae (Fig. 3.7.5.3 C, F), the antennal scapes (Fig. 3.7.5.2 A–C) usually reach or surpass the anterior margin of the eyes when folded backward, and the tibiae are mucronate or unarmed, sometimes retaining spurs. According to Thompson (1992) some characters of the adults, although not unique for the taxon, must be synapomorphic for Entiminae as well, the most important being the presence of deciduous processes on the mandibles. These processes also occur in several genera of Brachycerinae (i.e., *Brachycerus* Olivier, Brachycerini; *Hoplitotrachelus* Schoenherr, Byrsopini; *Desmidophorus* Dejean, Ocladiini) and are thought to have evolved independently (Thompson 1992; Marvaldi 1997). Adelognathous mouthparts are characteristic of the great majority of Entiminae but not unique to this subfamily, because they also occur in a number of other curculionoids (Thompson 1992), including several genera of Brachycerinae. Although it is possible that basal entimines retain phanerognathous mouthparts, it appears that adelognathy evolved early in the subfamily and was reversed secondarily in a few groups. A third imaginal feature characteristic of many Entiminae is the occurrence of true corbels on the hind tibiae, but this character is also present in some genera of Brachycerinae.

Recent phylogenetic studies based on morphological and/or molecular data (Marvaldi 1997; Marvaldi *et al.* 2002; McKenna *et al.* 2009) place entimines among the "higher curculionids", suggesting that brachycerines and erirhinines branched off earlier in the diversification of the family and form part of a paraphyletic basal grade that is close to, but not included in, the clade Entiminae. These studies also suggest that the closest relative of Entiminae is probably a group contained within the Cyclominae (including Amycterini, Hipporhinini, Listroderini, Rhythirrinini, etc.; Oberprieler 2010), but the currently available evidence is too weak to clearly identify the exact sister group.

The entimines and cyclomines share a number of biological and morphological features, along with some Brachycerinae, Thecesternini, *Brachyceropsis* Aurivillius (Molytinae) and some brentids such as Ithycerinae and Microcerinae. They do not use the rostrum for preparing an oviposition site in plant tissues, and their larval development is primarily in the soil. These biological traits are related to the shape and development of the rostrum and characterize most "broad-nosed weevils" as classified by Kuschel (1995) in his broadened concept of Brachycerinae (see also May 1993). The larvae of Entiminae and Cyclominae have the dorsal epicranial setae 3 (*des3*) placed on the frontal line or on the frons (not on the epicranium). This character occurs also in Brachycerinae (including Erirhinini), Bagoini and some genera currently in Molytinae (Oberprieler 2010) and may either be homoplasious or represent an ancestral feature of Curculionidae that is plesiomorphic for Entiminae and Cyclominae. The shape of male sternite IX is probably a synapomorphy for Entiminae and Cyclominae: its basal part is largely sclerotized, with the arms broad and usually lobe-shaped, whereas in other weevils the basal part is largely membranous and the arms of the fork are narrowly pigmented. Because Entiminae and Cyclominae have the pedal type of male terminalia, characterized by a number of derived traits (i.e., penis without tectum, the pedon navicular to tubular; apodemes of penis deflexed ventrad; tegmen dorsally with parameres absent or reduced to asetose lobes; spiculum gastrale (sternite IX) well developed, often much larger than manubrium), they may share a common ancestor with other "higher curculionids" rather than with Brachycerinae, which retain the plesiomorphic pedotectal type of male genitalia (penis with dorsal tectum, apodemes of penis arising from dorsal side and sometimes forming a bridge, tegmen with well developed and often setose parameres, spiculum gastrale smaller than tegmen). Although extreme reduction of the tectum and/or a tendency to form a tubular penis independently occurred several times in curculionoids and chrysomeloids (although, in these cases, by fusion of pedon and tectum), the morphological and molecular evidence currently available supports Entiminae belonging to a curculionid clade defined by the synapomorphic pedal type of genitalia. Phylogenetic studies to clarify both the position of Entiminae in the curculionid tree and the monophyly and relationships among the different groups within this weevil subfamily are needed.

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