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Re: Chapter on Entiminae. Received on 28 August 2007

Dear Dr. Marvaldi:

I am pleased to inform you that the chapter on Entiminae (Curculionoidea), by A. E. Marvaldi, A. A. Lanteri, M. G. Del Río, and R. G. Oberprieler, is accepted for publication in the Handbook of Zoology, Coleoptera II (R. Beutel & R. Leschen, Eds.), deGruyter Press.

Thank you for this contribution.

Sincerely,



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Entiminae Schoenherr, 1823

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Distribution. The Entiminae as a whole are cosmopolitan since they occur in all biogeographic regions (Nearctic, Palaearctic, Neotropical, Afrotropical, Oriental, Australian and Chile/southern Argentina). None of the tribes are worldwide distributed, of the 55 tribes recognized by Alonso-Zarazaga & Lyal (1999), 40 are represented mainly in a single region or in a particular area of this region, 10 occur in two biogeographic regions (e.g. Nearctic and Palaearctic; Palaearctic and Oriental; Afrotropical and Oriental; Afrotropical and Palaearctic; Australian and Chile/southern Argentina), and other five occur in more than three regions. As an example, Agraphini, Geonemini, Hormorini, Ophryastini are typically Nearctic; Holcorhinini, Otiorhynchini, Phyllobiini and Sciaphilini, Palaearctic; Anypotactini, Entimini, Eudiagogini, Eustylini, Lordopini and Naupactini, Neotropical; Cneorhinini, Cratopini, Embrtitini, Leptostethini, Myorhinini, Oosomini and Tanyrhynchini, Afrotropical; Mesostylini, Nastini, Omiini and Pachyrhynchini, Oriental; Celeuthetini, Eupholini, Ottistirini and Prypnini, Australian; and Anomophthalmiini is endemic to Chile/southern Argentina.

There are some tribes with reduced geographic ranges, such as Nothognathini, that only occurs in India, Ophthalmorrhynchini in Congo, Premnotrypini in the high Andes of northern South America, Typhlorhinini in Madagascar, Ectemnorhinini in small islands of the southern Indian Ocean (Kerguelen, Marion and Prince Edward Islands), Elytrurini in Polynesia, Laparocerini in Macaronesian islands (Azors, Madeira and Canary Islands), Polycatini in Philippines, and Rhyncogonini in various islands of the eastern Pacific (Marquesas, Hawaii and Tahiti). There is also one extinct tribe from the Upper Miocene of Germany (Alonso-Zarazaga & Lyal, 1999).

Notes.

“Broad-nosed weevils” of the subfamily Entiminae are characterized by the presence of a relatively short, broad rostrum and mandibular deciduous processes that leave a scar on

the outer mandibular surface. They include most weevils traditionally assigned to the Adelognathi = Otiornychinae, Brachyderinae, Eremninae, Tanymecinae, and Tanyrnynchinae of the old classifications.

Biology and Ecology (Fig. x.x.1 A-D). Larvae (Fig. x.x.1 A) of most Entiminae live freely in the soil, feeding externally on the roots of their host plants. Pupation (Fig. x.x.1 B) also occurs in the soil, in an earth cell lined with a larval secretion. Adults (Fig. x.x.1 C) feed on the aerial green parts of the plants, especially fresh leaves or flowers, cutting their edges in a characteristic “notching”.

Life cycles usually take about a year, but in some cases it is completed in two or three years (Young *et al.* 1938; May 1994). Larvae overwinter underground (usually as prepupae) and pupate in warmer months, teneral adults emerge from the soil during the spring- summer seasons. The longest part of the cycle occurs as larvae, which is the stage more injurious for the plants. The number of instars varies among species, *e.g.*

Premnotrypes latithorax four instars (Tisoc-Dueñas 1989) and *Naupactus leucoloma* eleven instars (Matthiessen 1991).

Females of Entiminae (as well as those of other broad-nosed weevils classified in Cyclominae) do not use the rostrum for preparing an oviposition site. There are two basic oviposition types within Entiminae: eggs deposited loosely and at random (“Sitona type”) and eggs deposited in batches between adjoining surfaces (“Brachyderes type”).

Oviposition inside plant tissues was never seen in this weevil subfamily (Emden 1950, 1952; Marvaldi 1999). Eggs laid randomly are usually placed on plants, surface litter, or soil, and become black as they develop; eggs laid in batches are covered with adhesive glutinous substance secreted during oviposition, they are hidden between adjoining surfaces (leaves, cracks in the soil, crevices, litter, or various niches near the soil) and remain pale (Marvaldi 1999). Each posture (Fig. x.x.1 D) consists on an agglutinate cluster of 20-80 eggs, a number that could vary depending on the food resources, time after emergence and other environmental conditions. The fecundity of the entimines is very high compared to other weevil subfamilies. Eggs hatch after 5 to 20 days, being affected by temperature and humidity.

Soil-dwelling larvae and polyphagy are characteristic features of the Entiminae, most of them feeding on a variety of plants (different families within the angiosperms) in both adult and larval stages. The biology of Pachyrhynchini and Ectemnorhinini differs from that of most members of Entiminae, since their larvae do not feed on roots in the soil, and their species show particular associations with cryptogams (symbiotic and for feeding, respectively).

The Pachyrhynchini have “arboreal” habits, the adults feed on leaves, young growth or flowers of jungle trees (some species of *Pantorhytes* became pest of cultivated cacao plants), the larvae tunnel in branches of the plants, and pupation occurs *in situ*, within a chamber covered with plant fibers and frass (May 1978). Oviposition is also divergent from other entimines, the eggs being apparently laid single in the bark (Emden 1952). Some species of *Pantorhytes* that live in humid forests at high elevations in the mountains, have an epizoic symbiosis with cryptogamic plants and microfauna (Gressitt 1966). Lichens, algae and mosses grow over weevil’s pronotum and elytra, providing camouflage and protection to the insects. Moreover, there are rotifers, nematods and acari living on the lichens that grow over the weevils.

The Ectemnorhinini have feeding habits that include angiosperm and cryptogam herbivory (Chown 1994). Larvae and adults mainly feed on bryophytes and lichens, some on cyanobacteria, algae, mosses, and only few species feed on angiosperms (Chown 1989; Chown & Scholtz 1989a). Members of the genera *Canonopsis*, *Christensenia* and *Ectemnorhinus* are the only ones that feed on angiosperms, but also incorporate bryophytes and other cryptogams in their diet (Chown 1989). They are polyphagous, except for *Palirhoeus eatoni*, which is oligophagous, feeding on three species of marine algae (Chown 1994). Eggs are deposited individually or in small groups, in ground litter below the host plant or among plant parts, they turn black as they develop. Larval development (seven instars reported for species of *Ectemnorhinus*) also occurs on or near the soil surface, usually among mat plants or plant detrits (Chown & Scholtz 1989a).

The Entiminae constitute a clade of angiosperm feeders, being primarily associated with angiosperm plant taxa (Marvaldi *et al.* 2002). Associations of entimine weevils with gymnosperms or with cryptogam plants most likely constitute secondary host-shifts, and / or represent expansions of the original host-plant range in polyphagous

species. Species of Entiminae feed on both monocots (e.g. Poaceae) and on a great variety of dicot families: Fabaceae, Fagaceae, Malvaceae, Rosaceae, Rutaceae, Solanaceae, etc. Legumes are among the main hosts of the Entiminae. It is not uncommon among polyphagous species that adult and larval stages feed on different plant taxa, ie. adults on leaves of various dicots and larvae on roots of monocots (pastures) (Marvaldi 1998b). The frequency of the host shifts depend not only of the physiology of plants and weevils, but also on the availability of these plants in a given area. *E.g.* adults of *Pantomorus ruizi* (Naupactini), known to feed on various dicots, have been recently found consuming pine needles in Patagonia, whereas larvae probably feed on roots of grasses growing around the trees (Gómez & Lanteri 2006), and adults of the Palaearctic species *Otiorhynchus kollari* were found feeding on cryptogams (ferns) (Muñiz 1970).

Even when polyphagous, they can show definite host preferences, *e.g.* South American species of *Pandeleiteius* (Tanymecini) are associated to trees and shrubs of the families Anacardiaceae (*Schinopsis* and *Schinus*), Asclepiadaceae (*Baccharis*) and Fabaceae (*Prosopis*), and those of *Enoplopactus* (Naupactini) are associated to shrubs of the subfamily Zygophyllaceae (*Larrea*) (Lanteri *et al.* 2002). *Phyllobius oblongus* (Phyllobiini) is very much common on elm (*Ulmus* spp: Ulmaceae) and blackthorn (*Prunus spinosa*: Rosaceae) than in other trees (Morris 1976). Species of *Sitona* are much more stenophagous than most Entiminae, being mainly associated with legumes (Fabaceae), the adults feed on leaves and the larvae on the nitrogen-fixing root nodules and on roots (Manglitz *et al.* 1963; Velázquez de Castro 2004; Velázquez de Castro *et al.* 2007). *Barynotus moerens* (Geonemini) is a rare example of monophagous species of Entiminae, only feeding on the roots of a European herb toxic to vertebrates (*Mercurialis perennis*: Euphorbiaceae) (Morris 1976).

Some pest species worldwide distributed are extremely polyphagous having hundreds of host plants, most of them cultivated. Adults do not injure plants seriously, except when they are very numerous, but the larval damage to roots is usually most harmful. Among the most serious pests classified in Entiminae are the “white fringed beetles” *Naupactus leucoloma*, *N. peregrinus* and *N. minor* (Naupactini); the “twobanded Japanese weevil” *Callirhopalus bifasciatus* (Trachyphloeini); the “black vine weevil”,

Otiorhynchus sulcatus (Otiorhynchini); and the “Andean potato weevils”, *Premnotrypes* spp (Premnotrypini).

The “White fringed beetles” are native to Southern South America, but they have reached a wide distribution, particularly in the cooler or more seasonal growing areas of southern USA, Australia, New Zealand and South Africa (Lanteri & Marvaldi 1995). They are considered serious pests of a number of crops. Adults feed on at least 385 species of plants, preferring those with large broad leaves, including peanut, soybean and many other leguminous crops (Young *et al.* 1938).

The “twobanded Japanese weevil” was first recorded for the United States at the beginning of the XX century and it is now firmly established in the eastern United States, where it feeds on a several ornamental plants and strawberry (Maier 1983; Wheeler & Boyd 2005).

The “black vine weevil” is native to Europe and has been a serious pest for the horticultural nursery industry during the past two decades. It damages a large number of horticultural species and perennial herbaceous plants, shrubs and climbers. Such a broad host range and the ability to develop on most gymnosperms and broad-leaved plants, has enable this beetle to establish itself in nurseries, greenhouses and landscapes around the world (Moorhouse *et al.* 1992; van Tol *et al.* 2004).

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 1997-1998). They occur only in South America (Argentina, Bolivia, Chile, Colombia, Ecuador, Perú and Venezuela), particularly in the high-altitude potato-growing areas about 3000 m on 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 of the genus are *P. latithorax* (in Perú) and *P. vorax* (in Venezuela).

Most Entiminae show habitat or stratum preferences rather than plant specializations. *E.g.* Flightless species of *Eurymetopus* and *Atrichonotus* (Naupactini) are prairie adapted, feeding on herbs and grasses (Lanteri *et al.* 2002), whereas full winged *Entimus* and *Phaedropus* (Entimini) are rain forest adapted, living and feeding on trees (Morrone 2002). *Galapaganus* species (Naupactini) inhabit along coastal deserts of the

Pacific of South America (Ecuador and Perú) and colonized the Galápagos islands, demonstrating high salt tolerance (Lanteri 1992; Sequeira *et al.* 2000) and *Otiorhynchus ligneus* inhabits halophylous environments where it feeds on unicellular and filamentous terrestrial algae (Muñiz 1970). Species of *Pandeteius* (Tanymecini) are mainly associated to trees and shrubs typical of xeric and semi-desert environments; *Otiorhynchus* subgenus *Troglohynchus* (Otiorhynchini) live on the ground under stones; and *Cylydrorhinus* (Cylydrorhinini), under stones, wood and cushions from steppes of grasses and shrubs of Patagonia (Muñiz 1970; Lanteri *et al.* 2002). Species of *Panthorhytes* (Pachyrhynchini) are arboreal feeders, being native of rainforests of the Papuan region (May 1978, 1994). The Ectemnorhinini are mostly cryptogam feeders in epilithic biotopes of Subantarctic islands of Indian Ocean (Chown 1989).

Parthenogenesis in Entiminae. Although most entimine species have sexual reproduction, there are some species in this subfamily that reproduce by parthenogenesis. Within the Curculionidae other two subfamilies include parthenogenetic species: Scolytinae (bark beetles) and Cyclominae (another broad-nosed weevil subfamily) (Suomalainen *et al.* 1987).

About 75 parthenogenetic weevil species have been cited thus far (Saura *et al.* 1993) and among them, over 50 are Entiminae (Smith & Virkki 1978; Lokki & Saura 1980; Bell 1982; Takenouchi 1986; Suomalainen *et al.* 1987). They belong to 13 tribes according to Alonso-Zarazaga & Lyal (1999): Blosyrini (*Blosyrus japonicus*), Cneorhinini (*Catapionus gracilicornis*), Cyphicerini (*Myllocerus nipponicus*, *M. fumosus*, *M. griseoides*, *Myosides serioehispidus*, *M. pyrus*, *Cyrtepistomus castaneus*), Geonemini= Barynotini (*Barynotus moerens*, *B. obscurus*, *B. squamosus*), Naupactini (*Aramigus tessellatus*, *Naupactus cervinus*, *N. leucoloma*, *N. peregrinus*), Otiorhynchini (*Otiorhynchus scaber*, *O. sulcatus*, other 15 spp of *Oriorhynchus*, *Sciopithes obscurus*), Peritelini (*Peritelus hirticornis*), Polydrusini (*Polydrusus mollis*, *Liophloeus tessulatus*), Sciaphilini (*Eusomus ovulum*, *Fourcartia squamulata*), Strophosomini (*Strophosoma melanogrammus*), Tanymecini (*Scepticus insularis*), Trachyphloeini (*Callirhopalus minimus*, *C. bifasciatus*, *C. obesus*, *C. setosus*), *Trachyphloeus aristatus*, *T. bifoveolatus*,

T. scabriculus, *Trachyrhinus* sp.), Tropiphorini (*Tropiphorus carinatus*, *T. cucullatus*, *T. terricola*).

A particularly high frequency of parthenogenetic lineages has been found in *Otiorhynchus* Germar, a diverse weevil genus native to the Old World, including some of the most serious insect pest for agriculture (Tomiuk & Loeschke 1992). *Otiorhynchus scaber* has been studied in much detail by geneticists and molecular biologists and it is frequently cited as a model of bisexual-parthenogenetic system in ecology and evolutionary studies (Stenberg et al. 2000, 2003).

Most parthenogenetic weevils have been reported for Central and Northern Europe and Japan, but this is probably an artifact caused by the distribution of the specialists that have been working in the subject. They also occur in Australia, New Zealand, North America and South America, the latter probably harboring several parthenogenetic Entiminae. Lanteri & Normark (1995) published a list of 34 South American species of Naupactini that are known (by rearing experiments and cytological studies) or suspected (unknown males in their population) to be parthenogenetic.

Parthenogenetic weevils are telytokous, this means that unfertilized eggs produce only females. Moreover, cytological studies have revealed that every weevil female reproduces by apomixis, and since no meiosis is involved, the offsprings are genetically identical unless mutation occurs (Smith & Virkki 1978; Suomalainen *et al.* 1987; Vepsäläinen & Järvinen 1979).

The morphological characters most strikingly correlated with parthenogenetic weevils are the reduction or absence of the metathoracic wings and the elytral humeri (Lanteri & Normark 1995; Scataglini *et al.* 2005). The only exceptions to this rule are *Polydrusus mollis* Stroem (Entiminae, Polydrusini) and *Listroderes costirostris* Schoenherr (Cyclominae, Listroderini) (Takenouchi 1970; Lokki et al. 1976). Flightlessness seems to evolve when the energetic cost of flight is high, e.g. cold and/or windy habitats (Roff 1990; Wagner & Liebherr, 1992; Lanteri & Normark 1995). Reduced vagility (loss of flight) may facilitate the origin of apomixis (Vepsäläinen & Järvinen 1979). Apomictic weevils are frequently polyploid, being triploidy the most common level of ploidy among them. Another morphological feature associated to

parthenogenesis is the larger body size or robustness of polyploids compare to diploids (Suomalainen 1969; Suomalainen et al. 1987).

There are two main hypotheses to explain the origin of parthenogenesis and polyploidy in weevils, the first assumes 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 as an irreversible change. There is a third hypothesis according to which endosymbiotic bacteria of the genus *Wolbachia* may play a role in the origin of apomixis. These bacteria maternally transmitted is responsible of several reproductive alterations in insects, such as feminization, cytoplasmic incompatibility, male killing and automictic parthenogenesis in hymenopteran wasps (Werren *et al.* 1995; Werren 1997), however, until present it has never been shown to induce apomictic parthenogenesis (Normark 2003). The finding of *Wolbachia* strains in *Otiorhynchus scaber* (Stenberg *et al.* 2003; Stenberg & Lundmark 2004), *Araucarioxylum tessellates* (Braig *et al.* 2002), *Naupactus cervinus* and other South American Naupactini (Rodriguero *et al.* 2005) is a starting point to elucidate the role of these bacteria in the origin of parthenogenetic weevils.

Whichever hypothesis holds true, parthenogenetic reproduction and polyploidy may be widespread in broad-nosed weevils because it arises repeatedly and/or because it creates novel possibilities for diversity and adaptation. 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 effect of mutations (these first two advantages result from gene duplication), and 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 related species, these forms, as a rule, have different distributions (Vandel 1928). Usually, the parthenogenetic form has a much broader distribution than the respective bisexual form, and such cases

are termed “geographical parthenogenesis” (Suomalainen 1969; Suomalainen & Saura 1973; Takenouchi 1976).

Studies on species of the *genus Otiorhynchus*, showing geographical parthenogenesis, like *O. scaber*, support the idea that polyploidy in it self is an important factor to explain the broad distribution of parthenogenetic races (Stenberg *et al.* 2000) and that polyploid clones are superior colonizers compared to sexual and diploid clones (Stenberg & Lundmark 2004). An exception to this pattern is seen in *Liophloeus tessulatus* (Polydrusini), with a parthenogenetic race restricted to mountains of central Europe and a bisexual race widespread in this continent, mainly at lower altitudes. There are also cases in which the bisexual and the parthenogenetic forms coexist (Suomalainen & Saura 1973).

“Geographical parthenogenesis” not only has been reported for European weevils but also for some Naupactini native to South America: *Aramigus tessellatus*, *Naupactus cervinus*, *N. leucoloma* and *N. peregrinus* (Lanteri 1984, 1993; Lanteri & Normark 1995). The introduction, establishment and posterior dispersal of clones of these species in Australia, New Zealand, the US and other countries far from their original distributions, is another example of the ability of parthenogens to colonize new environments. 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).

Morphology, Adults (Figs. x.x. 2 – x.x. 6) [Emden 1936, 1944; Heller 1925; Howden 1995; Kuschel 1995; Lanteri & del Rio, in press; Marshall 1945; Morimoto 1962; Morimoto & Kojima 2003; Muir 1918 ; Thompson 1992 ; Ting 1936; Velázquez de Castro *et al.* 2007; Zherikhin & Gratshev 1995]

Diagnosis. Weevils with a relatively short and broad rostrum (Fig. x.x. 2 A-D), with a deciduous process on each mandible (Fig. x.x. 3 A,B), that leaves a scar (Fig. x.x. 3 C, D) on mandibular surface after dehiscence. Mouthparts usually adelognathous, with prementum covering maxillae (Fig. x.x. 3 C, D). Antennal scape (Fig. x.x. 2 A-C) usually reaching or passing anterior margin of eye when laid backwards. Tibiae mucronate (Fig. x.x. 5 A, D) or unarmed.

General appearance (Fig. x.x. 2 A-D). Length about 4 – 30 mm. Body slightly flattened to moderately convex or strongly convex. Integument 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 deserts and high mountains usually dull colored, black or dark brown, covered with setae of various lengths but usually lacking scales. Species from rain forests usually colorful, covered with dense vestiture of greenish, bluish, golden, bright scales, in some cases with aposematic coloration.

Head and mouthparts (Figs. x.x. 3 A-D, x.x. 4 A-C). Head relatively large, not subspherical. Eyes slightly to strongly protuberant, variable in size and shape (ovate to subcircular), separated by about width of rostrum (usually facing outward on head). Rostrum broad, stout, short, at most about twice longer than wide, usually about as long to shorter than head, porrect (Fig. x.x. 1 C) or directed slightly downwards (Fig. x.x. 2 C), subcircular to subquadrate in cross-section. Antennal insertions (Fig. x.x. 3 B) lateral, concealed from above, sometimes dorsal. Scrobes well developed, exposed or partially concealed in dorsal view of head. Gular sutures confluent ((Fig. x.x. 2 D). Antennae (Fig. x.x. 2 B, x.x. 3 B) with 11 antennomeres, geniculate, scape usually more than 3 times as long as first funicular antennomere, almost reaching to exceeding anterior margin of eyes; funicle 7-segmented; club 3-segmented and compact. Mouthparts usually adelognathous (maxillae covered by prementum ((Fig. x.x. 3 C, D), which is usually large and not pedunculate); phanerognathous mouthparts (maxillae exposed continuously at sides of prementum) recorded for Sitonini, Ectemnorhinini, and some isolate genera of other tribes (Alophini, Cylydrorhinini, etc.). Labrum indistinct. Epistoma (clypeus) sometimes raised (Fig. x.x. 2 C) or impressed. **Mandibles** (Fig. x.x. 3 A-D) short and broad, plurisetose and / or squamose, partially visible from above and from lateral view, in many cases concave on their meso-ventral surface, without mola, moving in a near horizontal plane, inserted within distinct socket (pleurostomal sinus). Mandibular pharyngeal process (Fig. x.x. 4 A) about as long to shorter than mandible. Each mandible of teneral adults usually with a deciduous blade-like process (Fig. x.x. 3 A, B), smooth, bare and greatly variable in shape, being either straight (e.g. *Heterostylus*), incurved (e.g. *Naupactus*) or extrorse (e.g. Promecopini), sometimes with a tooth on inner edge, near

base (e.g. *Astycus lateralis*). Mandibular process usually well developed and present in both mandibles, or in left mandible only (e.g. some Sitonini: *Eugnathus* and *Catachenus*), minute or vestigial in some Entimini and Cylydrorhinini (e.g. *Leptostethus speciosus*, *Bothynorhynchus lascibus* and *Caneorhinus angulatus*), absent in Pachyrhynchini, *Sitona* and some Ectemnorhinini, and modified as accessory cusps in *Cecractes* and some Sitonini. Several Entiminae (e.g. some species of Tanymecini, Brachyderini, Otiorhynchini, Tanyrhynchini and Entimini) with deciduous processes mounted on a pedicel, punctate and setose (e.g. *Iphisomus*) or showing sexual dimorphism (e.g. *Prostomus scutellaris*). Early adults usually losing mandibular processes by active dehiscence, leaving a distinct well-defined rough area or scar (Fig. x.x. 3 C,D), sometimes very small (e.g. *Tanyrhynchus*) or worn away completely (e.g. some Alophini and *Otiorhynchus* spp.). Six entimine species (*Leptomias waltoni*, *Chlorophanus excisus*, *Prypnus trituberculatus*, *Stereogaster globosa*, *Bletonius hustachei* and *Anomonychus henoni*), with deciduous processes retained 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 to emerge up to the surface from its subterranean pupal cell (Thompson 1992 and references therein)]. **Maxillae** (Fig. x.x. 4 B) usually with a single apical lobe or mala; galea and lacinia fused, but sometimes differentiated by sclerotization and arrangement of setae or spines, or galea and lacinia broadly connate (partially divided) in Sitonini and some genera of Alophini and Naupactini; stipes fused with lacinia in its mesal margin; maxillary palpi three segmented; and apical maxillary palpomere cylindrical to fusiform. **Labium** (Figs. x.x. 3 C, D, x.x 4 C) usually adelognathous (with prementum enlarged and covering maxillae); phanerognathous type (maxilla exposed continuously at sides of prementum) only present in Sitonini, Alophini, Ectemnorhinini, Cylydrorhinini and some genera of other tribes. Postmentum short or indistinct, not pedunculate in adelognathous. Ligula indistinct or represented by membranous area between palps. Labial palpi (Fig. x.x. 4 C) three segmented (two segmented in *Amystax*, Tanymecini; *Episomus*, Episomini and *Blosyrus*, Blosyrini), attached to ental surface, usually near apex of prementum.

Thorax. Prothorax (dorsal and lateral views) (Fig. x.x. 2 A-C) with anterior margin and sides curved or straight; base distinctly narrower than elytral base, more or

less straight, evenly rounded or bisinuate. Maximum prothoracic width usually narrower than maximum elytral width. Sides usually lacking ocular lobes and vibrissae (ocular lobes (Fig. x.x. 2 C) present in some tribes like Tropiphorini, Cylydrohrinini, Premnotrypini, Entimini, Tanyrhynchini; vibrissae (Fig. x.x. 3 B) present in Tanyrhynchini and Tanymecini). **Prothorax (ventral view)** (Fig. x.x. 2 D) with prosternal process complete (extending behind coxae) or incomplete (ending before middle of coxae), having a transversal groove in some species; apex of prosternal process acute or broadly rounded, angulate or truncate. Procoxal cavities externally and internally closed; circular or longer than wide; contiguous or narrowly separated. **Pterothorax (dorsal and lateral views)** (Fig. x.x. 2 A-C). Scutellum well developed, absent or not visible. Elytra covering all abdominal tergites, usually with 10 rows or striae, usually punctuated (Fig. x.x. 2 C) (in some cases apunctuated); rarely with supernumerary striae. Hind wings well-developed (three or less free veins in medial area), reduced or absent. Flightlessness reported for Sciaphilini, Omiini, and Holcorhinini, and several genera or species of other tribes e.g. *Otiorhynchus* (Otiorhynchini), *Eurymetopus* and *Galapaganus* (Naupactini), *Sitona* (Sitonini). **Pterothorax (ventral view)** (Fig. x.x. 2 D). Mesocoxal cavities circular to slightly transversal, narrowly to widely separated. Metaventrite flat to convex, longer to slightly shorter than first abdominal ventrite. Metepisternal suture or lateral edge of metaventrite without sclerolepidia. Metacoxal cavities slightly to widely separate. Metendosternite with lateral arms moderately to very long; metendosternal laminae reduced or absent; ventrolateral processes absent or weakly developed; anterior process short or absent; anterior tendons widely separated; apical portion of metendosternite not or only slightly emarginate. **Legs.** Procoxae (Fig. x.x. 2 D) contiguous to slightly separate from each other. Profemur usually stouter than meso y metafemur; inner margin of profemur with one or more denticles in some genera (e.g. *Brachystylodes*, *Hoplopactus*). Apex of tibiae mucronate, with inner apical angle produced forming a tooth, the mucro (Fig. x.x. 5 A, D), or unarmed; tibial spurs usually absent, sometimes minute spurs present (Fig. x.x. 5 A) (e. g. Cylydrohrinini). Inner margin of tibiae simple, crenulate or denticulate (denticles could be present in protibiae or pro- and meso- tibiae or in all tibiae). Metatibial apex *simple* (with apical fringe of setae, but without outer bevel or inner flange) (Fig. x.x. 5 A), with *outer bevel* (swelling

area bare, setose or squamose, defined by one apical fringe of setae and a secondary, proximal, comb of setae) (Fig. x.x. 5 B, C), or with *inner flange* (with a bare smooth flange adjacent to tarsal socket delimiting a bare area with the apical fringe of setae) (Fig. x.x. 5 D). [The conditions tibial apex simple, with outer bevel, and with inner flange, are equivalent to Emden's (1944) "open corbel", "enclosed corbel", and "semi-enclosed corbel", respectively. However, under Thompson's (1992) interpretation, the inner flange is not the tibial apical edge that lost its setae, and the setose edge is not the proximal comb, but the true apical comb. This interpretation seems to be correct, because it allows that both outer bevel and inner flange can coexist in the same tibia, as observed in some species of *Lepropus* (Tanymecini) (Thompson 1992: p. 845)]. Mesotarsal empodium absent or concealed, or with two or less setae. Tarsal claws without setae near base, except in Sitonini (with "accessory claws" or modified setae, apically expanded and curve, inserted near base of claw on its outer view).

Abdomen. Tergites I-VII with different degrees of pigmentation, represented by median sclerites, without lateral or spiracular sclerites; terminal tergite (VII in female, VIII in male) covered by elytra in both sexes; female tergite VIII concealed under tergite VII (except partly exposed in Sitonini), male tergite VIII exposed beyond tergite VII. Spiracles present on segments I-VII, spiracles absent on tergite VIII, except vestigial in few cases (e. g. some species of *Entimus*). Abdominal ventrites (Fig. x.x. 2 D) 1 and 2 connate, with suture distinct; 3 to 5 free, articulated. Ventrite 1 at middle of metacoxa about as long as, to longer than ventrite 2; ventrites 1+2 longer than 3+4; ventrite 5 variable in shape, usually with sexual dimorphism.

Male genitalia (Fig. x.x. 6 A, B). Sternite VIII (Fig. x.x. 6 A) consisting of a divided plate (variable in shape, pigmentation and number and disposition of setae), in some cases with a vestigial apodeme (*spiculum relictum*). Sternite IX (Fig. x.x. 6 A) with its basal part sclerotized, arms broad and usually discontinuous with apodeme or median strut (*spiculum gastrale*), and median strut longer than apodeme of tegmen. Aedeagus (penis and phalobase or tegmen (Fig. x.x. 6 B)) of "gonatoceros type". Tegmen consisting of a complete, narrow, ring, with parameres absent or reduced to a pair of lobes fused to it. *Manubrium* (apodeme of tegmen) well developed but smaller than

spiculum gastrale. Penis without tectum (dorsal plate), pedon (ventral plate) trough-shaped or tubular, often dorsally membranous, with pair of proximal apodemes, deflexed in a distinct angle in lateral view. Endophallus membranous, with or without sclerites; flagellum usually absent. **Female genitalia** (Fig. x.x. 6 C-F). Sternite VIII (Fig. x.x. 6 C) variably in shape, sclerotization and distribution of setae; median strut or apodeme (*spiculum ventrale*) very long, to short or vestigial (e.g. Sitonini). Ovipositor (gonocoxites plus gonostyli) (Fig. x.x. 6 D, E) usually well developed, reduced in Sitonini and some species of Cylydrorhinini and Alophini, or absent in some species of *Trigonoscuta* (Brachyderini). Gonocoxites of variable length, undivided, with a dorsal incision, or divided into proximal and distal lobes (proximal and distal coxite). Proximal coxite (or valvifer) sclerotized or membranose (the latter smooth or wrinkled, with or without baculi). Distal coxite entire or divided into two sclerites (e. g. *Trachyrhinus*, *Arrhapogaster*). Gonostyli well developed, reduced or absent, apically or subapically attached (e.g. Ectemnorhinini).

Internal anatomy [Aslam 1961; Calder 1989, 1990]. *Male reproductive system*: Consisting of two bilobed testis (both lobes enclosed in a common sheath) and a variable number of follicles, from few (6-8) large ones to many (20-22) relatively small ones. Vasa efferentia distinct and usually enclosed within testicular sheath; anterior sections of vasa deferent free of testicular sheath or enclosed within it. Seminal vesicle multi-lobed (usually eight lobes). Accessory gland usually two-branched (one branch larger than another), entering vas deferens anteriorly or on anterior face of seminal vesicle. Ejaculatory duct of variable length, from very short to very long. *Female reproductive system*: Two ovaries with two ovarioles each, having terminal filaments; few exceptions with higher number of ovarioles (e.g. six in some species of *Leptopius*). Lateral oviducts joint in a common oviduct entering ventral face of the vagina-bursa copulatrix complex (= genital tract). Common oviduct with pouch structures on anterior part, in *Sitona*. Vagina tubular and sclerotized, rarely unsclerotized (e.g. Sitonini). Bursa copulatrix strongly developed to completely absent. Spermatheca (Fig. x.x. 6 F) variable in shape; spermathecal gland tubular, rarely ovoid (e.g. Sitonini); spermathecal duct usually long, membranous to sclerotized, entering ventral face of genital tract, near entry of common oviduct. *Nervous system*: With a discrete cerebrum, a suboesophageal ganglion, a usually

separated prothoracic ganglion, a fused meso-metathoracic ganglion and two discrete abdominal ganglia or one compound abdominal ganglion. Some groups with a compound meso-metathoracic-abdominal ganglion (some genera of Sitonini and Naupactini).

Alimentary canal: Fore gut short to moderately long (5-15% of total length of tract). Crop well developed to indistinct. Proventriculus bulbous, usually having well developed internal structures (eight sclerotized basal plates, each bearing two longitudinal brushes, usually with retaining bristles). Oesophagus usually covered with setae on anterior half. Mid gut usually shorter than hind gut (30-50% of total length of tract) and divided into two sections: a) a distended anterior ventriculus usually lacking pouches, with several pouches (e.g. *Naupactus cervinus* and *N. leucoloma*) or strongly lobed (e.g. *Leptopius*, *Parisomias*, *Stenocorynus*), having exterior surface mostly smooth or densely papillose in some species (e.g. some *Otiorrhynchus*, *Essolithna* and *Catasarcus*); b) a longer tubular posterior section having papillae variable in size, distribution and density. *Cryptonephric Malpighian tubules:* Six tubes located on the anterior extreme of hind gut, arranged in one group of four (entering a common chamber in some species such as *Eurymetopus birabeni*) and another group of two shorter tubes. Six tubes inserted posteriorly and arranged in two groups of three each, usually of ventrolateral position (excepting *Perperus* sp., *Stenocorynus* sp. and *Leptopius* spp., having dorsal tubes).

Morphology, Larvae (Figs. x.x. 7 A-G, x.x. 8 A-I, x.x. 9 A-F) [Chown & Scholtz 1989b, 1990; Emden 1952; May 1978, 1993, 1994; Marvaldi & Loiácono 1994; Marvaldi 1997, 1998 a, b]. *Abbreviations used in text:* Abdominal segments I-X (AI-X); *des* dorsal epicranial setae; *dms* dorsal malar setae; *fs* frontal setae; *mds* mandibular setae; *mes* median epipharyngeal setae; *pds* postdorsal setae; *pes* posterior epicranial setae; *prs* prodorsal setae; *vcs* ventral cranial setae; *vms* ventral malar setae.

Diagnosis. Antennal sensorium (Fig. x.x. 7 D) wider than long, cushion-like, usually truncate or widely rounded at apex; *des3* on frontal line (Fig. x.x. 7 B); postoccipital condyles present (Fig. x.x. 7 E); sensillum next to *des2* absent; maxillae (Fig. x.x. 8 H, I) with 4 *vms*; AI-VII (Fig. x.x. 7 A) with 3-4 dorsal folds; AVIII (Fig. x.x. 7 A) always bearing homologous *pds5* of preceding segments.

Note: The following description applies to larvae of most Entiminae (Entimini *sensu* Marvaldi 1997, 1998a), unless indicated.

Head (Fig. x.x. 7 B-G, x.x. 8 A, B) usually exposed, in some cases partially retracted into thorax (e.g. Naupactini). Frontal lines distinct, vestigial or absent. Endocarina (Fig. x.x. 7 F) usually absent or vestigial (but distinct in Sitonini and Alophini). Antennae with transverse position on anterior margin of head and ellipsoidal sensorium in apical view (Fig. x.x. 7 C, G) (oblique position and circular sensorium in apical view, in Pachyrhynchini, Ectemnorhinini and Alophini (Fig. x.x. 7 F)); antennal sensorium (Fig. x.x. 7 D) wider than long, cushion-like, usually truncate or widely rounded at apex (shortly ojival in Alophini); sensorium symmetric in mature larvae but projected outwards in earlier instars of most Entiminae (Fig. x.x. 7 G) (asymmetry persistent along the whole larval stage in Sitonini). Stemmata usually present as dark pigmented spots (Fig. x.x. 7 B, F) (large, under convex cornea in Pachyrhynchini and Ectemnorhinini). Cephalyc setae (Figs. x.x. 7 C, E-G, x.x. 8 A, B): *des1,2,3,4,5* present, being *des3* and *des5* the longest; *des3* on frontal line, sometimes contiguous to frons or to epicranium; *fs1,2,3,4,5* present, being *fs4* the longest, *fs5* also well developed (except reduced or vestigial in Pachyrhynchini and Ectemnorhinini); *vcs1* and *vcs2* usually very unequal, *vcs2* much smaller; sensillum next to *des2* absent. Labrum (Fig. x.x. 8 C) usually pigmented on two subtriangular areas (uniformly pigmented in Pachyrhynchini and Ectemnorhinini). Epipharynx (Fig. x.x. 8 D-F) with sensillum clusters between *mes1* and/or *mes2* (but between *mes2* and *mes3* in Pachyrhynchini and Ectemnorhinini). Labral rods usually subparallel, or divergent in their distal half (e. g. Brachyderini, Otiorhynchini, Polydrusini, Tanyrhynchini), and U-shaped in Naupactini. Mandibles bidentate at apex (unidentate in Pachyrhynchini, tridentate in Sitonini) and accessory teeth absent on cutting edge (but present in Pachyrhynchini and Ectemnorhynchini); mandibular scrobe weakly sclerotized, pale, and usually including both *mds1* and *mds2* (but sclerotized in Sitonini, Alophini, Pachyrhynchini and Ectemnorhynchini). Maxillary mala with 4 *vms*, and frequently with 8 *dms*. Posterior extension of premental sclerite with subparallel sides and truncate or expanded at apex in most Entiminae (subtriangular, with convergent sides and acute at apex (Fig. x.x. 8 H) in Sitonini, Alophini, Ectemnorhinini and Pachyrhynchini). Typical abdominal segments (Fig. x.x. 7 A) with 3-

4 dorsal folds; AVIII sometimes with one or more *pds* lost, but bearing the homologous *pds5* of preceding segments. Thoracic and abdominal spiracles (Fig. x.x. 9 A-F) with two annulated airtubes (airtubes reduced or absent in last instar larva of many Entiminae, but distinct and annulated in earlier larval instars and in all instars of Sitonini, Alophini, Pachyrhynchini and Ectemnorhinini), airtubes posteriorly or dorsoposteriorly directed (except dorsally directed in Pachyrhynchini and Ectemnorhinini). Spiracle of AVIII (Fig. x.x. 7 A) lateral (except on dorsum in Pachyrhynchini). Abdominal apex frequently with modifications (sclerotizations, particularly in soil-dwelling larvae). AX terminal or subterminal, usually 4-lobed (except 6-lobed in Pachyrhynchini).

Morphology, Pupae (Fig. x.x. 9 G, H) [May 1978, 1994; Marvaldi 1997]. Integument creamy white, usually changing to brown before adult emergence. Setae (varying in shape, number and disposition in different taxa) placed on tubercles on frons, rostrum, pronotum, femoral apex and dorsum of abdominal segments. Each mandibular theca (relatively large in comparison with other weevils) with 1-2 setae on dorsal surface. Femoral apex with 2 or less setae. Primary pterotheca (elytra) well developed; secondary pterotheca from well developed to very reduced (depending on hindwing development in the adult). Terminal abdominal segment with paired posterior processes (“pupal urogomphy” or “pseudocerci”), usually sclerotized and with an apical spine.

Phylogeny and Taxonomy. Entiminae Schoenherr, 1823 (=Polydrusinae Schoenherr, 1826) is the largest taxon of the curculionid beetles, with 1340 genera and more than 12000 species described (Alonzo-Zarazaga & Lyal 1999; O’Brien & Wibmer 1978; Yunakov & Nadein 2006). Several different classifications of this subfamily have been proposed during the last two decades. Zherikhin & Egorov (1990) and Thompson (1992), in agreement with Kuschel (1988 unpublished, see Thompson 1992: 883), expanded the concept of Entiminae (= Leptopiinae) by including other traditional subfamilies (Brachyderinae, Otiorhynchinae, and Eremninae), and demoted them into tribes. Thompson (1992) also considered Pachyrhynchini, Ectemnorhinini, and Sitonini within the Entiminae and gave a key to identify these tribes at the adult stage. According to this author the presence of deciduous mandibular processes (secondarily lost in few cases), in

combination with the derived type of male genitalia, suggest the monophyly of Entiminae in its largest concept. Kuschel (1995) included the Entiminae within the Brachycerinae in its broad sense. Marvaldi (1997, 1998a) followed Thompson (1992) and gathered all Entiminae into five tribes, diagnosing them by larval characters: Alophini, Pachyrhynchini, Ectemnorhinini, Sitonini and Entimini, the latter comprising the bulk of Entiminae. According to the catalogue of Alonso-Zarazaga & Lyal (1999) the Entiminae comprise 55 tribes. This systematic arrangement of the genera of Entiminae, although practical and necessary as starting point for further systematic work, will certainly be modified as phylogenetic studies on Entiminae progress. Definition of monophyletic tribes is hardly needed, as well as clarification of the placement of several genera, being many of the currently recognized tribes probably artificial. For example, Phyllobiini and Polydrusini might be paraphyletic, because they are groups based on symplesiomorphies; while Sciaphilini, Omiini, Holcorhinini, and Brachyderini are probably polyphyletic (Yunakov & Nadein 2006). Other tribes are most likely monophyletic and their limits are clearer, on the basis of recent and ongoing systematic studies, such as the Sitonini (Velázquez de Castro *et al.* 2007) and the Tanyrhynchini (Oberprieler 1988). Phylogenetic studies and natural classification of the taxon, particularly at tribal or subtribal levels, remain as challenging goals for the future.

In its present circumscription Entiminae is a monophyletic taxon mainly justified by the following larval synapomorphies: maxillary mala with four *vms* (other curculionids have five, with another seta near malar sensillum), and the antennal sensorium wider than long and cushion-like (Marvaldi 1997). Thompson's (1992) comparative study of weevil adult morphology leads to conclude that some adult characters, although not unique for the taxon, must be synapomorphic for the Entiminae. The monophyly of the subfamily is also recovered by combined analyses using molecular evidence of 18S rDNA gene sequences and morphological characters of adults and larvae (Marvaldi *et al.* 2002). The most important adult character defining the Entiminae is the presence of deciduous processes or the corresponding scar on the mandibles. The pupa of Entiminae is also characterized by having 1-2 setae on the mandibular theca, and this feature is apparently associated with the mandibular processes in this subfamily, being present even in pupae of those entimines lacking such processes in the adult stage (May

1978, 1994). Occurrence of mandibular processes is reported for a variety of curculionoid taxa, but the “deciduous” mandibular processes of Entiminae are considered homologous, and deemed to have evolved independently from those observed in some Brachycerinae (Thompson 1997, Marvaldi 1997). Similarly, adelognathous mouthparts occur in the great majority of tribes of Entiminae and they are not unique for this subfamily, since they also occur in other curculionoids (Thompson 1992). It may be possible that basal entimines retain phanerognathous mouthparts, but adelognathy apparently evolved early in the group with some few or isolated further reversals to phanerognathy.

The closest relative of Entiminae is probably a group or subgroup of weevils currently classified in Cyclominae (including Amycterinae, Rhythirrinae, etc.). The entimines and cyclomines share a number of biological and morphological features; along with some Brachycerinae/ini and some brentids like Ithycerinae and Microcerinae, they do not use the rostrum for preparing an oviposition site inside plant tissues, and their larval development is primarily soil-based. These biological features are obviously related with rostrum shape and development, and characterize the “broad-nosed weevils” grouped by Kuschel (1995) in his enlarged concept of Brachycerinae (see also May 1993). The larvae of Entiminae and Cyclominae have the *des3* on frontal line or on frons (not on epicranium). This larval feature is also characteristic of Brachycerinae and Eirrhinae (including Bagoiini), suggesting that it may be an ancestral feature for Curculionidae and thus plesiomorphic for Entiminae and Cyclominae. The shape of male sternite 9 is probably synapomorphic for Entiminae and Cyclominae: its basal part is largely sclerotized, with arms broad and usually discontinuous with the *spiculum gastrale* (while in other weevils the basal part is largely membranous, with arms narrow and fused with the apodeme). Because the Entiminae and Cyclominae have a number of derived male genitalic traits (“gonathoceros type”), they are deemed to share a more recent common ancestor with other “higher curculionids” than with the Brachycerinae and Eirrhinae, subfamilies that retain the “orthoceros type” of male genitalia.

Phylogenetic studies on both the position of Entiminae within the Curculionid tree and the relationships among the different groups within this weevil subfamily are badly needed.

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FIGURE LEGENDS

BIOLOGY

Fig. X.X.1. A, *Naupactus leucoloma*, mature larva in soil; B, *N. leucoloma*, pupa in earth cell; C, *N. cervinus*, adult feeding; D, *Atrichonotus taeniatus*, posture.

ENTIMINE ADULT GENERAL APPEARANCE

Fig. X.X.2. A –B, Adult general habitus. A, *Entimus sastrei* line= 5 mm; B, *Eurymetopus oblongus*, line= 5 mm; C, *Premnotrypes latithorax*, lateral, line= 1 mm; D, *Platyaspistes argentinensis*, ventral, line= 5 mm.

ADULT MORPHOLOGY

Fig. X.X.3 A-D, Adult morphology, head and mouthparts. A-C, *Platyaspistes argentinensis*. A, head, dorsal; B, head and antenna, lateral; C, rostrum and mouthparts, ventral; D, *Naupactus xanthographus*, rostrum and mouthparts, ventral. Lines = 1 mm.

Fig. X.X.4 A-C, *Naupactus leucoloma*, mouthparts. A, right mandible, with pharyngeal process, ventral, line= 0.5 mm; B, right maxilla, dorsal, line = 0.25 mm; C, Labium, inner face, line = 0.25 mm.

Fig. X.X.5. Adult morphology, metatibial apex. A, *Otiorhynchus* sp., simple, and with small mucro and minute spurs present, line= 0.5 mm; B, *Oxiderces argentinicus*, with bare outer bevel, line= 0.5 mm; C, *Entimus nobilis*, with setose outer bevel, line= 1 mm; C, *Premnotrypes latithorax*, with inner flange, and with well developed mucro, line= 0.5 mm.

Fig. X.X.6. Adult morphology, genitalia. A-B, *Galapagonotus cuneiformis*, male genitalia. A, sternite VIII (divided plate), sternite IX (bladal part plus *spiculum gastrale*) and tergite VIII, line = 1 mm; B, aedeagus (penis and tegmen), lateral view, line = 1 mm. C-F, *Phacepholis elegans*, female genitalia. C, sternite VIII, line = 1 mm; D, apex of ovipositor, ventral view, line = 1 mm; E, ovipositor (gonocoxites and gonostyli), lateral view, line = 1 mm; F, spermatheca, spermathecal duct and bursa copulatrix, line = 0.25 mm.

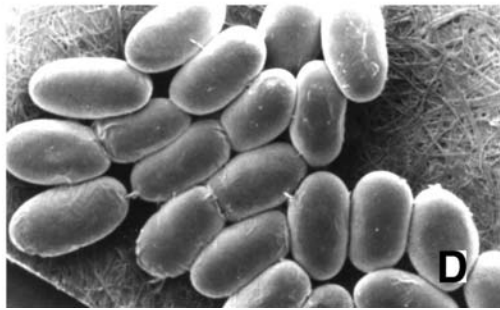
LARVAL (and pupal) MORPHOLOGY

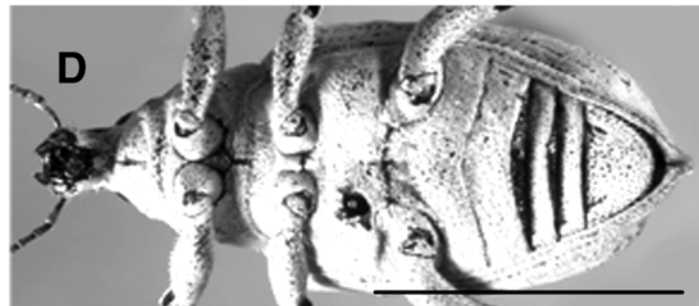
Fig. X.X.7. A-F, larval morphology. A, *Otiorhynchus sulcatus*, larva in lateral view, length = 10 mm; B, *O. sulcatus*, head and mouthparts, general aspect in anterolateral view, line = 0.5 mm; C-E, *Cylydrorhinus* sp., first instar. C, head, dorsal, line = 0.1 mm; D, antenna, line = 0.05 mm; E, head, ventral, line = 0.1 mm; F, *Alophus triguttatus*, first instar, head, dorsal, line = 0.1 mm; G, *Naupactus leucoloma*, first instar, head, dorsal, line = 0.1 mm.

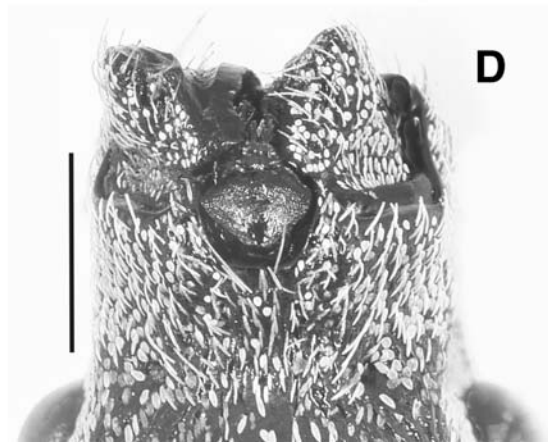
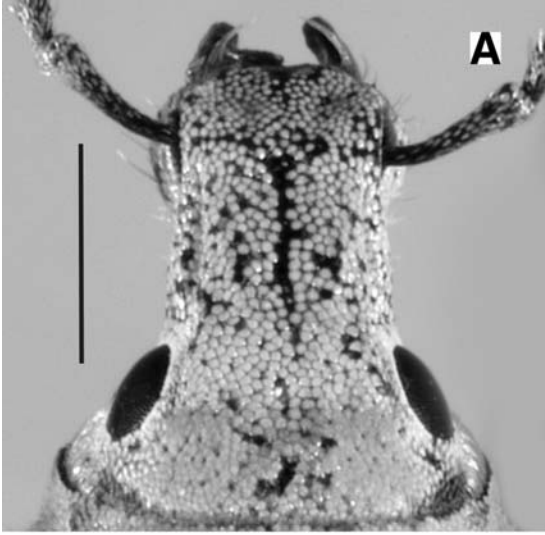
Fig. X.X.8 A-I. Larval morphology. A, *Naupactus leucoloma*, head, dorsal, line = 0.5 mm; B, *Diaprepes abbreviatus*, head, dorsal, line = 0.5 mm; C, *N. leucoloma*, clypeus and labrum, line = 0.1 mm; D, *Otiorhynchus sulcatus*, epipharynx, line = 0.1 mm; E, *Entimus sastrei*, epipharynx, line = 0.1 mm; F, *N. leucoloma*, epipharynx, line = 0.1 mm;

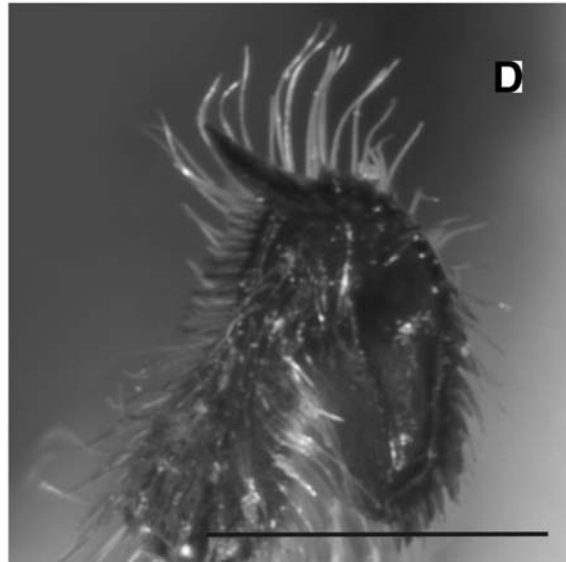
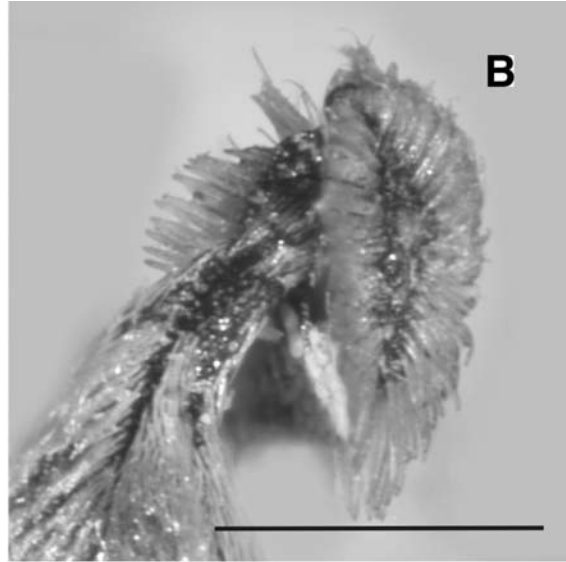
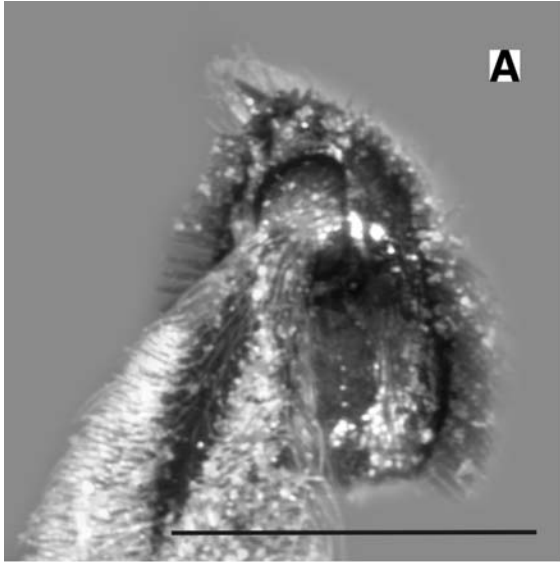
G, *O. sulcatus*, mandible, line = 0.5 mm; H, *Sitona gressorius*, maxilla and labium, ventral, and maxilla, dorsal, line = 0.1 mm; I, *N. leucoloma*, maxilla and labium, ventral, and maxilla, dorsal, line = 0.1 mm.

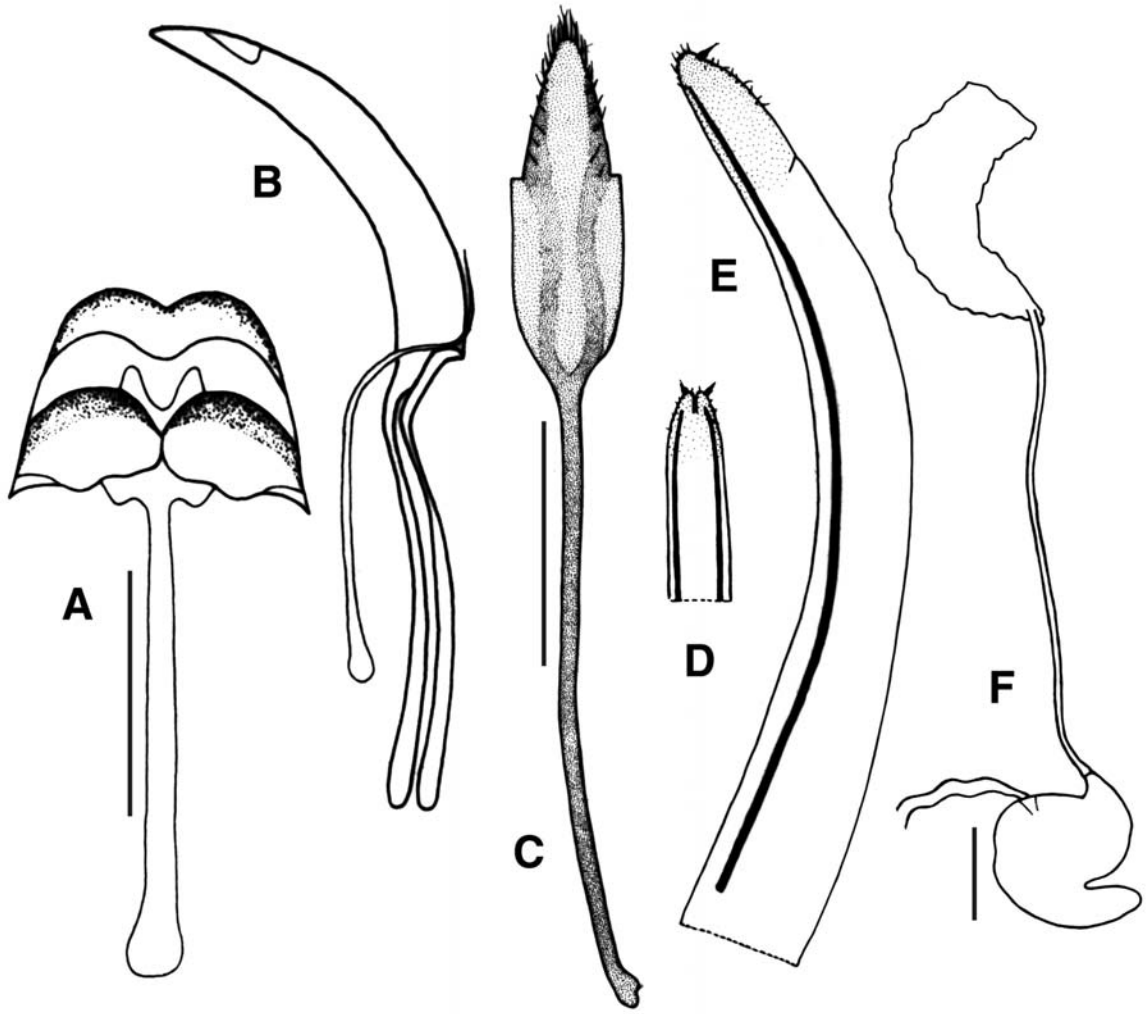
Fig. X.X.9 Larval spiracles and pupal morphology. A-F, *Naupactus leucoloma*, larval spiracles. A – C, first instar larva, line = 0.1 mm. A, thorax; B, AIV; C, AVIII. D – F, mature larva, line = 0.1 mm. D, thorax; E, AIV; F, AVIII. G-H, *Naupactus xanthographus*, pupa. G, ventral; B, dorsal, line = 5 mm.

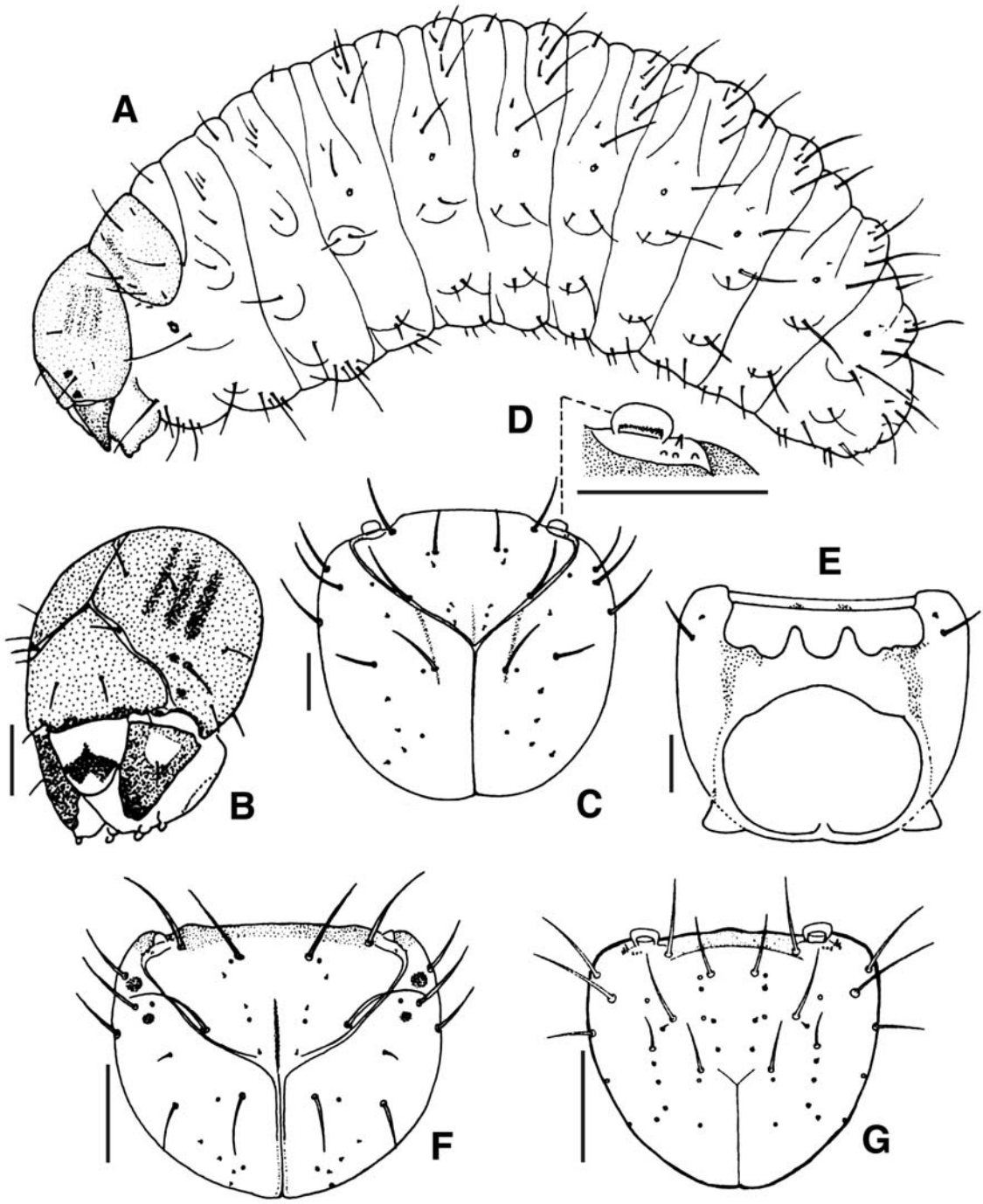


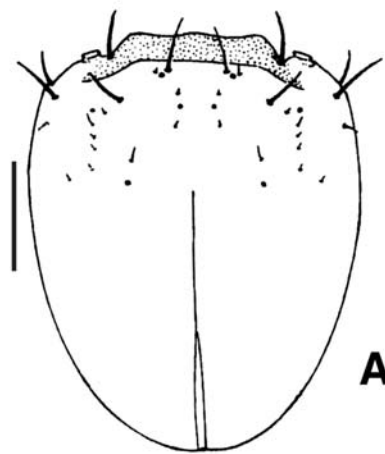




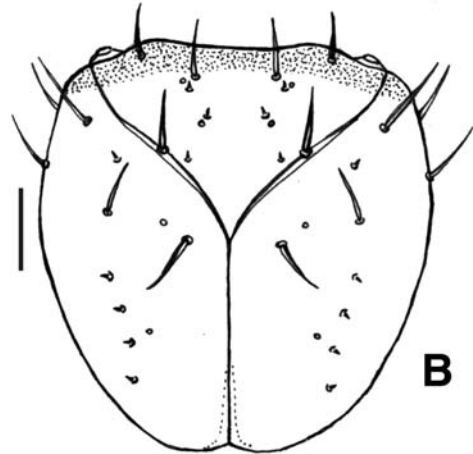




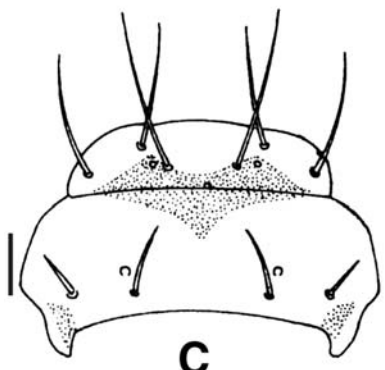




A



B



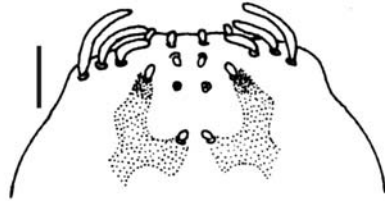
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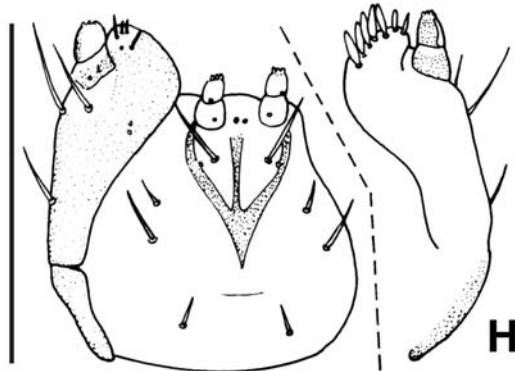
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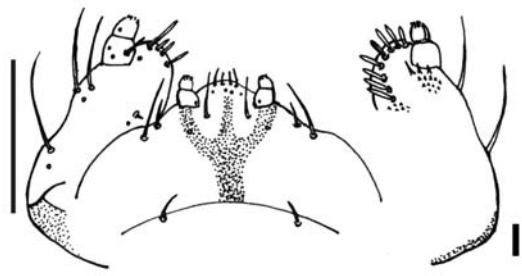
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G



H



I

