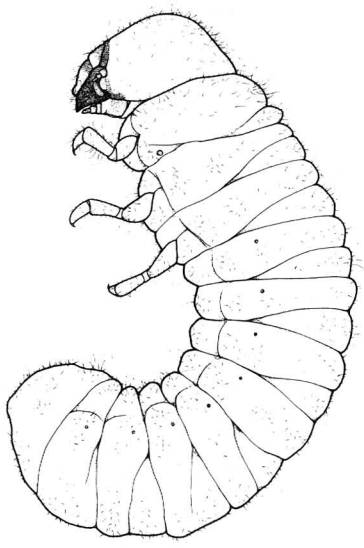

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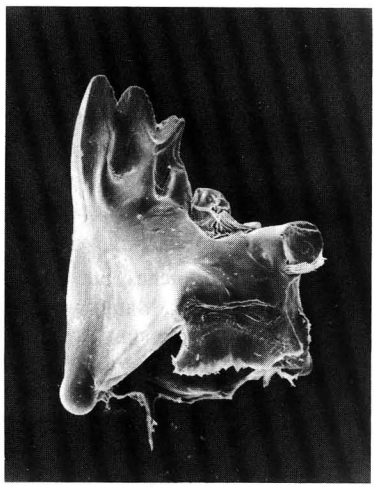

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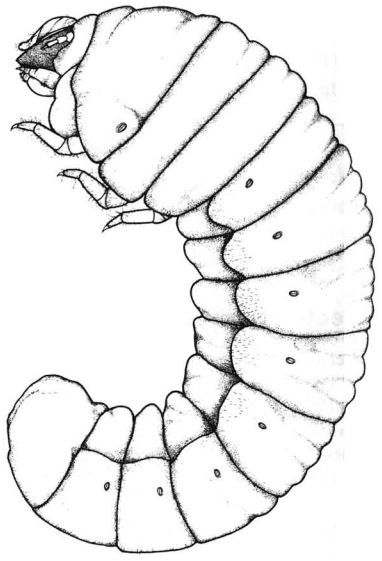

Figure 34.484

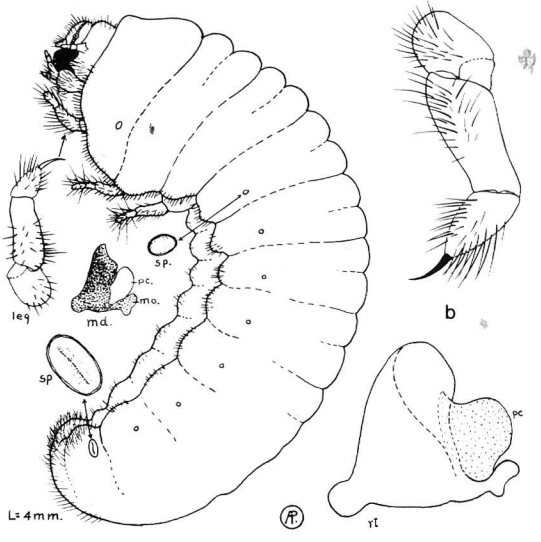

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Figure 34.485

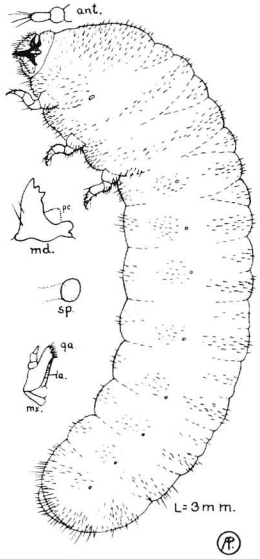

Figure 34.486

Figure 34.487

Figures 34.483a,b. Bostrichidae. *Endecatomus rugosus* Randall. Cedar Rapids, Linn Co., Iowa. Length = 5.8 mm. **a.** larva, lateral; **b.** right mandible, ventral.

Figure 34.484. *Psoa maculata* LeConte. San Luis Obispo Co., California. Larva, lateral. Length = 13.4 mm.

Figures 34.485a-c. Bostrichidae. *Lyctus planicollis* LeConte, Southern lyctus beetle. Length = 4 mm. **a.** larva, lateral (plus details); **b.** prothoracic leg; **c.** right mandible, ventral. Near white, including head except the area adjacent to the mouthparts; short, colorless, setae confined largely to the head, legs and ventrolateral aspects of each segment; labrum densely setiferous; prothoracic legs similar to those on mesothorax and metathorax but larger, more setiferous and with distinct, elongated, curved spinelike claws; spiracles on eighth abdominal segment much larger and more nearly oval than those on segments 1-7. Infests many kinds of dry or seasoned hardwood, especially ash, hickory and oak. (Figures 34.485a-c from Peterson, 1951)

Figure 34.486. Bostrichidae. *Rhyzopertha dominica* (Fabricius), lesser grain borer. Larva, lateral (plus details). Length = 3 mm. Near white except for the pigmented mouthparts, portions of the partially retracted head, and claws; a few, short light-colored setae on most parts of the body and head, longest and most abundant at caudal end and on ventral aspect; spiracles annuliform and very inconspicuous. Infests nearly all stored grains, especially wheat, and other products, namely cork, dried roots, drugs, leather goods and seeds. Also many penetrate paper boxes containing food. (From Peterson, 1951.)

Figure 34.487. Bostrichidae. *Xylobiops texanus* (Horn). Larva, lateral (plus details). Length = 5 mm. Infests dry mesquite wood. (from Peterson 1951)

2-segmented. Hypopharyngeal sclerome present or absent. Hypostomoal rods absent or very short. Ventral epicranial ridges absent. Gular region absent.

Thorax and Abdomen: Thorax usually enlarged with prothorax larger than meso- or metathorax (not so in *Endecatomus*). Prothorax in Bostrichinae with an oblique, sclerotized rod on each side. Legs relatively small, 5-segmented; tarsungulus slender, without setae or with 2 setae lying side by side. Meso- and metatergum and abdominal terga 1 to 6 or 7 each with 2 to 4 transverse plicae, but without patches of asperities. Abdominal segments 1–8 usually with well-developed pleural lobes. Segment A9 enlarged, almost always simple (small urogomphi or median process present in some first instars). Segment A10 reduced, usually with pair of longitudinal oval anal pads, but in Lyctinae with transverse pad as well.

Spiracles: Annular or annular-uniforous; thoracic spiracles located on posterior part of prothorax or on mesothorax; spiracles on segment A8 enlarged in Lyctinae.

Comments: The family includes about 90 genera and 700 species distributed worldwide, with 35 genera and about 100 species in N. America. There are 7 recognized subfamilies, which appear to form distinct groups: Endecatominae, Dysidinae-Psoinae, Dinoderine-Lyctinae, and Euderiinae-Bostrichinae. The genus *Endecatomus* is Holarctic; Dysidinae includes the S. American *Dysides* and the Oriental *Apoleon;* Psoinae are widespread, with individual groups in the Holarctic Region, tropical America, southeast Asia, and Chile; and *Euderia* is restricted to New Zealand. The Dinoderinae, Lyctinae, and Bostrichinae are all widely distributed.

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ANOBIIDAE (BOSTRICHOIDEA)

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Deathwatch Beetles, Furniture Beetles, Cigarette Beetle, Drugstore Beetle

Figures 34.488–495

Relationships and Diagnosis: Anobiidae, like Ptinidae and Bostrichidae, are characterized in the larval stage by the lightly sclerotized and more or less C-shaped or scarabaeiform body, usually with well-developed legs, and with a pair of longitudinally oval pads beneath the anus. Anobiid larvae may be distinguished from those of Bostrichidae by the combination of protracted and hypognathous head and very short antennae, which usually have only 1 evident segment. They differ from larvae of the closely related Ptinidae by the location of the thoracic spiracle posteriorly on the prothorax or between the prothorax and mesothorax, and usually by the presence of transverse bands of asperities on the abdominal terga. Scarabaeoid larvae differ from those of anobiids in having longer, 3- or 4-segmented antennae, a well-developed mandibular mola and accessory ventral process, and cribriform (or occasionally biforous) spiracles. Larvae of some Anthribidae resemble anobiid larvae in several respects but lack the longitudinal anal pads and tergal asperities; the same 2 features will separate legless *Caenocara* larvae from those of other curculionoids.

Biology and Ecology: Larvae of most Anobiidae feed on dead or dying wood, but some species attack conifer cones, twigs, vines, seeds, galls, fungus, fruiting bodies, or stored products of both animal and plant origin. Xylophagous species occur in all subfamilies, and include serious pests of furniture and structural timber, such as *Ernobius mollis* (L.), *Anobium punctatum* (De Geer), and *Xestobium rufovillosum* (De Geer). Larvae of the last species, as they tunnel through wood, produce a tapping sound once considered to be an omen of death; this is the origin of the common name deathwatch beetle. Within the Ernobiinae, *Ozognathus* species occur in stems, twigs, and galls, while some *Ernobius* attack the cones of conifers. The Dorcatominae include some wood-damaging forms, especially in the genus *Calymmaderus,* but the majority of species are mycophagous. In North America, species of *Dorcatoma* and *Byrrhodes* occur in the larger, more durable fruiting bodies of *Fomes, Ganoderma, Inonotus,* and *Phellinus,* while species of *Caenocara* are apparently restricted to puffballs (*Calvatia, Lycoperdon, Scleroderma,* etc.) (Benick, 1952; Lawrence, 1973; Matthewman and Pielou, 1971; Weiss, 1922; Weiss and West, 1920, 1921b). The subfamily Tricoryninae includes most of the seed-feeding anobiids, but *Tricorynus herbarius* (Gorham) damages books, leather, and stored foods, while *T. tabaci* (Guérin-Méneville)

*Deceased

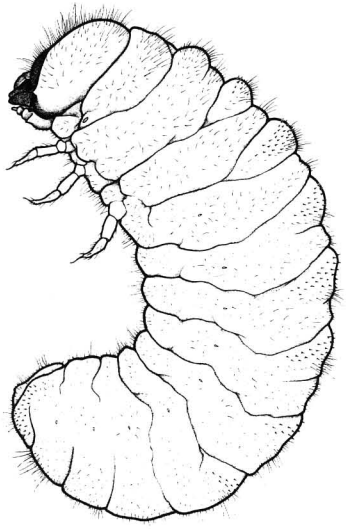


Figure 34.488

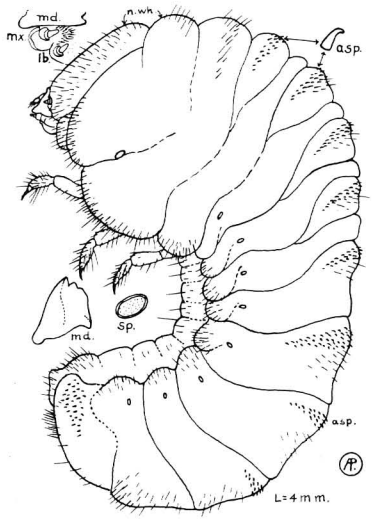


Figure 34.489

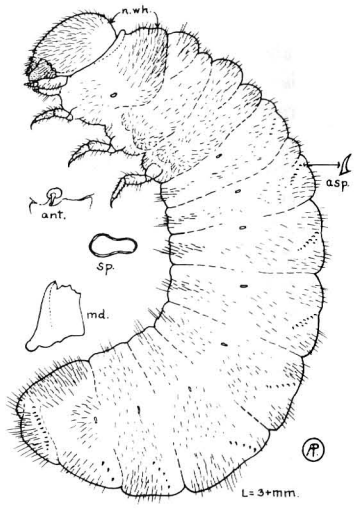
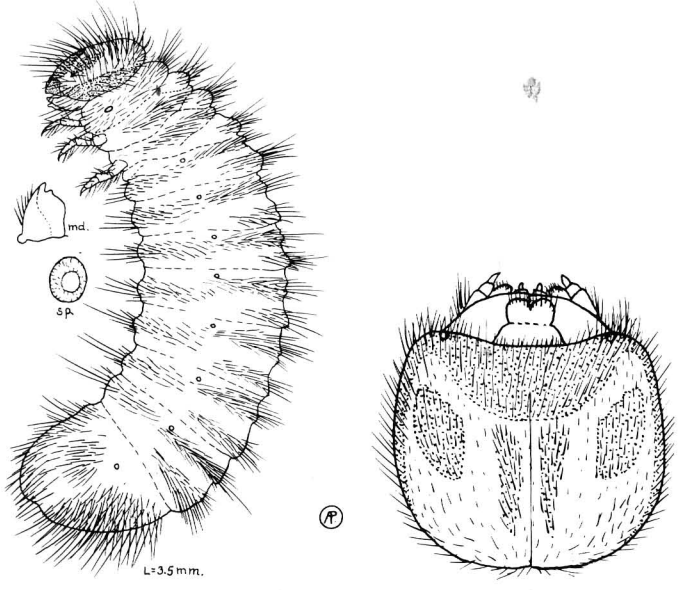


Figure 34.490



a

b

Figure 34.491

Figure 34.492

Figure 34.488. Anobiidae. *Dorcatoma* sp. Rensselaerville, Albany Co., New York. Larva, lateral. Length = 8.3 mm.

Figure 34.489. Anobiidae. *Hemicoelus carinatus* (Say). Larva, lateral (plus details). Length = 4 mm. Near white except cream head and moderately to deeply pigmented epistoma, mandibles, asperities and tarsi; short or long, light setae on all parts of body, most numerous on head, caudal segments and ventrad of spiracles on all segments; thorax enlarged; groups of short, curved asperities on dorsa of metathorax to abdominal segment 7, and on caudolateral apsects of caudal segment; spiracles oval and inconspicuous. Infests dry dead wood in buildings and elsewhere. Recorded chiefly from deciduous trees. (From Peterson, 1951).

Figure 34.490. Anobiidae. *Stegobium paniceum* (L.), drugstore beetle. Larva, lateral (plus details). Length = 3 mm. All segments subequal in diameter except the smaller prothorax. Near white except mouthparts and ventral margin of head capsule; numerous short to long, light colored setae on all areas of head, body and legs; inconspicuous, colored asperities present as single or narrow bands on dorsa of all abdominal segments; inconspicuous peanut-shaped spiracles present. Attacks a wide variety of dry plant products including book covers containing glue, paste or casein, leather, and bamboo. (From Peterson, 1951)

Figures 34.491a,b. Anobiidae. *Lasioderma serricorne* (Fabricius) cigarette beetle. **a.** larva, lateral (plus details), length = 3.5 mm; **b.** head, anterior. Wrinkled, segments subequal in diameter; near white including head capsule except for yellowish-brown pigmented areas; very numerous, long, light setae on all parts of body, head and legs; spiracles annuliform to oval with thoracic pair on prothorax. Infests mainly dried vegetable products. Destructive to cured leaf tobacco or tobacco products, especially in storage. Also known to infest dried yeast cakes, seeds, dried botanical specimens, dried fish, leather goods, rugs, tapestry, and upholstered furniture. (From Peterson, 1951).

Figure 34.492. Anobiidae. *Byrrhodes* sp. Concord, Massachusetts. Left mandible, mesoventral.

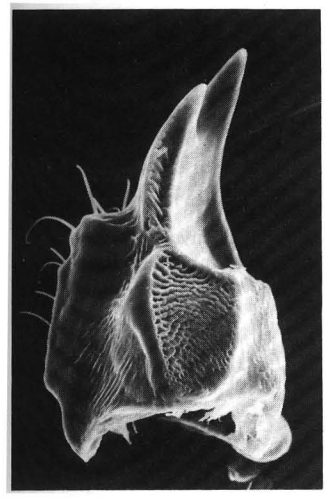


Figure 34.493

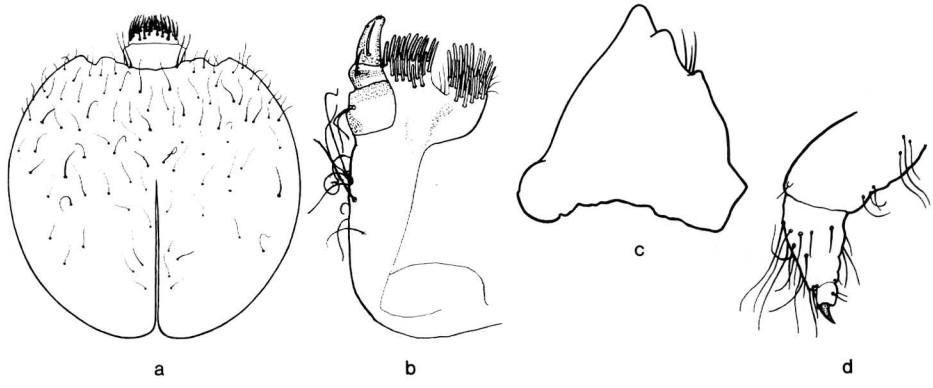


Figure 34.494

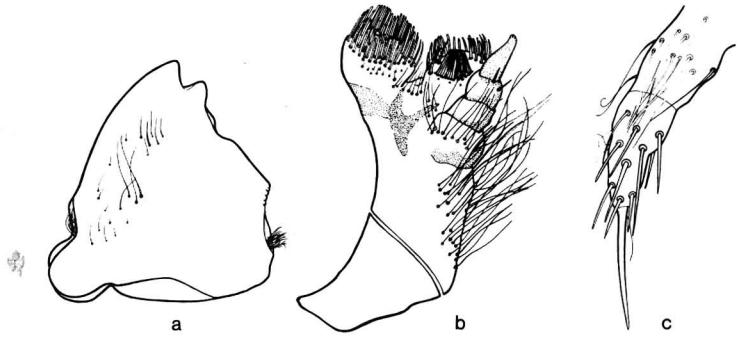


Figure 34.495

Figure 34.493. Anobiidae. *Caenocara* sp. Gloucester, Massachusetts. Left mandible, mesal.

Figures 34.494a-d. Anobiidae. *Grynobius planus* (Fabricius). **a.** head, dorsal; **b.** right maxilla, ventral; **c.** left mandible, dorsal; **d.** apex of prothoracic leg.

Figures 34.495a-c. Anobiidae. *Nicobium villosum* (Brullé). **a.** left mandible, dorsal; **b.** right maxilla, dorsal; **c.** apex of leg.

is found in various stored herbs, bulbs, and seeds (White, 1982). The 2 most common and widespread pests of stored products are the drugstore beetle, *Stegobium paniceum* (L.) (fig. 34.490) (Anobiinae) and the cigarette beetle, *Lasioderma serricorne* (Fabricius) (fig. 34.491a,b) (Xyletininae). These species damage a wide variety of plant and animal products, including tobacco, drugs, spices, seeds, grains, and leather (White, 1982). Many anobiids exhibit an advanced type of digestive physiology, in which intracellular symbionts play a large part in breaking down cellulose and providing B vitamins (Blewett and Fraenkel, 1944; Buchner, 1965; Parkin, 1940); however little is known about the physiology of the primitive Hedobiinae and Dryophilinae. Hedobiinae are apparently unique in forming a silk-like cocoon for pupation (actually formed of chitinous threads produced by the peritrophic membrane); the fact that *Ptinus* species construct a similar cocoon has been used to support the union of the Anobiidae and Ptinidae (Crowson, 1981; Hickman, 1974; Viedma, 1973).

Description: Mature larvae 2 to 12 mm. Body elongate, more or less parallel-sided, subcylindrical to slightly flattened, moderately to strongly curved ventrally (C-shaped), lightly sclerotized, except for buccal region, whitish to yellowish; vestiture consisting of short, simple setae or longer, fine hairs, often dense in places.

Head: Protracted and hypognathous (rarely retracted and prognathous), globular to somewhat flattened. Epicranial stem long; frontal arms usually indistinct or absent, sometimes V-shaped. Median endocarina coincident with epicranial stem. Stemmata absent or 1 on each side. Antennae very short, usually 2-segmented, with sensorium on segment 1 longer than segment 2, sometimes 1-segmented with sensorium at apex. Frontoclypeal suture present; labrum free; clypeolabral region narrow. Mandibles usually symmetrical, robust, unidentate to tridentate (occasionally 4-dentate), without accessory ventral process; mesal surface of mandibular base usually simple or with brush of hairs (penicillus); occasionally a mola (pseudomola) present which may be ridged or tuberculate. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, and articulating area narrow, indistinct, or absent; maxillary palp usually 3-segmented, occasionally 2-segmented, or 4-segmented where palpifer is completely articulated; galea and lacinia fixed; galea rounded or truncate; lacinia rounded to falciform,

sometimes with sclerotized spur or spine at apex, occasionally vestigial. Labium more or less free to base of mentum; ligula short and broad; labial palps 2-segmented. Hypopharyngeal sclerome usually absent. Hypostomal rods absent. Ventral epicranial ridges absent. Gular region absent.

Thorax and Abdomen: Prothorax not much larger than meso- or metathorax, without sclerotizations. Legs usually well-developed, 5-segmented, occasionally highly reduced or absent; tarsungulus usually with 2 setae lying side by side, sometimes with numerous setae; basal portion of tarsungulus (arolium) sometimes expanded and bladder-like, replacing claw-like portion entirely. Meso- and metaterga and abdominal terga 1–7 usually with 2 transverse plicae. Meso- and metaterga, abdominal terga 1–7 or 8, and sometimes lateral portions of segments 9 and 10, usually with patches or transverse bands of asperities (usually located on anterior plica). Segment A9 well-developed, rounded, without urogomphi or median process. Segment A10 reduced, terminal, with pair of longitudinally oval anal pads separated by groove below anus and sometimes with bow-like sclerite at ventral edge of anal pads.

Spiracles: Usually annular or annular-uniforous; occasionally annular-multiforous. Thoracic spiracle located on posterior part of prothorax or between prothorax and mesothorax.

Comments: The Anobiidae include about 150 genera and 1600 species worldwide, and 52 genera and 332 species were included in a recent N. American catalogue (White, 1982). The family is currently divided into 9 subfamilies on the basis of adult characters (White, 1974b): Hedobiinae, Dryophilinae, Anobiinae, Ptilininae, Alvarenganiellinae, Xyletininae, Dorcatominae, and Tricoryninae; except for the Hedobiinae, however, none of these divisions have been characterized using larval features (Böving, 1954; Viedma, 1973, 1977). The major work on anobiid larvae is that of Böving (1954), which includes representatives of more than 40 genera.

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PTINIDAE (BOSTRICHOIDEA)

(INCLUDING GNOSTIDAE, ECTREPHIDAE)

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Spider Beetles

Figures 34.496-497

Relationships and Diagnosis: The family Ptinidae is very closely related to the Anobiidae, and Crowson (1955, 1981) has suggested that the families be merged because of the larval similarities in the 2 groups, the presence of a pupal cocoon in both Ptinidae and hedobiine Anobiidae, and the adult features of the genus *Xylodes*, which are intermediate between the 2 groups. Ptinid larvae may be distinguished from those of anobiids mainly by the position of the thoracic spiracle near the anterior edge of the prothorax, but also by the absence of tergal asperities present in most anobiid larvae.

Biology and Ecology: Ptinidae are primarily scavengers and feed on a wide variety of animal and plant products. It is thought that wood-boring may be the ancestral habit of the group (Crowson, 1955), and at least a few species of *Ptinus*, such as *P. palliatus* Perris and *P. lichenum* Marsham, do occur in wood (Belles, 1980; Hinton, 1941e). It is much more common, however, for Ptinidae to feed on feces, hair, feathers, arthropod cuticle, or other organic debris, especially that accumulating in caves or in the nests of mammals, birds, spiders or insects. In arid regions, caves and animal nests provide them with access to drinking water, without which they cannot produce eggs (Howe, 1959). Some species, such as *Ptinus sexpunctatus* Panzer and *P. californicus* Pic, which occur in the nests of bees, have become depredators, feeding on the pollen stores (Linsley, 1944; Linsley and MacSwain, 1942). According to Hickman (1974), the Australian *Ptinus exulans* Erichson lives in the nests of a salticid spider (*Plexippus validus* Urquhart), where both larvae and adults feed on dead arthropods and spider eggs. Myrmecophily has evolved at least 5 times in the family, and the more highly specialized forms, such as the Australian Ectrephinae, are probably fed by the ants, at least as adults (Lawrence and Reichardt, 1969). The best known ptinids are those which have become pests of stored products and have been spread worldwide by human transport. Examples are *Mezium americanum* Laporte, *Gibbium psylloides* (Czenpinski), *Niptus hololeucus* (Falderman),

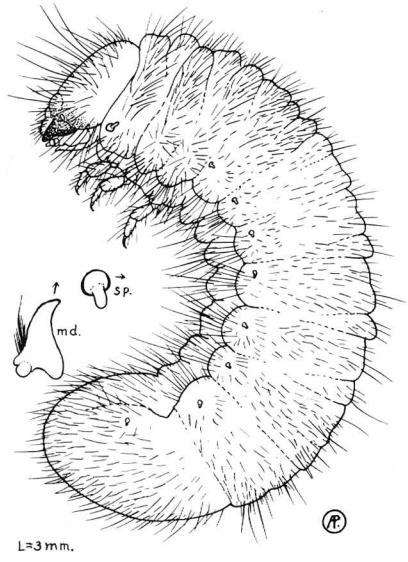

Figure 34.496. Ptinidae. *Ptinus brunneus* Duftschmid. Illinois. Larva, lateral (plus details). Length = 3 mm. Collected from tankage in Illinois. (from Peterson 1951)

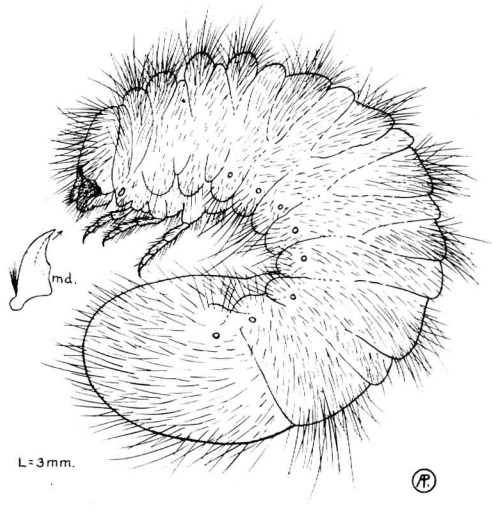

Figure 34.497. Ptinidae. *Mezium americanum* Laporte. Cleveland, Ohio. Larva, lateral (plus details). Length = 3 mm. Reared from rat pellets. (from Peterson 1951)

Ptinus fur (Linnaeus), *P. villiger* Reitter, and *P. tectus* Boieldieu. According to Howe (1959), ptinids cause only minor damage to most goods, either by the accumulation of feces or silk, or by the larvae boring into materials to pupate. The "silken" cocoon formed for pupation has been shown to be composed of chitin and produced by the peritrophic membrane (Crowson, 1981).

Description: Mature larvae 2 to 6 mm. Body elongate, more or less parallel-sided, subcylindrical to slightly flattened, moderately to strongly curved ventrally (C-shaped), lightly sclerotized, whitish to yellowish; vestiture of moderately long, fine hairs, densely and more or less uniformly distributed.

Head: Protracted and hypognathous. Epicranial stem long; frontal arms absent. Median endocarina coincident with epicranial stem. Stemmata absent. Antennae very short, 1-segmented, with well-developed sensorium at apex. Frontoclypeal suture present; labrum free; clypeolabral region narrow. Mandibles symmetrical, robust, wedge-like, with simple, unidentate apex, oblique incisor edge, and no accessory ventral process; mesal surface of mandibular base simple; mola absent. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, narrow or indistinct articulating area, and 3-segmented palp; galea truncate and lacinia falciform with sclerotized, spine-like apex. Labium free to base of mentum; ligula absent; labial palps 2-segmented. Hypopharyngeal sclerome absent. Hypostomal rods absent. Ventral epicranial ridges absent. Gular region absent.

Thorax and Abdomen: Prothorax not enlarged and without sclerotizations. Legs well-developed, 5-segmented; tarsungulus usually with 1 seta, sometimes with 2. Meso- and metaterga and abdominal terga 1–7 with 2 transverse plicae; tergal asperities absent. Segment A9 well-developed, rounded, without urogomphi or median process. Segment A10 reduced, terminal, with pair of longitudinally oval anal pads separated by groove below anus and with U-shaped or V-shaped sclerite (preanal sclerite) at ventral edge of pads.

Spiracles: Annular or annular-uniforous. Thoracic spiracles located near anterior end of prothorax.

Comments: The family contains about 50 genera and 500 species, with 11 genera and about 50 species occurring in America north of Mexico. The subfamily and tribal classification is still in doubt. Belles (1981) has divided the family into 9 informal groups based on the genera *Xylodes, Gynopterus, Maheoptinus, Ptinus, Niptus, Casopus, Trigonogenius, Sphaericus,* and *Gibbium.* This breakdown does not include the myrmecophilous groups, such as *Gnostus* and *Fabrasia* in the New World, *Diplocotidus* in South Africa, or the Australian Ectrephinae.

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LYMEXYLIDAE (LYMEXYLOIDEA)

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Lymexylid Beetles, Ship-Timber Beetles

Figures 34.498-501

Relationships and Diagnosis: The Lymexylidae is a primitive family of the Cucujiformia of uncertain phylogenetic relationship, reflected by their present status as a separate superfamily, Lymexyloidea. Authors studying larval characters have noted similarities with Cucujoidea, while those studying adults have observed similarities with Cleroidea (and previously "Malacoderm" families) (e.g., Böving and Craighead, 1931; Bright, 1979). Lymexyloidea is regarded here as a monofamilial superfamily, although Crowson (1981) has proposed inclusion of Stylopidae (Strepsiptera). Crowson (1955, 1960b, 1981) places Lymexylidae in the series Cucujiformia near Cleroidea (cf. Crowson, 1964) and Cucujoidea (Clavicornia + Heteromera). This situation is presently an unresolved trichotomy. Wheeler (1986) discusses phylogenetic relationships of world genera and recognizes 3 subfamilies: Hylecoetinae (*Hylecoetus*), Lymexylinae (*Lymexylon, Atractocerus*), and Melittomminae (a new subfamily for *Melittomma* and related genera *Protomelittomma, Melottommopsis,* and *Australymexylon*). North American Lymexylidae include *Hylecoetus lugubris* and *Melittomma sericeum* in the U.S. and Canada, and *Atractocerus brasiliensis* in Mexico.

The large hoodlike pronotum, elongate body form, lateral folds, and highly modified ninth abdominal segment (figs. 34.498–500) distinguish the Lymexylidae from most other Coleoptera. Three major structural configurations of the ninth abdominal segment exist: (1) a long, heavily sclerotized, serrated swordlike form in Hylecoetinae (fig. 34.499); (2) a large, bulbous, membranous to lightly sclerotized form in Lymexylinae (fig. 34.500); and a truncate, cylindrical, heavily sclerotized (at least apically) and often toothed form in Melittomminae (sensu Wheeler 1986; cf. fig. 34.498). Some lymexylids (*Hylecoetus* and *Atractocerus*) have plurisetose tarsunguli (fig. 34.501), and late-instar larvae lack stemmata.

Biology and Ecology: All Lymexylidae are wood-boring as larvae, and believed to be symbiotic associates of fungi and microbes. *Hylecoetus dermestoides* L., a Palearctic species, is best understood, and the North American *H. lugubris* is apparently identical in habits. *Hylecoetus* is fungus-growing (Wilson, 1971), cultivating *Ascoidea hylecoeti* in tunnels in many hardwoods and most softwoods (cf. Batra & Francke-Grosmann, 1961; Batra, 1967; Francke-Grosmann, 1967; Lyngnes, 1958). Spores are transmitted to eggs in a sticky substance, and host spores are stored by the female in fungus-pouches of the genitalia (cf. Francke-Grosmann, 1967; Wheeler, 1986). First instar larvae differ from later instars in body proportion, having stemmata, and sometimes bearing trichobothria. Pupation occurs in the wood. Some larvae may live for as many as 6 years or more, and have an indeterminate number of instars. The short-lived adults have bizarre maxillary palp organs which seem to function in chemoreception (Germer, 1912; Slifer et al., 1975). Efforts to determine the symbiotic associates of lymexylids have sometimes proven difficult (e.g., Simmonds, 1956).

Description: Mature larvae 12–20 mm (tropical species up to 50 mm). Body elongate, cylindrical, orthosomatic, definitely sclerotized and pigmented with lateral abdominal folds (figs. 34.498–500). Colors from nearly white to creamy yellow to dark brown. Sparse setae, spines, and asperities on integument.

Head: Large, hypognathous, retracted into large, hoodlike pronotum (fig. 34.499). Stemmata present in first instar larvae, but absent in later instars. Cranium oval, with short postero-medial epicranial suture (sometimes broken or hidden by pronotum), and pale lines on dorsum. Antennae small, 3-segmented (or apparently 2-segmented), and posterodorsal to mandibles; segment 2 (first clearly visible segment) with large digitiform sensorium and few other sensilla; segment 3 only slightly larger than sensorium on 2. Labrum elongate, simple. Epipharynx membranous, with dense setae. Mandible broad, short, and heavily sclerotized; with distinct molar part covered by transverse grooves or minute spines; prostheca absent. Maxilla with distinct cardo; stipes and mala fused; mala partially divided at apex in some taxa, and mesal surface with double row of long setae and membranous area between; maxillary palp 3-segmented. Labium small, lightly sclerotized; labial palp 2-segmented; ligula broad, membranous.

Thorax and Abdomen: Prothorax large, hoodlike, partially covering head; with sparse spines and asperities, especially anteriorly. Meso- and metathorax smaller than prothorax. Three pairs of small but well-developed legs; legs with many spines and setae, terminating in heavily sclerotized tarsungulus which is bisetose or plurisetose (*Hylecoetus* and *Atractocerus*).

Abdomen elongate, subcylindrical, with 9 large segments, each with lateral fold (fig. 34.500), and a minute tenth segment inferior to ninth and restricted to area surrounding anus. Ninth segment with 3 structural types: long, heavily sclerotized, swordlike and spinose (e.g., *Hylecoetus,* fig. 34.499); large, bulbous, lightly sclerotized, usually with dense asperities (e.g., *Atractocerus,* fig. 34.500); and cylindrical, truncate, and often with large teeth around apical rim (e.g., *Melittomma,* fig. 34.498).

Spiracles: Present on abdominal segments 1–8; lateral, annular or annular-multiforous, elliptical.

Comments: The Lymexylidae includes about 7 genera and 50 species worldwide. The family is primarily tropical, with only two species established in the United States and Canada (*Hylecoetus lugubris* Say and *Melittomma sericeum* Harris), easily identified by the form of the ninth abdominal segment (cf. figs. 34.498, 34.499). *Atractocerus brasiliensis* is a widespread species in Mexico and Central and South America. In Europe, *Hylecoetus dermestoides* is sometimes a serious pest of stored lumber, but *H. lugubris* has only rarely been a problem in N. America. *Melittomma sericeum* used to infest up to 90% of the trees in local stands of chestnut in N. America, but is today an uncommon species. Although many lymexylid larvae have been described

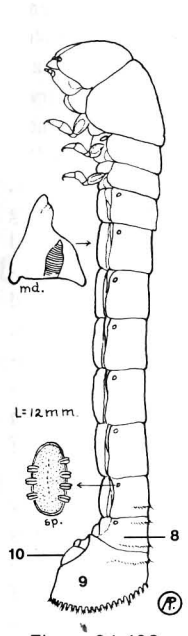

Figure 34.498

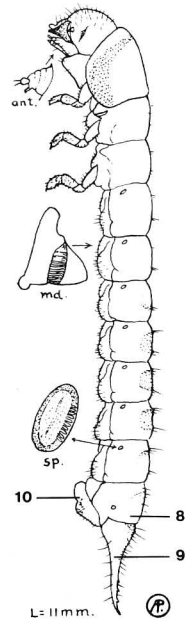

Figure 34.499

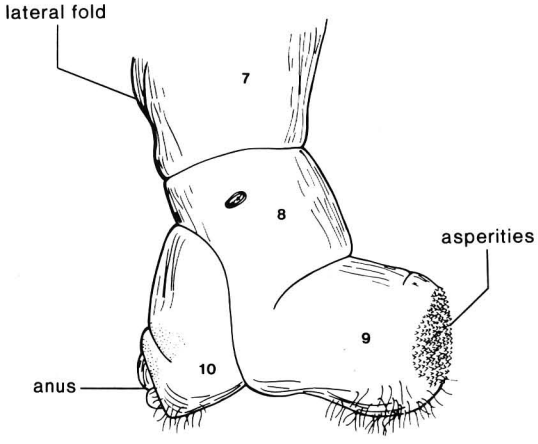

Figure 34.500

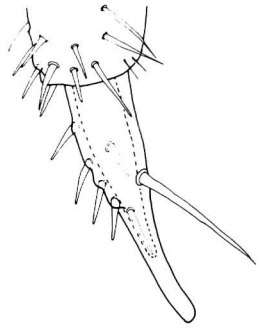

Figure 34.501

Figure 34.498. Lymexylidae. *Melittomma sericeum* Harris, chestnut timberworm. Larva, lateral. Formerly a serious pest of chestnut, now uncommon, chiefly in white oak. (From Peterson, 1951)

Figure 34.499. Lymexylidae. *Hylecoetus lugubris* Say. Larva, lateral. Infests assorted softer hardwoods, including poplar, birch, tulip-poplar, basswood, walnut and buckeye. (From Peterson, 1951)

Figure 34.500. Lymexylidae. *Atractocerus brevicornis* Palisot de Beauvois. Apex of abdomen (lateral) showing lymexyline type of ninth segment. (From Wheeler, 1986)

Figure 34.501. *Hylecoetus dermestoides* L. Tarsungulus, showing plurisetose condition. (From Wheeler, 1986)

(*see* review in Wheeler, 1986.), there remains much work to be done before the full range of structural and biological variability is known. The genera have recently been revised (Wheeler 1986).

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PHLOIOPHILIDAE (CLEROIDEA)

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This family includes the single genus *Phloiophilus*, containing the European species *P. edwardsi* Stephens and a second species from North Africa. The group is considered to be the most primitive member of the Cleroidea, and it shares a number of features with protopeltine Trogossitidae.

Larvae are 4 to 4.5 mm in length, and are elongate, slightly flattened, and lightly sclerotized, except for the head and tergum A9. The head is transverse, strongly rounded laterally, without an epicranial stem, and with lyriform frontal arms and a long median endocarina. There are 6 stemmata on each side, and the antennae are relatively short. The mandibles lack a mola, but each has 3 short, acute processes at the base. The ventral mouthparts are retracted, with the stipes longer than the cardo, and the maxillary mala bears a pedunculate seta. The gular and paragular regions are lightly

sclerotized, and the hypostomal rods are slightly diverging and extend almost to the posterior edge of the head. The protergal plate is barely indicated. The legs are relatively short, with a unisetose tarsungulus. Tergum A9 is moderately sclerotized, with a pair of short, upturned, fixed urogomphi. Spiracles are annular-uniforous.

Phloiophilus edwardsi is known to feed as both adult and larva beneath the relatively thin and fleshy fruiting bodies of the wood-rotting fungus *Phlebia merismoides* (Basidiomycetes: Meruliaceae); pupation occurs on the ground.

Selected Bibliography

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TROGOSSITIDAE (CLEROIDEA)

(= TROGOSITIDAE; INCLUDING LOPHOCATERIDAE, OSTOMIDAE, PELTIDAE, TEMNOCHILIDAE)

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Bark-Gnawing Beetles, Cadelles

Figures 34.502–504

Relationships and Diagnosis: The family Trogossitidae is used here in its broadest sense, encompassing the families Peltidae and Lophocateridae, as defined by Crowson (1964d, 1966a, 1970). This family and the related Phloiophilidae include the more primitive types of larval Cleroidea, which are similar to those of some cucujoids, as well as the predaceous, clerid-like larvae of Trogossitini. Trogossitid larvae may be distinguished from those of Cleridae and Chaetosomatidae by having the ventral mouthparts retracted, and from those of Melyridae and Phycosecidae by lacking a long epicranial stem and having the gular and paragular regions as heavily sclerotized as the epicranium.

Biology and Ecology: Although most of the better known Trogossitidae are predatory, several are mycophagous and 2 have become stored products pests. The New Zealand *Protopeltis* is apparently a fungus feeder, like the related Phloiophilidae. Little is known about the south temperate Rentoniinae; the single presumed larva was collected in leaf litter but assumed to have dropped from an arboreal habitat (Crowson, 1966a). Adults of the S. American Decamerinae are apparently pollen feeders, as are those of the N. American *Eronyxa*. Members of the Peltinae and Calitinae feed on the fruiting bodies of various Polyporaceae. *Thymalus marginicollis* Chevrolat breeds mainly in the birch bracket fungus (*Piptoporus betulinus*), but has been found in other polypores as well. *Ostoma pippingskoeldi* (Mannerheim) and *Calitys scabra* (Thunberg) are usually associated with *Fomitopsis pinicola*, a common brown rot of conifers, while *O. ferruginea* (Linnaeus) and *C. minor* Hatch were collected together in *Tyromyces leucospongia* brackets and *O. columbiana* Casey was found in *Hapalopilus alboluteus*. The Lophocaterinae are often found beneath bark, and evidence suggests that at least some are predaceous (Crowson, 1964d). The south temperate Egoliinae vary considerably in form and their habits are not well known; *Egolia* and *Acalanthis* larvae are very similar to those of typical trogossitines and are almost certainly predaceous. Trogossitinae are primarily predators as adults and larvae, and they are usually found under bark, in rotten wood, and in the galleries of various wood-boring insects, such as Cerambycidae, Bostrichidae, Scolytidae, and Siricidae (Hymenoptera). Some of the small, narrow trogossitines, like species of *Nemosoma, Corticotomus, Airora,* and *Cylidrella,* are specialized predators of smaller bark beetles. Species of *Temnochila* and *Tenebroides* are important predators of Scolytidae and other xylophagous insects in both conifer and hardwood forests. *Temnochila chlorodia* (Mannerheim) is often found in the small fruiting bodies of *Cryptoporus volvatus,* where it feeds on the mycophagous inhabitants (Nitidulidae, Ciidae, Tenebrionidae); it apparently plays a role in the dissemination of the spores of this fungus (Borden and McClaren, 1970, 1972). The cadelle, *Tenebroides mauritanicus* (L.) (figs. 34.502a–c), is a predator of stored products pests but also feeds on grain and cereal products.

Description: Mature larvae 2 to 50 mm (usually 10 to 30 mm). Body elongate, subcylindrical to slightly flattened, occasionally with enlarged thoracic region. Usually lightly sclerotized, except for head, protergum, and part of tergum A9 (occasionally without sclerotizd areas); paired sclerotizations often present on meso- and metaterga (and rarely terga A6–8); color usually cream or white, but varying to purple in some surface-active forms. Surfaces smooth; vestiture consisting of shorter and longer, scattered setae.

Head: Protracted and prognathous, slightly elongate and parallel-sided in Trogossitinae, transverse with strongly rounded sides in Peltinae, with intermediate conditions occurring in *Calitys* and Lophocaterinae. Epicranial stem usually absent (very short in some Peltinae); frontal arms V-shaped. Median endocarina extending between frontal arms in most species; a Y-shaped endocarina coincident with the short epicranial stem and the frontal arms in most Peltinae; paired endocarinae located between frontal arms in *Thymalus*. Stemmata usually 2 or 5 on each side; sometimes absent and occasionally 3, 4, or 6. Antennae well-developed, 3-segmented, very short in Peltinae. Frontoclypeal suture absent except in some Peltinae; labrum free. Mandibles heavy and subtriangular, bidentate, without a mola or accessory ventral process; inner edge of mandibular base bearing 1 to several hyaline processes forming a lacinia mobilis (also called lacinia mandibulae). Ventral mouthparts more or less retracted, the maxillolabial complex at least as long as gula; cardo transverse, stipes elongate, maxillary articulating area usually absent, and mala simple and rounded or truncate, with or without a pedunculate seta; maxillary palp almost always 3-segmented (2-segmented in Rentoniinae). Labium with mentum and submentum fused; postmentum elongate in Trogossitinae; labial palps almost always 2-segmented (1-segmented in Rentoniinae); ligula usually absent. Gula longer than wide, except in Peltinae. Hypostomal rods usually subparallel and extending to posterior edge of head, delimiting sclerotized paragular plates; hypostomal rods absent

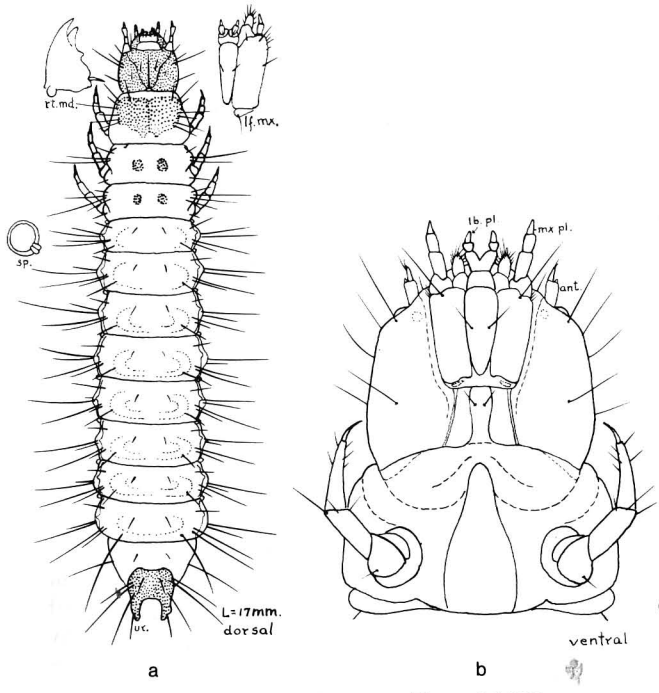
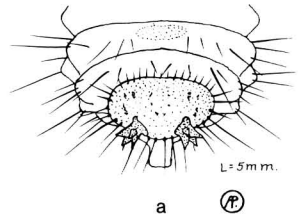


Figure 34.502



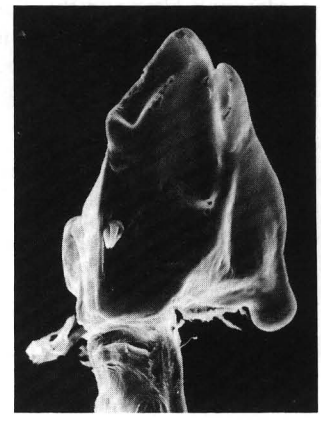
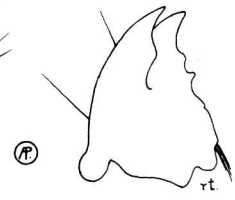


Figure 34.503



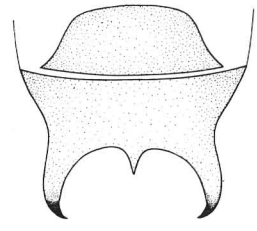


Figure 34.504

Figures 34.502a-c. Trogossitidae. *Tenebroides mauritanicus* (Linnaeus), the cadelle. **a.** larva, dorsal, length = 17 mm; **b.** head and prothorax, ventral; **c.** right mandible, ventral. Dirty white, with head, pronotum, anal plate and urogomphi deep brown; long, colorless setae on all segments, especially the lateral aspects; anal plate bearing 2, thick, rounded urogomphi with small pointed tips. Infests stored grains, rice, flour, meal, and may injure paper and wood containers, silk bolting cloth and similar materials associated with food products. (From Peterson, 1951)

Figures 34.503a,b. Trogossitidae. *Thymalus marginicollis* Chevrolat. **a.** abdominal apex, dorsal; **b.** left mandible, mesal. Concord, Massachusetts. (Figure 34.503a from Peterson, 1951)

Figure 34.504. Trogossitidae. (Lophocaterinae). Abdominal apex, dorsal.

in some Peltinae. Ventral epicranial ridges present in Trogossitinae and *Calitys*.

Thorax and Abdomen: Protergum with sclerotized plate in *Thymalus, Calitys,* and Trogossitinae; mesotergum with single plate in Trogossitini but with paired plates in *Calitys* and Egoliini; metatergum usually with paired plates in Trogossitini. Prothorax enlarged in *Ostoma* and related genera. Ventral regions of thorax with various sclerotizations in Trogossitinae. Legs moderately well-developed, somewhat reduced in some Peltinae, widely separated; tarsungulus with 1 seta. Abdominal terga 1–6 or 7 sometimes with paired ampullae. Paired, coiled, tubular glands (not easily visible) often present on abdominal terga 1–8. Tergum A9 usually with sclerotized basal plate (absent in most Peltinae) and always with paired urogomphi, which bear accessory processes in *Calitys* and *Thymalus*. In Lophocaterinae, basal plate transversely divided and median, posteriorly projecting tooth present between urogomphi. Sternum A9 well-developed; segment A10 ventrally located, small, circular.

Spiracles: Annular-biforous or apparently annular.

Comments: The family includes about 60 genera and 600 species worldwide, with 14 genera and about 60 species known from America north of Mexico. The classification has been subject to dispute in recent years. Barron (1971, 1975) divided the family along traditional lines, with 2 groups based on adult structure: Peltinae, with a more or less broadly oval body and explanate elytra, and Trogossitinae, with a narrower, more elongate body. The first group, with the exception of *Calitys* also has open procoxal cavities. Crowson (1964d, 1966a, 1970) divided the family into 8 groups, which he recognized as 3 separate families: Peltidae, with the subfamilies Decamerinae (including *Eronyxa*), Protopeltinae, Rentoniinae, and Peltinae (including *Ostoma* and *Thymalus*); Lophocateridae (including *Lophocateres, Lycoptis,* and *Grynocharis*); and Trogossitidae, with the subfamilies Calitinae (*Calitys*), Egoliinae, and Trogossitinae (equivalent to that of Barron). Crowson's 8 groups are all considered subfamilies here. Decamerinae are primarily S. American, with the western N. American *Eronyxa* somewhat doubtfully included; Protopeltinae, Rentoniinae, and Egoliinae are restricted to the Southern Hemisphere; Lophocaterinae and Trogossitinae are worldwide; and Peltinae and Calitinae are Holarctic.

There are 2 economically important species: the cadelle (*Tenebroides mauritanicus,* figs. 34.502a–c), which is a primary pest of stored grains and cereal products (in spite of its

predatory habits), and the Siamese grain beetle, (*Lophocateres pusillus* (Klug), which is a secondary grain pest, especially common in rice.

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CHAETOSOMATIDAE (CLEROIDEA)

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The family Chaetosomatidae includes the monotypic New Zealand genera *Chaetosoma* and *Chaetosomodes,* and the Madagascar genera *Malgassochaetus* and *Somatochaetus,* with 5 and 2 species, respectively. The family is thought to be most closely related to Cleridae.

Larvae are elongate, parallel-sided, slightly flattened, white or pink, and lightly sclerotized, except for head, protergal plate, A9 tergum, and lightly sclerotized plates on meso- and metatergum. The head is elongate, with a short epicranial stem, V-shaped frontal arms, and a median endocarina. The base of the mandible has no mola but bears 2 slender spines and a seta. Ventral mouthparts are strongly protracted, with the cardo longer than the stipes, and the mala has a pedunculate seta. The hypostomal rods are subparallel and extend to the posterior edge of the head. Gular and paragular plates are well-sclerotized. Legs are 5-segmented, with a unisetose tarsungulus. Paired gland openings are absent from the abdominal terga, and tergum A9 is concave, with a pair of upturned urogomphi. Spiracles are annular-biforous.

Chaetosomatid larvae live in the galleries of wood-inhabiting beetles and are apparently predaceous. A larva of *Chaetosoma scaritides* Westwood has been found in the galleries of a cossonine weevil.

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CLERIDAE (CLEROIDEA)
(INCLUDING CORYNETIDAE, KORYNETIDAE)

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Checkered Beetles

Figures 34.505-508

Relationships and Diagnosis: The Cleridae are advanced members of the Cleroidea, whose larvae are distinguished from all other members of the superfamily (with the exception of the closely related Chaetosomatidae) by the strongly prognathous ventral mouthparts with transverse stipites and the elongate gular region, which is as heavily sclerotized as the epicranial region. Surface-active clerid larvae are usually reddish or mottled with shades ranging from blue to red, so that they superficially resemble melyrid larvae occurring in the same habitats. Melyrid larvae differ from those of most clerids, however, by having a long epicranial stem and no median endocarina, and from those of all clerids by having the ventral mouthparts more retracted with elongate stipites and the gular region more lightly sclerotized than the epicranium (head lacking a ventral closure). Gallery-inhabiting clerid larvae are subcylindrical and lightly pigmented, and they may have dorsal ampullae similar to those of some wood-boring, xylophagous beetles on which they prey; but the features of the head capsule and mouthparts are still diagnostic in these forms. The larva of *Chaetosoma* differs from those of Cleridae in having hypostomal rods which extend to the posterior edge of the head capsule.

Biology and Ecology: With the exception of some species of *Necrobia,* all Cleridae are predaceous as adults and larvae. The majority are xylophilous and prey on a variety of wood-boring and subcortical insects, but some are restricted to other habitats and others are wide-ranging predators. Members of the Thaneroclerinae usually prey on small mycophagous insects and are found under bark or in fungus fruiting bodies; one of these, *Thaneroclerus buqueti* (Lefevre), is associated with stored products, where it feeds on various pest species, especially *Lasioderma serricorne* (Fabricius) (Anobiidae). Xylophilous clerid larvae fall into 2 groups: those which are relatively unspecialized and capable of moving rapidly on surfaces or in tunnels or galleries, and those which have become specially adapted for living within the tunnels of wood-boring insects. The second type has evolved several times in the subfamilies Tillinae (*Cylidrus,*

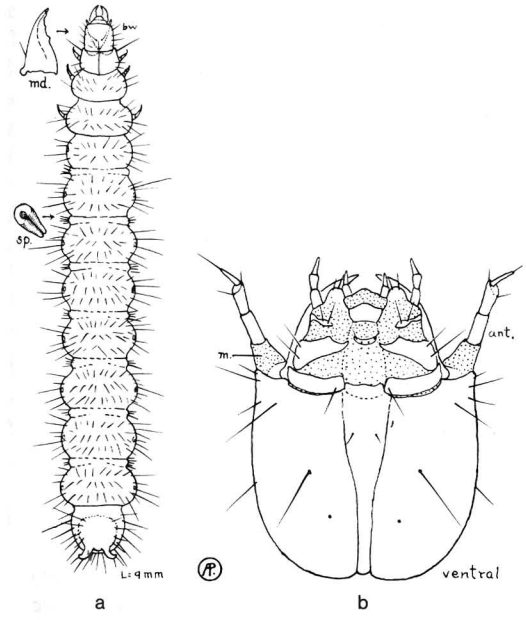

Figure 34.505

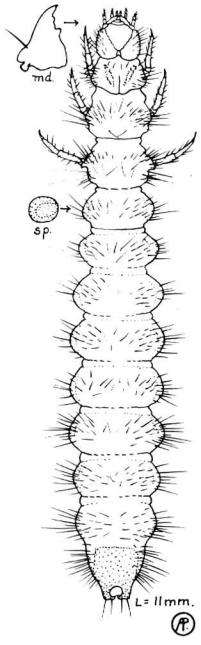

Figure 34.506

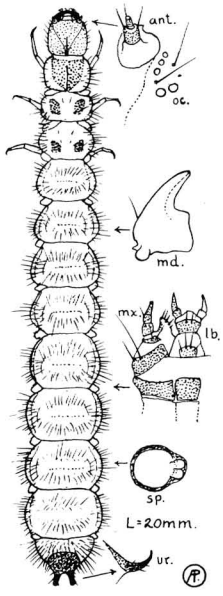

Figure 34.507

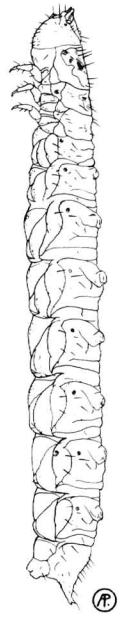

Figure 34.508

Figures 34.505a,b. Cleridae. *Necrobia rufipes* (De Geer), the redlegged ham beetle. Length = 9 mm. **a.** larva, dorsal; **b.** head, ventral. *See* "Comments." (from Peterson 1951)

Figure 34.506. Cleridae. *Cymatodera* sp. Arizona. Larva, dorsal, length = 11 mm. (from Peterson 1951)

Figure 34.507. Cleridae. *Enoclerus* sp. Massachusetts. Larva, dorsal, length = 20 mm. (from Peterson 1951)

Figure 34.508. Cleridae. *Priocera castanea* (Newman). Larva, lateral, length = 13 mm. (from Peterson 1951)

Monophylla), Epiphloeinae (*Neichnea, Phlogistosternus*), Enopliinae (*Pelonium, Chariessa, Cregya, Orthopleura, Tenerus*), Tarsosteninae (*Tarsostenus, Paratillus*), and Clerinae (*Priocera*).

There may be strong preferences for habitat or prey type. Some genera like *Chariessa* are associated with deciduous trees, while *Thanasimus* are restricted to conifers. Species of *Monophylla* and *Cylidrus* are predators of Bostrichidae; *Paratillus carus* (Newman) and *Tarsostenus univittatus* (Rossi) are associated with lyctine Bostrichidae; and *Thanasimus* species prefer bark beetles (Scolytidae). Within the genus *Enoclerus, E. sphegeus* (Fabricius) and related species occur on conifers, where several are important bark beetle predators, *E. eximus* (Mannerheim) occurs in riparian situations and preys on anobiids in alder and willow, *E. coccineus* (Schenklin) and *E. acerbus* Wolcott occur in the roots of rabbit brush, where they prey on cerambycid larvae, and *E. abdominalis* (Chevrolat) preys on yucca moth larvae in the pods and weevil larvae in the stems of *Yucca*. Many *Cymatodera* species are apparently associated with wood borers, but they have also been reported from cynipid galls and the cells of megachilid bees. Species of *Phyllobaenus* are also wide-ranging predators, and may occur not only in woody habitats, but in leaf litter, galls, or the webbing of Lepidoptera. *Lecontella cancellata* has been recorded from the cells of 7 species of aculeate Hymenoptera. Species of *Trichodes* occur primarily in the cells of bees, but *T. oregonensis* Barr and *T. nutalli* (Kirby) prey on the eggs of slantfaced grasshoppers. *Aulicus terrestris* Linsley feeds on the eggs of lubber grasshoppers.

Within the subfamily Corynetinae, *Corynetes coeruleus* occurs in wood and preys on Anobiidae, but some species of *Necrobia* frequent carrion and are scavengers as well as predators (*see* "Comments").

Description: Mature larvae 5 to 25 mm. Body elongate and parallel-sided to somewhat fusiform or clavate and subcylindrical to slightly flattened; lightly sclerotized, except for head (only rarely as lightly sclerotized as rest of body), prothorax, which bears a protergal plate and usually paired meso- and metatergal plates, and tergum A9, which usually bears a sclerotized basal plate and/or urogomphi. Color white or cream in gallery-inhabiting forms, but often with varying amounts of red or blue pigments in free-living species. Surfaces smooth, and vestiture of numerous short, fine hairs or longer, scattered hairs.

Head: Protracted and prognathous, often elongate and flattened, with subparallel sides, but sometimes subconical or globular, with modified upper surface. Posterior edge of head sometimes emarginate or notched. Epicranial stem usually absent (well-developed in Thaneroclerinae and some exotic Enopliinae); frontal arms V-shaped, usually contiguous at base, sometimes narrowly separated, widely separated in Phyllobaeninae. Median endocarina extending between frontal arms in all but Thaneroclerinae. Stemmata varying from 1 to 5 on each side or occasionally absent, usually arranged in 2 subvertical rows. Antennae well-developed, 3-segmented. Frontoclypeal suture usually distinct; labrum free. Mandibles heavy, subtriangular, unidentate, with apex acute or somewhat rounded; retinaculum, if present, weakly

developed; mola and accessory ventral process absent; mesal edge of mandibular base sometimes with 2 or more spine-like, hyaline processes forming a lacinia mobilis (or lacinia mandibulae). Ventral mouthparts protracted or sometimes slightly retracted, with transverse cardines, sometimes reduced, transverse stipites, and no maxillary articulating areas; mala simple and rounded, with a pedunculate seta; maxillary palp 3-segmented. Mentum and submentum distinct, the latter usually membranous; labial palps 2-segmented and moderately broadly separated; ligula weakly developed. Gula longer than wide, often very narrow; gular and paragular areas usually heavily sclerotized, so that head capsule appears to be broadly closed behind. Hypostomal rods usually short and subparallel, sometimes absent.

Thorax and Abdomen: Prothorax usually with a large, sclerotized tergal plate occupying most of the dorsal surface and divided only by a median ecdysial line; plate sometimes reduced and occasionally (*Orthopleura, Tenerus*) absent. Meso- and metaterga with or without paired, subcircular sclerotizations of varying size. Legs moderately well-developed, widely separated; tarsungulus with 1 seta. Abdomen sometimes enlarged near posterior end (clavate), occasionally very long and narrow; paired ampullae sometimes present on abdominal terga 2–8. Tergum A9 almost always with a sclerotized basal plate and usually with a pair of urogomphi (reduced or absent in *Phyllobaenus* and some Thaneroclerinae), which vary from long, hooked structures to short, blunt projections, and may be widely separated or occasionally joined at base. Segment A10 reduced, ventrally or posteroventrally situated, and oval or subcircular.

Spiracles: Usually annular or annular-biforous with very small accessory openings; occasionally (Korynetinae) with well-developed accessory openings.

Comments: The family includes about 150 genera and 4000 species worldwide, with 37 genera and about 300 species occurring in America north of Mexico. Crowson (1964d) gave a key to the 8 subfamilies based on adults, and later (1972a) discussed their phylogenetic relationships based on studies of the alimentary canal made by Ekis and Gupta (1971).

Two species of Cleridae have been recorded as stored products pests: *Necrobia ruficollis* (Fabricius), the red shouldered ham beetle, and *N. rufipes* (De Geer) the red legged ham beetle (figs. 34.505a,b). The former occurs mainly on animal matter, and is relatively scarce in plant products, while the latter is a common insect in copra, oilseeds, oilcake, and cocoa beans, where it feeds on other pests, as well as on the products themselves.

Selected Bibliography

Aitken 1975 (species in stored products).
Balduf 1935 (biology of various predators).
Barr 1961 (review of Pacific Northwest species).
Beeson 1926 (biology of Indian species).
Böving and Champlain 1921 (North American larvae; 32 species in 15 genera).
Böving and Craighead 1931.
Craighead 1950 (predators of forest pests).
Crowson 1964d, 1972a.
Ekis 1977 (*Perilyphus* revision; larval description).
Ekis and Gupta 1971.
Foster 1976a (larvae of Thaneroclerinae), 1976b (larvae of Tillinae), 1976c (*Trichodes* revision; larval description).
Furniss and Carolin 1977 (predators of forest pests).
Gardner 1937a (larvae of Indian species).
Kline and Rudinsky 1964 (predators of forest pests).
Linsley and MacSwain 1943 (biology and larva of *Trichodes ornatus* Say).
Scott 1919 (biology and larva of *Necrobia ruficollis*).

PHYCOSECIDAE (CLEROIDEA)

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This family includes the single genus *Phycosecis*, with 1 species from New Zealand and 3 more from Australia. In spite of the cucujoid appearance of the adult, larval characters of *Phycosecis* indicate a close relationship to the cleroid family Melyridae.

Larvae are elongate, narrow, slightly flattened, and lightly sclerotized, except for the head and protergal plate. The head is subquadrate and flattened, with a Y-shaped epicranial suture and no median endocarina. There are 6 stemmata on each side and the mandible lacks a mola but has a plumose process at the base. The ventral mouthparts are retracted with the stipes much longer than the cardo, and the mala bears a pedunculate seta. The gular and paragular regions are lightly sclerotized, so that the head capsule appears open behind, and the hypostomal rods extend to the posterior edge of the head. The protergal plate is weakly developed, and thoracic and abdominal terga lack paired gland openings. Tergum A9 is slightly more heavily sclerotized than the preceding terga and has a pair of subparallel, posteriorly projecting urogomphi, slightly curved at apex. Spiracles are annular.

Phycosecids live along coastlines among sand dunes, and adults may be active during the day but are difficult to see because of their covering of grayish scales or scale-like setae. Larvae and adults are scavengers and have been found on dead birds and fishes along the beach. Crowson (1964d) found insect parts in the larval gut of *P. limbata* (Fabricius), but I have reared *P. littoralis* Pascoe through an entire generation in a closed container with fresh fish, lettuce, and bran (larvae were usually clustered beneath the rotting pieces of fish).

Selected Bibliography

Crowson 1964d (relationships, larva), 1970 (key to larval Cleroidea).
Hudson 1934 (habits of *P. limbata*).

ACANTHOCNEMIDAE (CLEROIDEA)

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This family is based on a single species, *Acanthocnemus nigricans* Hope, which is native to Australia, but has been introduced into southern Europe, North Africa, southern

Africa, Madagascar, India, Burma, Thailand, and New Caledonia. The group is considered to have affinities with both Trogossitidae and Melyridae. An unassociated first instar larva has been described by Crowson (1970), but this is not described here because of the questionable identification. *Acanthocnemus* adults often fly to lights and one series was taken from the hot ashes of a campfire; in addition, they have been found under bark on several occasions. Crowson's larva was found in litter around the base of a *Eucalyptus*. An unusual adult feature which may provide a clue to the niche occupied by this widespread species is the presence on each pronotal hypomeron of a deep cavity, which is almost totally blocked by a thin cuticular flap, attached at one point to the rim of the cavity.

Selected Bibliography

Champion 1922 (distribution).
Crowson 1970 (relationships, putative larva).

MELYRIDAE (CLEROIDEA)

(INCLUDING DASYTIDAE, MALACHIIDAE, PRIONOCERIDAE, RHADALIDAE)

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John F. Lawrence,
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Soft-winged Flower Beetles

Figures 34.509-510

Relationships and Diagnosis: The family Melyridae is one of the more derived groups of Cleroidea and appears to be most closely related to Acanthocnemidae and Phycosecidae, both of which are endemic to the Australian Region. Melyrid larvae (and also those of Phycosecidae) may be distinguished from those of other cleroids by the distinctive head capsule, which is somewhat parallel-sided and flattened, with a long-stemmed, Y-shaped epicranial suture and no endocarina, and is well-sclerotized dorsally with membranous gular and paragular regions ventrally; this type of head capsule is sometimes described as lacking a ventral closure. Additional features distinguishing melyrid larvae from those of Cleridae and Chaetosomatidae are the retracted ventral mouthparts with elongate stipites, and shorter, broader gula. Phycosecid larvae differ from those of melyrids in having well-developed hypostomal rods and 6 stemmata on each side.

Biology and Ecology: Adult Melyridae are active and usually diurnal inhabitants of surfaces, often occurring in flowers or on foliage. The large subfamily Malachiinae contains many brightly colored, aposematic species, which have eversible defense glands; this same group is characterized by having a variety of glandular structures on the head, antennae, or elytra of the male, which are used in courtship (Matthes, 1970a, 1970b). Adult melyrids may feed on pollen or other insects; Crowson (1964d) found pollen grains in the guts of representatives of all 5 subfamilies and insect fragments in at least some Haplocneminae, Dasytinae, and Malachiinae.

Larval melyrids occur in a variety of habitats where they are either scavengers or predators. Larvae of species of *Dasytes, Anthocomus, Malachius,* and *Hypebaeus* have all been collected under bark or in the galleries of wood-boring beetles, but melyrids in general are less common than Cleridae and Trogossitidae in this habitat. A number of larvae occur on the ground or in soil and leaf litter, where they feed on living or dead animals (insects, molluscs, worms, carrion). They are particularly common in sandy soils and on beaches; *Amecocerus* larvae were found in soil beneath dune vegetation. *Endeodes* species occur in the debris accumulated at the high tide mark on beaches along the Pacific Coast (Moore, 1956; Moore and Legner, 1977). A larva belonging to a species of *Rhadalus* was collected from rotting *Yucca* stems in Arizona. Adults of the European *Psilothrix viridicaeruleus* (Geoffroy) deposit eggs in dead flower heads or inflorescences, and the first instar is immobile and non-feeding; later instars become scavengers on the ground, and the last instar bores into the stems of herbaceous plants where it pupates (Fiori, 1971). *Anthocomus horni* (Fall) has been collected under pine bark, but also in tephritid galls on sagebrush and in the nests of black-billed magpies (Foster and Antonelli, 1973). *Malachius bipustulatus* (L.) has been collected in *Artemisia* stems inhabited by larvae of *Mordellistena* (Mordellidae), and *M. aeneus* (L.) is known to be a predator on insect larvae in grasses. Larvae of *Collops* species are predaceous in a variety of situations, including grasses, beaches, termite nests, and refuse chambers of harvester ants. At least 3 species prey on important economic pests: *C. bipunctatus* (Say) on the alfalfa weevil (*Hypera postica* (Gyllenhal)), *C. hirtellus* LeConte on the pea leaf weevil (*Sitona lineata* (Linnaeus)), and *C. vittatus* (Say) on the alfalfa caterpillar (*Colias erytheme* Boisduval). *Dicranolaius villosus* (Lea) occurs in soil in Australia, where it is an egg pod predator of the Australian plague locust (*Choroicetes terminifera* (Walker)) (Farrow, 1974).

Description: Mature larvae 2.5 to 25 mm (usually 5 to 10 mm). Body elongate and usually narrow, sometimes wider at middle, subcylindrical to slightly flattened. Lightly sclerotized except for head, usually tergum A9, and paired plates (or pigmented areas) on thoracic terga; color cream to pink, red, or purple; vestiture of fine hairs, usually short and scattered but sometimes long and dense.

Head: Protracted and prognathous, subquadrate or slightly elongate, parallel-sided and more or less flattened. Epicranial stem long and frontal arms V-shaped; median endocarina absent. Stemmata usually 4 or 5 on each side, arranged in 2 subparallel, vertical rows, sometimes fewer (2 in Haplocneminae). Antennae relatively short, 3-segmented, with first 2 segments usually subequal and the last much narrower and usually longer; sensorium broadly conical. Mandibles broadly triangular, bidentate, without a mola and with a serrate and/or bifurcate lacinia mobilis at base of mesal edge. Ventral mouthparts retracted. Maxilla with transverse, subtriangular cardo, elongate stipes, no articulating area, and

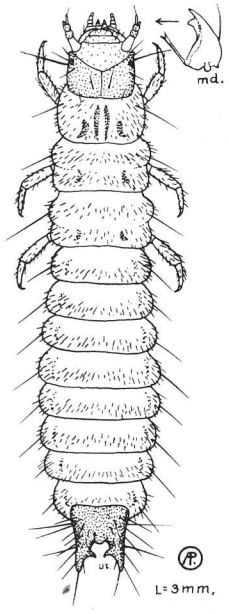

Figure 34.509

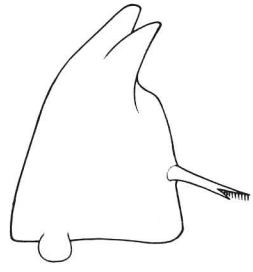

Figure 34.510

Figure 34.509. Melyridae. *Collops* sp. Larva, dorsal, length = 3 mm. (From Peterson, 1951)

Figure 34.510. Melyridae. (Malachiinae). Mandible, ventral.

simple, rounded mala; maxillary palp 3-segmented. Labium with submentum more or less distinct and mentum connate with stipites for most of its length; labial palps 2-segmented, broadly to narrowly separated. Gula subquadrate to slightly elongate; gular and paragular areas lightly sclerotized, in contrast with dorsal surface, so that head capsule appears to be "open" ventrally (lacking a sclerotized ventral closure). Hypostomal rods absent; ventral epicranial ridges occasionally present. Hypopharyngeal bracon present; hypopharyngeal sclerome absent.

Thorax and Abdomen: Protergum often with 1 to 3 pairs of sclerites or pigmented areas, a larger, elongate median pair, and 1 or 2 oval or crescent-shaped lateral ones; rarely with single prothoracic plate. Meso- and metaterga often with 1 pair of small plates or pigmented areas (rarely with 2). Legs well-developed, widely separated; tarsungulus with 1 seta. Thoracic terga and abdominal terga 1–8 or A1 and A8 often with 1 or 2 pairs of gland openings. Abdominal terga 1–8 rarely (Prionocerinae) with paired plates or pigmented areas. Tergum A9 usually with sclerotized basal plate and almost always with paired urogomphi, which may be arcuate or hooked and sometimes have mesally projecting teeth near the base. Basal plate or urogomphal bases occasionally with 1 (Haplocneminae) or 2 (Prionocerinae) pairs of membranous, tubular appendages. Sternum A9 simple. Segments A10 ventrally or posteroventrally situated, transversely oval.

Spiracles: Annular.

Comments: The family includes about 200 genera and 5000 species worldwide, with 47 genera and about 450 species known from America north of Mexico. Crowson (1964d, 1970) divided the group into 5 subfamilies: Haplocneminae (including *Rhadalus*), Melyrinae (including *Melyrodes* and *Eurelymis*), Prionocerinae (exotic), Dasytinae, and Malachiinae. Melyrinae are most diverse in S. America and Africa, Prionocerinae occur in southern Eurasia and tropical Africa, Dasytinae are particularly abundant in the Mediterranean region and southwestern N. America, and the Malachiinae is the largest and most widespread group and the only one to have radiated extensively in Australia. There are no economically important species, but *Zygia oblonga* (Fabricius) occurs in stored carob, barley, dried fruit, and lentils in the Mediterranean region.

Selected Bibliography

Aitken 1975 (stored products records).
Balduf 1935.
Böving and Craighead 1931 (larvae of *Malachius bipustulatus* (Linnaeus), *Anthocomus auritus* (LeConte), *Collops nigriceps* (Say), and *Dasytes caeruleus* (De Geer)).
Crowson 1964d, 1970.
Farrow 1974 (larva of *Laius villosus* Lea).
Fiori 1963, 1971 (larva of *Psilothrix viridicoeruleus* (Fourcroy)).
Foster and Antonelli 1973 (larva of *Anthocomus horni* (Fall)).
Gardner 1929 (larvae of *Idgia* spp.), 1931b (larva of *Carphurus almorensis* (Champion).
Matthes 1970a (courtship in *Malachius bipustulatus* (L.), 1970b (courtship in *Troglops albicans* (L.)).
Medvedev and Galata 1969 (larva of *Simoderus reflexicollis* Gebl)
Moore 1956 (habitat and larvae of *Endeodes*).
Moore and Legner 1977 (larvae and pupae of *Endeodes*).
Vinson 1957 (larva of *Pelecophora pikei* Vinson).

PROTOCUCUJIDAE (CUCUJOIDEA)

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This family is based on the genus *Ericmodes* (= *Protocucujus*), which includes 2 species from Chile and a third from Australia, but several species and probably an additional genus remain to be described from these regions. It is one of the more primitive cucujoid families and is thought to be closely related to the Sphindidae.

Adult protocucujids have been collected in leaf litter, in flight intercept traps, and at lights, but little is known of the biology and immature states have not been described. Tillyard (1926) reported *Ericmodes australis* Grouvelle from *Uromycladium* rust galls on *Acacia*.

Selected Bibliography

Crowson 1955.
Sen Gupta and Crowson 1969a, 1979.
Tillyard 1926.

SPHINDIDAE (CUCUJOIDEA)
(INCLUDING ASPIDIPHORIDAE)

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Figure 34.511

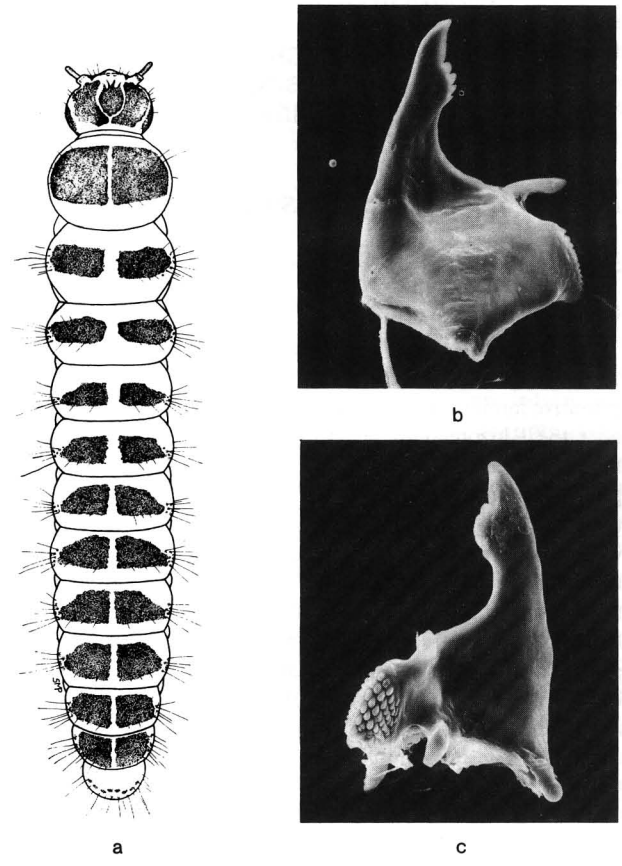
Relationships and Diagnosis: The family Sphindidae is one of the more primitive groups of Cucujoidea, and may be related to Protocucujidae, Boganiidae, or Phloeostichidae. Larvae may be distinguished by the 6 stemmata, blunt mala, relatively narrow, hyaline prostheca, and annular spiracles, and most of them are further distinguished by lacking urogomphi and having paired tergal plates on the thoracic and abdominal segments.

Biology and Ecology: Both larval and adult Sphindidae appear to be restricted to the fruiting bodies of slime molds, where they feed on the spore mass. They have been recorded from a number of Myxomycetes, including species of *Arcyria, Fuligo, Lycogala, Reticularia,* and *Stemonitis* (Lawrence and Newton, 1980; Russell, 1979; Sen Gupta and Crowson, 1979).

Description: Mature larvae 2 to 5 mm. Body elongate, parallel-sided or somewhat fusiform, straight, slightly flattened; dorsal surfaces smooth, usually with head plus paired thoracic and abdominal tergal plates darkly pigmented; body occasionally very lightly pigmented, with darker head and a few small, tergal maculae. Vestiture usually consisting of scattered, simple setae; body sometimes densely clothed with long, fine hairs.

Head: Protracted and prognathous, moderately broad, slightly flattened. Epicranial stem short or absent; frontal arms lyriform and contiguous at base. Median endocarina absent. Stemmata 6 on each side. Antennae well-developed, 3-segmented, with segment 2 slightly to much longer than 1 or 3. Frontoclypeal suture absent; labrum free. Mandibles symmetrical, unidentate or bidentate, sometimes with serrate incisor edge, and with accessory ventral process; mola well-developed, tuberculate or asperate, prostheca a narrow, fixed, hyaline process, acute at apex. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and broad and obtuse mala. Labium free to base of mentum; ligula short and broad; labial palps 2-segmented, widely separated. Hypopharyngeal sclerome a transverse bar. Hypostomal rods usually long and slightly to strongly diverging, occasionally very short or absent. Ventral epicranial ridges absent. Gula very short and indistinct.

Thorax and Abdomen: Thoracic terga and abdominal terga 1–8 with large, paired, pigmented plates in *Sphindus* and *Protosphindus*. Thoracic terga expanded laterally in *Aspidiphorus*. Legs well-developed, 5-segmented; tarsungulus with 2 setae lying one distal to the other; coxae moderately to widely separated. Abdominal segments 1–8 each with 2 pairs of lateral processes in *Aspidiphorus*. Tergum A9 unpigmented or with a few small maculae, usually simple, occasionally (*Odontosphindus* and *Protosphindus*) with pair of slightly upturned, fixed urogomphi; sternum A9 well-developed, simple. Segment A10 short, circular, posteriorly oriented.



Figures 34.511a-c. Sphindidae. *Sphindus americanus* LeConte. Bedford, Middlesex Co., Massachusetts. Length = 3.2 mm. **a.** larva, dorsal; **b.** left mandible, dorsal; **c.** left mandible, ventral.

Spiracles: Usually annular and located at ends of short, conical tubes; thoracic spiracles in *Odontosphindus* annular-uniforous.

Comments: The family includes 6 genera and about 35 species worldwide, with 3 genera and 6 species occurring in America north of Mexico. *Odontosphindus* and *Sphindus* are both found in the Holarctic Region, but the latter extends into S. America, India, tropical Africa, and Madagascar; *Eurysphindus* and *Aspidiphorus* are restricted to the New World and Old World, respectively, while *Protosphindus* is endemic to Chile and *Sphindophorus* to South Africa. Undescribed genera have been seen from Australia and tropical America.

Selected Bibliography

Böving and Craighead 1931 (larva of *Sphindus americanus* LeConte).
Emden 1943 (larvae of *Aspidiphorus orbiculatus* (Gyllenhal) and *Sphindus dubius* (Gyllenhal)).
Lawrence and Newton 1980 (slime mold associations).
Perris 1877 (larvae of *Aspidiphorus lareyniei* Jacquelin DuVal and *Sphindus dubius*).
Peyerimhoff 1921 (larvae of *A. orbiculatus* and *S. dubius*).
Russell 1979 (slime mold associations).
Sen Gupta and Crowson 1979 (larva of *Odontosphindus clavicornis* Casey; larval key).

NITIDULIDAE (CUCUJOIDEA)

(INCLUDING BRACHYPTERIDAE, CATERETIDAE, CYBOCEPHALIDAE, SMICRIPIDAE)

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Sap Beetles, Dried Fruit Beetles

Figures 34.512-522

Relationships and Diagnosis: The Nitidulidae are a distinctive group generally considered to be one of the more primitive families of cucujoid beetles. They are usually placed near the Rhizophagidae on the basis of adult features, but there are considerable differences between larvae of the 2 groups. Almost all nitidulid larvae may be distinguished by the unique ventral head structure (figs. 34.516b, 34.519c), in which the hypostomal ridges are strongly convergent posteriorly, the retracted mouthparts are pushed forward by the longitudinal cardines, the maxillary mala is blunt, and the labial palps are 1-segmented. In addition, the mandibular prostheca is usually complex, consisting of comb-hairs or fringed membranes (fig. 34.514c), the frontal arms are usually distant at base, the spiracles are often placed on raised tubes, and the urogomphi often have a pair of tubercles or pregomphi in front of them. The only nitidulid larvae lacking the characteristic ventral mouthparts are species of the genus *Smicrips*, which is usually excluded from the family (Crowson, 1955; Kirejtshuk, 1982). In the *Smicrips* larva, the mouthparts are truly protracted, without distinct cardines, as in Phalacridae and Cucujidae-Laemophloeinae; it may be distinguished from phalacrid larvae by the long, parallel hypostomal rods and from those of Laemophloeinae by the structure of the abdominal apex, in which segment 8 is not elongate and tergum 9 does not form a hinged plate. Larvae of the Cybocephalinae, which have also been removed from the family by various authors (Böving and Craighead 1931; Kirejtshuk, 1982), do not differ significantly from those of other Nitidulidae. Rhizophagid larvae differ from those of nitidulids in having retracted ventral mouthparts, transverse cardines, a falciform mala, a narrow mandibular prostheca, which may be acute or serrate, and the usual presence of ventral epicranial ridges.

Biology and Ecology: Nitidulids have one of the largest feeding repertoires among the Coleoptera. In general, they are saprophagous, feeding on decaying or fermenting plant tissue or occasionally carrion, but many species feed on fungal fruiting bodies or spores, and some may be predaceous or may attack healthy leaves, flowers, or fruits. The most characteristic habit of nitidulids is an association with yeasts and other fungi causing fermentation in tree wounds, under bark, or among decaying leaves, fruits, and flowers. Species of *Brachypeplus, Cillaeus, Colopterus, Epuraea, Prometopia, Soronia, Cryptarcha,* and *Glischrochilus* occur most commonly in rancid sap or under fermenting bark, while *Amphicrossus* may be restricted to slime fluxes, where they occur with *Nosodendron. Haptoncus, Lasiodactyla,* and *Stelidota* are particularly abundant in leaf litter and other accumulations of rotting vegetation, *Camptodes* has been found breeding in rotting cactus (*Opuntia*), and decaying flowers form the food source for some *Conotelus, Macrostola, Mystrops,* and *Smicrips*. Fermenting fruits are attractive to many nitidulids, especially species of *Carpophilus, Epuraea, Haptoncus, Aethina,* and *Lobiopa*. The dried-fruit beetle, *Carpophilus hemipterus* (L.) (figs. 34.514a–c), the corn sap beetle, *Carpophilus dimidiatus* (Fabricius), the dusky sap beetle, *Carpophilus lugubris* Murray, and several related forms are serious pests of stored fruits, grains, and other plant products (Böving and Rozen, 1962; Bondar, 1940a; Connell, 1956; Hayashi, 1978; Hinton, 1945b; Horion, 1960; Lepesme, 1944; Schedl, 1962).

Several species occurring in the habitats mentioned have been implicated in the transmission of pathogenic fungi. Some *Colopterus, Carpophilus, Haptoncus,* and *Glischrochilus* are involved in the transmission of *Ceratocystis* (Ascomycetes: Ophiosomatales) in oak, aspen, and sugarcane, while *Glischrochilus* are known to transmit *Fusarium* (Hyphomycetes) in corn. Some species of *Epuraea* are attracted to the nectar exuding from the spermagonia of rusts, such as *Cronartium* and *Peridermium* (Basidiomycetes: Uredinales), and they may aid in the transmission of these diseases in pines. (Chang and Jensen, 1974; Crowson, 1984a; Dorsey and Leach 1956; Dorsey *et al.*, 1953; Hinds, 1972; Jewell, 1956; Parsons, 1969b; Powell, 1971; Powell *et al.*, 1972; Windels *et al.*, 1976).

Mycophagy in the Nitidulidae involves most of the major fungal groups, including those mentioned above. Other ascomycete specialists include some species of *Epuraea,* which feed on conidia of molds (Eurotiales), *Prometopia,* which has been associated with an *Hypoxylon* (Xylariales) (Lawrence, 1977a), and several New Zealand species, including *Soronia hystrix* Broun, which feed on the black hyphal masses of sooty molds (Dothideales: Capnodiaceae) growing on tree trunks.

Some nitidulids occur on the softer fruiting bodies of higher Basidiomycetes (Agaricales and Aphyllophorales), especially those which are decaying, and certain genera appear to be restricted to this habitat. *Phenolia grossa* (Fabricius) has been collected in *Pleurotus, Bondarzewia, Laetiporus,* and *Hydnum,* while *Pallodes, Neopallodes, Cychramus,* and *Cyllodes* are found in gilled fungi, such as *Armillaria, Lampteromyces, Pleurotus, Pholiota,* and *Russula.* Most of these species feed on hyphal tissue, but species of *Aphenolia* feed on the spores of the polypore *Cryptoporus volvatus* (Böving and Rozen, 1962; Gillogly and Gillogly, 1954; Hayashi, 1978; Palm, 1959; Weiss and West, 1921a).

Gasteromycetes serve as hosts for certain Nitidulidae. Species of *Psilopyga,* for instance, are found on the fruiting structures of Phallaceae, while *Pocadius* species feed on the spores of puffballs (*Calvatia, Lycoperdon,* and *Scleroderma*). The genus *Thalycra* is restricted to the hypogean fruiting bodies of Hymenogastraceae (*Rhizopogon* and *Gautieria*), and it is likely that the Australian *Thalycrodes* has similar habits. (Donisthorpe, 1935; Fogel and Peck, 1975; Hayashi, 1978; Howden, 1961; Palm, 1959; Rehfous, 1955).

Although some nitidulids feed on rotting flowers, pollen- and nectar-feeding occur primarily in the subfamilies Cateretinae and Meligethinae. Cateretinae occur on a variety of

angiosperms, such as Papaveraceae (*Amartus, Brachyleptus*), Agavaceae (*Anthonaeus*), Scrophulariaceae (*Brachypterolus*), Compositae, Urticaceae, and Umbelliferae (*Brachypterus*), or Rosaceae and Caprifoliaceae (*Cateretes* and *Heterhelus*). Species of *Meligethes* attack many types of flowers, including those of Rosaceae, Cruciferae, Ranunculaceae, Caprifoliaceae, Campanulaceae, and Labiatae, while *Pria* have been recorded from solanaceous flowers. Adults of *Conotelus* (Carpophilinae) feed and oviposit in live solanaceous flowers, but larvae develop after the flowers begin to rot. Floricolous habits are much less common in the Nitidulinae, but the Australian genera *Circopes* and *Macroura* breed in the male cones of cycads and the flowers of Malvaceae (*Hibiscus* and *Alyogyne*), respectively, while the S. American *Neopocadius nitiduloides* Grouvelle occurs in the flowers of *Prosopanche* (Hydnoraceae), which give off the odor of carrion (Böving and Rozen, 1962; Bruch, 1923; Hayashi, 1978; Horion, 1960; Jourdheuil, 1962; Peyerimhoff, 1926). Other associates of living plants include members of the genera *Xenostrongylus* and *Anister,* which are leafminers of various Brassicaceae (Hinton, 1942; Peyerimhoff, 1910).

Predatory habits occur in members of the Cybocephalinae, which attack various mealybugs and scale insects (Homoptera: Coccoidea) (Horion, 1960; Silvestri, 1910) and the nitiduline *Cychramptodes murrayi* Reitter, which is a predator of the wattle tick scale (*Cryptes baccatus* (Maskell)) in Australia. In the United States *Cybocephalus nipponicus* has been established, and both larvae and adults are effective predators against euonymus scale, *Unaspis euonymi* (Comstock), feeding beneath the scale covers (R. M. Hendrickson, personal communication to FWS). Species of *Epuraea, Glischrochilus,* and *Pityophagus* have been recorded as predators of scolytid eggs and larvae (Beaver, 1967; Kleine, 1908, 1909, 1944; Horion, 1960), but it is doubtful that any of these are obligate predators. Carrion feeding occurs in the genera *Omosita* and *Nitidula* (Böving and Rozen, 1962; Hayashi, 1978; Horion, 1960), while *Brachypeplus auritus* Murray and certain species of *Epuraea* are known to inhabit the nests of bees (Böving and Rozen, 1962; Murray, 1864). The European *Amphotis marginata* (Fabricius) is an associate of the ant *Lasius fuliginosus* (Latreille); adults induce food-laden ants to regurgitate food by tapping the ant's labium and are protected from the ant's attack by the flattened body form (Hölldobler, 1971; Horion, 1960).

Description: Mature larvae 1 to 20 mm, usually less than 15 mm. Body elongate, parallel-sided or fusiform, straight or slightly curved ventrally, occasionally curved dorsally (*Pallodes, Pocadius*), subcylindrical to strongly flattened. Dorsal surfaces smooth to granulate or tuberculate, usually lightly pigmented, except for head, protergum, and tergum A9, occasionally with single or paired plates on all exposed terga. Vestiture of scattered, simple setae.

Head: Protracted and prognathous, usually transverse and slightly flattened. Epicranial stem almost always absent (present in *Pocadius*); frontal arms lyriform or V-shaped, distant at base except in *Pocadius,* some Cateretinae and Cybocephalinae. Median endocarina absent, except in some Cateretinae, where it is simple or in *Pocadius,* where it is forked (Y-shaped) and coincident with epicranial stem and bases of frontal arms. Stemmata 2 to 4 on each side. Antennae usually well developed and always 3-segmented. Frontoclypeal suture absent, except in Cybocephalinae; labrum almost always free, partly fused to head capsule in Cybocephalinae, completely so in Meligethinae. Mandibles symmetrical, unidentate or bidentate, sometimes with serrate incisor edge, without accessory ventral process; mola well developed, usually with tubercles or asperities, which often form transverse rows; basal armature usually extending onto both dorsal and ventral surfaces; prostheca usually consisting of a brush of simple or complex hairs or several fringed membranes; in Meligethinae it is a simple membranous lobe, and in Cateretinae, Cybocephalinae and Smicripinae it is absent. Ventral mouthparts almost always retracted, in that their bases are located well behind the mandibular articulations, but appear protracted because of the longitudinally oblique cardines, which displace the stipes and mala farther forward; ventral mouthparts truly protracted in Smicripinae. Cardines absent in Smicripinae, longitudinally oblique in all other nitidulids. Stipes usually elongate, wider than long in Smicripinae, Cybocephalinae, and some Cateretinae; articulating area more or less reduced or absent; maxillary palp usually 3-segmented, 2-segmented in Smicripinae and Cybocephalinae. Mala obtuse, usually with mentum and submentum fused; postmentum partly connate with maxillae; ligula present or absent; labial palps 1-segmented. Hypopharyngeal sclerome usually a transverse bar, sometimes tooth-like. Hypostomal rods usually absent, long and parallel in Smicripinae, long and diverging in Cybocephalinae and Cateretinae. Ventral epicranial ridges absent. Gula indistinctly separated from labium in most nitidulids, longer than wide in Smicripinae.

Thorax and Abdomen: Protergum usually with pigmented plate; meso- and metaterga with or without plates or maculae. Meso- and metathorax and abdominal segments 1–8 sometimes with paired dorsal or lateral tergal processes, or paired pleural processes. Legs well developed, 5-segmented, usually not very long, tarsungulus usually with 2 setae, which may be unequal, with one or both forming adhesive lobe, sometimes with single seta; coxae usually moderately widely separated. Tergum A9 usually with paired, fixed urogomphi, which may be simple, bifid, or complex, and which often have a pair of pregomphi in front of them; tergum A9 simple in Cateretinae, Meligethinae, and Cybocephalinae. Segment A10 short, circular, ventrally or posteroventrally oriented.

Spiracles: Biforous or annular biforous, placed at the ends of short to moderately long tubes in Carpophilinae, Cryptarchinae and most Nitidulinae.

Comments: The family includes about 160 genera and 3000 species worldwide, with 36 genera and about 150 species occurring in N. America. In addition to the Smicripinae and Cybocephalinae, the family is usually divided into 5 more subfamilies—Cateretinae, Carpophilinae, Meligethinae, Nitidulinae, and Cryptarchinae, and Kirejtshuk (1982) has proposed an additional subfamily for the genus *Calonecrus.* Most of the subfamilies are widely distributed, but Calonecrinae are restricted to the Philippines and East Indies, Smicripinae occur in the warmer parts of the New World, and Cateretinae are found in the temperate parts of the Northern and Southern Hemispheres.

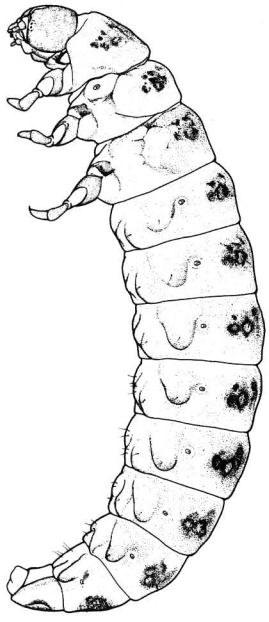


Figure 34.512

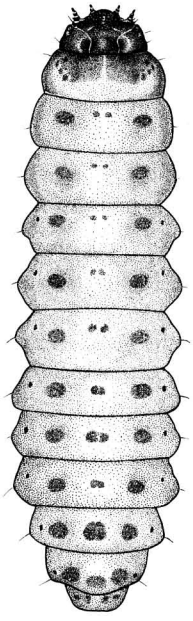
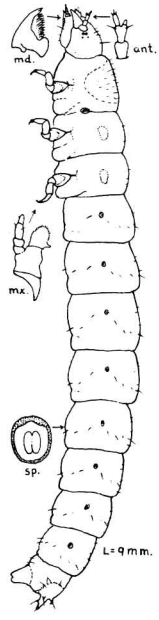


Figure 34.513



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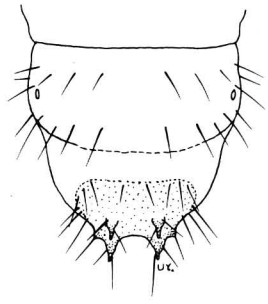

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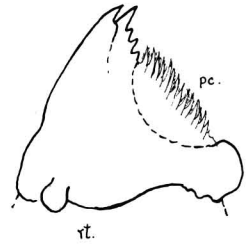

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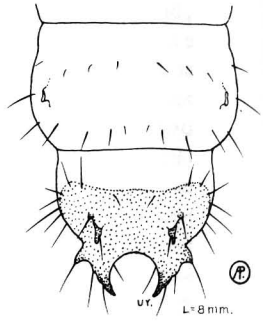
Figure 34.514



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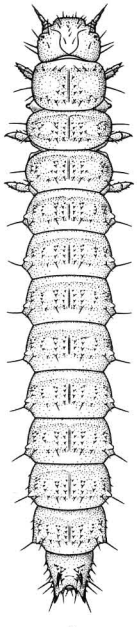

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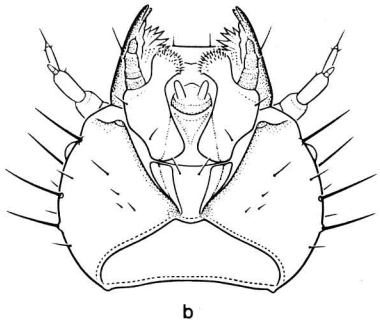

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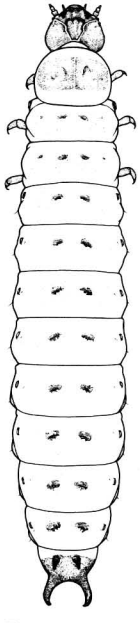
Figure 34.516



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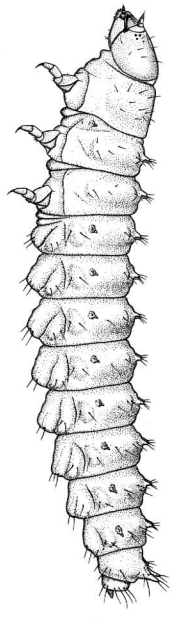

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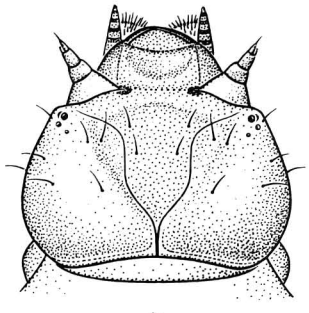

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Figure 34.518

Figure 34.512. Nitidulidae. *Amartus rufipes* LeConte. Point Reyes National Seashore, Marin Co., California. Larva, lateral. Length = 6.3 mm.

Figure 34.513. Nitidulidae. *Meligethes* sp. El Cerrito, California. Larva, dorsal. Length = 3.7 mm.

Figures 34.514a-c. Nitidulidae. *Carpophilus hemipterus* (L.). Length = 9 mm. **a.** larva, lateral view (plus details); **b.** abdominal apex, dorsal; **c.** right mandible, ventral. Infests various kinds of ripe and dried stored fruits, especially raisins, prunes, figs, dates, apples and other stored food products; also found in decayed fruits. (From Peterson, 1951)

Figure 34.515. Nitidulidae. *Carpophilus niger* (Say). Abdominal apex, dorsal. It and *C. lugubris* (Murray) commonly infest insect-damaged sweet corn and other decaying vegetation. (From Peterson, 1951)

Figures 34.516a,b. Nitidulidae. *Epuraea* sp. Mt. Rainier, Pierce Co., Washington. **a.** larva, dorsal; **b.** head, ventral. Length = 4.6 mm.

Figure 34.517. Nitidulidae. *Phenolia grossa* (Fabricius). Dorset, Bennington Co., Vermont. Larva, dorsal. Length = 12.8 mm.

Figures 34.518a,b. Nitidulidae. *Pocadius* sp. Tamborine Mountain, Queensland. **a.** larva, lateral; **b.** head, dorsal. Length = 3.3 mm.

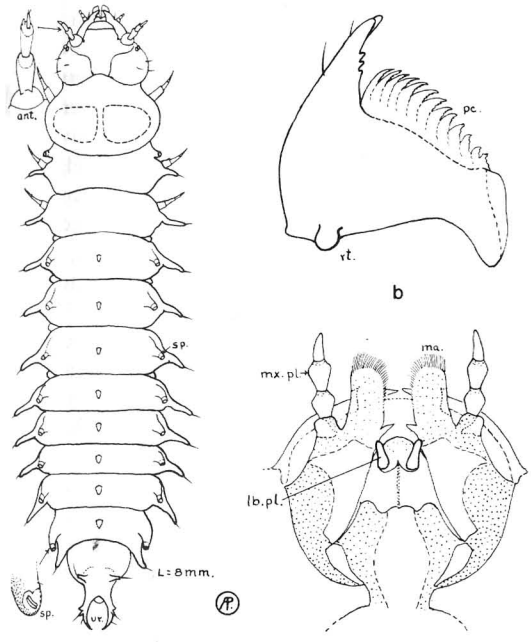

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Figure 34.519

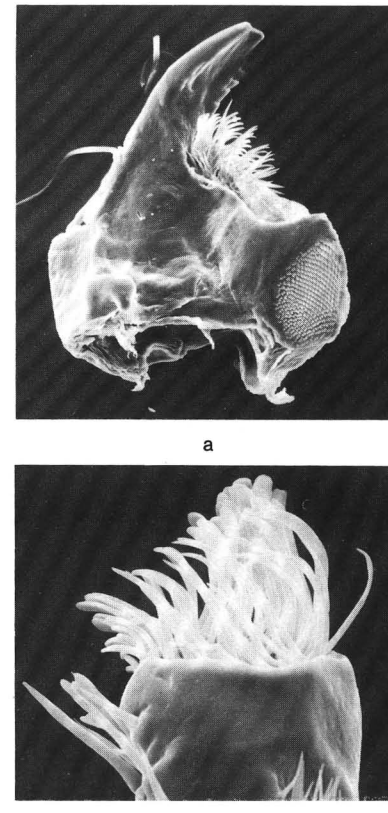

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Figure 34.521

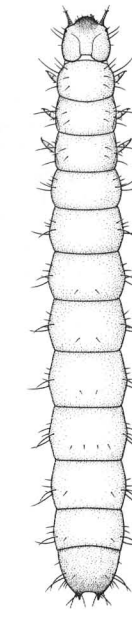
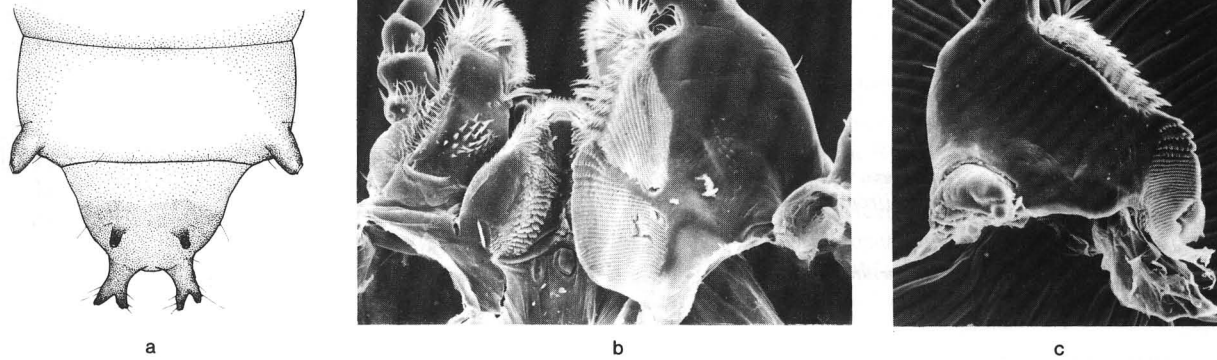


Figure 34.522



a b c

Figure 34.520

Figures 34.519a-c. Nitidulidae. *Cryptarcha ampla* Erichson. **a.** larva, dorsal (plus details); **b.** right mandible, ventral; **c.** maxillo-labial complex, ventral. Length = 8 mm. (from Peterson 1951)

Figures 34.520a-c. Nitidulidae. *Glischrochilus* sp. Great Smoky Mountains National Park, Tennessee. **a.** abdominal apex, dorsal; **b.** right mandible and maxillo-labial complex, dorsal; **c.** right mandible, ventral. Adult *G. quadrisignatus* (Say) and *G. fasciatus* (Olivier) are the common, black with yellow spots, "picnic" beetles.

Figures 34.521a,b. Nitidulidae. *Aphenolia monogama* (Crotch). Wasco Co., Oregon. **a.** right mandible, ventral; **b.** apex of maxillary mala.

Figure 34.522. Nitidulidae. *Smicrips* sp. Madera Canyon, Santa Rita Mts., Arizona. Larva, dorsal. Length = 3.1 mm.

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RHIZOPHAGIDAE (CUCUJOIDEA)

(INCLUDING MONOTOMIDAE)

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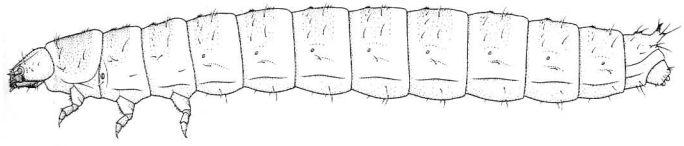
Figures 34.523-525

Relationships and Diagnosis: The family Rhizophagidae is usually considered to be closely related to the Nitidulidae on the basis of adult similarities, but larval characters indicate a closer relationship to other primitive cucujoids, such as Cryptophagidae or Biphyllidae. Larval rhizophagids differ from those of nitidulids in having transverse cardines, a falciform mala, ventral epicranial ridges, and mandibles having an accessory ventral process and a narrow, simple or serrate prostheca. *Rhizophagus* larvae resemble those of most cryptophagine Cryptophagidae, but the latter differ in having 1-segmented labial palps and no ventral epicranial ridges. Monotomine larvae have a granulate or tuberculate upper surface, similar to that of euxestine Cerylonidae, teredine Bothrideridae, xenosceline and cryptophiline Languriidae, and the endomychid genus *Mycetaea*. All of these groups differ in having the frontal arms absent or contiguous at the base and the labial palps 2-segmented; languriids have a broader prostheca; euxestines, teredines, and *Mycetaea* lack ventral epicranial ridges and have a single tarsungular seta; euxestines and teredines lack a prostheca: and *Mycetaea* has a truncate mala.

Biology and Ecology: Larvae of *Rhizophagus* are usually found under bark in decaying or fermenting cambium and often in association with the galleries of bark beetles. Several species have been implicated as predators of scolytid larvae (Kleine, 1909, 1944), but it is more likely that they feed on fungi or fungal biproducts (Beaver, 1967). The few records on fruiting bodies of macrofungi are probably incidental. *Rhizophagus bipustulatus* Fabricius is reported to damage wine corks (Lepesme, 1944). Larvae of *Shoguna* sp. have been taken under bark of logs in the fermenting stage in Australia, and *S. conradti* Grouvelle has been collected in the galleries of ambrosia beetles (Platypodidae and *Xyleborus*) in Africa (Schedl, 1962). *Lenax* adults have been taken among fine debris under the bark of *Nothofagus* logs. Monotomine larvae may also occur under bark, but they are usually associated either with the fruiting bodies of pyrenomycete fungi or with fungi growing in accumulations of grass cuttings or other types of decaying vegetation. *Bactridium ephippigerum* (Guérin-Méneville) was found feeding in the stromata of an *Hypoxylon* (Ascomycetes: Xylariaceae) (Lawrence, 1977a), while species of *Hesperobaenus* have been taken in fruiting bodies of *Hypoxylon* and *Daldinia* (Xylariaceae). *Monotoma* species are well-known inhabitants of grass piles, compost heaps, and even decaying seaweed (Chandler, 1983; Horion, 1960; Kuschel, 1979), and have been widely dispersed by man. The European *M. conicollis* Guérin-Méneville is apparently a commensal in the nests of ants (*Formica*) (Horion, 1960).

Description: Mature larvae 2 to 6 mm. Body elongate, parallel-sided or somewhat fusiform, straight, subcylindrical to slightly flattened. Dorsal surfaces lightly pigmented, usually whitish, sometimes with weakly developed yellowish tergal plates in *Rhizophagus,* usually granulate or tuberculate (smooth in *Rhizophagus*). Vestiture consisting of scattered, long, simple setae, sometimes mixed with stout, expanded setae.

Head: Protracted and prognathous, moderately broad and transverse, sometimes sharply constricted posteriorly (*Monotoma*). Epicranial stem absent; frontal arms lyriform, separated at base. Median endocarina absent. Stemmata usually 2 or 4 on each side, sometimes absent. Antennae well-developed, 3-segmented. Frontocylpeal suture absent; labrum



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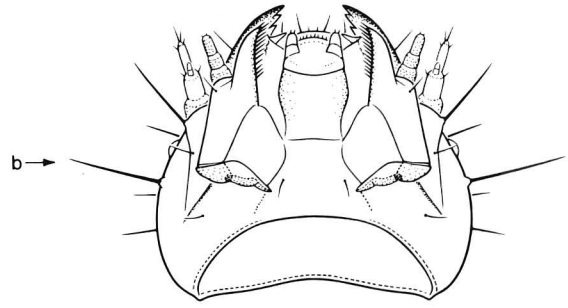
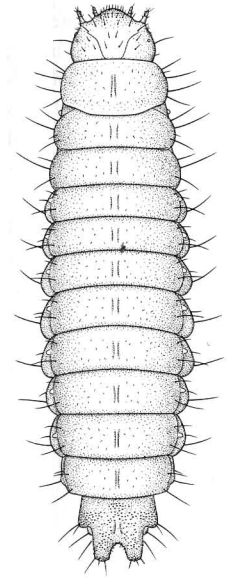


b

Figure 34.523



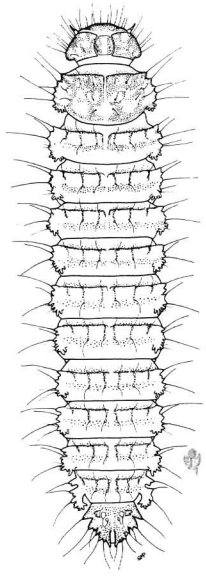


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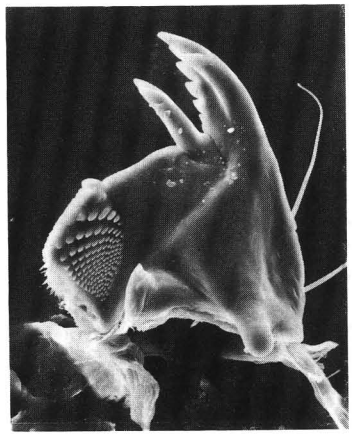
Figure 34.524



b

Figure 34.525

Figures 34.523a,b. Rhizophagidae. *Rhizophagus* sp. West side Mt. Rainier, Pierce Co., Washington. **a.** larva, lateral, length = 5.6 mm; **b.** head, ventral.

Figure 34.524. Rhizophagidae. *Bactridium epphipigerum* (Guérin-Méneville). Savannah, Georgia. Larva, dorsal. Length = 2.4 mm.

Figures 34.525a,b. Rhizophagidae. *Monotoma americana* Aube. Bedford, Middlesex Co., Massachusetts. **a.** larva, dorsal, length = 3.1 mm; **b.** left mandible, ventral.

free. Mandibles symmetrical, bidentate, sometimes with serrate incisor edge, with accessory ventral process; mola well-developed, asperate or tuberculate; prostheca a fixed, narrow, hyaline process, which is acute, bifid, or serrate. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and falciform mala. Labium free to base of mentum; ligula short and broad; labial palps usually 1-segmented (2-segmented in *Rhizophagus*), widely separated. Hypopharyngeal sclerome a transverse bar. Hypostomal rods usually short to moderately long and diverging (absent in *Monotoma*). Ventral epicranial ridges present. Gula strongly transverse.

Thorax and Abdomen: Thoracic terga and abdominal terga 1–9 each with a pair of lateral processes in *Monotoma*. Legs well-developed, 5-segmented; tarsungulus with 2 setae lying side by side; coxae moderately to widely separated. Tergum A9 with pair of urogomphi, which are usually complex, with accessory tubercles; sternum A9 well-developed, simple. Segment A10 short, circular, posteroventrally oriented.

Spiracles: Biforous or annular-biforous, usually raised on short, conical tubes.

Comments: The Rhizophagidae includes about 20 genera and 250 species, of which 9 genera and 53 species occur in America north of Mexico. The bulk of the genera are placed in the subfamily Monotominae, which occurs in most regions of the world. The subfamily Rhizophaginae includes the Holarctic genus *Rhizophagus*, and the Thioninae (*Thione* and *Shoguna*) occur in the warmer parts of the New and Old Worlds. The fourth subfamily, Lenacinae, contains the New Zealand genus *Lenax*, which is unknown in the larval stage and somewhat doubtfully included in the family. A larva described as *Myrmechixenus* by Klausnitzer (1975b) is almost certainly a misidentified *Monotoma* (*see* Doyen and Lawrence, 1979, and Nikitsky, 1983a).

Selected Bibliography

Beaver 1967 (predaceous species).
Böving and Craighead 1931 (larvae of *Hesperobaenus* sp. and *Rhizophagus grandis* Gyllenhal).
Chandler 1983 (larva of *Monotoma producta* LeConte).
Doyen and Lawrence 1979.

Hayashi 1980 (larva of *Rhizophagus japonicus* Reitter and *Mimemodes monstrosus* Reitter).
Horion 1960.
Klausnitzer 1975b.
Kleine 1909 (predaceous species), 1944 (predaceous species).
Kuschel 1979.
Lawrence 1977a (association with Ascomycetes).
Lepesme 1944 (stored products pests).
Nikitsky 1983a.
Peacock 1977.
Saalas 1917.
Schedl 1962 (association with bark beetles).
Verhoeff 1923.

BOGANIIDAE (CUCUJOIDEA)

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The Boganiidae includes the Australian genera *Boganium* and *Paracucujus*, and the South African genera *Afroboganium* and *Metacucujus* (Endrödy-Younga and Crowson 1986). The group is considered to be one of the more primitive famiies of Cucujoidea, and *Paracucujus rostratus* Sen Gupta and Crowson bears a marked resemblance to the Jurassic fossil *Parandrexis parvula* Martynov from Central Asia (Rodendorf and Ponomarenko, 1962).

Larvae of *P. rostratus* are elongate, more or less parallel-sided, and slightly flattened, with a sclerotized head and pigmented tergal plates on the thorax and abdominal segments 1 to 9. The head lacks an epicranial stem or median endocarina and has lyriform frontal arms; antennae are moderately long and 3-segmented, with a small sensorium, and there are 6 stemmata on each side. Mandibles are unidentate, without an accessory ventral process and with a tuberculate mola and acute prostheca. Ventral mouthparts are retracted; the maxilla has a relatively short stipes, an articulated, falciform mala, and a 3-segmented palp with well-developed palpifer; and the labium has a broadly rounded ligula and long, 2-segmented palps. Hypostomal rods are short and slightly diverging. Legs are well-developed but relatively thin and widely separated, with a bisetose tarsungulus. Tergal plates are smooth and even, and those on the meso- and metathorax and abdominal segments 1 to 8 bear a transverse carina near the anterior edge. Tergum A9 bears a pair of short, posteriorly projecting urogomphi. Segment A10 is posteriorly oriented and bears a pair of long, tubular pygopods. Spiracles are small, annular-biforous, and not placed at the ends of tubes.

Paracucujus rostratus occurs in the male cones of the cycad *Macrozamia riedlei*, where both larvae and adults feed on pollen, while the South African *Metacucujus encephalarti* feeds on the pollen of another cycad, *Encephalartos lanatus*. Species of *Afroboganium* occur on flowering shrubs, but little is known of the habits of *Boganium*.

Selected Bibliography

Crowson 1981.
Endrödy-Younga and Crowson 1986.
Rodendorf and Ponomarenko 1962.
Sen Gupta and Crowson 1966, 1969a.

PHLOEOSTICHIDAE (CUCUJOIDEA)

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The Phloeostichidae is comprised of 4 distinct groups: *Phloeostichus* with a single species (*P. denticollis* Redtenbacher) from central and southern Europe; Hymaeinae, including *Hymaea*, with 3 Australian species, and *Rhopalobrachium clavipes* Boheman from Chile; Agapythinae with a single species (*A. foveicollis* Broun) from New Zealand; and Priasilphinae, including the New Zealand *Priasilpha obscura* Broun and the Tasmanian *Priastichus tasmanicus* Crowson. It is doubtful that this family is monophyletic, and affinities of individual components seem to be with Cucujidae, Cryptophagidae, and Helotidae.

Larvae are elongate and parallel-sided to fusiform and subovate, slightly to strongly flattened, with dorsal surfaces lightly pigmented, except in Priasilphinae, which also has long, curved, spinose tergal processes on the thorax and abdominal segments 1 to 8. The head lacks an epicranial stem or median endocarina, and the frontal arms are lyriform; antennae are moderately long and there are 5 or 6 stemmata on each side. Mandibles may be bidentate or tridentate, with an accessory ventral process, transversely ridged or tuberculate mola, and relatively narrow and acute prostheca. The ventral mouthparts are retracted, the mala falciform, and the maxillary palps 3-segmented. The labial palps are 2-segmented. Hypostomal rods are moderately long and diverging, except in Priasilphinae, where they are very short or absent. Weak ventral epicranial ridges occur in Priasilphinae. The legs are widely separated, with a bisetose tarsungulus. Dorsal surfaces are covered with elongate, setiferous tubercles forming patterns in Priasilphinae; the anterior 5 or 6 abdominal terga and sterna in Hymaeinae each has a pair of semicircular bands of asperities; surfaces are smooth in *Agapytho*, except for a pair of elongate, setiferous tubercles in front of each urogomphus. Tergum A9 has a pair of urogomphi, widely separated and upcurved in Hymaeinae, approximate, diverging, and upcurved in Agapythinae, and straight and posteriorly oriented in Priasilphinae. Spiracles are biforous and not or only slightly raised, except in Priasilphinae, where they are annular and placed at the ends of the long lateral processes. Segment A10 is ventrally or posteroventrally oriented and somewhat transverse.

Phloeostichus and the Hymaeinae occur under the bark of dead trees and probably feed on fungal hyphae and conidia or dead cambium. *Agapytho* occurs on sooty molds (Ascomycetes: Capnodiaceae, etc.). Larvae and adults of *Priasilpha* and *Priastichus* occur in leaf litter and moss; their feeding habits are unknown.

Selected Bibliography

Cekalovic 1976 (larva of *Rhopalobrachium*).
Crowson 1973a (Priasilphinae).
Sen Gupta and Crowson 1966 (larva of *Hymaea*), 1969a (larvae of *Agapytho* and *Rhopalobrachium*).
Weise 1897 (larva of *Phloeostichus*).

HELOTIDAE (CUCUJOIDEA)

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This family includes the single genus *Helota,* with about 100 species occurring in the warmer parts of the Old World from Japan to India and tropical Africa. It is usually placed with the more primitive cucujoid families and may be related to Phloeostichidae.

Larvae of helotids are of moderate size (10 to 20 mm), elongate and slightly flattened, with lateral processes on the meso- and metathorax and abdominal segments 1 to 8. The head is broad, without an epicranial stem or median endocarina, the frontal arms are lyriform and distant at base, the antennae are moderately long, and there are 6 stemmata on each side; the labrum is fused to the clypeus, except laterally. The mandibles are bidentate, with a large, tuberculate mola, an accessory ventral process, and a narrow, acute prostheca. The ventral mouthparts are retracted and the mala is obliquely truncate at apex and partly divided, with a dense fringe of hairs along the inner edge and several curved spines at the apex; maxillary palps are 3-segmented and labial palps are 2-segmented. Hypostomal rods are absent and ventral epicranial ridges are present. Tergum A9 has a pair of long, diverging, spinose urogomphi. Spiracles are annular-biforous.

Helotids feed as adults and larvae on the sap exuding from trees.

Selected Bibliography

Crowson 1973a.
Hayashi *et al.* 1959 (larva).
Olliff 1882 (larva).
Roberts 1958 (larva in key).

CUCUJIDAE (CUCUJOIDEA)

(INCLUDING CATOGENIDAE, LAEMOPHLOEIDAE, PASSANDRIDAE, SILVANIDAE)

John F. Lawrence,
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Flat Bark Beetles

Figures 34.526–533

Relationships and Diagnosis: The Cucujidae includes a diverse assemblage of beetles which have been placed in several families by Crowson (1955, 1981) and by Böving and Craighead (1931). Larval characters support the recognition of 4 distinct groups: Passandrinae, Cucujinae, Laemophloeinae, and Silvaninae. Closely related families include the Phalacridae and Phloeostichidae. Diagnostic features of cucujid larvae include the reduction of the 9th abdominal segment, usually with the loss or concealment of the sternum, the somewhat flattened, elongate body, more or less protracted ventral mouthparts, relatively broad head, and well-developed legs and antennae; none of these characters, however, occur in all members of the family.

Flattened, subcortical larvae in the tenebrionoid (heteromeran) families Prostomidae, Pythidae, Pedilidae, Pyrochroidae, Othniidae, Inopeplidae, Salpingidae, Mycteridae, and Tenebrionidae may be confused with some cucujids, but most of these larvae have a well-developed 9th sternum bearing at least 1 pair of basal asperities, while those tenebrionids with a reduced sternum have a distinct frontoclypeal suture and lack both the falciform mala and symmetrical mandibles of the Cucujinae and Uleiotini and the prognathous mouthparts of the Laemophloeinae. The exotic Hymaeinae Phloeostichidae have the abdominal rings of asperities like those in Laemophloeinae and mouthparts similar to those of cucujines and brontines, but the frontal arms are distant at the base, and the 9th abdominal segment has a well-developed sternum. Some flattened Nitidulidae differ from cucujids in having unique, longitudinal cardines, distant frontal arms and a complex prostheca. Smicripine nitidulids have prognathous mouthparts and long, parallel hypostomal rods as in Laemophloeinae, but they lack the paired endocarinae and articulated 9th tergum of that group. Some Phalacridae (*Litochrus* and their allies) resemble laemophloeine cucujids in general shape, presence of a sclerotized, articulated 9th tergum, long hypostomal rods, protracted ventral mouthparts, and mandibular structure; these phalacrids differ in having a median endocarina, diverging hypostomal rods, and a completely concealed 9th sternum. Some lophocaterine Trogossitidae are also cucujid-like, but have V-shaped frontal arms, a median endocarina, and a transversely divided plate on tergum A9.

Biology and Ecology: Cucujidae are commonly found under bark, in leaf litter, or in stored products; they are primarily mycophagous, but some can be reared on grains or cereals, and others have become predaceous or ectoparasitic.

Members of the Laemophloeinae usually feed on fungal spores or hyphae growing under bark or in the galleries of bark beetles. Several laemophloeines have been associated with the fruiting bodies of Ascomycetes, apparently feeding on the sporulating surfaces; larvae of *Laemophloeus biguttatus* (Say) were found feeding on conidia produced by a species of *Hypoxylon, Placonotus illustris* Casey was collected on *Daldinia* stromata, and similar habits have been reported for several European species (Dajoz, 1966; Lawrence, 1977a; Palm, 1959). A number of laemophloeines are known to be stored products pests; *Laemophloeus janeti* (Grouvelle) attacks cocoa beans and a *Planolestes* has been reported from legume pods, but the most serious economic pests are species of *Cryptolestes* (fig. 34.529), including the rusty grain beetle, *C. ferrugineus* (Stephens), which cause major damage to stored grains. Some species of *Cryptolestes* may also be facultative predators (Bräuer, 1970; Howe and Lefkovitch, 1957; Lefkovitch, 1957a, 1957b, 1958, 1959, 1962a, 1962b, 1962c, 1964). Laemophloeine larvae are unique among the Coleoptera in producing silk for pupation from paired prothoracic glands (Bishop, 1960; Roberts and Rilett, 1953).

The Cucujinae are found exclusively under bark, and at least some of them appear to be predaceous. Smith and Sears (1982) studied the larval gut contents of *Cucujus clavipes* (Fabricius) (figs. 34.528a–d) and found only animal matter, including insect parts; in my own dissections, insect remains were also common, but these were mixed with some plant

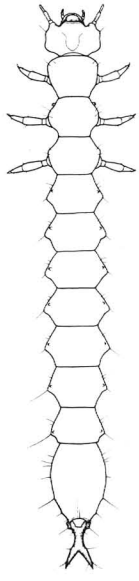


Figure 34.526

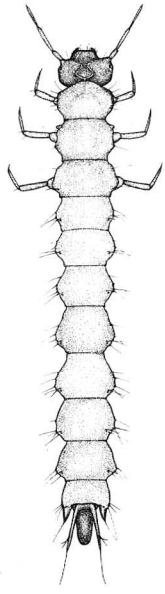


Figure 34.527

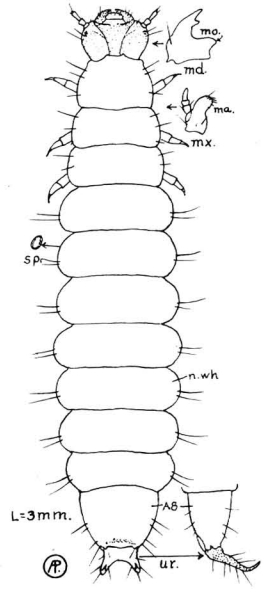


Figure 34.529

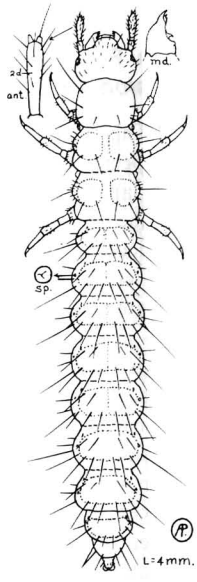
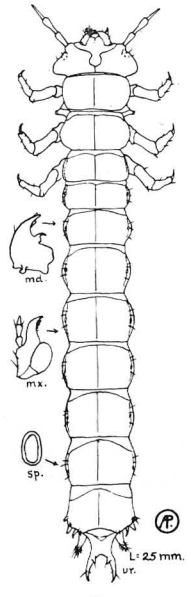


Figure 34.530



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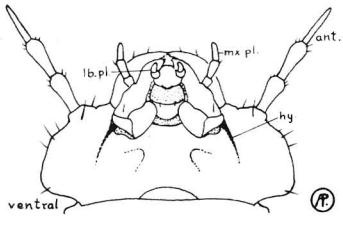

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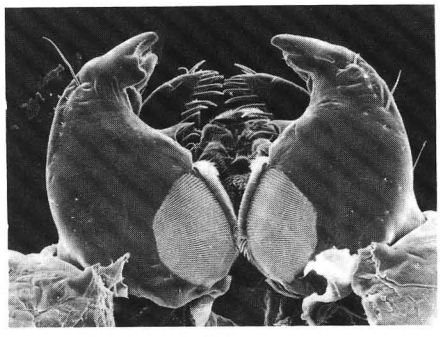

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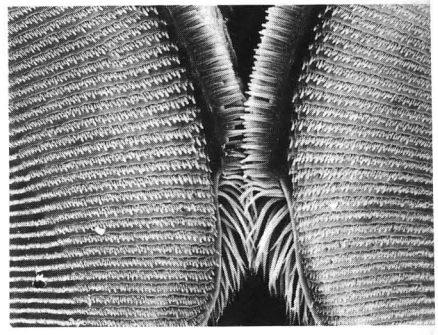

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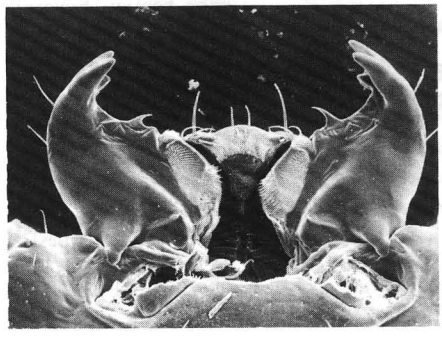

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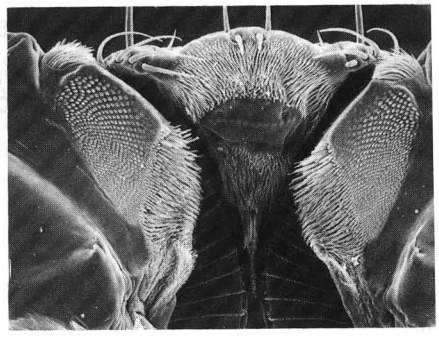

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Figure 34.528

Figure 34.526. Cucujidae. *Pediacus* sp. Peddler Hill, Amador Co., California. Larva, dorsal. Length = 6 mm.

Figure 34.527. Cucujidae. *Dendrophagus americanus* Mannerheim. Blodgett Forest, near Georgetown, El Dorado Co., California. Larva, dorsal. Length = 10.3 mm.

Figures 34.528a-f. Cucujidae. *Cucujus clavipes* Fabricius. **a.** larva, dorsal (plus details), length = 25 mm; **b.** head, ventral; **c.** anterior portion of head capsule, dorsal, with clypeolabral region removed, showing mandibular molae engaged; **d.** details of mandibular bases; **e.** anterior portion of head capsule, ventral, with maxillo-labial complex removed and mandibles spread, showing epipharynx and pharynx; **f.** details of mandibular bases. epipharynx and pharynx. Lives under bark of logs and dead trees. (Figures 34.528a, b from Peterson, 1951)

Figure 34.529. Cucujidae. *Cryptolestes* sp. Larva, dorsal (plus details). Length = 3 mm. (From Peterson, 1951)

Figure 34.530. Cucujidae. *Oryzaephilus surinamensis* (L.), saw-toothed grain beetle. Larva, dorsal (plus details). Length = 4 mm. Infests grains and cereal products, dried fruits, nuts, yeast, candy, tobacco, dried meats and many other food products. (From Peterson, 1951)

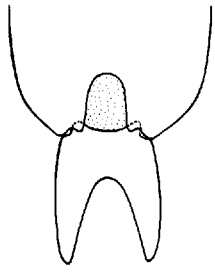

Figure 34.531

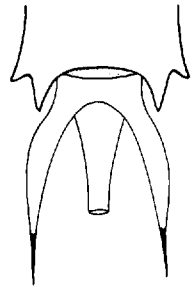

Figure 34.532

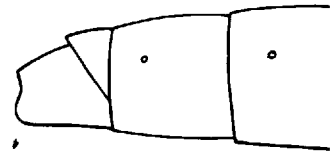

Figure 34.533

Figure 34.531. Cucujidae. Laemophloeinae. Abdominal apex, ventral.

Figure 34.532. Cucujidae. Uleiotini. Abdominal apex, dorsal.

Figure 34.533. Cucujidae. Silvanini. Abdominal apex, lateral.

fragments, fungal hyphae, and hyphomycete conidia. *Cucujus* larvae are probably facultative predators, whose feeding apparatus is still of the microphagous type, unlike those of most predaceous forms, which practice liquid feeding. The Passandrinae are true obligate predators with ectoparasitic larvae, and are usually found in the tunnels of wood-boring insects. *Catogenus rufus* (Fabricius) is known to attack larvae of a braconid wasp and cerambycid beetles (Baker, 1977; Wheeler, 1921a), while *Hectarthrum trigeminum* (Newman) has been associated with a cryptorrhynchine weevil (*Mechistocerus*) (Gravely, 1916). *Laemotmetus rhizophagoides* (Walker) is known to inhabit rattan canes and bamboo, where it feeds on larvae of Lyctinae and *Dinoderus* (Bostrichidae) (Aitken, 1975; Beeson, 1941).

Among the Silvaninae, members of the tribe Uleiotini are subcortical fungus feeders like the laemophloeines, but the larvae are larger and more active. Crowson and Ellis (1969) showed that *Dendrophagus crenatus* (Paykull), which lives under the bark of old conifers, carries spores of the fungi on which it feeds in the mandibular cavities of the adult; larvae were reared through to the adult stage on *Ceratocystis* grown from spores obtained from these mandibular cavities. Although some other Silvaninae also occur under bark, the Cryptamorphini, Psammoecini, and many Silvanini are found in leaf litter and decaying vegetation, and a number of species have become pests of stored products. Species of economic importance include the foreign grain beetle, *Ahasverus advena* (Waltl), the squarenecked grain beetle, *Cathartus quadricollis* (Guérin-Méneville), the sawtoothed grain beetle, *Oryzaephilus surinamensis* (L.) (fig. 34.530), and the merchant grain beetle, *O. mercator* (Fauvel). A unique habit occurs in the so-called social beetles of the Neotropical Region; *Coccidotrophus socialis* Schwarz and Barber and *Eunausibius wheeleri* Schwartz and Barber live in the enlarged petioles of the ant-plant (*Tachigalia*), where they feed not only on the nutritive parenchyma, but also on the honeydew produced by a species of *Pseudococcus* (Homoptera) (Wheeler, 1921a).

Description: Mature larvae 2 to 30 mm, usually less than 20 mm. Body elongate, usually more or less parallel-sided (physogastric in Passandrinae), straight, slightly to strongly flattened, usually uniformly lightly pigmented (with heavily pigmented abdominal apex in Laemophloeinae and some Cucujinae) or uniformly heavily pigmented in *Cucujus;* surfaces smooth; vestiture of scattered, simple setae.

Head: Protracted and prognathous, slightly to strongly transverse, sometimes strongly flattened, and usually as wide as or wider than thorax. Epicranial stem very short or absent; frontal arms usually lyriform and contiguous at base, subparallel and distant at base in Laemophloeinae, absent in Passandrinae. Paired, subparallel endocarinae present in Laemophloeinae. Stemmata usually 5 or 6 on each side, sometimes absent. Antennae usually long and 3-segmented, sometimes longer than head width, very short in Passandrinae; terminal segment reduced or antenna 2-segmented in some Silvanini. Frontocylpeal suture absent; labrum usually free, sometimes partly (Uleiotini) or completely (Passandrinae) fused to head capsule. Mandibles symmetrical, bidentate or tridentate, with accessory ventral process; mola usually well-developed, tuberculate or asperate, with slender, acute, fixed, hyaline prostheca; mola replaced by single hyaline process in Passandrinae or by several processes in Laemophloeinae. Ventral mouthparts usually retracted, strongly protracted in Laemophloeinae and Passandrinae. Maxilla usually with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and falciform mala; cardo and articulating area absent, stipes short and broad, and mala obtuse in Laemophloeinae and Passandrinae, palp reduced in latter. Labium more or less free to base of mentum; ligula short and broad; labial palps 2-segmented and widely separated. Hypopharyngeal sclerome usually a tooth-like structure. Hypostomal rods short to moderately long and usually diverging, long and subparallel in Laemophloeinae. Ventral epicranial ridges absent. Gula usually transverse, sometimes elongate.

Thorax and Abdomen: Legs usually well-developed, 5-segmented, and widely separated (reduced and indistinctly segmented in Passandrinae); tarsungulus usually with 2 setae lying side by side. Abdomen with 9 or 10 segments, with segment 8 sometimes enlarged and segment 9 usually reduced. Abdominal terga and sterna 1–7 in Laemophloeinae with paired rows of asperities forming incomplete rings which are longitudinally oriented. Tergum A9 with pair of urogomphi in some Passandrinae, *Cucujus,* Laemophloeinae, Uleiotini (fig. 34.532) and Cryptamorphini; urogomphi absent in Silvanini (fig. 34.533), Psammoecini, and some Passandrinae, and replaced by median forked process in some Cucujinae. Tergum A9 in Cucujinae and Laemophloeinae forming sclerotized, articulated plate. Sternum A9 reduced, sometimes completely concealed. Segment A10 well-developed, more or less tubular, posteriorly oriented, and visible from above in Passandrinae and Silvaninae, reduced and concealed from above in Cucujinae and Laemophloeinae; sternum A9 and segment A10 in Laemophloeinae (fig. 34.531) membranous and located in deep emargination of sternum A8.

Spiracles: Usually annular and raised on short tubes, annular-biforous in Laemophloeinae; spiracles on segment A8 more or less posteriorly placed, except in Silvanini and Passandrinae.

Triungulin (Passandrinae): Passandrine triungulins have not been examined but apparently resemble those of Bothrideridae, except for the shorter 3rd antennal segment, biforous spiracles, and presence of 5 or 6 stemmata on each side (Crowson, *in litt.*).

Comments: The family includes about 75 genera and 1200 species, of which 17 genera and 140 species occur in North America. The subfamily Passandrinae contains the N. American genera *Catogenus* and *Scalidia*, plus various exotic groups, like *Passandra, Hectarthrum,* and *Laemotmetus. Cucujus, Pediacus,* and the exotic *Platisus* belong in the Cucujinae. Laemophloeinae includes *Laemophloeus* and a number of related genera, such as *Cryptolestes, Placonotus, Narthecius, Lathropus, Sysmerus,* and *Rhinomalus.* The Silvaninae is divided into 4 tribes: Uleiotini (*Uleiota, Dendrophagus*), Psammoecini (*Psammoecus, Telephanus*), Cryptamorphini (*Cryptamorpha*), and Silvanini (the bulk of the genera, including *Silvanus, Oryzaephilus, Cathartus, Monanus, Ahasverus,* and *Nausibius*). Several genera have been removed to other families: these include *Hemipeplus* (to Mycteridae), *Prostomis* (to Prostomidae), *Inopeplus* (to Inopeplidae), and *Hypocoprus* (to Cryptophagidae) (Böving and Craighead, 1931; Crowson, 1955, 1973a, 1981; Crowson and Viedma, 1964; Lefkovitch, 1961, 1962c).

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Böving and Craighead 1931 (larvae of *Cucujus clavipes* Fabricius, *Brontes* sp., *Oryzaephilus surinamensis,* and those listed for Böving, 1921).
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Crowson 1955, 1973a, 1981.
Crowson and Ellis 1969 (mycangia in *Dendrophagus crenatus* (Paykull)).
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Cutler 1971 (larvae of *Ahasverus advena, Cathartus quadricollis, Oryzaephilus surinamensis,* and *O. mercator*).
Dajoz 1966 (association with Ascomycetes).
Drooz 1985 (habits of *Catogenus rufus*).
Emden 1931 (larva of *Telephanus costaricensis* Nevermann).
Gravely 1915 (larva of *Uleiota indica* Arrow; key to *Uleiota* larvae), 1916 (larva of *Hectarthrum trigeminum* (Newman)).
Halstead 1973 (revision of *Silvanus* and relatives), 1980 (revision of *Oryzaephilus* and relatives).
Hayashi 1980 (larvae of *Cucujus coccinatus* Lewis, *Uleiota arborea* Reitter, *Dendrophagus longicornis* Reitter, *Pediacus japonicus* Reitter, *Silvanus lateritius* Reitter, and *Laemophloeus* sp.).
Howe and Lefkovitch 1957.
Hudson 1934 (larvae of *Cryptamorpha brevicornis* (White) and *Dendrophagus capito* Pascoe (as *Parabrontes setiger* Broun; *see* Lefkovitch, 1961)).
Iablokov-Khnzorian 1977.
Lawrence 1977a (association of *Laemophloeus* with Ascomycetes).
Lefkovitch 1957a (biology of *Cryptolestes ugandae* Steel and Howe), 1957b (Laemophloeinae in stored products), 1958, 1959 (revision of European Laemophloeinae), 1961, 1962a (biology of *Cryptolestes capensis* (Waltl)), 1962b (biology of *Cryptolestes turicus*), 1962c (revision of African Laemophloeinae), 1964 (biology of *Cryptolestes pusilloides* (Steel and Howe)).
Lepesme 1944 (stored products pests).
Olliff 1882 (larva of *Cucujus coccinatus* Lewis).
Palm 1959.
Peterson 1951 (larvae of *Cucujus clavipes, Laemophloeus* sp., and *Oryzaephilus surinamensis*).
Reid 1942b (stored products laemophloeines).
Roberts and Rillett 1953 (silk glands in *Cryptolestes ferrugineus*).
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PROPALTICIDAE (CUCUJOIDEA)

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This family includes the genus *Propalticus* with about 25 described species from Asia, the East Indies, the Pacific Region, Australia, Madagascar, and Africa, and *Discogenia* with about 10 species occurring only in Africa. Adults are minute, broad and strongly flattened, and are capable of jumping using the front pair of legs. On the basis of adult structure, the group appears to be related to Cucujidae-Laemophloeinae, but a relationship to Languriidae-Cryptophilinae was suggested by Crowson and Sen Gupta (1969), based on larvae collected in fungusy bark of a dead tree with adults of an Australian *Propalticus.*

Selected Bibliography

Crowson 1955.
Crowson and Sen Gupta 1969 (putative larva; relationships).
John 1960.
Sen Gupta and Crowson 1971.

PHALACRIDAE (CUCUJOIDEA)

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Shining Flower Beetles

Figures 34.534-538

Relationships and Diagnosis: The systematic position of the Phalacridae is still in doubt, but the family is generally considered to be one of the more primitive groups of Cucujoidea, with possible affinities with the Nitidulidae and Cucujidae. In general, the group is well defined, but the inclusions

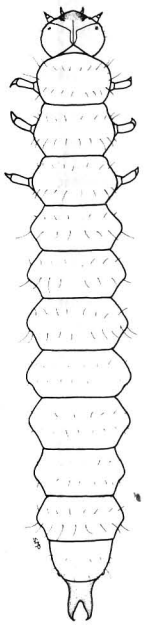
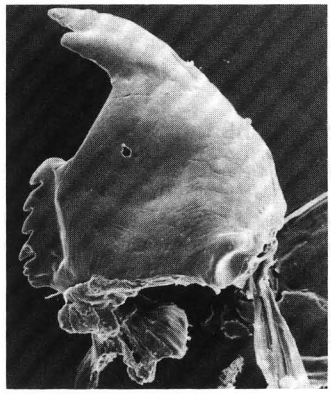


Figure 34.534



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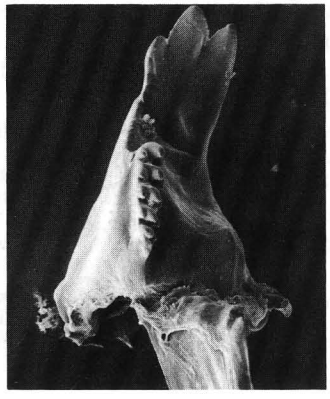

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Figure 34.535

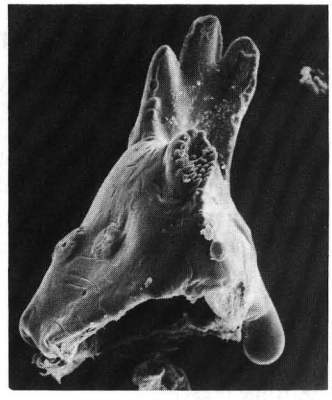
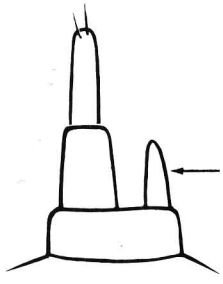


Figure 34.536



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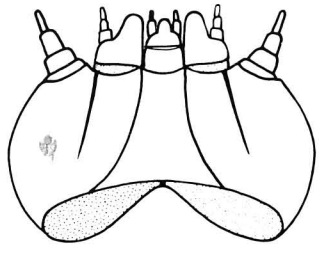

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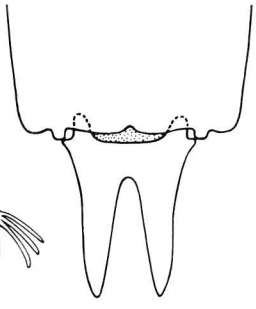

c

Figure 34.538

Figure 34.534. Phalacridae. *Litochropus clavicornis* Casey. Welder Wildlife Refuge, near Sinton, Texas. Larva, dorsal. Length = 4.8 mm.

Figures 34.535a,b. Phalacridae. *Phalacropsis dispar* (LeConte). Lee Vining, California. **a.** right mandible, dorsal; **b.** left mandible, mesal.

Figure 34.536. Phalacridae. *Acylomus pugetanus* Casey? Bedford, Massachusetts. Left mandible, mesal.

Figure 34.537. Phalacridae. *Phalacrus* sp. Antenna (showing sensorium on segment 1).

Figures 34.538a-c. Phalacridae. *Litochrus* sp. **a.** head, ventral; **b.** right mandible, ventral; **c.** abdominal apex, ventral.

of the Australian *Phalacrinus* and the New Zealand *Cyclaxyra* are still open to question (Crowson, 1955; Sen Gupta and Crowson, 1966). Phalacrid larvae are usually distinguished from those of other cucujoids by the combination of protracted ventral mouthparts, reduced cardines, long, diverging hypostomal rods, enlarged and posteriorly oriented 8th spiracles, and concealed 9th sternite and anal region. Protracted ventral mouthparts also occur in laemophloeine Cucujidae, the nitidulid genus *Smicrips,* and the family Cleridae, but these groups do not have lyriform frontal arms which are contiguous at the base or a concealed anal region (in Laemophloeinae it is exposed by a notch in sternum 8). Antennae of the Phalacrinae (*Phalacrus* and *Phalacropsis*) are unique in the Coleoptera, in that the sensorium is located on the first and not the second segment.

Biology and Ecology: Most Phalacridae are associated with ascomycete and primitive basidiomycete fungi, including molds, mildews, sooty molds, ergots, smuts, and rusts, but some feed in rotten wood or bark and others occur in the flowers heads of Compositae. Species of *Phalacrus* are often found in the spore masses of smuts (*Ustilago, Tilletia, Cintractia*) infesting various monocots, such as *Carex,* rye, wheat, corn, and sugarcane, but at least 2 Australian species feed on spores formed on the galls of *Uromycladium* rusts. The related genus *Phalacropsis* is associated with the aecia of pine stem rusts (*Peridermium* spp.). Most species of *Acylomus* and *Stilbus* feed on the spores of molds and mildews occurring on dead or dying leaves, seed clusters, etc. An exception is *A. pugetanus* Casey, whose larvae feed within the sclerotia (ergots) of *Claviceps purpurea.* Species of *Litochropus* feed on spores and stromatal tissue of *Daldinia* spp. (Xylariaceae), while Australian species of *Litochrus* occur in rotten wood or bark. Species of *Olibrus* breed in the flower heads of various Compositae (*Aster, Cirsium, Eupatorium, Solidago*), and the European *Tolyphus* apparently have similar habits. *Olibrus* larvae feed on fresh flowers, and no spores or other fungal material have been found in the gut. Pupation may occur on surfaces (*Acylomus*), within the food mass (*Phalacrus, Acylomus pugetanus, Litochropus, Litochrus*), or in the ground (*Olibrus*) (d'Aguilar, 1944; Crowson, 1981,

1984a; Lambert and McIlveen, 1976; Löben Sels, 1934; Peyerimhoff, 1926; Steiner, 1984; Thompson, 1958; Thompson and Marshall, 1980).

Description: Mature larvae 2 to 10 mm, usually less than 5 mm. Body elongate, more or less parallel-sided or somewhat fusiform, slightly to moderately flattened; usually lightly pigmented, except for head and abdominal apex, occasionally with pigmented plates on protergum or on all visible terga; surfaces smooth and vestiture consisting of scattered or dense, simple setae or longer hairs.

Head: Protracted and prognathous, moderately broad and somewhat flattened. Epicranial stem very short or absent; frontal arms lyriform and contiguous at base. Median endocarina present or absent (paired endocarinae present in *Cyclaxyra*). Stemmata 5 or 6 on each side. Antennae short to moderately long, 3-segmented; antennal sensorium occasionally (Phalacrini) situated on 1st, rather than 2nd segment. Frontoclypeal suture absent or vaguely indicated; labrum usually free, sometimes partly or completely fused to head capsule. Mandibles symmetrical, usually tridentate with apex perpendicular to plane of movement, and usually without accessory ventral process (present in Phalacrini); mola usually more or less reduced, either narrow or sub-basal, tuberculate or asperate, and without prostheca; mola sometimes absent and replaced by 2 or more slender, hyaline processes. Ventral mouthparts strongly protracted. Maxilla with cardo indistinct or absent, stipes wider than long, articulating area absent, palp 3-segmented, and mala fixed and obtuse. Labium usually with mentum and submentum fused; ligula present; labial palps 2-segmented and widely separated. Hypopharyngeal sclerome absent or consisting of transverse bar. Hypostomal rods long and diverging. Ventral epicranial ridges absent. Gula elongate.

Thorax and Abdomen: Legs short to moderately long, 5-segmented, widely separated; tarsungulus with single seta or 2 setae of unequal lengths. Abdominal segments 1–7 occasionally with paired rows of asperities forming incomplete rings on terga and sterna. Segment A9 much narrower and usually shorter than segment A8; tergum A9 almost always with pair of urogomphi (absent in *Cyclaxyra*), sometimes forming sclerotized plate which articulates with A8. Sternum A9 and segment A10 more or less concealed beneath sternum A8 (except in *Cyclaxyra*).

Spiracles: Annular-biforous, those on segment A8 usually enlarged and posteriorly situated.

Comments: The family is comprised of about 55 genera and 600 species worldwide, with 13 genera and 122 species occurring in N. America. Although there is no generally accepted subfamilial classification, the Phalacrinae (*Phalacrus* and *Phalacropsis*), *Tolyphus, Phalacrinus,* and *Cyclaxyra* form distinctive groups on the basis of adult characters, and in the case of Phalacrinae and *Cyclaxyra* this is supported by features of the larvae. The remaining phalacrids, whose larvae are known, fall into 2 groups: those having a median endocarina and lacking a mandibular mola (with 2 or more hyaline processes at the mandibular base) (*Litochrus, Litochropus, Olibrus*); and those lacking a median endocarina but having a mandibular mola (*Acylomus, Stilbus*). Steiner (1984) illustrated mandibles of several genera and discussed the relationship between morphological features and larval feeding habits.

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Emden 1928 (larva of *Phalacrus grossus* Erichson).
Lambert and McIlveen 1976 (*Acylomus* associated with ergot).
Löben Sels 1934 (larva of *Olibrus* sp., as *Phalacrus politus* Melsheimer).
Peterson 1951 (larva of *Olibrus* sp., as *Phalacrus*).
Peyerimhoff 1926 (habits of *Tolyphus*).
Steiner 1984 (biology of Phalacridae; larvae of several species).
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Urban 1926 (biology, larva of *Olibrus* spp.).

HOBARTIIDAE (CUCUJOIDEA)

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This family is based on two monotypic Australian genera, *Hobartius* and *Hydnobioides,* but undescribed species of *Hobartius* are known from Australia, Chile, and Argentina.

Larvae are elongate, somewhat fusiform, and slightly flattened, with a relatively lightly pigmented upper surface which is granulate and/or tuberculate. The head lacks an epicranial stem and median endocarina and has lyriform frontal arms, distant at base, 5 stemmata on each side, and well-developed antennae. The mandibles have a simple or serrate incisor edge, a well-developed tuberculate mola, accessory ventral process, and narrow, acute, hyaline prostheca (reduced in *Hobartius*). The ventral mouthparts are retracted, the mala falciform or narrowly rounded, and the maxillary palps 3-segmented. The labial palps are only 1-segmented. The hypostomal rods are short to moderately long and diverging, and there are no ventral epicranial ridges. The legs have a bisetose tarsungulus. Abdominal terga are armed with transverse rows of short to very long setiferous processes, and tergum 9 has a pair of upturned, fixed urogomphi; segment 10 is circular and more or less ventrally oriented. Spiracles are biforous and borne on short spiracular tubes.

Hobartiids are known to breed in soft, rotting fruiting bodies of some basidiomycete fungi, including Tricholomataceae (*Pleurotus*), Polyporaceae (*Grifola*), and Clavariaceae, but adults may be attracted in large numbers to carrion traps. The larva described as *Hydnobioides pubescens* by Sen Gupta and Crowson (1969a) was misidentified.

Selected Bibliography

Crowson 1981.
Sen Gupta and Crowson 1966, 1969a.

CAVOGNATHIDAE (CUCUJOIDEA)

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This family includes 5 described species: *Taphropiestes fusca* Reitter from Chile, *Cavognatha pullivora* Crowson from Australia, *Neocercus electus* Broun from New Zealand, and the New Zealand genus *Zeonidicola* with 2 species; other forms have been seen from Brazil, Argentina, and Chile. The group is usually placed near the Cryptophagidae.

Cavognathid larvae are elongate, more or less parallel-sided, and slightly flattened, with a darkly pigmented head and tergal plates on the thorax and abdominal segments 1 to 9. The head is short and broad, with moderately long antennae, 6 stemmata on each side, lyriform frontal arms, which are distant at base, and no epicranial stem or median endocarina. The mandibles are bidentate, with an additional subapical tooth, and the mola is absent, being replaced by 2 hyaline processes, one rounded and setose and the other narrow and acute. The ventral mouthparts are retracted, the mala is falciform, maxillary palps are 3-segmented and the labial palps 2-segmented. Hypostomal rods are moderately long and diverging. The legs are moderately widely separated and the tarsungulus bears 2 setae, one distal to the other. Tergum A9 has a pair of posteriorly projecting urogomphi, and segment A10 is circular and more or less posteriorly oriented. Spiracles are biforous and placed at the ends of very short tubes.

Cavognathids occur in the nests of birds and may be attached to nestlings. They have been associated with a number of bird species. *Z. chathamensis* has been found in the nests of the pipit (Motacillidae), sooty shearwater, fairy prion, giant petrel, and royal albatross (Procellaridae) on the Chatham Islands; *Z. dumbletoni* has been associated with the spotted shag (Phalacrocoracidae); a species identified as "*Taphropiestes* sp." was found with the weebill (Acanthizidae); and *C. pullivora* has been found in the nests of the magpie (Cractidae), white-winged triller (Campephagidae), regent honeyeater (Meliphagidae), and a finch. Cavognathids are widely distributed in Australia but they appear to be more common in the arid inland regions.

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Chisholm 1952 (bird nest record).
Crowson 1964b (larva of *Cavognatha pullivora*), 1973a.
Sen Gupta and Crowson 1966, 1969a.
Watt 1980 (larva of *Zeonidicola dumbletoni* Crowson).

CRYPTOPHAGIDAE (CUCUJOIDEA)

(INCLUDING CATOPOCHROTIDAE, HYPOCOPRIDAE)

John F. Lawrence,
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Silken Fungus Beetles

Figures 34.539–542

Relationships and Diagnosis: Because of recent studies on cucujoid phylogeny (Crowson, 1955, 1980; Sen Gupta, 1967, 1968a; Sen Gupta and Crowson, 1971), the constitution of the Cryptophagidae has undergone considerable change, and of those North American genera listed by Arnett (1968), *Cryptophilus, Toramus, Loberus, Hapalips,* and *Pharaxonotha,* have been transferred to Languriidae, while the genus *Hypocoprus* (Rhizophagidae in Arnett) has been added to the family. The group is a relatively primitive one, sharing plesiomorphic features with Cavognathidae and Phloeostichidae, but differing from all basal cucujoids in the adult stage by the outward closure of the mesocoxal cavities by the sterna. Cryptophagid larvae may be distinguished from those of other cucujoid families by the combination of falciform mala, narrow-based, hyaline prostheca (which may be simple, bifid, or serrate), 2 tarsungular setae, no ventral epicranial ridges, and either 1-segmented labial palps or annular spiracles.

Biology and Ecology: Cryptophagidae are usually found under bark or in leaf litter, compost heaps, animal nests, or stored products, where they feed on fungal spores and hyphae, but a few are known to feed on pollen or fern spores, and others have been associated with the fruiting bodies of higher fungi. Hinton and Stephens (1941a) found the adults of *Cryptophagus acutangulus* Gyllenhal fed on spores of many fungi, but larvae were reared on molds (*Penicillium* and *Botrytis*). Many of the species recorded from the larger fruiting bodies of Basidiomycetes were probably feeding on hyphae and conidia of surface molds. Exceptions include the Californian *Cryptophagus maximus* Blake and the closely related Japanese species, *C. enormis* Hisamatsu, which feed on the spore mass of the pouch fungus, *Cryptoporus volvatus* (Hisamatsu, 1962); *Pteryngium* species, which are consistently associated with *Fomitopsis pinicola* (Scheerpeltz and Höfler, 1948); and *Crosimus* species, which have been taken on a variety of trametoid Polyporaceae (Weiss and West, 1920). *Cryptophagus lycoperdi* (Scopoli) is a frequent inhabitant of the gasteromycete *Scleroderma vulgare,* but it has also been recorded from the hypogean fruiting body of *Choiromyces meandriniformis* (Tuberales) (Donisthorpe, 1935). *Cryptophagus ruficornis* Stephens was collected on the early stage, sporulating stromata of *Daldinia* sp. (Ascomycetes: Xylariaceae), while *C. dentatus* (Herbst) was associated with older fruiting bodies (Hingley, 1971). A number of *Cryptophagus* species have been taken from the nests of birds (Hicks, 1959, 1962, 1971), mammals, and social insects; species of *Antherophagus* are apparently restricted to *Bombus* nests (Horion, 1960; Meer Mohr and Lieftinck, 1947); and *Emphylus glaber* (Gyllenhal) occurs in nests of various *Formica* species (Eichelbaum, 1907; Horion, 1960). Some atomariines, such as *Anchicera ruficornis* (Marsham) and *A. lewisi* (Reitter), occur in compost heaps and grass cuttings, and have been widely distributed by man (Evans, 1961). *Atomaria linearis* Stephens has been recorded as a pest of mangels and some other food plants (Newton, 1932). Species apparently belonging to an undescribed genus were collected on sporangia of a fern (*Cystopteris fragilis*) on Juan

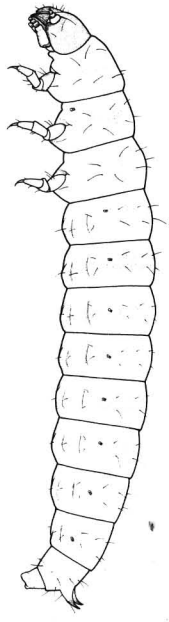

Figure 34.539

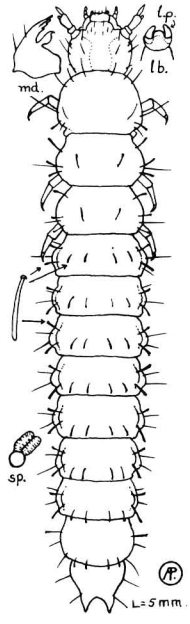

Figure 34.540

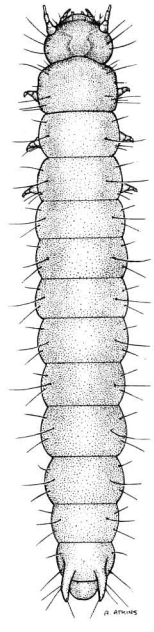

Figure 34.541

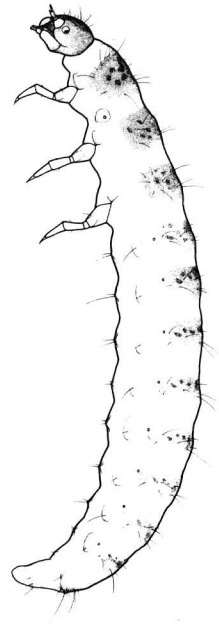

Figure 34.542

Figure 34.539. Cryptophagidae. *Antherophagus* sp. Manotick, Ontario. Larva, lateral. Length = 9.5 mm.

Figure 34.540. Cryptophagidae. *Cryptophagus* sp. Larva, dorsal (plus details). Length = 5 mm. (From Peterson, 1951)

Figure 34.541. Cryptophagidae. *Atomaria longipennis* (Casey). 7.5 mi. S Los Gatos, Santa Clara Co., California. Larva, dorsal. Length = 3.1 mm.

Figure 34.542. Cryptophagidae. *Anchicera lewisi* Reitter. Bedford, Middlesex Co., Massachusetts. Larva, lateral. Length = 3.3 mm.

Fernandez; sporangia were found on the mouthparts and fern spores in the gut. The N. American and European species of *Telmatophilus* feed in the flower heads of aquatic monocots, such as *Carex, Typha,* and *Sparganium* (Hatch, 1962; Horion, 1960). *Henoticus californicus* (Mannerheim), and several species of *Cryptophagus* and *Anchicera* are known to be pests in stored products (Hinton, 1945b).

Description: Mature larvae 2 to 6 mm. Body elongate, more or less parallel-sided or slightly wider in middle, straight, subcylindrical to slightly flattened; surfaces lightly pigmented, occasionally with yellowish-brown tergal plates which may be maculate, smooth, and clothed with scattered, simple, setae.

Head: Protracted and prognathous, moderately broad and slightly flattened. Epicranial stem absent; frontal arms lyriform, usually contiguous at base. Median endocarina absent. Stemmata usually indistinct or absent, sometimes 1, 2, or 5 or each side. Antennae well-developed, 3-segmented. Frontocylpeal suture absent; labrum free. Mandibles symmetrical, bidentate, with accessory ventral process and often with serrate incisor edge; mola well-developed, tuberculate or asperate, sometimes with brush of hairs at base; prostheca consisting of slender, fixed, hyaline process, which may be acute, bifid, or serrate. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and falciform mala. Labium free to base of mentum; ligula present; labial palps 1-segmented (Cryptophaginae) or 2-segmented (Atomarinae), widely separated. Hypopharyngeal sclerome usually tooth-like. Hypostomal rods moderately long and diverging. Ventral epicranial ridges absent. Gula transverse.

Thorax and Abdomen: Legs well-developed, 5-segmented; tarsungulus with 2 setae, either side by side or with one distal to the other; coxae moderately close together. Tergum A9 usually with pair of strongly upturned, fixed urogomphi, simple and sclerotized at apex only, occasionally reduced or absent. Sternum A9 well-developed, simple. Segment A10 well-developed, circular, posteriorly or posteroventrally oriented.

Spiracles: Annular or annular-biforous, not raised on tubes.

Comments: The family includes about 30 genera and 600 species for the world, and 16 genera and 140 species occur in the United States and Canada. The subfamily and tribal classification is currently being revised by Sen Gupta and Crowson, and several genera remain to be described, especially from the Southern Hemisphere. Crowson (1980) has divided the group into 4 subfamilies: Hypocoprinae (the Holarctic *Hypocoprus*), Alfieriellinae (the Palearctic *Alfieriella*), Cryptophaginae and Atomariinae; the last 2 groups have been reconstituted by Crowson, so that *Caenoscelis* and related genera fall into the former, along with the New Zealand *Pirotus* and *Thortus,* while *Ephistemus* and its allies, as well as various Southern Hemisphere forms related to

Salltius are included in the latter (Crowson, 1980). The family exhibits an amphipolar distribution, with tribes restricted to either North Temperate (Cryptophaginae: Cryptophagini and Caenoscelini; Atomariinae: Atomariini) or South Temperate (Cryptophaginae: Cryptosomatulini and Picrotini; Atomariinae: Salltiini) Regions. Exceptions occur in the cryptophagine genera (*Mnioticus* (East Africa) and *Micrambe* (extending into tropical Africa and Asia).

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Coombs and Woodroffe 1955.
Crowson 1955, 1967, 1980 (amphipolar distribution).
Donisthorpe 1935 (mycophagy).
Eichelbaum 1907 (larva of *Emphylus glaber* (Gyllenhal)).
Evans 1961 (larva of *Anchicera ruficornis*).
Falcoz 1922 (larva of *Henoticus californicus* (Mannerheim)), 1924 (larvae of *Cryptophagus* spp.).
Hatch 1962.
Hingley 1971 (association with Ascomycetes).
Hinton 1945b (stored products pests).
Hinton and Stephens 1941a (larva of *Cryptophagus acutangulus* Gyllenhal).
Hisamatsu 1962 (association with *Cryptoporus*, a polypore).
Horion 1960.
Klippel 1952 (association with molds; larvae and pupae of *Cryptophagus* spp.).
Meer Mohr and Lieftinck 1947 (larva of *Antherophagus ludekingi* Grouvelle).
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Peterson 1951 (larva of *Cryptophagus* sp.).
Scheerpeltz and Höfler 1948 (mycophagy).
Sen Gupta 1967, 1968a.
Sen Gupta and Crowson 1971.
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LAMINGTONIIDAE (CUCUJOIDEA)

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This family is based on *Lamingtonium binnaburrense* Sen Gupta and Crowson, which was collected under the bark of a dead standing tree in southern Queensland, Australia. On the basis of adult features, it was considered to be a link between primitive Cucujoidea and the family Languriidae (Sen Gupta and Crowson, 1969b). Larvae have not been described.

Selected Bibliography

Lawrence and Newton 1982.
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LANGURIIDAE (CUCUJOIDEA) (INCLUDING CRYPTOPHILIDAE)

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Figures 34.543-547

Relationships and Diagnosis: The Languriidae, as defined by Sen Gupta and Crowson (1971), includes not only the typical languriines, but also a number of genera formerly placed in Cryptophagidae (Arnett, 1968), such as *Pharaxonotha, Hapalips, Loberus, Cryptophilus,* and *Toramus.* The family appears to be closely related to Erotylidae, and some members of the Xenoscelinae are difficult to distinguish in the larval stage from dacnine erotylids. Larvae of both Erotylidae-Dacninae and Languriidae may be distinguished by the presence of a well-developed, tuberculate or asperate, mandibular mola, accompanied by a characteristic, fixed, hyaline prostheca, which is broad at base and more or less angulate at the apex; languriid larvae differ from those of dacnines in having a falciform, rather than a truncate maxillary mala. Xenosceline and cryptophiline larvae usually have a more or less granulate or tuberculate upper surface, resembling the condition found in many other cucujoids, such as *Monotoma* (Rhizophagidae), *Epuraea* (Nitidulidae), *Teredolaemus* (Bothrideridae), or *Mycetaea* (Endomychidae), but in all of these groups the prostheca is differently formed (narrow and acute, serrate, complex) or absent.

Biology and Ecology: Members of the subfamily Xenoscelinae have a variety of feeding habits but are usually associated with decaying plant tissue. The European *Eicolyctus brunneus* (Gyllenhal) feeds in red-rotten wood of maple, alder and birch (Horion, 1960; Lundberg, 1973; Sen Gupta and Crowson, 1967). The widespread *Leucohimatium arundinaceum* (Forskål) has been recorded in oats and barley, and was found breeding in a smut (*Ustilago*) on *Spinifex* in Australia, while *Leucohimatops javanus* Heller was commonly found in tea shipments in Java (Aitken, 1975; Heller, 1923). Several xenoscelines feed on the pollen of cycadaceous gymnosperms; *Pharaxonotha floridana* (Casey) occurs on *Zamia* in N. America, *Pharaxonotha* sp. on *Encephalartos* in South Africa, and *Xenocryptus tenebroides* Arrow and *Hapalips* spp. on *Macrozamia* in Australia (Roberts, 1939; Sen Gupta and Crowson, 1971). Various other *Hapalips* species have been recorded from corn stalks, banana leaves, cactus flowers, and palm leaf bases, while the stored products pest *Pharaxonotha kirschi* Reitter is known to cause damage to cotton bolls, corn meal, edible tubers, stored maize, wheat, and beans (Grouvelle, 1914; Hinton, 1945b; Sen Gupta, 1968a; Sen Gupta and Crowson, 1971). Perhaps the most bizarre habits are those of the Mexican *Loberopsyllus traubi* Martinez and Barrera, a blind and apterous commensal of the volcano mouse (*Neotomodon*), which attaches itself to the fur and feeds on dead skin and other organic matter (Barrera, 1969).

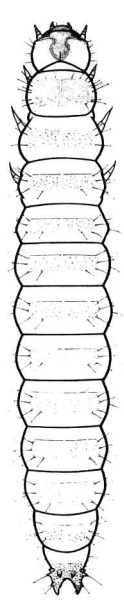

Figure 34.543

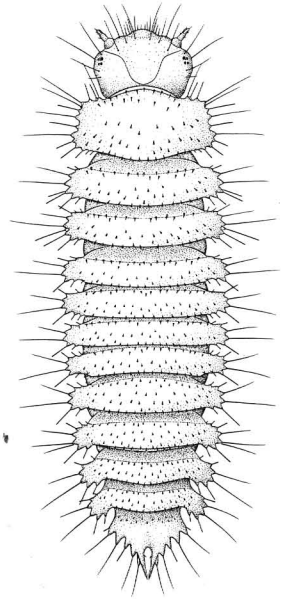

Figure 34.544

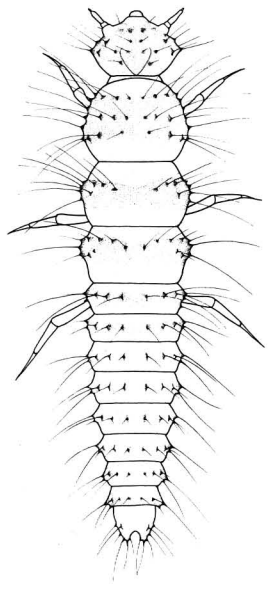

Figure 34.545

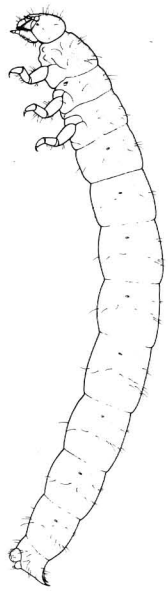

Figure 34.546

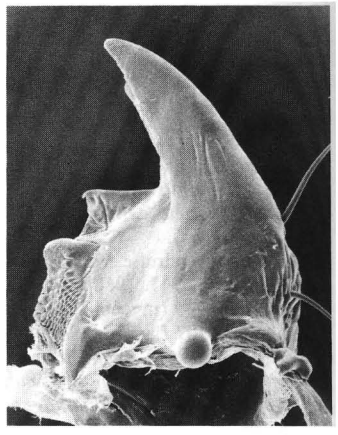

Figure 34.547

Figure 34.543. Languriidae. *Pharaxonotha floridana* (Casey). Crescent City, Florida. Larva, dorsal. Length = 8.3 mm.

Figure 34.544. Languriidae. *Cryptophilus* sp. Shipton's Flat, North Queensland. Larva, dorsal. Length = 2.7 mm.

Figure 34.545. Languriidae. *Loberoschema* sp. Barro Colorado Is., Canal Zone, Panama. Larva, dorsal. Length = 1.2 mm.

Figure 34.546. Languriidae.. *Acropteroxys gracilis* (Newman). Bedford, Middlesex Co., Massachusetts. Larva, lateral. Length = 17.5 mm.

Figure 34.547. Languriidae. *Hapalips* sp. Galapagos Is. Left mandible, ventral.

The only member of the Setariolinae, *Setariola sericea* (Mulsant and Rey), occurs under bark and in dead leaves and vegetable detritus in southern Europe (Falcoz, 1921). The closely related groups Cryptophilinae and Toraminae are also found in decaying vegetation and may be associated with molds. *Cryptophilus integer* (Heer) has been implicated as a stored products pest because of its occurrence in cellars and warehouses, sometimes in association with dried fruit or cereals (Aitken, 1975; Hinton, 1945b), and Peyerimhoff (1919) reared the species from larvae found on the underside of a bracket fungus (*Fomes fomentarius*). *Cryptophilus seriatus* Casey has been found on rotten fruiting bodies of *Polyporus squamosus* and *Steccherinum septentrionale,* where it was apparently feeding on surface molds. *Cryptophilus* species are also commonly collected in leaf litter. Adults and larvae belonging to the toramine genera *Loberoschema* and *Empocryptus* were taken in numbers in the rotting fallen flowers of a tropical tree (*Pseudobombax*) in Panama. The subfamily Languriinae includes those species which feed in the living stems of various herbaceous angiosperms, and a number of them may be pests of garden vegetables or forage crops (Hinton, 1945b; Lawrence and Vaurie, 1983; Vaurie, 1948).

Description: Mature larvae 2 to 25 mm. Body moderately to very elongate, more or less parallel-sided or sometimes narrowed posteriorly, straight, and cylindrical to slightly flattened. Dorsal surfaces usually granulate or tuberculate (smooth in Languriinae and *Leucohimatium*), lightly pigmented, sometimes with darker head and tergal plates; vestiture of long, fine, scattered hairs, occasionally mixed with expanded or frayed setae.

Head: Protracted and prognathous, moderately broad, slightly flattened. Epicranial stem usually absent (long in Languriinae); frontal arms usually lyriform (V-shaped in Languriinae) and contiguous at base (separated at base in some Loberini); epicranial suture sometimes indistinct. Median endocarina extending between frontal arms in some Xenoscelinae (*Eicolyctus, Leucohimatium, Pharaxonotha*). Stemmata usually 5 or 6 on each side, occasionally 2 or 0. Antennae moderately long, 3-segmented. Frontoclypeal suture absent; labrum free. Mandibles symmetrical, bidentate or tridentate, usually with accessory ventral process (absent in Languriinae); mola well-developed, tuberculate or asperate, with tubercles or asperities sometimes forming transverse rows, sometimes with hyaline lobe at base; prostheca usually a fixed, hyaline process, broad at base and obtusely angulate at apex (broadly triangular), sometimes reduced. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and falciform mala. Labium more or less free to base of mentum; ligula short and broad; labial palps 2-segmented and widely separated. Hypopharyngeal sclerome tooth-like. Hypostomal rods moderately to very long and diverging. Ventral epicranial ridges absent, except in Cryptophilinae and Toraminae.

Thorax and Abdomen: Thoracic and abdominal terga sometimes with weak (Toraminae) or strong (Cryptophilinae) lateral processes. Legs well-developed, 5-segmented, moderately widely separated; tarsungulus usually with 2 setae lying more or less side by side, sometimes (Toraminae and Cryptophilinae) with 2 unequal setae lying one distal to the other. Tergum A9 well-developed, with pair of fixed urogomphi, which are strongly upturned (not so in Toraminae and Cryptophilinae) and unpigmented or pigmented at apex only; accessory setiferous tubercles or pregomphi often present in front of urogomphi (absent in Languriinae). Segment A10 usually more or less circular and posteroventrally oriented (somewhat transverse in Languriinae).

Spiracles: Biforous or annular-biforous, not raised on tubes.

Comments: The family contains about 85 genera and 900 species, with 9 genera and 38 species occurring in America north of Mexico. Five subfamilies are currently recognized: Xenoscelinae, with the tribes Xenoscelini (= Pharaxonothini), Loberini, and Loberonothini; Setariolinae, with the European genus *Setariola;* Languriinae, with the tribes Languriini, Cladoxenini, and Thallisellini; Cryptophilinae, with the tribes Cryptophilini and Xenoscelinini; and Toraminae (Lawrence and Vaurie, 1983; Sen Gupta, 1967, 1968a, 1968b; Sen Gupta and Crowson, 1967, 1969b, 1971). Unlike the Cryptophagidae, with which the group was formerly confused, Languriidae are widely distributed throughout the warmer parts of the world, and are not as common in cool temperate regions. The larvae described by Sen Gupta and Crowson (1971) as *Cryptophilus integer* and *Xenoscelinus australiensis* Sen Gupta and Crowson, were apparently misidentified.

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Falcoz 1921 (relationships of *Setariola sericea* (Mulsant)).
Gardner 1931b.
Grouvelle 1914 (habitat of *Hapalips*).
Heller 1923 (*Leucohimatops javanus* in tea).
Hinton 1945b (stored products pests).
Horion 1960.
Kingsolver 1973.
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Peyerimhoff 1919 (habits of *Cryptophilus integer*).
Roberts 1939 (larvae of *Pharaxonotha floridana, Bolerus angulosus* Arrow, *Hapalips* sp., and several Languriinae), 1958 (various genera in key).
Sen Gupta 1967 (Toraminae), 1968a (Loberini; larva of *Hapalips prolixus* Sharp), 1968b (Cladoxenini).
Sen Gupta and Crowson 1967 (larva of *Eicolyctus brunneus*), 1969b, 1971 (family revision).
Vaurie 1948 (North American Languriinae).
Villiers 1943 (Languriinae).

EROTYLIDAE (CUCUJOIDEA) (INCLUDING DACNIDAE)

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Pleasing Fungus Beetles

Figures 34.548-553

Relationships and Diagnosis: Larvae of the Erotylidae may be distinguished from those of the closely related Languriidae by the presence of a truncate, rather than a falciform maxillary mala, and by the absence of a mandibular mola in all groups but the Dacninae. Dacnine larvae may be separated from those of most other groups (Languriidae excluded) by the presence of a characteristic prostheca, which consists of a fixed, hyaline lobe with a broad base and more or less angulate apex. Some erotylid larvae without a mola may be confused with those of certain Tenebrionoidea, such as Tetratomidae (*Penthe*) and Melandryidae (Eustrophinae), but they differ from those of either group in having either a median endocarina or a hypognathous head, cleft mala, and tridentate mandibles.

Biology and Ecology: The Erotylidae appear to feed exclusively on the larger fruiting bodies of basidiomycete fungi in the orders Aphyllophorales and Agaricales. Most larvae are internal feeders on the supportive (context) tissue, but those of the New World Erotylinae feed externally on the soft hymenial or spore-bearing surfaces. Those occurring under bark are usually associated with basidiomycete hyphal masses. Many species of *Dacne, Thallis, Tritoma,* and *Triplax* feed on the fruiting bodies of wood-inhabiting mushrooms (*Pleurotus, Panus,* etc.) or on the softer bracket fungi, like *Polyporus, Tyromyces, Hapalopilus, Laetiporus,* and *Piptoporus;* others occur in woodier sporophores, like those of *Phellinus* (*Microsternus* spp.) or *Ganoderma* (*Megalodacne* spp.). Some species of *Dacne* are known to be pests in commercial dried mushrooms. Pupation usually occurs within the fungal matrix or in the soil, but at least some erotylines, such as *Cypherotylus californicus* (Lacordaire), pupate on the surface, partly enclosed within the larval skin. Adults of most species and larvae of Erotylinae are aposematically colored with red and yellow pigments and probably contain defensive compounds. The surface-grazing erotyline larvae also have a covering of spines.

Description: Mature larvae 3 to 25 mm. Body elongate, more or less parallel-sided or fusiform, subcylindrical to slightly flattened, straight or slightly curved ventrally. Dorsal surfaces usually lightly pigmented but covered with granules or setiferous tubercles, sometimes with darkly pigmented tergal plates and/or complex, branched spines.

Head: Protracted and moderately to strongly declined (hypognathous), globular to slightly flattened. Epicranial stem usually long, absent in Triplacinae and some Dacninae; frontal arms lyriform or V-shaped, contiguous at base; epicranial suture sometimes indistinct or absent. Median endocarina

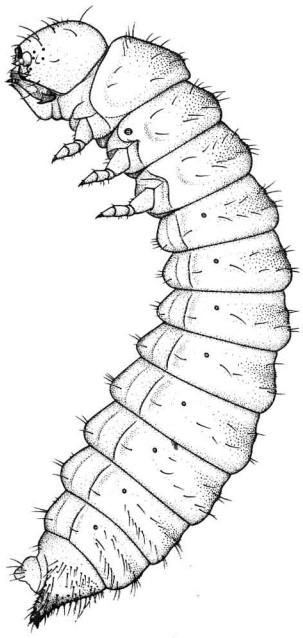


Figure 34.548

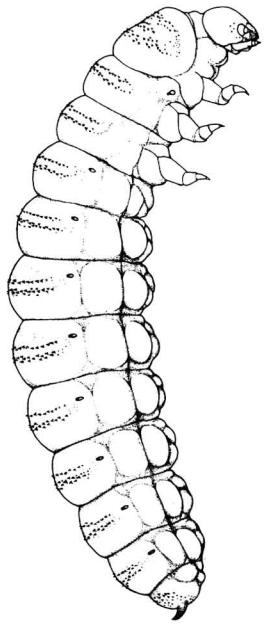


Figure 34.549

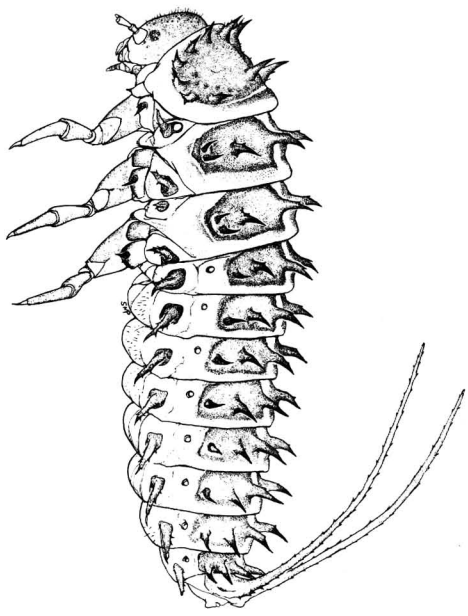


Figure 34.550

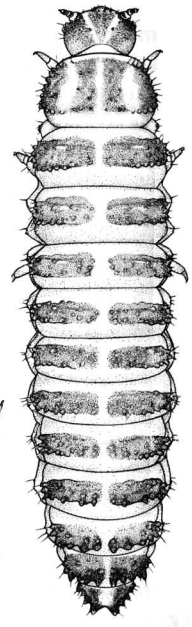


Figure 34.551

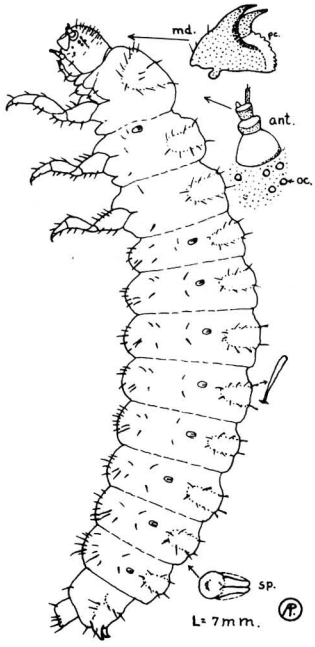
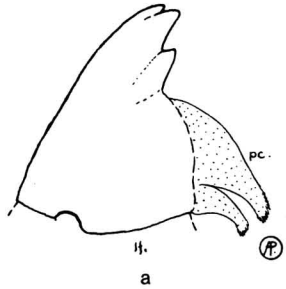
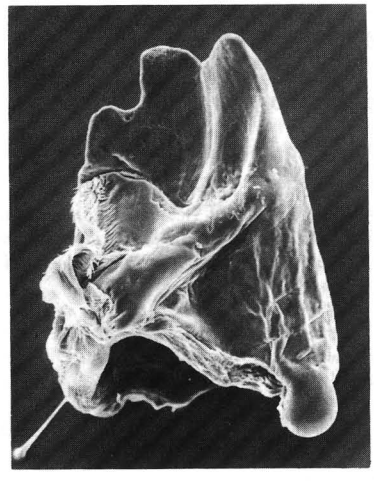


Figure 34.552



a



b

Figure 34.553

Figure 34.548. Erotylidae. *Microsternus ulkei* (Crotch). Cincinnati, Ohio. Larva, lateral. Length = 7.5 mm.

Figure 34.549. Erotylidae. *Megalodacne* sp. Barro Colorado Is., Canal Zone, Panama. Larva, lateral. Length = 25 mm.

Figure 34.550. Erotylidae. *Cypherotylus californicus* (Lacordaire). Sunnyside Canyon, Huachuca Mts., Arizona. Larva, lateral. Length = 17 mm.

Figure 34.551. Erotylidae. *Ischyrus quadripunctatus* (Olivier). Dead Lake, Chipola Park, Calhoun Co., Florida. Larva, dorsal. Length = 11 mm. (From Peterson 1951)

Figure 34.552. Erotylidae. *Tritoma* sp. Larva, lateral (plus details). Length = 7 mm.

Figures 34.553a,b. Erotylidae. *Cypherotylus californicus* (Lacordaire). **a.** left mandible, dorsal; **b.** left mandible, mesoventral. Sunnyside Canyon, Huachuca Mts., Arizona. (Figure 34.553a from Peterson, 1951)

sometimes present between frontal arms and extending anterad of epicranial stem, when the latter is present; endocarina absent in some Dacninae and many Erotylinae. Stemmata 5 or 6 on each side. Antennae short to moderately long, 3-segmented. Frontoclypeal suture absent or vaguely indicated; labrum free. Mandibles symmetrical, usually tridentate, and usually without accessory ventral process (present in *Cryptodacne, Dacne,* and *Thallis*); mola usually absent, replaced by membranous setose lobe and sometimes an additional brush of hairs; mola in *Cryptodacne, Dacne,* and *Thallis* well-developed, armed with asperities or tubercles, which may form transverse rows, and accompanied by fixed, hyaline prostheca, which is broadly triangular. Ventral mouthparts retracted. Maxilla with transverse cardo (which may be divided), elongate stipes, and 3-segmented palp; articulating area present or absent; mala blunt, often cleft, and variously armed with teeth, spines, and setae. Labium sometimes with mentum and submentum fused, usually more or less free to base of mentum; ligula usually short and broad, sometimes absent; labial palps 2-segmented and narrowly to widely separated. Hypopharyngeal sclerome usually absent, sometimes consisting of a transverse bar or tooth-like structure. Hypostomal rods usually absent, occasionally short and diverging. Ventral epicranial ridges present or absent. Gula transverse.

Thorax and Abdomen: Legs short to moderately long, 5-segmented, and narrowly separated; tarsungulus with 2 setae lying side by side. Thoracic and abdominal terga sometimes with granulate plates, rows or patches of asperities, or 2 to several pairs of simple or branched spines. Tergum A9 usually with pair of fixed urogomphi, which are usually short and strongly upturned, but may be long and narrow (some Erotylinae), sometimes with single median, sclerotized process (some Dacninae); sternum A9 well-developed, simple. Segment A10 circular, posteroventrally oriented.

Spiracles: Usually annular-biforous, sometimes (Erotylinae) annular.

Comments: The family contains about 30 genera and 2500 species, of which 10 genera and 50 species occur in America north of Mexico. There are at least 4 distinct groups: Dacninae (including *Cryptodacne*), Megalodacninae, Triplacinae, and Erotylinae. The Dacninae occur in the North and South Temperate Regions, while the Megalodacninae are pantropical, but most diverse in the Indo-Australian Region. The Triplacinae are usually found in the warmer parts of the New and Old Worlds, while the Erotylinae are primarily Neotropical, with a single species of *Cypherotylus* extending into the southwestern United States.

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Weiss 1920b (fungus hosts).
Weiss and West 1920 (fungus hosts).

BIPHYLLIDAE (CUCUJOIDEA)

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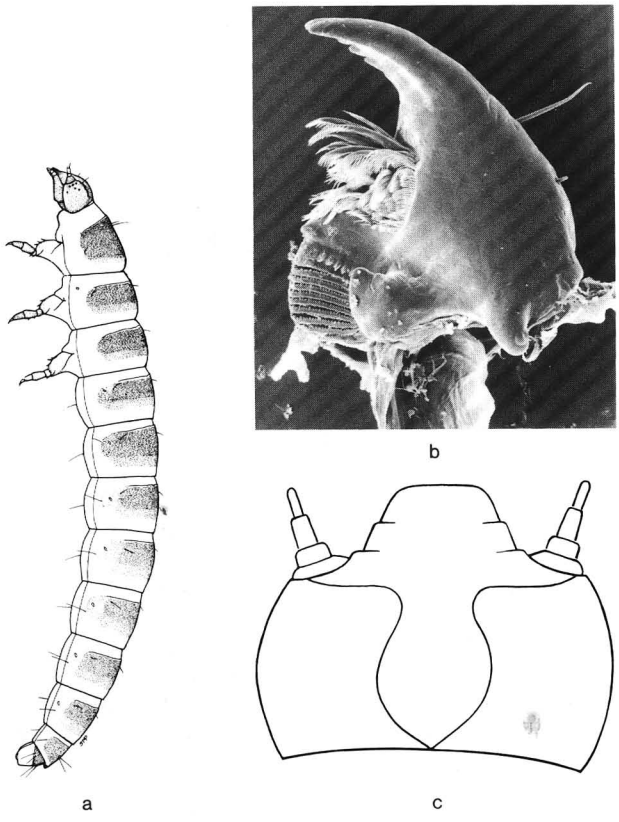
Division of Entomology, CSIRO

Figures 34.554a-c

Relationships and Diagnosis: The family Biphyllidae is a sharply defined group, which has been associated with the cucujoid families Erotylidae (Roberts, 1958), Languriidae (Cryptophilinae) (Crowson, 1955; Sen Gupta and Crowson, 1971), and Byturidae (Falcoz, 1926), but has also been placed in the Tenebrionoidea by Crowson (1960b) and Abdullah (1966). Several features of both larva and adult also indicate a relationship to the Bothrideridae and possibly the euxestine Cerylonidae. Falcoz (1926) presented a reasonable argument for the close relationship of Biphyllidae and Byturidae, but biphyllid larvae differ from those of byturids in having an accessory ventral process on the mandible, a basal hyaline mandibular lobe, which is neither projecting nor setose, well-developed ventral epicranial ridges, and enlarged, posteriorly oriented 8th spiracles, which may be raised on short tubes. The complex prostheca, consisting of comb-hairs, distinguishes byphyllid larvae from those of most other cucujoid families; a similar type of prostheca may be found in Nitidulidae, which have longitudinally oblique cardines and a truncate mala. Although distinct urogomphi are present in the 2 European larvae which have been previously described, these structures are absent in *Anchorius,* several Neotropical *Goniocoelus,* and Australian species presently included in the genera *Biphyllus* and *Diplocoelus.*

Biology and Ecology: Biphyllidae are mycophagous and appear to be associated with various types of Ascomycetes. Larvae of *Anchorius lineatus* Casey were found under the fermenting bark of mesquite (*Prosopis*) in Arizona, while several Neotropical biphyllids (*Goniocoelus* spp.) have also been found under bark in the fermenting stage. The European species *Biphyllus lunatus* (Fabricius) and *Diplocoelus fagi* Guérin-Méneville feed on the spores and stromata of the xylariaceous Ascomycetes *Daldinia concentrica* and *Tuberculariа confluens,* respectively (Donisthorpe, 1935; Hingley, 1971; Horion, 1960; Palm, 1959), and several Australian species of *Biphyllus* and *Diplocoelus* appear to have similar habits. Some Australian species have been found on the rotting flower stalks of a monocot *Xanthorrhoea* and in rotting cycad cones, where they may be feeding on molds or other fungi.



Figures 34.554a-c. Biphyllidae. *Anchorius lineatus* Casey. 1 mi. NW Arivaca, Pima Co., Arizona. **a.** larva, lateral view. Length = 7 mm; **b.** left mandible, ventral; **c.** head, dorsal.

Description: Mature larvae 2.5 to 10 mm. Body elongate, parallel-sided, cylindrical to very slightly flattened, straight or slightly curved ventrally; dorsal surfaces lightly to moderately heavily pigmented, smooth, with scattered, simple setae.

Head: Protracted and prognathous, moderately broad, slightly flattened. Epicranial stem absent or very short; frontal arms lyriform and contiguous at base. Median endocarina absent. Stemmata 6 on each side. Antennae well-developed, 3-segmented. Frontoclypeal suture absent; labrum partly fused to head capsule. Mandibles symmetrical, bidentate, with accessory ventral process and sometimes with serrate incisor edge; mola well-developed, transversely ridged, with hyaline lobe at base; prostheca consisting of a brush of complex comb-hairs. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and falciform mala. Labium free almost to base of mentum; ligula short; labial palps 2-segmented, widely separated. Hypopharyngeal sclerome consisting of a transverse bar. Hypostomal rods short and diverging. Ventral epicranial ridges present. Gula transverse.

Thorax and Abdomen: Legs well-developed, 5-segmented, moderately close together, clothed with short spines; tarsungulus with 1 seta. Mesotergum, metatergum, and abdominal terga 1–8 each with a transverse carina near anterior edge. Tergum A9 usually without urogomphi; sometimes with a pair of short, fixed urogomphi; sternum A9 well-developed, simple. Segment A10 more or less cylindrical, posteriorly or posteroventrally oriented.

Spiracles: Annular-biforous, those on segment A8 raised on short tubes and posteriorly or posterodorsally placed.

Comments: The family includes 6 genera and about 200 species worldwide, with *Anchorius lineatus* and 3 species of *Diplocoelus* occurring in America north of Mexico.

Selected Bibliography

Abdullah 1966.
Crowson 1955, 1960b, 1981.
Donisthorpe 1935 (mycophagy).
Falcoz 1926 (relationships).
Hingley 1971 (association with Ascomycetes).
Horion 1960.
Nikitsky 1983b (larva of *Biphyllus flexuosus* Reitter).
Palm 1959.
Perris 1851 (larva of *Biphyllus lunatus*).
Roberts 1958 (larvae of *Biphyllus lunatus* and *Diplocoelus fagi* in key).
Sen Gupta and Crowson 1971 (relationships).

BYTURIDAE (CUCUJOIDEA)

John F. Lawrence,
Division of Entomology, CSIRO

Fruit Worms

Figures 34.555-556

Relationships and Diagnosis: The family Byturidae is generally considered to be most closely related to the Biphyllidae (Falcoz, 1926), and both groups are now placed in the superfamily Cucujoidea (Crowson, 1981; Lawrence and Newton, 1982). Byturid larvae differ from those of Biphyllidae in lacking an accessory ventral process on the mandible, ventral epicranial ridges, and modified 8th abdominal spiracles, and in having a projecting and setose, hyaline process at the base of the mandibular mola.

Biology and Ecology: Species of *Byturus* are known to breed in the fruits of *Rubus* species, and may be pests of blackberries and raspberries, while larvae of *Byturellus grisescens* (Jayne) feed in the catkins of oak (*Quercus* species) in California (d'Aguilar, 1962a; Barber, 1942; Schöning, 1953).

Description: Mature larvae 4 to 10 mm. Body elongate, parallel-sided or slightly wider in middle, subcylindrical to slightly flattened, straight or slightly curved ventrally; dorsal surfaces moderately heavily pigmented, somewhat granulate and tuberculate, with vestiture of scattered, simple setae.

Head: Protracted and prognathous. Epicranial stem very short or absent; frontal arms lyriform and contiguous at base. Median endocarina absent. Stemmata almost always 6 on each side (rarely 5). Antennae well-developed, 3-segmented. Frontoclypeal suture absent; labrum free or partly fused to head capsule. Mandibles symmetrical, with bidentate apex, serrate incisor edge and no accessory ventral process; mola sub-basal, tuberculate, with hyaline, setose lobe at base; prostheca absent or consisting of a few hyaline processes or brush

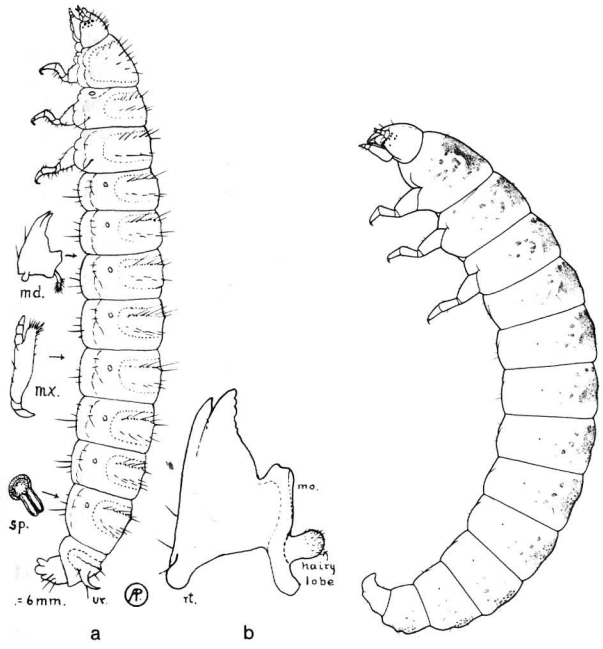


Figure 34.555

Figure 34.556

Figures 34.555a,b. Byturidae. *Byturus* sp. **a.** larva, lateral (plus details), length = 6 mm; **b.** right mandible, ventral. (From Peterson, 1951)

Figure 34.556. Byturidae. *Byturellus grisescens* (Jayne). Strawberry Canyon, Berkeley, California. Larva, lateral. Length = 6 mm.

of hairs. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and falciform mala, which may be somewhat obtuse with 2 spines at inner angle. Labium free almost to base of mentum; ligula present; labial palps 2-segmented, widely separated. Hypopharyngeal sclerome a transverse bar or tooth-like structure. Hypostomal rods moderately long and diverging. Ventral epicranial ridges absent. Gula transverse.

Thorax and Abdomen: Legs well-developed, 5-segmented, moderately close together; tarsungulus with 1 seta. Tergum A9 usually with pair of upturned, fixed urogomphi (absent in *Byturellus*); sternum A9 well-developed, simple. Segment A10 circular, posteriorly or posteroventrally oriented.

Spiracles: Annular, biforous, not raised on tubes, those on segment A8 laterally placed.

Comments: The family includes 7 genera: the Holarctic *Byturus, Byturellus* from California, *Byturodes* from western China, *Xerasia* and *Terobyturus* from Japan, and *Platydascillus* and *Dascillocyphon* from Sumatra.

Selected Bibliography

Abdullah 1966.
d'Aguilar 1962b (agricultural pests; larva of *Byturus tomentosus* (De Geer)).
Barber 1942 (revision).
Böving and Craighead 1931 (larvae of *Byturus tomentosus* and *B. unicolor* Say).
Crowson 1981.
Falcoz 1926 (relationships).
Lawrence and Newton 1982.
Peterson 1951 (larva of *Byturus* sp.).
Schöning 1953 (larvae of *B. fumatus* (Fabricius) and *B. tomentosus*).
Springer and Goodrich 1983 (North American revision).
Verhoeff 1923 (larva of *B. tomentosus*).

BOTHRIDERIDAE (CUCUJOIDEA)

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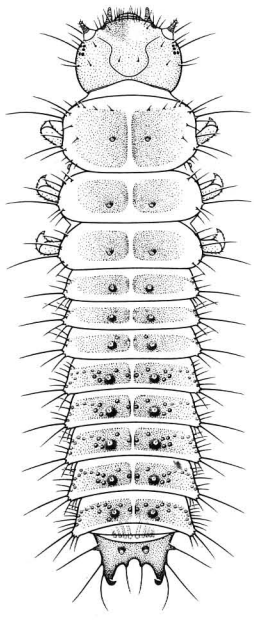
Figures 34.557-558

Relationships and Diagnosis: Although Craighead (1920) treated this group as a distinct family, subsequent authors (Arnett, 1968; Crowson, 1955, 1981) considered it to be a subfamily of Colydiidae. Lawrence (1980) presented evidence for placing Bothrideridae in the Cucujoidea, but their relationships within that superfamily are still unclear, and it is not at all certain that the Teredinae and Bothriderinae, as delimited below, form a monophyletic unit. Teredine larvae have a number of features in common with Sphaerosomatidae and some Cerylonidae (Euxestinae), while adult teredines are reminiscent of Metacerylinae (Cerylonidae). The Biphyllidae must also be considered as a possible sister group of the Bothrideridae. The ectoparasitic larvae of Bothriderinae are similar to those of Cucujidae: Passandrinae, but differ in having retracted ventral mouthparts and lacking hypostomal rods.

Biology and Ecology: All species of Bothrideridae appear to be associated with the galleries or tunnels of wood-boring insects; especially Coleoptera, and most are ectoparasitoids of larvae or pupae. Larvae of Teredinae are apparently free-living, and do not show any of the modifications associated with ectoparasitism; those of *Oxylaemus, Teredolaemus,* and *Teredomorphus* are associated with the tunnels of ambrosia beetles (Platypodidae and some Scolytidae), while *Teredus* larvae live in the galleries of a number of wood-borers, including Scolytidae (*Dryocoetes*), Anobiidae (*Ptilinus, Xestobium, Anobium*), and Cerambycidae (*Callidium*) (Dajoz, 1977; Horion, 1961; Schedl, 1962). *Teredolaemus leae* (Grouvelle) was reared from tunnels of *Platypus subgranosus* Schedl in a *Nothofagus* log from Tasmania; the pupa was not enclosed in a cocoon (Lawrence, 1985b). Species of *Sosylus* also inhabit the tunnels of Platypodidae and other ambrosia beetles, but they are hypermetamorphic, with active triungulins and later instars modified as ectoparasitoids, which construct a waxen chamber for pupation. The related *Asosylus rhysodoides* (Grouvelle) has similar habits, but its host is a brentid (*Carcinopisthius kolbei* Senna), which is, in turn, a nest parasite of Platypodidae (Browne, 1962; Roberts, 1968, 1969, 1980; Schedl, 1962). Larvae of *Dastarcus, Deretaphrus,* and the genera of Bothriderini are all ectoparasitoids of wood-borers (usually excluding ambrosia beetles), and they spin a silken cocoon for pupation. *Dastarcus* larvae have been associated with a cerambycid host (Lieu, 1944), but they have also been found parasitizing larvae of carpenter bees (*Xylocopa*) in Asia (Piel, 1938). *Deretaphrus* larvae are known



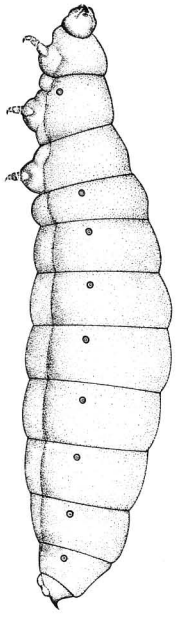
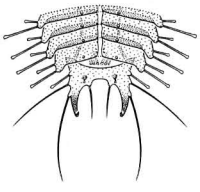


Figure 34.558



b

Figure 34.557

Figures 34.557a,b. Bothrideridae. *Teredolaemus leae* (Grouvelle). Arve Valley, Tasmania. **a.** larva, late instar, dorsal, length = 2.6 mm. **b.** first instar, abdominal apex, dorsal.

Figure 34.558. *Deretaphrus oregonensis* Horn. Giant Forest, California. Larva, lateral. Length = 15 mm.

to attack Cerambycidae, Buprestidae, and some of the larger Scolytidae (*Dendroctonus*), while bothriderine larvae are often found in the tunnels of Bostrichidae, but may also feed on larvae or pupae of Cerambycidae, Buprestidae, Anobiidae, Curculionidae, or Scolytidae (Burke, 1919; Craighead, 1920; Dajoz, 1977; Horion, 1961; Rasmussen, 1967; Schedl, 1962).

Description: *Free-living Larvae (Teredinae).* Mature larvae 3–4 mm. Body elongate, more or less parallel-sided and moderately to strongly flattened. Dorsal surfaces moderately pigmented and granulate-tuberculate; vestiture of longer and shorter, simple setae.

Head: Protracted and prognathous, moderately broad and somewhat flattened. Epicranial stem very short; frontal arms lyriform. Median endocarina absent. Stemmata usually 5 on each side (occasionally with an indistinct 6th stemma). Antennae short, 3-segmented. Frontoclypeal suture absent; labrum free. Mandibles symmetrical, bidentate, with 2 to several teeth along incisor edge and with large accessory ventral process. Mola well-developed and asperate; prostheca absent. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and falciform mala. Labium more or less free to base of mentum; ligula short and broad; labial palps 2-segmented and widely separated. Hypopharyngeal sclerome well-developed with pair of characteristic anterior horns. Hypostomal rods long and diverging. Ventral epicranial ridges absent. Gula transverse.

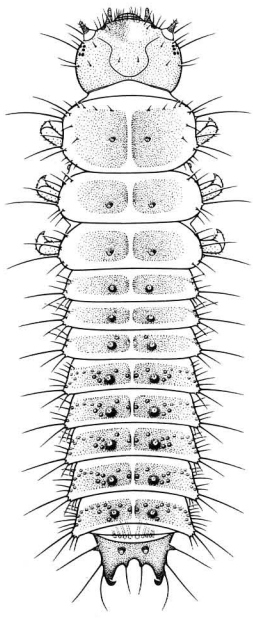
Thorax and Abdomen: Legs moderately well-developed, widely separated; tarsungulus with 1 seta. Thoracic terga and abdominal terga 1–9 each with a pair of sharp, paramedian tubercles, in addition to smaller tubercles and granules. Thoracic terga slightly expanded at sides; abdominal terga 1–8 more strongly expanded laterally forming tergal processes which are somewhat posteriorly directed. Tergum A9 with pair of well-developed, widely separated urogomphi, each with a lateral and mesal accessory process at base (in addition to paramedian tubercles). Anterior edge of tergum A9 with a transverse row of internal processes (visible under transmitted light). Sternum A9 well-developed, simple. Segment A10 oval, posteroventrally oriented.

Spiracles: Annular biforous, with long accessory openings, borne on tubular processes; those on segment A8 somewhat larger than others.

First Instar: Body broader and flatter, with smoother and more heavily pigmented dorsal surfaces, and with several pleural and sternal pigmented plates. Vestiture including modified setae which are expanded at apex and probably glandular. Lateral tergal processes on thorax and first 8 abdominal segments more well-developed, forming flattened plates. Paramedian tubercles on thorax and abdomen reduced, except for those on tergum A9. Accessory basal processes of urogomphi reduced. Spiracles located at the ends of longer tubes.

Ectoparasitic Larvae (Bothriderinae): Mature larvae 3 to 15 mm. Body elongate, subcylindrical, but with abdomen enlarged (physogastric), very slightly sclerotized, smooth, with vestiture of short, scattered setae.

Head: Protracted and prognathous, reduced in size, somewhat flattened. Epicranial stem absent; frontal arms usually indistinct or absent, sometimes V-shaped and distant at base. Median endocarina absent. Stemmata absent or 1 on each side. Antennae very short, usually 2-segmented, with long sensorium on segment 1, occasionally 1-segmented. Frontoclypeal suture absent; labrum usually free. Mandibles symmetrical, unidentate or bidentate, without accessory ventral process or mola; mesal surface of mandibular base simple or with fixed, hyaline or partly sclerotized, acute process. Ventral mouthparts retracted. Maxilla usually with transverse or oblique cardo, slightly elongate stipes, well developed articulating area, 2-segmented palp (sometimes with distinct palpifer and appearing 3-segmented), and a blunt but narrowly rounded mala; in *Sosylus,* cardo, stipes and articulating area indistinct, mala sometimes absent, and palp sometimes absent or represented by minute papilla. Labium usually free to base of mentum, with ligula longer than labial palps which are 2-segmented; in *Sosylus,* labium may not be subdivided, ligula is absent, and labial palps may be absent



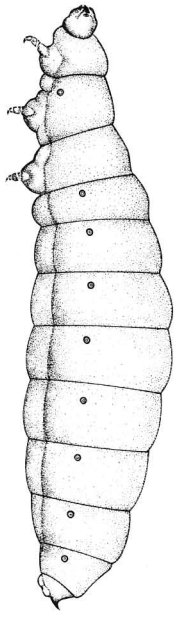
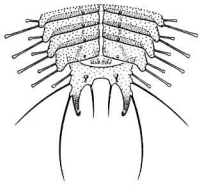


Figure 34.558



b

Figure 34.557

Figures 34.557a,b. Bothrideridae. *Teredolaemus leae* (Grouvelle). Arve Valley, Tasmania. **a.** larva, late instar, dorsal, length = 2.6 mm. **b.** first instar, abdominal apex, dorsal.

Figure 34.558. *Deretaphrus oregonensis* Horn. Giant Forest, California. Larva, lateral. Length = 15 mm.

to attack Cerambycidae, Buprestidae, and some of the larger Scolytidae (*Dendroctonus*), while bothriderine larvae are often found in the tunnels of Bostrichidae, but may also feed on larvae or pupae of Cerambycidae, Buprestidae, Anobiidae, Curculionidae, or Scolytidae (Burke, 1919; Craighead, 1920; Dajoz, 1977; Horion, 1961; Rasmussen, 1967; Schedl, 1962).

Description: *Free-living Larvae (Teredinae).* Mature larvae 3–4 mm. Body elongate, more or less parallel-sided and moderately to strongly flattened. Dorsal surfaces moderately pigmented and granulate-tuberculate; vestiture of longer and shorter, simple setae.

Head: Protracted and prognathous, moderately broad and somewhat flattened. Epicranial stem very short; frontal arms lyriform. Median endocarina absent. Stemmata usually 5 on each side (occasionally with an indistinct 6th stemma). Antennae short, 3-segmented. Frontoclypeal suture absent; labrum free. Mandibles symmetrical, bidentate, with 2 to several teeth along incisor edge and with large accessory ventral process. Mola well-developed and asperate; prostheca absent. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and falciform mala. Labium more or less free to base of mentum; ligula short and broad; labial palps 2-segmented and widely separated. Hypopharyngeal sclerome well-developed with pair of characteristic anterior horns. Hypostomal rods long and diverging. Ventral epicranial ridges absent. Gula transverse.

Thorax and Abdomen: Legs moderately well-developed, widely separated; tarsungulus with 1 seta. Thoracic terga and abdominal terga 1–9 each with a pair of sharp, paramedian tubercles, in addition to smaller tubercles and granules. Thoracic terga slightly expanded at sides; abdominal terga 1–8 more strongly expanded laterally forming tergal processes which are somewhat posteriorly directed. Tergum A9 with pair of well-developed, widely separated urogomphi, each with a lateral and mesal accessory process at base (in addition to paramedian tubercles). Anterior edge of tergum A9 with a transverse row of internal processes (visible under transmitted light). Sternum A9 well-developed, simple. Segment A10 oval, posteroventrally oriented.

Spiracles: Annular biforous, with long accessory openings, borne on tubular processes; those on segment A8 somewhat larger than others.

First Instar: Body broader and flatter, with smoother and more heavily pigmented dorsal surfaces, and with several pleural and sternal pigmented plates. Vestiture including modified setae which are expanded at apex and probably glandular. Lateral tergal processes on thorax and first 8 abdominal segments more well-developed, forming flattened plates. Paramedian tubercles on thorax and abdomen reduced, except for those on tergum A9. Accessory basal processes of urogomphi reduced. Spiracles located at the ends of longer tubes.

Ectoparasitic Larvae (Bothriderinae): Mature larvae 3 to 15 mm. Body elongate, subcylindrical, but with abdomen enlarged (physogastric), very slightly sclerotized, smooth, with vestiture of short, scattered setae.

Head: Protracted and prognathous, reduced in size, somewhat flattened. Epicranial stem absent; frontal arms usually indistinct or absent, sometimes V-shaped and distant at base. Median endocarina absent. Stemmata absent or 1 on each side. Antennae very short, usually 2-segmented, with long sensorium on segment 1, occasionally 1-segmented. Frontoclypeal suture absent; labrum usually free. Mandibles symmetrical, unidentate or bidentate, without accessory ventral process or mola; mesal surface of mandibular base simple or with fixed, hyaline or partly sclerotized, acute process. Ventral mouthparts retracted. Maxilla usually with transverse or oblique cardo, slightly elongate stipes, well developed articulating area, 2-segmented palp (sometimes with distinct palpifer and appearing 3-segmented), and a blunt but narrowly rounded mala; in *Sosylus,* cardo, stipes and articulating area indistinct, mala sometimes absent, and palp sometimes absent or represented by minute papilla. Labium usually free to base of mentum, with ligula longer than labial palps which are 2-segmented; in *Sosylus,* labium may not be subdivided, ligula is absent, and labial palps may be absent

CERYLONIDAE (CUCUJOIDEA)

(= CERYLIDAE; INCLUDING ACULAGNATHIDAE, ANOMMATIDAE, DOLOSIDAE, EUXESTIDAE, MURMIDIIDAE)

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Figures 34.559-562

Relationships and Diagnosis: The Cerylonidae are a diverse group of cucujoid beetles, which probably should be placed in two or more families. Larvae of the subfamily Ceryloninae are easily distinguished by the highly modified mandibles and maxillae, which are stylet-like and either endognathous or enclosed in a tubular proboscis. Adults of Anommatinae and Metaceryloninae exhibit characters indicating a relationship to Bothrideridae, while larvae of Anommatinae and Metaceryloninae are not easily distinguished from free-living forms of the bothriderid subfamily Teredinae (Pal and Lawrence 1986). The positions of the Anommatinae and Murmidiinae are not clear, and larvae of the latter are disc-like, resembling those of the family Discolomidae. Current studies in progress by Crowson, Sen Gupta, Lawrence, Pal, and Slipinski may shed light on the phylogenetic relationship of these groups.

Biology and Ecology: Cerylonidae occur commonly in leaf litter, in rotten wood, or under bark, and probably feed on fungal hyphae and spores. *Hypodacne punctata* LeConte has been found in the galleries of carpenter ants (*Camponotus*) in rotten oak and elm logs (Stephan, 1968), while Australian species of this genus are collected in samples of leaf litter. *Euxestus erithacus* Chevrolat was found breeding in bat guano in a cave in Jamaica, and the African *Elytrotetrantus chappuisi* (Jeannel and Paulian) has been collected in the nests of mole rats. Species of *Cerylon, Philothermus,* and *Mychocerus* are most common under bark, while species of *Lapethus* are characteristic inhabitants of leaf litter and have been taken in the refuse deposits of leaf-cutter ants (*Atta*). *Murmidius ovalis* (Beck) occurs in granaries and warehouses, where it has been associated with stored products, such as corn, wheat, rice, flour, hay, pepper, ginger, and various fruits and seeds; it also occurs in dead leaves and cut grass and is probably a mold feeder (Halstead, 1968a; Hinton, 1945b). *Anommatus duodecimstriatus* (Müller) is known from damp soil beneath railroad ties, in grass roots, grass cuttings, tree holes, and leaf litter; it has apparently been distributed by man in soil samples (Kuschel, 1979; Lawrence and Stephan, 1975).

Description: Mature larvae 1 to 5 mm. Body oblong and fusiform to broadly ovate, slightly to strongly flattened. Dorsal surfaces usually lightly sclerotized, sometimes with pigmented tergal plates, often granulate or tuberculate; vestiture often including frayed or clavate setae, or occasionally (*Murmidius*) barbed setae.

Head: Protracted and prognathous to strongly hypognathous or opisthognathous, sometimes completely concealed from above by prothorax, slightly flattened. Epicranial stem usually absent, occasionally short; frontal arms usually absent, sometimes lyriform and contiguous at base. Median endocarina present in *Murmidius*. Stemmata usually absent, sometimes 1 to 3 on each side. Antennae short to moderately long, 3-segmented, usually with sensorium longer than segment 3. Frontoclypeal suture usually absent; labrum usually free, forming long, tapered, tubular proboscis in most Ceryloninae, apparently fused to head capsule in *Cerylon*. Mouthparts in Ceryloninae highly modified, either enclosed within proboscis or endognathous (*Cerylon*); mandibles andmaxillae both forming narrow stylets; maxillary palps 3-segmented and labial palps usually 2-segmented (1-segmented in *Cerylon*). Mouthparts in unspecialized forms (Euxestinae, *Murmidius, Anommatus*) as follows: mandibles symmetrical, bidentate or tridentate, with well-developed mola, which is tuberculate, asperate, or transversely ridged, usually with an accessory ventral process, and occasionally (*Murmidius*) with a fixed, hyaline prostheca; ventral mouthparts retracted; maxilla with transverse or oblique cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and blunt mala; labium free to base of mentum, with ligula and 2-segmented palps; hypopharyngeal sclerome a transverse bar or tooth-like structure. Hypostomal rods usually absent (short and subparallel in *Murmidius*). Gula transverse.

Thorax and Abdomen: Thoracic and abdominal terga usually with lateral or dorsal and lateral processes. Legs well-developed, 5-segmented; tarsungulus with 1 seta. Tergum A9 usually simple, with short, complex urogomphi in *Anommatus*, and with long urogomphi bearing accessory tubercles or processes in Euxestinae; sternum A9 relatively short, simple. Segment A10 circular, ventrally oriented.

Spiracles: Annular or annular-biforous, occasionally raised on tubes, located laterally beneath lateral tergal processes, when present.

Comments: The family, as here defined, includes about 55 genera and 650 species worldwide, with 10 genera and 18 species occurring in N. America. The subfamily Euxestinae is worldwide and includes such genera as *Euxestus, Hypodacne,* and *Elytrotetrantus*. The Anommatinae are native to Europe, but the species *Anommatus duodecimstriatus* (Müller) has been introduced into N. America, South Africa, Chile, and Australia. Species of Ostomopsinae, Metaceryloninae and Murmidiinae occur in the warmer parts of the Old and New Worlds, but *Murmidius ovalis* has been widely introduced with stored products. The Ceryloninae is the largest and most widespread subfamily, and includes such genera as *Cerylon, Lapethus,* and *Philothermus*. The genus *Eidoreus* (= *Eupsilobius*) was transferred to the family Endomychidae by Sen Gupta and Crowson (1973). The larva described and illustrated by Peterson (1951) as *Murmidius ovalis* is actually a corylophid.

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Böving and Craighead 1931 (larva of *Murmidius ovalis*).
Dajoz 1963, 1968 (larva of *Anommatus duodecimstriatus*).
Halstead 1968a (biology of *M. ovalis*).
Hinton 1945b (stored products pests).

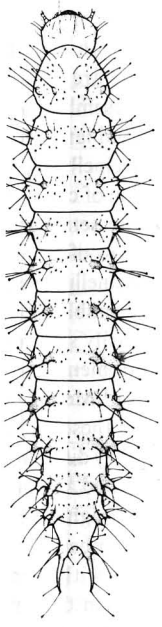


Figure 34.559

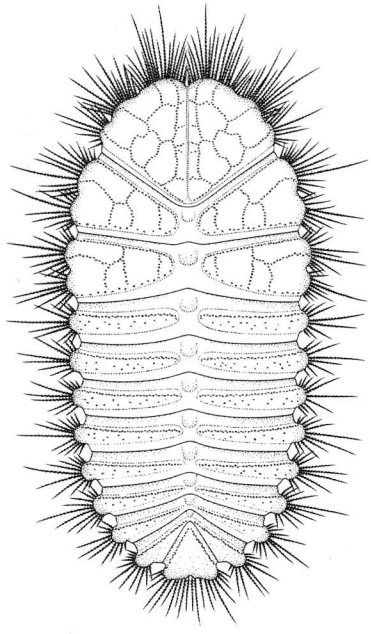
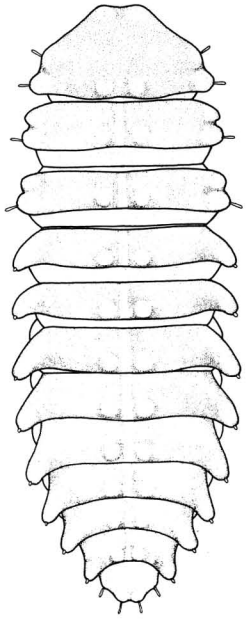
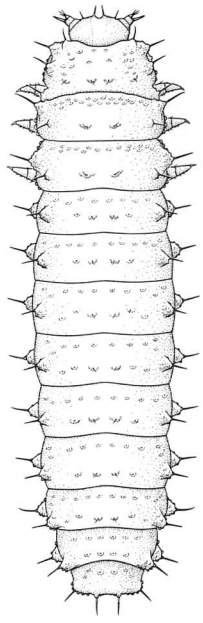


Figure 34.560



a



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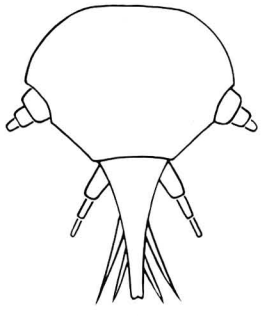
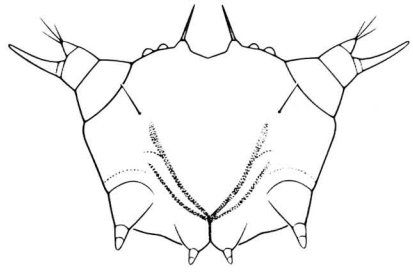


b

Figure 34.561



b

Figure 34.562

Figure 34.559. Cerylonidae. *Euxestus erithacus* Chevrolat. Bandon Hill Cave, St. James Parish, Jamaica. Larva, dorsal. Length = 4.9 mm.

Figure 34.560. Cerylonidae. *Murmidius ovalis* (Beck). Slough, England (in culture). Larva, dorsal. Length = 1.9 mm.

Figures 34.561a,b. Cerylonidae. *Lapethus* sp. 21 km. W El Hato del Volcan, Panama. **a.** larva, dorsal, length = 2.3 mm; **b.** head, dorsal (anteroventral view).

Figures 34.562a,b. Cerylonidae. *Cerylon unicolor* (Ziegler). 5.4 mi. N Shady Lake Recreation Area, Polk Co., Arkansas. **a.** larva, dorsal. Length = 2.4 mm; **b.** head, ventral.

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Slipinski 1984 (larva of *Lapethus ferrugineus* (Hinton and Ancona)).
Stephan 1968 (habits of *Hypodacne punctata*).

DISCOLOMIDAE (CUCUJOIDEA)

(= NOTIOPHYGIDAE)

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The family Discolomidae is comprised of 18 genera and about 400 species distributed throughout the warmer parts of the world, but is much more diverse in the Eastern Hemisphere. Of the 5 subfamilies, Notiophyginae and Aphanocephalinae have representatives in the Neotropical, Ethiopian, and Indo-Australian Regions, Discolominae occur in tropical Africa and America, Cephalophaninae are restricted to Southeast Asia and the East Indies, and Pondonatinae occur only in Africa. Both larval and adult features indicate a possible relationship with *Murmidius* and its relatives (Cerylonidae).

Larvae are small to minute, broadly ovate, strongly flattened, and disc-like, with the dorsal surfaces pigmented, granulate, and clothed with various kinds of modified setae or scales, and the lateral edges lined with scale-like setae. The head is prognathous but concealed from above by the pronotum, with no epicranial stem or median endocarina, and with lyriform frontal arms, approximate at base. The antennae are long and 2-segmented, and there are 3 stemmata on each side. The mandibles are tridentate, with a well-developed, tuberculate mola and a hyaline prostheca, which is acute at the apex. The ventral mouthparts are retracted, with an obtuse mala, which is usually cleft, 2- or 3-segmented maxillary palps and 2-segmented labial palps. The legs are widely separated with a unisetose tarsungulus. Paired dorsal gland openings are present on all visible terga, on the protergum and abdominal terga 1 to 4, or on abdominal terga 4 to 8. Urogomphi are absent and segment A10 is circular and ventrally oriented. Spiracles are annular.

Discolomids may be collected under the loose bark of trees or sometimes in leaf litter, but species of *Notiophygus* have been recorded from lichens, and *Katoporus* are myrmecophilous. Adults and larvae of *Aphanocephalus hemisphaericus* Wollaston were found feeding on the surface of the polypore fungus *Favolus arcularius*, while other species of *Aphanocephalus* and *Fallia* have been found on various polypores.

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Fukuda 1969 (larva of *Aphanocephalus hemisphaericus;* larval comparisons; feeding habits).
John 1954 (family characters and relationships), 1959 (genera), 1964.

ENDOMYCHIDAE (CUCUJOIDEA)

(INCLUDING MEROPHYSIIDAE, MYCETAEIDAE)

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Handsome Fungus Beetles

Figures 34.563-569

Relationships and Diagnosis: Endomychidae, as defined here, excludes the European genus *Sphaerosoma* (Sphaerosomatidae), but includes *Agaricophilus reflexus* Motschulsky (removed by Mamaev, 1977) and *Eidoreus* (= *Eupsilobius*) (formerly placed in Cerylonidae), as well as those genera (*Merophysia, Coluocera, Holoparamecus,* etc.) currently comprising the family Merophysiidae (Crowson, 1955, 1981; Lawrence, 1982c; Sasaji, 1971; Sen Gupta and Crowson, 1973). The family forms part of Crowson's cerylonid series and is thought to be related to Sphaerosomatidae and Coccinellidae.

Endomychid larvae are highly variable in form, sculpture, and vestiture, and they may be confused with a number of other cucujoids. Typical endomychid larvae are fusiform to broadly ovate, without urogomphi, and resemble many coccinellids. Except in *Endomychus,* endomychid larvae have a more well-developed mola than those of Coccinellidae, and in addition they lack such features as the fusion of cardo and stipes, enlarged tibia bearing group of clavate setae, small tarsungulus with broad base, and transverse row of 6 protuberances on most abdominal segments. Like coccinellids, many endomychids are surface dwellers, and thus resemble certain Chrysomelidae with similar habits; they are easily separated by the presence of a gula and a distinct mola (or membranous lobe in *Endomychus*). Larvae of Leiestinae and Merophysiinae are more or less cylindrical and resemble those biphyllids and cryptophagids which lack urogomphi; they differ from members of either family in having no prostheca and an obtuse mala. The larva of *Mycetaea hirta* (Marsham) might be confused with Sphaerosomatidae or with some members of the families Rhizophagidae and Languriidae (those with a more or less tuberculate upper surface). It differs from the larva of *Sphaerosoma* in lacking raised spiracular tubes or paired tubercles on tergum A8, and from both rhizophagids and languriids in having an obtuse mala and small, annular spiracles. Larvae of Cerylonidae: Ceryloninae resemble endomychids in general body form, but they have highly modified mouthparts, which are either endognathous or enclosed within a tubular beak. *Murmidius ovalis* (Beck) has a disc-like larva resembling that of *Agaricophilus,* but the latter has a much shorter basal antennal segment and lacks a median endocarina and barbed setae. Those corylophid larvae which have a disc-like body differ from *Agaricophilus* in having paired gland openings on abdominal segments 1 and 8.

Biology and Ecology: Endomychidae are basically mycophagous, feeding on a wide variety of fungal types, but some occur with ants or termites, a few are predators, and others are pests on stored products. Most endomychids are associated with rotten wood, and they may occur under bark, in rotting wood, or more often on wood or bark surfaces (especially at night). Their specific food source usually consists of the less conspicuous cryptograms and is thus difficult to determine; *Aphorista morosa* LeConte was found in association with a yellow plasmodium of a slime mold (Myxomycetes), while a Neotropical species of *Amphix* was found feeding on spore capsules of an ascomycete fungus. The more obvious Basidiomycetes are also fed upon by some endomychids. *Endomychus* species are known to breed in the fruiting bodies of *Hirneola mesenterica* (Auriculariaceae) and *Schizophyllum commune* (Schizophyllaceae); species of *Symbiotes* have been collected in *Pleurotus* mushrooms (Tricholomataceae); and species of *Phymaphora, Rhanidea, Mycetina, Bystus,* and *Eumorphus* have been associated with various bracket fungi (Polyporaceae) (Donisthorpe, 1935; Weiss and West, 1920). The last group represents several different larval types, some (*Phymaphora, Rhanidea*) feeding internally in a relatively soft matrix, and others (*Eumorphus*) feeding on surface tissue. Species of *Lycoperdina* have distinctive, internally feeding larvae, which occur in puffballs

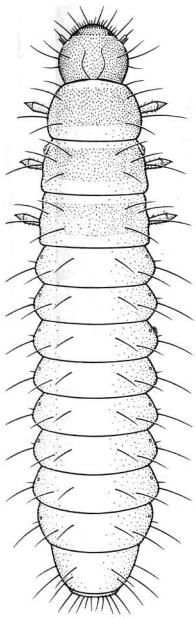


Figure 34.563

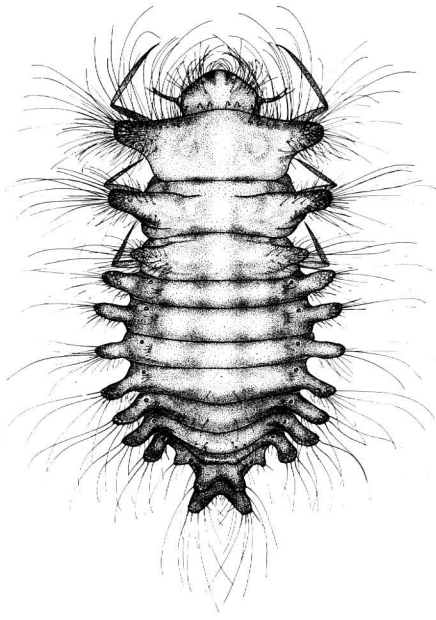


Figure 34.564

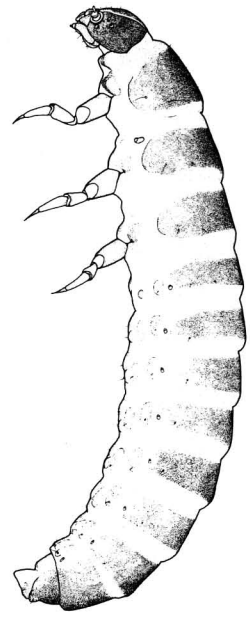


Figure 34.565

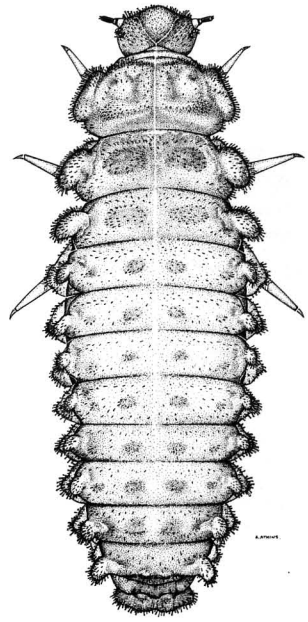


Figure 34.566

Figure 34.563. Endomychidae. *Holoparamecus* sp. Island MUD2, Monroe Co., Florida. Larva, lateral. Length = 1.9 mm.

Figure 34.564. Endomychidae. *Bystus* sp. Barro Colorado Is., Canal Zone, Panama. Larva, lateral. Length = 4.7 mm.

Figure 34.565. Endomychidae. *Rhanidea unicolor* (Ziegler). Rancocas, Burlington Co., Vermont. Larva, lateral. Length = 3.3 mm.

Figure 34.566. Endomychidae. *Aphorista morosa* LeConte. Mt. Bigelow, Santa Catalina Mts., Arizona. Larva, dorsal. Length = 8.9 mm.

of the genus *Lycoperdon* (Donisthorpe, 1935; Weiss and West, 1920). Various endomychids turn up regularly in leaf litter samples and feed on molds and other fungi on decaying plant products. Among the mold feeders, *Mycetaea hirta* (Marsham) and various species of *Holoparamecus* have become stored products pests, occurring in granaries and warehouses and causing minor damage to a variety of stored goods (Aitken, 1975; Hinton, 1945b; Klippel, 1952). Species of *Trochoideus* occur in termite nests, while *Coluocera* and *Merophysia* are myrmecophiles, but little is known of the food habits of either group (Kemner, 1924; Silvestri, 1912). *Saula japonica* Gorham has developed predaceous habits and feeds on scale insects and phytophagous mites (Sasaji, 1978b).

Description: Mature larvae 2 to 20 mm, usually 10 mm or less. Body elongate and subcylindrical, oblong, or fusiform and slightly flattened, or broadly ovate and strongly flattened. Dorsal surfaces lightly to darkly pigmented, sometimes with distinct tergal plates, smooth or sometimes granulate, with vestiture variable, consisting of short, fine setae, long, fine hairs, stout spines, or specialized (barbed, clavate, frayed) setae or scales.

Head: Protracted and prognathous or slightly declined to strongly hypognathous, usually broad and sometimes narrowed anteriorly. Epicranial stem very short or absent; frontal arms usually lyriform (V-shaped in *Mycetaea* and contiguous at base (separated at base in *Endomychus*), sometimes indistinct or absent. Median endocarina absent. Stemmata usually 2 to 4 on each side, 1 or 0 in Mychotheninae and Merophysiinae. Antennae usually well-developed, 3-segmented, occasionally short and broad, often with segment 2 very long and 3 reduced; antennal insertions often distant from mandibular articulations. Frontoclypeal suture present or absent; labrum free. Mandibles symmetrical, unidentate to tridentate or occasionally 4-dentate, with incisor edge sometimes serrate and accessory ventral process usually absent; mola almost always well-developed, bearing tubercles or asperities, which may form transverse rows or ridges, rarely (*Endomychus*) reduced and replaced by membranous lobe; prostheca usually a narrow, fixed, hyaline process, which may be acute or bifid, sometimes a fringed membrane, occasionally absent. Ventral mouthparts retracted. Maxilla usually with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and obtuse mala, which is sometimes densely fringed with setae at apex; mala falciform in Mychotheninae. Labium with mentum and submentum fused; ligula present, often longer than labial palps, which are usually 2-segmented (1-segmented in *Lycoperdina* and Merophysiinae). Hypopharyngeal sclerome usually consisting of a distinct tooth-like structure. Hypostomal rods usually long and diverging, sometimes almost parallel. Ventral epicranial ridges absent. Gula transverse.

Thorax and Abdomen: Abdominal or thoracic and abdominal terga and sometimes abdominal pleura with lateral processes, which may be dehiscent; *Lycoperdina* with paired,

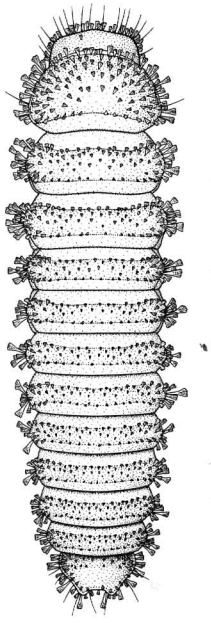


Figure 34.567

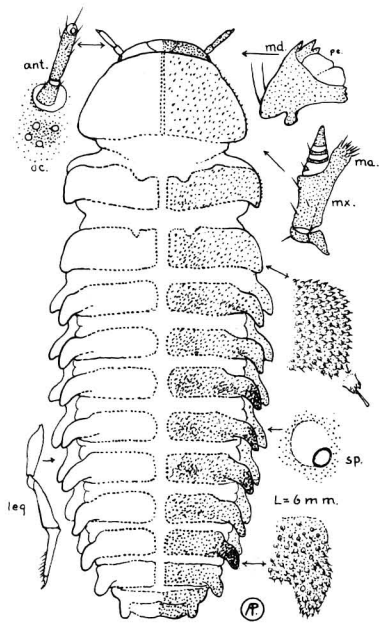
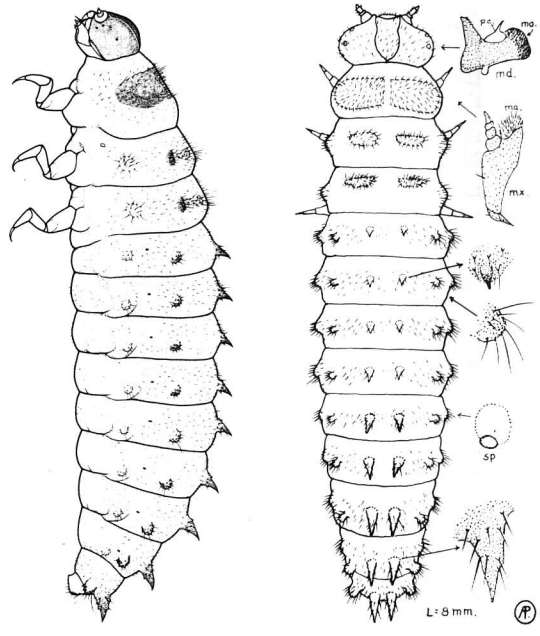


Figure 34.568



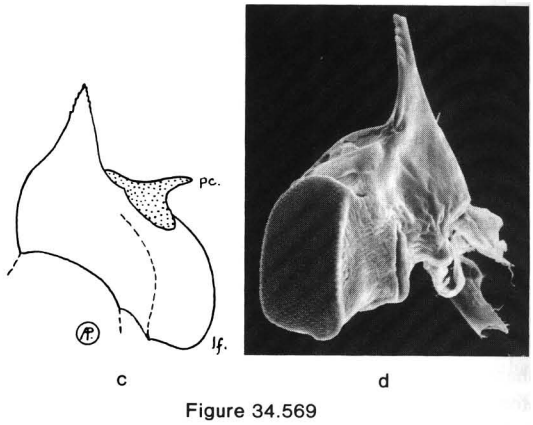


Figure 34.569

Figure 34.567. Endomychidae. *Mycetaea hirta* (Marhsam). Isle of Rhum, Scotland. Larva, dorsal. Length = 2.3 mm.

Figure 34.568. Endomychidae. *Endomychus biguttatus* Say. Larva, dorsal (plus details). Length = 6 mm. (From Peterson, 1951)

Figures 34.569a-d. Endomychidae. *Lycoperdina ferruginea* LeConte. East Lansing, Michigan. **a.** larva, lateral, length = 9.3 mm; **b.** larva, dorsal (plus details); **c.** left mandible, dorsal; **d.** left mandible, mesoventral. Great Smoky Mts. National Park, Tennessee. (figures 34.569b, c from Peterson, 1951)

acute, dorsal processes on terga A1–9, the last being the urogomphi. Legs well-developed, 5-segmented; tarsungulus with 1 seta. Tergum A9 usually without urogomphi (except in *Lycoperdina, Mycetaea,* and some Mychotheninae); sternum A9 short, simple. Segment A10 circular, ventrally or posteroventrally oriented.

Spiracles: Annular, not raised on tubes (except in some Mychotheninae).

Comments: The family includes about 120 genera and 1300 species worldwide, with 19 genera and about 45 species occurring in America north of Mexico. The subfamily classification currently in use is that of Strohecker (1953, and in Arnett, 1968), but more recent changes have been made by Crowson and Sen Gupta (1973), Lawrence (1982c, and this work), and Sasaji (1978a). The following groups are presently included in the family, but their constitution, rank, and arrangement are only tentative: Leiestinae (*Leiestes, Phymaphora, Rhanidea,* etc.); Holoparamecinae (*Holoparamecus, Lycoperdinella,* etc.); Merophysiinae (*Merophysia, Coluocera,* etc.); Eupsilobiinae (*Eidoreus*); Mycetaeinae (*Mycetaea*); Mychotheninae (*Mychothenus, Bystus, Symbiotes, Clemmus,* etc.); Agaricophilinae (*Agaricophilus*) Xenomycetinae (*Xenomycetes*); Trochoideinae (*Trochoideus*); Eumorphinae (*Eumorphus, Lycoperdina, Mycetina Aphorista, Amphix,* etc.); Stenotarsinae (*Stenotarsus, Danae, Epipocus,* etc.); and Endomychinae (*Endomychus,* etc.).

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Donisthorpe 1935 (fungus hosts).
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Verhoeff 1923 (larva of *M. hirta*).
Weiss and West 1920 (fungus hosts).

COCCINELLIDAE (CUCUJOIDEA)

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The Lady Beetles, Lady Birds

Figures 34.570–624

Relationships and Diagnosis: The Coccinellidae, commonly known as ladybird beetles, belong to the superfamily Cucujoidea, and are closely related to the Endomychidae and Corylophidae (van Emden 1949; Crowson 1955). There are about 490 genera and 4200 world species (Sasaji 1971) of which about 425 are known from the United States and Canada. Coccinellid larvae usually have a reduced mola on the mandible (absent in Epilachninae) (figs. 34.593–34.599), a gular area between the labium and the thorax (fig. 34.586), and the median epicranial stem (coronal suture) is absent in most genera (figs. 34.583–34.585). The most distinctive characteristics of coccinellid larvae are a great development of the body armature into setose processes in most tribes, a campodeiform and usually brightly colored body, and mandibles of a predaceous type in most tribes (acute at apex). Except in Epilachnini and Psylloborini, they are usually very active predators.

Many galerucine and some alticine larvae in the Chrysomelidae superficially resemble larvae of coccinellids. However, chrysomelid larvae have short legs, none or only 1 pair of stemmata, no setose processes on the body (rarely with processes covered by fine setae) and the mandibles lack a mola, whereas coccinellid larvae which may be mistaken for chrysomelid larvae have long legs, 3 pairs of stemmata, large setose body processes covered by robust setae, and a mandibular mola.

Biology and Ecology: It is not possible to treat here in detail the bionomics and ecology of Coccinellidae. See the excellent reviews by Balduf (1935), Hagen (1962), and Hodek (1967, 1973).

The eggs, usually oval or spindle-shaped, vary in colour from yellowish to reddish orange, and are mostly laid in clusters on the underside of leaves or in bark crevices in the vicinity of prey.

In general, there are 4 larval instars which last about 10 days each, but with great variation according to species and ecological factors. A unique feature among coccinellid larvae is the presence of secretory structures that produce a visible coating of waxy threads in the larvae of several tribes; these probably have primarily a defensive role against predators (Pope 1979). Cannibalism is frequent in coccinellid larvae and increases the chances of survival when there is a very low density of prey (Hodek 1973; Dimetry 1976). Larvae perceive their prey only by contact (Fleschner 1950; Putman 1955a, 1955b; Dixon 1959; Kaddou 1960; Frazer et al. 1981). With the development of biological control programs, attempts have been made to rear larvae on artificial diets or dried food. Several recent experiments gave excellent results (Smith 1960; Fisher 1963; Shands et al. 1966; Hodek 1973 (review); Kariluoto 1980).

Different types of pupae occur in Coccinellidae. Coccinellinae and Sticholotini have naked pupae attached by the cauda to the substrate. Pupae of the Chilochorini and Noviini are partly covered by the skin of the last larval instar, and the Hyperaspini and Scymnini have pupae completely covered by larval skins. The pupa is not entirely immobile; if irritated, the head region is raised several times by upward jerks of the body.

The number of generations varies greatly according to species and latitudes; types of voltinism were summarized by Hagen (1962). Perhaps the most fascinating phenomenon coccinellid adults display is the formation of aggregations. Species involved usually feed mostly on aphids, exhibit long dormancy or diapause periods, and mate at the aggregation site before the beetles disperse or migrate (Hagen 1962; Hodek 1967, 1973; Benton & Crump 1979; Lee 1980).

The role of coccinellids in natural control has been demonstrated many times. Various interrelated factors affect the ability of coccinellids to check pest infestations. However, it seems that the most important factor involved, temperature, was probably also the most neglected in theories of insect predation (Baumgaertner et al. 1981).

Since the bionomics, general habitus and food preference are generally distinctive for each tribe, a key to tribes is presented below, followed by a short synopsis of each tribe.

Body Armature: Gage's terminology (Gage 1920) is generally followed for different structures on the body of larvae. A *seta* (fig. 34.610) is situated directly on the body surface; a *chalaza* is a seta mounted on a small base (fig. 34.611). A *verruca* or *tubercle* is a small protuberance covered by setae instead of chalazae (fig. 34.612). A *struma* appears to be a mound-like projection of the body-wall upon which are situated a few chalazae (fig. 34.613). A *parascolus* (fig. 34.614) is an elongate process covered by chalazae, but less than 3 times as long as wide. A *scolus* (fig. 34.616) is a branched projection, usually more than 5 times as long as wide; each branch bears at its distal end a single stout seta. A *sentus* (fig. 34.615) is a projection of the body-wall which is not branched like a scolus but bears stout setae on its trunk. Larvae may have structures intermediate between scoli, senti, parascoli or strumae.

KEY TO TRIBES OF NORTH AMERICAN LARVAE OF COCCINELLIDAE

1.	Body with scoli (figs. 34.570, 34.616); mandible without mola (fig. 34.597)	Epilachnini
	Body without scoli (figs. 34.572–34.575); mandible with mola (figs. 34.593–34.596)	2
2(1).	Epicranial suture present (figs. 34.582, 34.583, 34.585)	3
	Epicranial suture absent (fig. 34.584)	11
3(2).	Epicranial suture V-shaped (fig. 34.585)	4
	Epicranial suture U-, Y-, or lyre-shaped (figs. 34.582, 34.583)	6
4(3).	Antennae large, conspicuous, second and third segments elongate (fig. 34.600)	Scymnillini
	Antennae small, inconspicuous, second and third segments short (fig. 34.585)	5
5(4).	Mature larvae small, less than 3 mm (fig. 34.575); tibiotarsi with a pair of apical flattened setae (fig. 34.618); maxillary palps 3-segmented (fig. 34.608)	Sticholotini
	Mature larvae larger, more than 6 mm (fig. 34.574); tibiotarsi with several apical clavate setae (fig. 34.617); maxillary palps 2-segmented (fig. 34.609)	Noviini
6(3).	Pores of repugnatorial glands present in the coria between abdominal segments on the antero-lateral margin (fig. 34.587); body always with long senti (figs. 34.587, 34.615)	Chilochorini
	Pores of repugnatorial glands absent, body usually with strumae (fig. 34.613) or parascoli (fig. 34.614), rarely with senti (fig. 34.615)	7
7(6).	Apex of mandible simple (fig. 34.594)	8
	Apex of mandible bidentate (figs. 34.596, 34.599)	10
8(7).	Body densely covered with fine hairs and long setae (fig. 34.624); tibiotarsi slender and narrowing apically	Serangiini
	Body covered with few large setae located on tubercles or strumae (figs. 34.623, 34.573); tibiotarsi short, stout, and truncated apically (fig. 34.588)	9
9(8).	Three pairs of conspicuous, pigmented, sclerotized plates (strumae) on abdominal segments 1–8 (fig. 34.623); body not covered by wax-like secretions	Stethorini
	Three pairs of inconspicuous, not pigmented, tubercles on abdominal segments 1–8; body covered by wax-like secretions	(in part) Scymnini
10(7).	Few large chalazae on disk or posterior margin of abdominal segment 9 (fig. 34.622); body dull yellowish; third antennal segment always well-developed and cupola-like (fig. 34.602)	Coccidulini
	Numerous setae and/or small chalazae on abdominal segment 9 (fig. 34.621); body brightly colored with black, brown, red, yellow or orange; third antennal segment usually much reduced, antenna appearing 2-segmented (fig. 34.606)	Coccinellini
11(2).	Apex of mandible multidentate (fig. 34.595); body without wax-like secretions	Psylloborini
	Apex of mandible simple (fig. 34.594); body covered with wax-like secretions	12
12(11).	Labial palp very small, dome-shaped, 1-segmented (fig. 34.592)	Hyperaspini
	Labial palp normal, 2-segmented (fig. 34.591)	(in part) Scymnini

Tribal Information

Unlike other coccinellids, the **Epilachnini** (Epilachninae) have an unusual porcupine-like appearance (fig. 34.570), and are phytophagous. Furthermore, in this tribe the mandible (fig. 34.597) lacks a mola and has a multidentate apex. *Epilachna borealis* (Fabricius), the squash beetle, attacks squash and pumpkins, and *E. varivestis* (Mulsant), the Mexican bean beetle, is a serious pest of beans including soybeans (Guyon & Knull 1925). The European alfalfa beetle, *Subcoccinella vigintiquatuorpunctata* (L.) was discovered in 1972 in Pennsylvania (Annonymous 1974). While an important pest of alfalfa and clover in Europe, it has been found feeding only on bouncing bet, *Saponaria officinalis*, campion, *Lychnus alba*, and oatgrass, *Arrhenatherum elatius* in the United States (Annonymous 1974).

Chilochorini (Chilochorinae) superficially resemble Epilachnini when senti are well-developed as in *Chilochorus* (fig. 34.571), or some Coccinellini when senti are more reduced. However, the presence of large pores of repugnatorial glands (fig. 34.587) on the abdomen will separate them easily from both. Chilochorini feed primarily on aphids and scales, therefore are used for biological control (Huffaker & Doutt 1965). For example, *Exochomus flavipes* Thungerg, indigenous to South Africa (Geyer 1947a, 1947b), was successfully used in the United States against mealybugs infesting commercial

greenhouses (Doutt 1951). *E. quadripustulatus* (L.) was released against the wooly aphid *Adelges piceae* (Ratz). The twice-stabbed lady beetle, *Chilochorus stigma* (Say), is an important predator of the Florida red scale, *Chrysomphalus aonidum* (L.) which infests citrus groves (Muma 1955a, 1955b).

Coccinellini (Coccinellinae) are the best known coccinellid larvae because they live exposed, are very active, relatively large, and brightly coloured. The body armature is very diverse in this tribe (figs. 34.572, 34.579–34.581) and all structures are represented except scoli. These larvae can be distinguished from those of other tribes by the lyre-shaped epicranial suture of the head (fig. 34.583), the bidentate apex of the mandible (fig. 34.599), the reduced, inconspicuous third antennal segment (fig. 34.606) and the well-developed body armature. All native Coccinellini are beneficial and several foreign species have been introduced to aid in control of pests (DeBach 1964; Hodek 1967, 1973). Some species are widely distributed and well known. *Anatis mali* (Say), the eye-spotted lady beetle, bears senti on the body similar to fig. 34.580, and occurs on conifers where it is able to survive at low prey densities (Smith 1965; Watson 1976). The spotted ladybird, *Coleomegilla maculata* (De Geer) (fig. 34.621), eats pollen as well as aphids and is usually found on herbaceous plants, wild and cultivated, where its food is abundant (Smith 1965). *Hippodamia* species are important aphid predators (Cuthright 1924; Hodek 1973) and a common species, *Hippodamia convergens* Guérin, the convergent lady beetle (fig. 34.579), can keep aphids in check in alfalfa fields (Cooke 1963). *Adalia bipunctata* (L.) (fig. 34.581), the 2-spotted ladybird, is a widespread polymorphic species (Hodek 1973) which prefers trees above 2 m. Consequently, it is especially beneficial in orchards and groves where it is the most important coccinellid aphid predator (Smith 1958; Putman 1964; Hodek 1973). *Coccinella* species (fig. 34.572) are known as aphid predators (Palmer 1914; Clausen 1916; McMullen 1967), and some have become established after repeated releases over large areas; others like *C. undecimpunctata* L., are becoming well established on their own, along with the aid of man's commerce (Watson 1979; Wheeler & Hoebeke 1981).

Coccidulini (Coccidulinae) much resemble Coccinellini but differ by the features of the last abdominal segment (fig. 34.622) and antenna (fig. 34.602), their dull coloration, and the presence of a thin powdery coating of wax (Pope 1979). Their biology is not well known. *Coccidula* live in wet habitats. *Rhyzobius ventralis* (Erichson) has been introduced from Australia to California and Hawaii for control of scale insects (Pope 1981; Richards 1981).

Scymnini and **Hyperaspini** larvae are strikingly different from others because of their thick coating of wax (fig. 34.577) which is absent or inconspicuous in other tribes.

Scymnini (Scymninae) larvae have very sharp unidentate mandibles (fig. 34.594) and very small tubercles on the abdomen (fig. 34.573). *Scymnus* species feed mainly on aphids; some are useful predators in red pine plantations (Gagné & Martin 1968), cotton fields (Davidson 1921b) or sugarbeet fields (Buntin & Tamaki 1980); others attack psyllids and are beneficial in pear orchards (Westigard et al. 1968) while a few feed on mealybugs in citrus groves (Muma 1955a), or on phylloxera on wild grape (Wheeler & Jubb 1979).

Hyperaspini (Scymninae) larvae are separated from all others by the unique dome-shaped, 1-segmented labial palps (fig. 34.592). *Hyperaspis* (figs. 34.576, 34.577) species are known as efficient predators of scale insects (Simanton 1916; Böving 1917; Phillips 1963).

Noviini (Coccidulinae) is the only tribe where the larvae have only 2 pairs of sclerotized tubercles and 1 pair of soft lateral projections on the abdominal segments (fig. 34.574). *Rodolia cardinalis* Mulsant, the vedalia lady beetle, is a famous classic example of successful use of coccinellids in biological control of coccids (DeBach 1964).

Psylloborini (Coccinellinae) larvae are immediately recognized by the multidentate apex of their mandibles (fig. 34.595). They differ from other tribes in that they are mycophagous and feed on mildew. They are beneficial because they eat destructive fungi (Davidson 1921a).

Larvae of the 4 remaining tribes are usually overlooked because of their small size. *Microweisea* larvae (fig. 34.575) in the tribe **Sticholotini** (Sticholotinae) are easily identified by the 2 large flattened setae at the apex of the tibiae (fig. 34.618). They are beneficial scale feeders (Burgess & Collins 1912; Muma 1955a; Sharma & Martel 1972).

Serangiini (Sticholotinae) larvae have the body densely covered with fine setae (fig. 34.624) and their tibiae are unusually slender (fig. 34.590), characters which distinguish them from all others. *Delphastus* species in this tribe are predators of Aleyrodidae (Muma 1955a, 1955b).

Stethorini (Scymninae) larvae resemble superficially the Serangiini but are separated from them and all other tribes by the few large setae fixed on small tubercles covering the body (figs. 34.578, 34.623) and their short tibiae, apically truncated (fig. 34.588). They feed chiefly on mites, and many *Stethorus* species are active predators of these pests (Fleschner 1950; Robinson 1953; Putman 1955a, 1955b; Putman & Herne 1966; Tanigoshi & McMurtry 1977).

Scymnillini (Coccidulinae) larvae are distinguished by their unusual, large, antennae (fig. 34.600). Their biology is poorly known. *Scymnillus aterrimus* Horn has been reported as an incidental predator of scale insects in citrus groves (Muma 1955b).

Description: Coccinellid larvae are extremely diverse as described in the previous section, and illustrated in the family key, where they key out at several couplets. Therefore, they cannot be distinguished altogether by only 1 or 2 characters as in many beetle families. On the other hand, larvae of each tribe show a distinctive general habitus and have morphological features which are shared by all members of the tribe. The striking flattened larvae of the Palaearctic Platynaspini do not occur in North America.

Head: Hypognathous, usually rounded (fig. 34.582), sometimes elongate (fig. 34.585) as in *Microweisea*, or transverse as in Hyperaspini, Platynaspini, and some Scymnini (fig. 34.584). In most species, the head is completely sclerotized, but sometimes it may be partly or only very slightly sclerotized. The epicranial suture is usually distinct, V-shaped (fig. 34.585), Y-shaped (fig. 34.582), lyre-shaped (fig. 34.583), or absent (fig. 34.584) but the epicranial stem is usually absent.

The antenna of the typical form of coccinellid larvae consists of 3 sclerotized segments (figs. 34.600, 34.602, 34.603), and bears a large spine-like seta on the membranous apical area of the second segment. However, they may appear to be 2-segmented (figs. 34.601, 34.605, 34.606) or even 1-segmented (fig. 34.604) when the third, and sometimes the second and third segments are reduced and not sclerotized; in those cases the homology of the segments apparently missing is often difficult to establish (Sasaji 1968b). The labrum is distinct and transverse (fig. 34.582).

The mandible is either apically simple and acute (figs. 34.593, 34.594), bidentate (figs. 34.596, 34.599), or multidentate in plant feeders (figs. 34.595, 34.597); the mola is usually present but reduced (figs. 34.595, 34.596 34.598, 34.599), highly reduced in *Microweisea* (fig. 34.593) and absent in *Epilachna* (fig. 34.597); a retinaculum may be either absent (figs. 34.593, 34.594), developed with 1 tooth (fig. 34.596), or multidenticulate (fig. 34.595). The maxillary palps are generally 3-segmented, but are 2-segmented in Noviini (fig. 34.609). The labial palps are either 1- or 2-segmented (figs. 34.591, 34.592). The labium has the submentum fused with the ligula (fig. 34.586).

Thorax and Abdomen: Pronotum with 2 or 4 plates. Meso- and metanotum each with 2 plates and distinct armature. Legs usually long and slender (figs. 34.589, 34.590), short in Hyperaspini and Stethorini (fig. 34.588), consisting of 5 segments (coxa, trochanter, femur, tibia and claw-like tarsungulus). Tarsungulus curved (fig. 34.620), with a robust quadrangular tooth in some species (fig. 34.619). The apex of the tibiae usually bears clavate or flattened setae which are important in taxonomy (figs. 34.588, 34.617, 34.618).

Abdomen 10-segmented, widest basally, tapering to caudal end, dorsally with distinct armature, usually characteristic for each tribe. The tenth segment may be modified as a proleg or a sucking disk. Pores of repugnatorial glands may occur on each antero-lateral margin of terga in the coria between segments (fig. 34.587).

Spiracles: Small, annular, and located on abdominal segments 1–8 (fig. 34.587).

Comments: The larval stage of most coccinellid species consists of 4 instars. The first instar can be recognized by the paired egg-bursters on pronotum, and differences in proportions in size of head, abdomen, legs, setae, etc. Changes occur in coloration, proportions and armature of the body between successive instars. Larvae of the first and second instars are monochrome, with sclerotization and armature less developed than in older instars. Larvae of the third and fourth instars are usually brightly coloured and well sclerotized.

Palearctic coccinellid larvae are now fairly well known with the recent contributions of several authors (van Emden 1949; Savoiskaya 1957, 1960, 1962, 1964a, 1964b; Kamiya 1965; Sasaji 1968a, 1968b; Klausnitzer 1970; Savoiskaya & Klausnitzer 1973). The taxonomy of the Nearctic coccinellid larvae has not been comprehensively studied; only the early works of Böving (1917) and Gage (1920) provide a general treatment of the family. With the field key of Storch (1970) one can identify the larvae of 5 common native species. Phuoc and Stehr (1974) studied the morphology and the phylogenetic relationships of coccinellid pupae based on their morphology and suggested the need for a similar study of the larvae.

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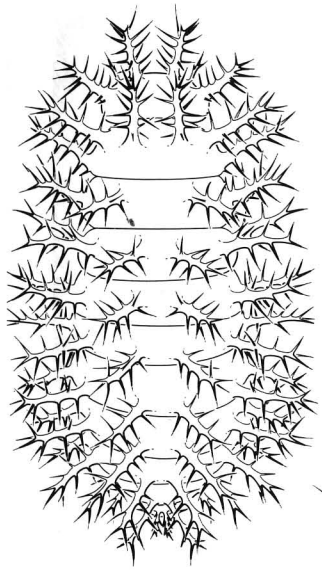
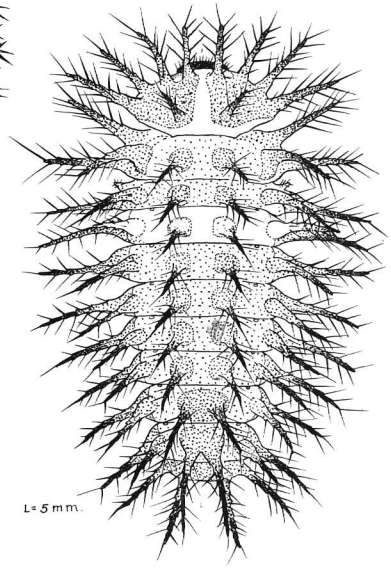
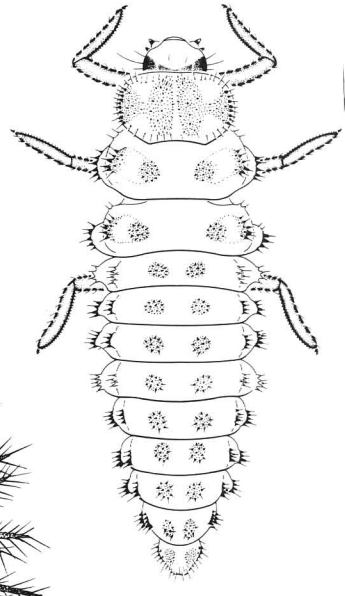


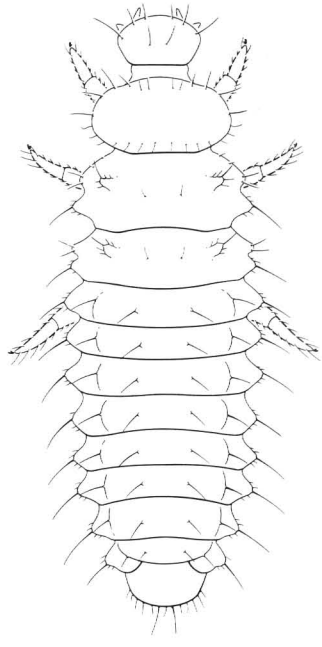
Epilachna
Figure 34.570



Chilochorus
Figure 34.571



Coccinella
Figure 34.572



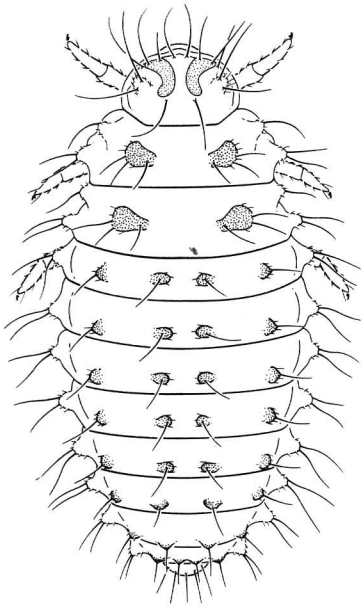
Scymnus
Figure 34.573

Figure 34.570. *See* also figures 34.597, 34.601, 34.616. Coccinellidae. *Epilachna varivestis* Mulsant. Mexican bean beetle. (Epilachnini) Length 11 mm; cyphosomatic, yellow, brownish around stemmata and tips of scoli; abdominal segments 1-8 each bearing 6 scoli; 4 scoli on prothorax, 6 on both meso- and metathorax; light slender setae on head, legs, and verrucae of all segments; 1 pair of verrucae on sterna of each thoracic and abdominal segment 1; 3 pairs on abdominal segments 2-7, 2 pairs on 8; caudal segment in the form of a sucker-like protuberance; spiracles inconspicuous, annular, and ventrad of supraspiracular scoli. It can be a serious defoliator of many kinds of beans, including soybeans. Jerome, Idaho, 25-VII-1960, Gibson & Evans.

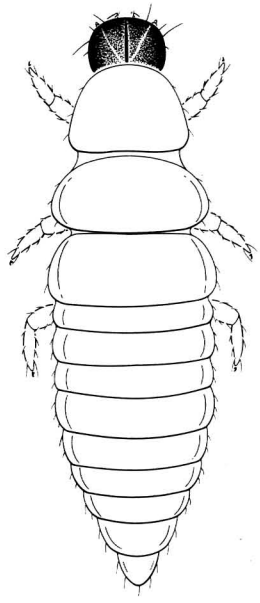
Figure 34.571. Coccinellidae. *Chilocorus stigma* (Say), twice-stabbed lady beetle. (Chilochorini) Length = 5 ± mm. Cyphosomatic, oval, and covered with prominent senti; color brownish with most senti and pinacula near black, mid-dorsal line and dorsum of first abdominal segment yellow to near white; prothorax with 5 pairs of prominent senti, mesothorax and metathorax with 4 pairs of senti; pinacula of dorsal senti on abdominal segments 1-5 separated, contiguous on segments 6-8; all senti deep brown to near black except the yellow to near white dorsal and supraspiracular senti on the first abdominal segment; all abdominal segments with 3 pairs of senti except the eighth where lateral senti are wanting; 7 pairs of conspicuous, circular openings to glands are found in the coriae between abdominal segments 1-8; less conspicuous circular spiracles occur on the mesothorax and abdominal segments 1-8 cephaloventrad of the supraspiracular senti. Feeds on scale insects, especially soft bodied scales and immatures. (From Peterson, 1951)

Figure 34.572. Coccinellidae. *Coccinella transversoguttata* Faldermann. (Coccinellini) Transverse lady beetle, an aphid predator. Length = 11 mm. Fusiform with ground color bluish-gray, all processes on abdominal segments black except for lateral and dorsolateral ones on abdominal segments 1 and 4; basal portion of head black, labrum and frons cream to white; epicranial suture lyre-shaped; medial plates on prothorax separated by narrow yellowish stripe, sclerotized plates on both meso- and metathorax well-separated; dorsal and dorsolateral aspects of abdominal segments 1-8 each provided with parascoli or strumae, ventral aspect with verrucae or chalazae; legs well-developed, robust, and black; basal portion of claw with a distinct rectangular tooth. Ottawa, Ontario, 20-VIII-1980, on potatoes, L. LeSage.

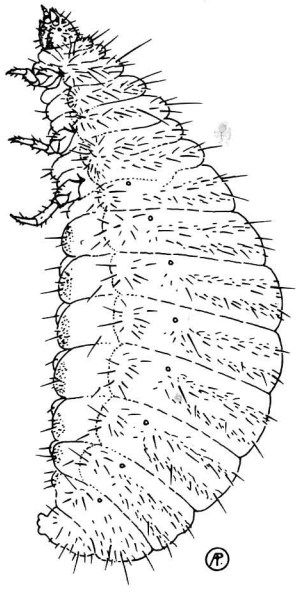
Figure 34.573. Coccinellidae. *Scymnus hemorrhous* LeConte, a predator. (Scymnini) Length = 3 mm. Shape fusiform; head, body and legs yellowish; epicranial suture absent; prothorax transverse, ovoid, with a row of marginal setae; meso- and metathorax each with a pair of dorsal sclerotized tubercles and 2 pairs of lateral and moderately developed tubercles; abdominal segments 1-8 each with 3 pairs of weakly developed tubercles, each bearing a large seta and a few small setae; legs relatively short and rather stout. Baton Rouge, Louisiana, 15-VIII-1952, (reared), O.L.C.



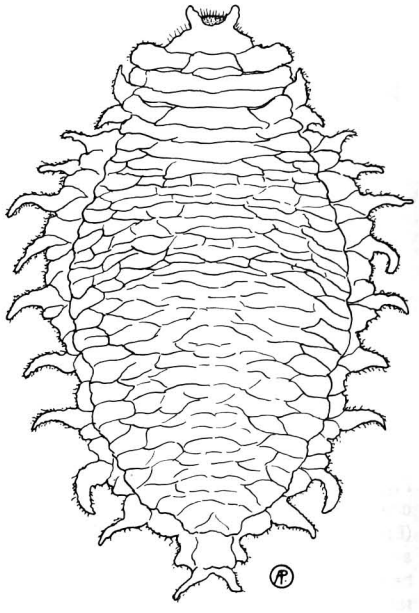
Rodolia
Figure 34.574



Microwesia
Figure 34.575



Hyperaspis
Figure 34.576

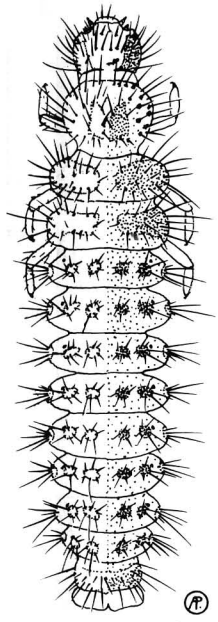


Hyperaspis
Figure 34.577

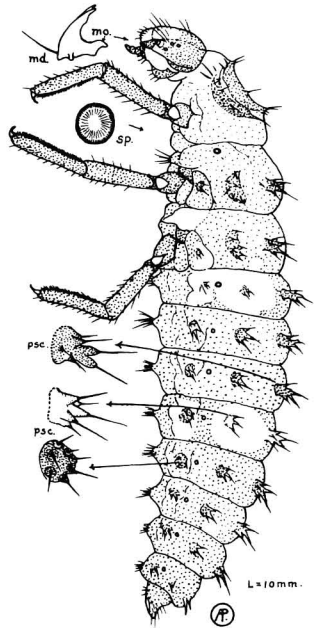
Figure 34.574. Coccinellidae. *Rodolia cardinalis* (Mulsant). (Noviini) Vedalia lady beetle, a predator on the cottony-cushion scale, *Icerya purchasi* Raaskell. Length = 7 mm. Shape elliptical and weakly convex above; dorsum dark red with brown sclerotized plates and tubercles; head black, subquadrate; epicranial suture V-shaped; maxillary palpi 2-segmented; each thoracic segment with a pair of sclerotized plates, meso- and metathorax each bearing 2 additional pairs of soft lateral projections; abdominal segments 1-8 each with 2 pairs of dorsal plates and 1 pair of soft lateral projections bearing 2 long setae. Los Angeles, California, July 1892, D. V. Coquillet.

Figure 34.575. Coccinellidae. *Microweisea* sp. (Stilochotini) Length = 3 mm. Shape fusiform, yellowish throughout except the dark brown head; head elongate with a V-shaped epicranial suture; prothorax trapezoidal, meso- and metathorax transverse; lateral margin of each thoracic segment with a fringe of inconspicuous fine setae; legs well-developed; tibiotarsi with a pair of large flattened setae at the apex; abdominal segments 1-8 similar, but becoming successively smaller, bearing a few inconspicuous small setae. New Orleans, Louisiana, 13-VII-1923, Quaintance.

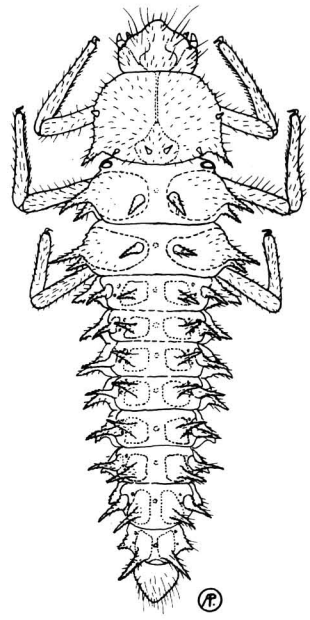
Figures 34.576, 34.577. Coccinellidae. *Hyperaspis signata* Olivier. (Hyperaspini) Length = 5 mm. Cyphosomatic, greatest width near mid-abdominal region and entire dorsal aspect covered with a near white, cottony, wax covering; body cream to greenish color (may be pinkish in preserved specimens), head mottled brown and legs brown especially the 2 distal segments; numerous short, brown setae scattered over lateral and dorsal aspects of all segments and also on the head, only a few setae on venter of abdomen; legs small, well developed but not projecting beyond sides of body; caudal segment with an eversible sucking disk; inconspicuous circular spiracles on lateral aspects dorsad of lateral ridge. Larvae feed on mealybugs, and soft scales, especially immatures. (From Peterson, 1951).



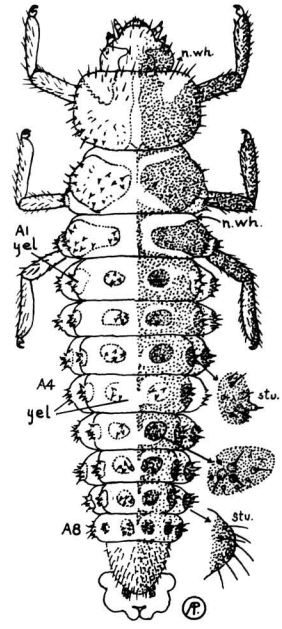
Stethorus
Figure 34.578



Hippodamia
Figure 34.579



Anatis
Figure 34.580



Adalia
Figure 34.581

Figures 34.578, and 34.623. Coccinellidae. *Stethorus punctum* LeConte. (Stethorini) Length = 2.5-3 mm. Somewhat fusiform with greatest diameter in metathorax and first abdominal segments; light gray to light brown with brown to gray verrucae and brown to gray areas on thorax and head; head light brown laterally and mottled on frons; solid brown to mottled brown pigment areas laterad of the meson on all thoracic segments; 6 verrucae on the dorsal and lateral aspects of abdominal segments 1-8; numerous, light colored, elongate setae on the head, dorsum of thorax, on all verrucae and venter of the abdomen; well developed legs possess a few setae and are partially pigmented; spiracles circular and located ventrad of supraspiracular verrucae. Feeds on plant-infesting mites, common on apple. (From Peterson, 1951)

Figure 34.579. Coccinellidae. *Hippodamia convergens* Guérin-Méneville, convergent lady beetle. (Coccinellini) Length = 10-11 mm. Somewhat fusiform, subcylindrical with greatest diameter in region of metathorax; dark brown to black with a bluish cast, light areas ranging from orange, to yellow to near-white; prothorax oval, wider than long and with 4 longitudinal dark areas with light yellow areas between, cephalad, and caudad of dark areas. Chalazae on the cephalic and lateral portions and on the pigmented areas; parascoli on caudolateral margin of metathorax cream colored; each abdominal segment 1-8 with 3 pairs of parascoli, subdorsal, supraspiracular and subspiracular, all deeply pigmented except the supraspiracular and subspiracular on the first and fourth abdominal segments and the subdorsal on the fourth segment; the light colored parascoli and the areas about them plus the areas between the subdorsal and supraspiracular parascoli on the 6th and 7th segments are yellow to deep orange; sterna on segments 2-8 with transverse rows of 6 verrucae; legs well developed, elongate and tarsal claws without appendiculate teeth. Feeds on aphids and soft bodied insects. (From Peterson, 1951)

Figure 34.580. Coccinellidae. *Anatis quindecimpunctata* Olivier. (Coccinellini) Length = 17-18 mm. Elongate, widest at metathorax and tapering toward both ends; color on dorsal half a deep brown except for light spots and median line, ventral half near white to yellow; head one-half diameter of prothorax, flattened, light on frontal area and dark on caudolateral portions; prothorax with parascoli on caudolateral margin and a light spot on the caudomeson bearing 2 chalazae; mesothorax and metathorax bearing 2 pairs of senti and 1 extreme, lateral pair of parascoli; abdominal segments 1-8 with 2 pairs of senti dorsad of the spiracles and 1 pair of senti or parascoli immediately ventrad of spiracles; thoracic sterna similar, each bearing a pair of verrucae adjacent to the meson; thoracic legs long, slender, nearly 1.5 times as long as the metathorax is wide. Feeds chiefly on aphids. (From Peterson, 1951)

Figure 34.581. Coccinellidae. *Adalia bipunctata* (L.), two-spotted lady beetle. (Coccinellini) Length = 9 ± mm. Fusiform with greatest width in region of 2nd to 4th abdominal segments; dark brown to bluish-gray, mottled with yellow to cream spots, dorsal half of head deeply pigmented and ventral portion of frons and clypeus cream to white; prothorax with a medium yellow stripe and 2 cephalolateral yellow areas; each abdominal segment 1-8 with 2 pairs of strumae dorsad of the spiracles and 1 pair ventrad; each struma may have 3-8 chalazae and additional setae; 2 of the lateral strumae on first abdominal segment cream to yellow, and on the fourth abdominal segment the most lateral strumae and the pair adjacent to the meson are light colored or yellow; ninth segment deeply pigmented, setiferous and giving rise to a large, eversible, fleshy protuberance. Feeds chiefly on aphids. (From Peterson, 1951)

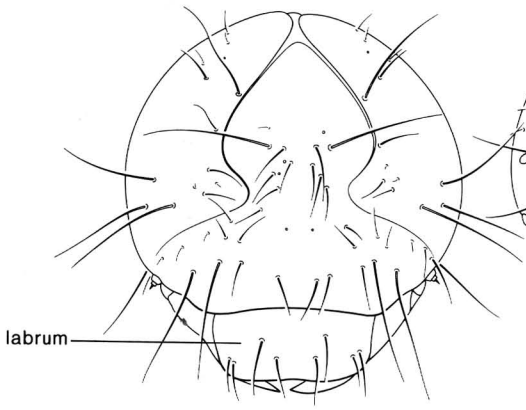
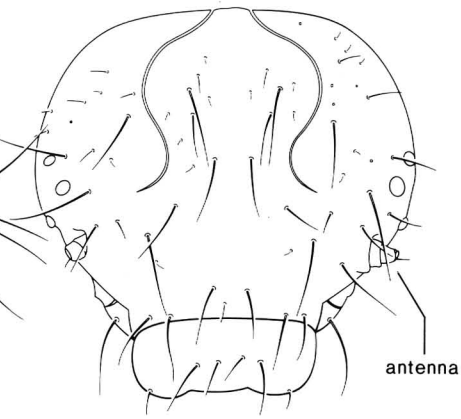


Figure 34.582



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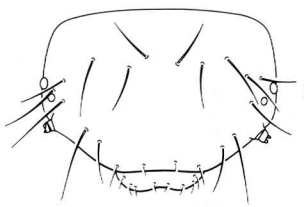

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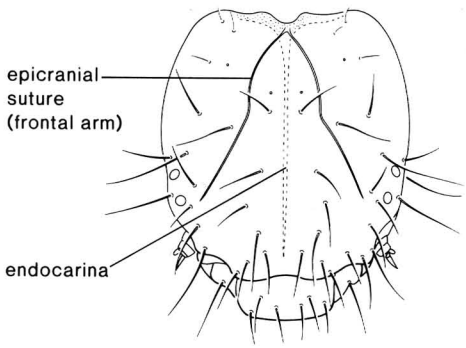
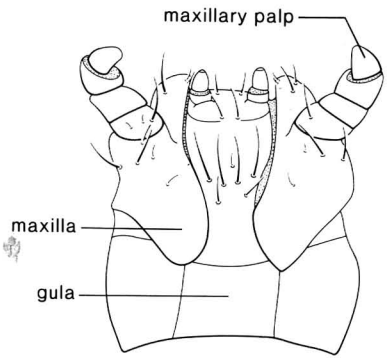


Figure 34.585



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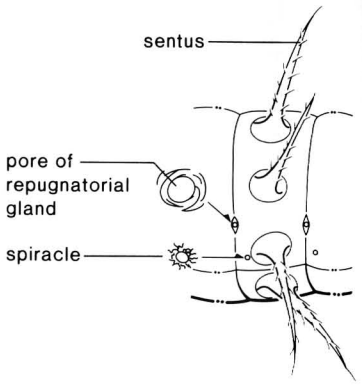

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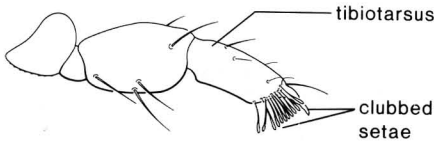


Figure 34.588

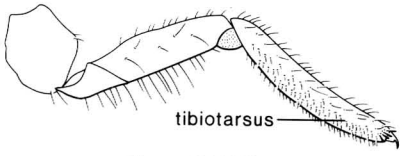
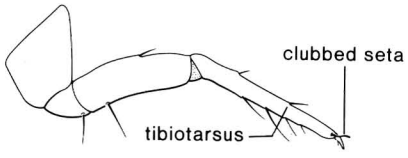


Figure 34.589



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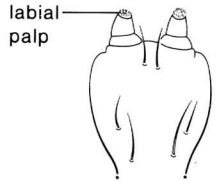


Figure 34.591

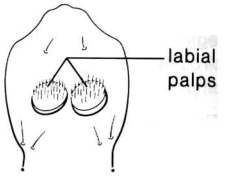


Figure 34.592

Figures 34.582–34.592. Coccinellidae. Structures of larvae.

Figure 34.582. *Chilochorus cacti* (L.), head capsule, dorsal. (Chilocorini)

Figure 34.583. *Coccinella transversoguttata* Faldermann, head capsule, dorsal. (Coccinellini)

Figure 34.584. *Scymnus creperus* Mulsant, head capsule, dorsal. (Scymnini)

Figure 34.585. *Microweisea* sp., head capsule, dorsal. (Sticholotini)

Figure 34.586. *Hippodamia tredecimpunctata* (L.), head capsule, ventral. (Coccinellini)

Figure 34.587. *Chilochorus cacti* (L.), third abdominal segment, lateral. (Chilochorini)

Figure 34.588. *Stethorus histrio* Chazeau, foreleg. (Stethorini)

Figure 34.589. *Coccinella transversoguttata* Faldermann, foreleg. (Coccinellini)

Figure 34.590. *Delphastus sonoricus* Casey, foreleg. (Serangiini)

Figure 34.591. *Scymnus collaris* Melsheimer, labium. (Scymnini)

Figure 34.592. *Hyperaspis binotata* Say, labium. (Hyperaspini)

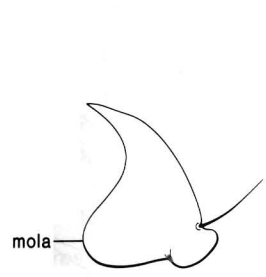


Figure 34.593

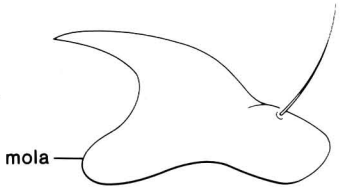
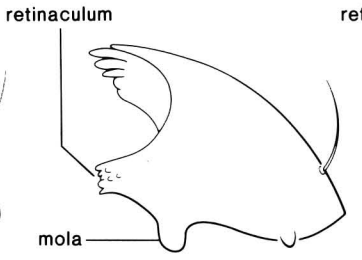


Figure 34.594



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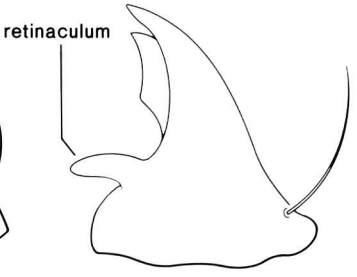
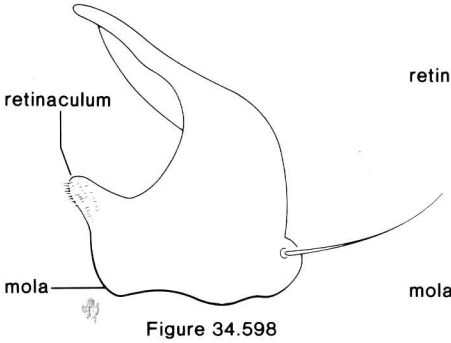


Figure 34.596

Figure 34.597



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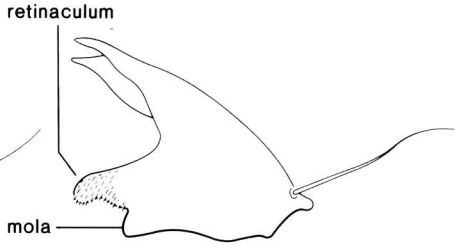

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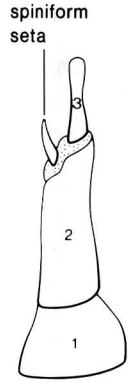

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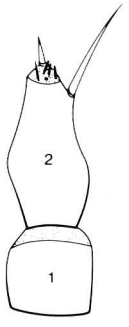

Figure 34.601

Figure 34.602

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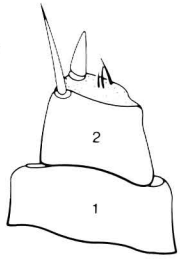
Figure 34.605



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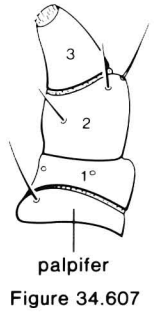

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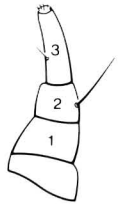


Figure 34.608

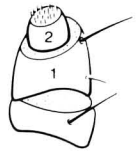


Figure 34.609

Figures 34.593–34.609. Coccinellidae. Structures of larvae.

Figure 34.593. *Microweisea,* mandible. (Stilochotini)

Figure 34.594. *Scymnus creperus* Mulsant, mandible. (Scymnini)

Figure 34.595. *Psyllobora* sp., mandible. (Psylloborini)

Figure 34.596. *Lindorus lophantae* Blaisdell, mandible. (Coccidulini)

Figure 34.597. *Epilachna varivestis* Mulsant, mandible. (Epilachnini)

Figure 34.598. *Hyperaspis binotata* Say, mandible. (Hyperaspini)

Figure 34.599. *Coccinella* sp., mandible (Coccinellini)

Figure 34.600. *Zagobla ornata* (Horn), antenna (Scymnillini)

Figure 34.601. *Epilachna varivestis* Mulsant, antenna. (Epilachnini)

Figure 34.602. *Lindorus lophantae* Mulsant, antenna. (Coccidulini)

Figure 34.603. *Scymnus creperus* Mulsant, antenna. (Scymnini)

Figure 34.604. *Chilochorus cacti* (L.), antenna. (Chilochorini)

Figure 34.605. *Rodolia cardinalis* (Mulsant), antenna. (Noviini)

Figure 34.606. *Coccinella transversoguttata* Faldermann, antenna. (Coccinellini)

Figure 34.607. *Coccinella transversoguttata* Faldermann, maxillary palp. (Coccinellini)

Figure 34.608. *Microweisea* sp., maxillary palp. (Stilochotini)

Figure 34.609. *Rodolia cardinalis* (Mulsant), maxillary palp. (Noviini)

seta

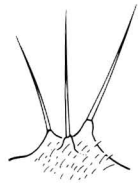
Figure 34.610

chalaza

Figure 34.611

tubercle

Figure 34.612



struma

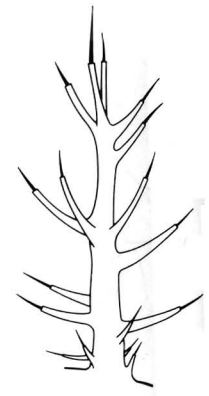
Figure 34.613

parascolus

Figure 34.614

sentus

Figure 34.615



scolus

Figure 34.616

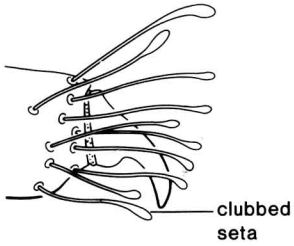


Figure 34.617

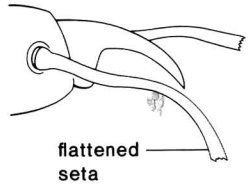


Figure 34.618

Figure 34.619

Figure 34.620

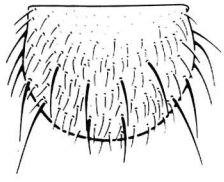


Figure 34.621

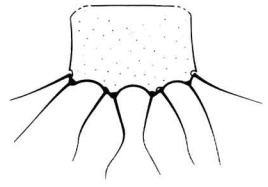


Figure 34.622

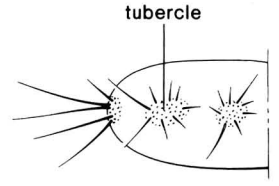


Figure 34.623

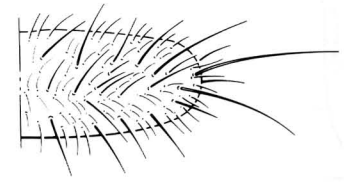


Figure 34.624

Figures 34.610–34.624. Coccinellidae. Structures of larvae.

Figure 34.610. *Hippodamia tredecimpunctata* (L.), seta. (Coccinellini)

Figure 34.611. *Hippodamia tredecimpunctata* (L.), chalaza. (Coccinellini)

Figure 34.612. *Microweisea* sp., verruca. (Stilochotini)

Figure 34.613. *Coleomegilla maculata* (De Geer), struma. (Coccinellini)

Figure 34.614. *Coccinella transversoguttata* Faldermann, parascolus. (Coccinellini)

Figure 34.615. *Chilochorus cacti* (L.), sentus. (Chilorchorini)

Figure 34.616. *Epilachna varivestis* Mulsant, scolus. (Epilachnini)

Figure 34.617. *Rodolia cardinalis* (Mulsant), apex of tibiotarsus. (Noviini)

Figure 34.618. *Microweisea* sp., apex of tibiotarsus. (Stilochotini)

Figure 34.619. *Coccinella transversoguttata* Faldermann, apex of tibiotarsus. (Coccinellini)

Figure 34.620. *Coleomegilla maculata* (De Geer), apex of tibiotarsus. (Coccinellini)

Figure 34.621. *Coleomegilla maculata* (De Geer), ninth abdominal tergite. (Coccinellini)

Figure 34.622. *Lindorus lophantae* Mulsant, ninth abdominal tergite. (Coccidulini)

Figure 34.623. *Stethorus punctum* (LeConte), third abdominal tergite, left half. (Stethorini)

Figure 34.624. *Delphastus sonoricus* (LeConte), third abdominal tergite, right half. (Serangiini)

CORYLOPHIDAE (CUCUJOIDEA)

(= ORTHOPERIDAE)

John F. Lawrence,
Division of Entomology, CSIRO

Minute Fungus Beetles

Figures 34.625-629

Relationships and Diagnosis: Corylophidae is a family whose relationships are somewhat obscured by the structural modifications accompanying small size. The group has been included in the "cerylonid" series (Crowson, 1955) and is usually placed near the Coccinellidae, but there are some larval features resembling Lathridiidae, and the lathridiid genus *Hyplathrinus* is actually a corylophid (Pakaluk, 1985). Larvae are highly variable, some being broadly ovate and strongly flattened like those of *Murmidius* (Cerylonidae), *Agaricophilus* (Endomychidae), and Discolomidae, and others more elongate and resembling some Lathridiidae, Endomychidae, and Coccinellidae. All corylophid larvae may be distinguished by the presence of paired dorsal or dorsolateral gland openings on abdominal segments 1–7, 1 and 8, or 2 and 8.

Biology and Ecology: Corylophids are primarily spore feeders in both larval and adult stages, and they are usually collected in leaf litter, refuse heaps, or on surfaces covered with sporulating fungi of various kinds. Species of *Sericoderus* and *Orthoperus* are often associated with molds. Hinton (1945b) reared *S. lateralis* (Gyllenhal) in the laboratory on spores of *Mucor mucedo* (Zygomycetes: Mucorales) and conidia of *Penicillium glaucum* (Ascomycetes: Eurotiales), and the same species has been associated with *Penicillium* occurring in vegetable detritus (Peyerimhoff, 1919, 1921). *Orthoperus scutellaris* LeConte has been collected on *Pencillium,* and Chandler (1983) found the species in decaying seaweed feeding on *Alternaria* and *Helminthosporium* conidial types; other *Orthoperus* have been found in lawn clippings and in sorghum heads. *Corylophodes marginicollis* LeConte was found breeding beneath the leaves of European horse chestnut on a powdery mildew, *Uncinula flexuosa* (Ascomycetes: Erysiphales) (Morrill, 1903). *Arthrolips obscurus* (Sahlberg) was found by Peyerimhoff (1919) feeding on spores falling out of the pore tubes of *Fomes fomentarius* (Basidiomycetes: Polyporaceae) and being caught on the viscous filaments produced by the mycetophilid fly, *Ceroplatus tipuloides* Bosc. *Arthrolips aequalis* Wollaston was reported feeding on the stromata of *Nummulariola bulliardii* (Ascomycetes: Xylariaceae), and various other corylophids have been observed on xylariaceous fruiting bodies. Paulian (1950) noted the occurrence of certain African species in the infloresences of *Lobelia* and *Senecio* and others associated with scale insects (*Chionaspis* and *Lecanium*). *Foadia maculata* Pakaluk has been collected under the bark of mangroves in the Florida Keys (Pakaluk, 1985). Other corylophids have been collected in rotten reeds (*Rypobius* and *Corylophus*), tussock grass (*Holopsis*), and tree ferns (*Holopsis*) (Endrödy-Younga, 1964; Horion, 1949). Pupae of Corylophidae are obtect and are attached to the substrate, enclosed basally by the larval exuvia, as in most Coccinellidae (Hinton, 1941b; Morrill, 1903).

Description: Mature larvae 1 to 3 mm. Body elongate, somewhat fusiform and slightly flattened, or broadly ovate and strongly flattened. Dorsal surfaces usually lightly pigmented, except for head and maculae on protergum and abdominal tergum 9, sometimes entirely pigmented or maculate, smooth to granulate, with vestiture of fine simple setae, usually mixed with various types of expanded setae or scales.

Head: Protracted and prognathous, but sometimes concealed from above by prothorax, elongate to strongly transverse, slightly to strongly flattened. Epicranial stem absent; frontal arms, if present, V-shaped and distant at base. Median endocarina absent. Paired, subparallel endocarinae sometimes present. Stemmata absent or 2 on each side. Antennae moderately to very long, 2- or 3-segmented, sometimes with very long 2nd segment. Frontoclypeal suture absent; labrum free or occasionally completely fused to head capsule. Mandibles symmetrical, usually broad at base and narrow at apex, bidentate or tridentate, without accessory ventral process and with tuberculate or asperate mola and prostheca absent or consisting of 2 hyaline processes; mandibles occasionally narrow and falcate, endognathous. Ventral mouthparts usually protracted. Maxilla with cardo, stipes, and articulating area usually indistinctly separated; mala obtuse or falciform; maxillary palp 2- or 3-segmented, with apical segment much longer than penultimate. Labium usually consisting of single plate; labial palps 2-segmented with apical segment much longer than basal, or occasionally 1-segmented. Hypopharyngeal area often with complex internal skeleton. Hypostomal rods usually absent, sometimes long and diverging. Ventral epicranial ridges absent. Gula sometimes longer than wide; gular sutures usually well-marked by parallel internal ridges.

Thorax and Abdomen: Legs well-developed, 5-segmented, moderately widely separated; tarsungulus with 1 seta, usually clavate. Thoracic and abdominal terga sometimes broadly expanded at edges forming contiguous flat plates, so that body has a disc-like form. Paired dorsal gland openings present on abdominal terga 1 and 8, or sometimes 2 and 8 or 1–7. Tergum A9 simple, without urogomphi, sometimes with pigmented plate or macula; sternum A9 short, simple. Segment A10 circular, ventrally oriented.

Spiracles: Annular, those on abdomen dorsally placed.

Comments: The family includes about 35 genera and 400 species worldwide, with 12 genera and about 60 species occurring in America north of Mexico. The subfamilial, tribal, and generic concepts are badly in need of revision. On the basis of larval characters, Böving and Craighead (1931) divided the group into Arthrolipinae (*Arthrolips* and *Orthoperus*) with gland openings on segments A1–7, and Corylophinae (*Corylophodes, Molamba, Sacium,* and *Sericoderus*) with openings on A1 and A8 only. This is in conflict with the adult classification proposed by Matthews (1899) and Casey (1900) and modified by Paulian (1950), where *Arthrolips* falls into the same group as *Sacium* and *Molamba.*

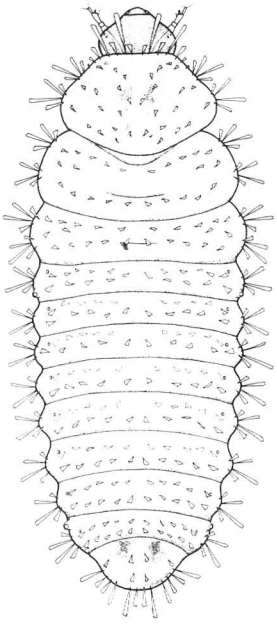


Figure 34.625

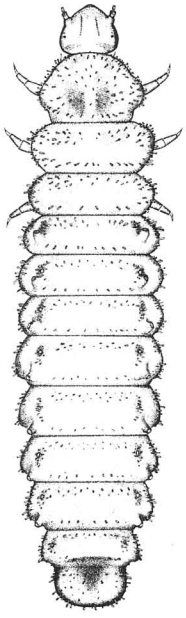
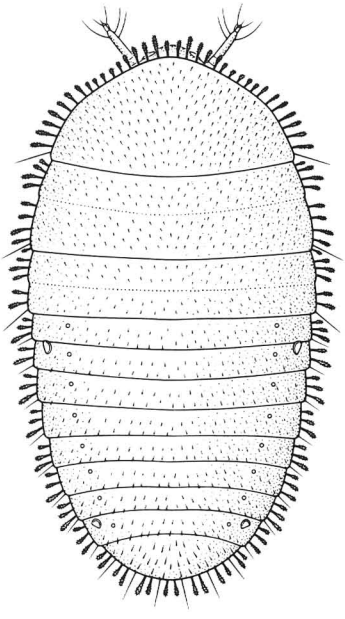


Figure 34.626



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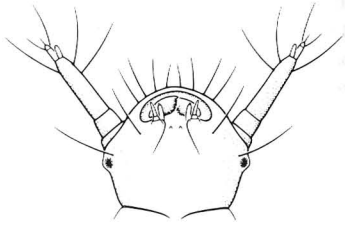

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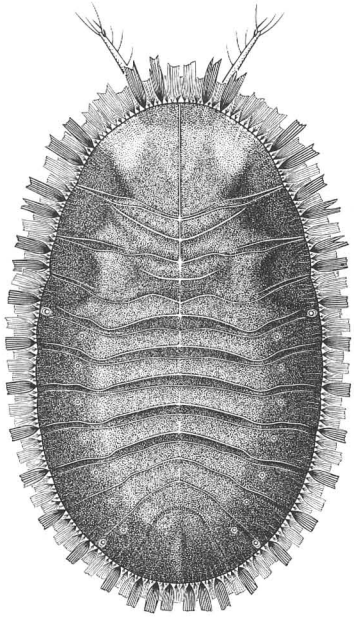
Figure 34.627



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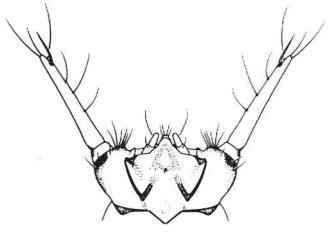

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Figure 34.628

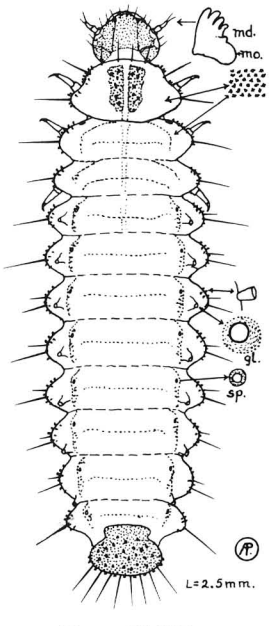

Figure 34.629

Figure 34.625. Corylophidae. *Sericoderus lateralis* (Gyllenhal). Bedford, Middlesex Co., Massachusetts. Larva, dorsal. Length = 1.7 mm.

Figure 34.626. Corylophidae. *Arthrolips* sp. Ysleta, Texas. Larva, dorsal. Length = 2.3 mm.

Figures 34.627a,b. Corylophidae. *Corylophodes* sp. Mt. Gingera, Australian Capital Territory. **a.** larva, dorsal, length = 1.2 mm; **b.** head, ventral.

Figures 34.628a,b. Corylophidae. Genus? Lamington National Park, Queensland. **a.** larva, dorsal, length = 1.9 mm; **b.** head, ventral.

Figure 34.629. Corylophidae. *Arthrolips* sp. Larva, dorsal (plus details). Length = 2.5 mm. (From Peterson, 1951)

It is possible, however, that Böving's illustrations of *Molamba lunata* LeConte and *Sacium* sp. were based on misidentifications, since there is no information available on how the determinations were made. Paulian recognized 4 subfamilies: Peltinoidinae (*Peltinoides* from North Africa), Corylophinae (including Peltinini, Orthoperini, Corylophodini, Corylophini, and Rypobiini), Sericoderinae and Saciinae (including *Arthrolips*); Casey's Aenigmaticini (Phanerocephalina of Matthews, 1899) was included in Orthoperini. A more thorough study of corylophid larvae and the discovery of the larval forms of critical genera, such as *Rypobius* and *Corylophus* would greatly help in understanding this difficult group.

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Casey 1900.
Chandler 1983 (larva of *Orthoperus scutellaris*).
Crowson 1955.
Endrödy-Younga 1964.
Gressitt and Samuelson 1964a (larvae of *Holopsis oblongus* Endrödy-Younga).
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Pakaluk 1985.
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Peyerimhoff 1919 (habits of *S. lateralis*), 1921 (larva of *S. lateralis*).

LATHRIDIIDAE (CUCUJOIDEA)

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Minute Brown Scavenger Beetles

Figures 34.630-631

Relationships and Diagnosis: The Lathridiidae, as defined by Belon (1909) and Arnett (1968), contains several genera which belong to other families. These include *Dasycerus* (considered to be a staphylinoid family Dasyceridae by Crowson, 1955), *Merophysia, Holoparamecus,* and their allies (placed in Merophysiidae by Crowson, 1955, but here considered as part of the family Endomychidae), and *Hyplathrinus,* which is closely related to the corylophid genus *Aenigmaticum* on the basis of both larval and adult characters. Lathridiid larvae are usually distinguished by their small size, 4 stemmata or fewer on each side of the head, truncate or rounded maxillary mala, tuberculate mandibular mola with a broad, hyaline prostheca, reduced mandibular apex which is partly or entirely unsclerotized, moderately to strongly protracted mouthparts, with hypostomal rods more laterally placed than is usual, single tarsungular seta, annular spiracles, and lack of urogomphi or sclerotized abdominal tergites.

Biology and Ecology: Lathridiids are often found in leaf litter, decaying vegetation, animal nests, or human habitations, or on the surfaces of leaves, bark, or wood, where they feed on the spores of a variety of fungi. Spores of Myxomycetes are fed upon by *Revelieria californica* Fall and by several species of *Enicmus* in N. America, Europe, Australia, and New Zealand (Andrews, 1976a; Crowson and Hunter, 1964; Dajoz, 1960; Lawrence and Newton, 1980; Russell, 1979). Most lathridiids feed on spores or conidia of Zygomycetes (Mucorales) and Ascomycetes (Eurotiales, Erysiphales, Pyrenomycetes, and their imperfect stages). Species of *Metophthalmus, Lithostygnus, Adistemia, Cartodere, Dienerella,* and *Corticaria* have been reared on various "molds", including *Mucor, Aspergillus, Penicillium,* and *Botrytis* (Andrews, 1976b; Hammad, 1953; Hinton, 1941c, 1945b; Kerr and McLean, 1956; Klippel, 1952). *Enicmus maculatus* LeConte was reared on *Nodulisporium* type conidia produced by a pyrenomycete fungus (*Hypoxylon*) (Lawrence, 1977a), while 2 European *Enicmus* were recorded from *Nummulariola bulliardii* (Dajoz, 1966). Chandler (1983) collected large numbers of *Corticaria valida* Fall in rotting seaweed and found conidia of the *Helminthosporium* and *Alternaria* types in their guts. Several *Corticaria* and *Melanophthalma* may be collected by sweeping leaves and other vegetation, where they are probably feeding on mildews. Gordon (1938) recorded *Dienerella filum* (Aube) from herbarium specimens of smuts (*Ustilago* and *Tilletia*) and puffballs (*Lycoperdon*), while a Californian species of *Corticaria* is known to breed in the spore masses produced by a polypore (*Cryptoporus volvatus*). Many of the mold-feeding lathridiids are commonly found in cellars, warehouses, and granaries, either on moldy walls or in stored grains or other foods; these stored products species include *Aridius nodifer* (Westwood), *Lathridius minutus* (Linnaeus), *Cartodere constricta* (Gyllenhal), *Dienerella argus* (Reitter), *Corticaria pubescens* (Gyllenhal) and *Migneauxia orientalis* Reitter (Aitken, 1975; Hinton, 1941c, 1945b; Klippel, 1952). One species of lathridiid, *Eufallia seminivea* Motschulsky, has been reported biting humans in Florida; these bites apparently produced red, itching lesions (Parsons, 1969a).

Description: Mature larvae 1 to 3 mm. Body elongate and fusiform or elongate-oval and slightly flattened. Dorsal surfaces usually very lightly pigmented, sometimes with darker head and protergal macula, smooth, with vestiture of scattered long setae, occasionally mixed with expanded or frayed hairs.

Head: Protracted and prognathous, usually more heavily sclerotized dorsally than ventrally, slightly flattened. Epicranial stem usually short to moderately long; frontal arms usually V-shaped; epicranial suture sometimes absent. Median endocarina absent. Stemmata 1 to 5 on each side (usually 3 or 4), sometimes absent. Antenna well-developed, often long, 3-segmented, usually with 2nd segment much longer than 1st or 3rd. Frontoclypeal suture absent; labrum free. Mandibles symmetrical, usually with 1 to 4 teeth at apex, sometimes with apical portion rounded and hyaline, without accessory ventral process, and sometimes with 2 long setae arising from outer edge; mola well-developed and tuberculate or asperate;

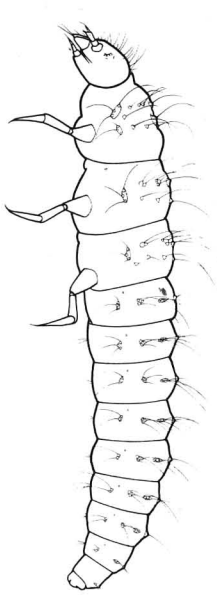
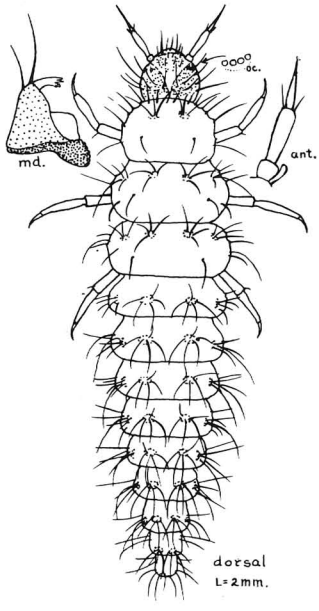


Figure 34.630



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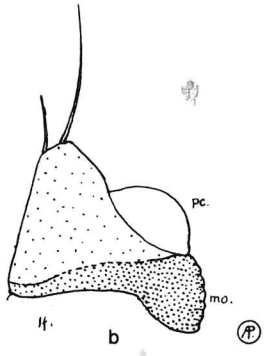

b

Figure 34.631

Figure 34.630. Lathridiidae. *Lathridius minutus* (L.). Lake of the Clouds, Mt. Washington, New Hampshire. Larva, lateral. Length = 3.3 mm.

Figures 34.631a,b. Lathridiidae. *Cartodere* sp. Poland. **a.** larva, lateral, length = 2 mm; **b.** left mandible, dorsal. (From Peterson, 1951)

prostheca consisting of a broad, rounded or acute, fixed hyaline process. Ventral mouthparts retracted or strongly protracted. Maxilla with cardo present or absent, stipes elongate or broader than long, articulating area present or absent, palp 3-segmented, and mala usually obtuse, sometimes falciform, and occasionally cleft at apex. Labium usually with mentum and submentum fused, sometimes consisting of a single plate only; ligula present or absent; labial palps 1- or 2-segmented and widely separated. Hypopharyngeal sclerome a transverse bar. Hypostomal rods usually long and diverging, sometimes absent. Ventral epicranial ridges absent. Gula sometimes elongate.

Thorax and Abdomen: Legs well-developed, 5-segmented; tarsungulus with 1 seta. Tergum A9 without urogomphi; sternum A9 well-developed. Segment A10 circular and posteriorly or terminally oriented.

Spiracles: Annular, not raised on tubes.

Comments: The family includes about 25 genera and 500 species worldwide, and appears to be most diverse in the northern and southern temperate regions; in America north of Mexico, there are 15 genera and about 120 species. There are 2 well-defined subfamilies—Lathridiinae and Corticarinae, but the generic concepts have been relatively unstable, and several well-known genera and species have undergone recent name changes (Walkley, 1952; Pope, 1977). Widespread human introduction into new territory has added to the taxonomic confusion in the group.

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Belon 1909 (genera).
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Chandler 1983 (larva of *Corticaria valida* LeConte).
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Crowson and Hunter 1964.
Dajoz 1960 (association with Myxomycetes), 1966 (association with Ascomycetes).
van Emden 1942b (larval mandible of *Aridius nodifer*).
Gordon 1938 (feeding habits of *Dienerella filum*).
Hammad 1953 (larva of *Lithostygnus serripennis* Broun).
Hinton 1941c (stored products species; larval key; larvae and pupae of *Aridius nodifer, Lathridius minutus, Adistemia watsoni* (Wollaston), *Dienerella filum, D. filiformis* (Gyllenhal), and *Corticaria fulva* (Comolli)), 1945b (stored products species; larvae as in 1941c).
Kerr and McLean 1956 (biology, control).
Klippel 1952 (association with molds; larvae of *Aridius nodifer* and *Corticaria fulva*).
Lawrence 1977a (association with Ascomycetes).
Lawrence and Newton 1980 (association with Myxomycetes).
Lefkovitch 1960 (*Adistemia watsoni* in bird nest).
Parsons 1969a (*Eufallia seminivea* biting humans).
Peterson 1951 (larvae of *Dienerella?* sp., as *Cartodere* sp.).
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Russell 1979 (association with Myxomycetes).
Saalas 1923 (biology of various species; larvae).
Verhoeff 1923 (larva of *Lathridius minutus*).
Walkley 1952 (generic concepts).

MYCETOPHAGIDAE (TENEBRIONOIDEA)

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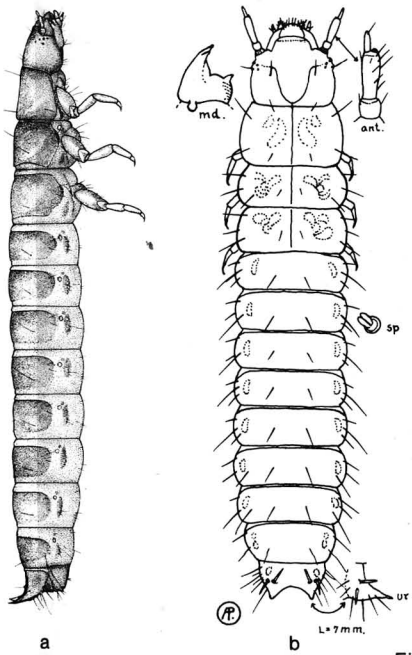
Hairy Fungus Beetles

Figures 34.632-633

Relationships and Diagnosis: The Mycetophagidae is one of the more primitive tenebrionoid families whose affinities appear to be with the Tetratomidae and Archeocrypticidae (Crowson, 1964c, 1966b; Lawrence and Newton, 1982; Miyatake, 1960; Watt, 1974b). Larvae of *Penthe* and the Tetratominae differ from those of mycetophagids in lacking a mandibular mola (replaced by membranous lobe or group of hyaline processes), while larvae of the pisenine tetratomids



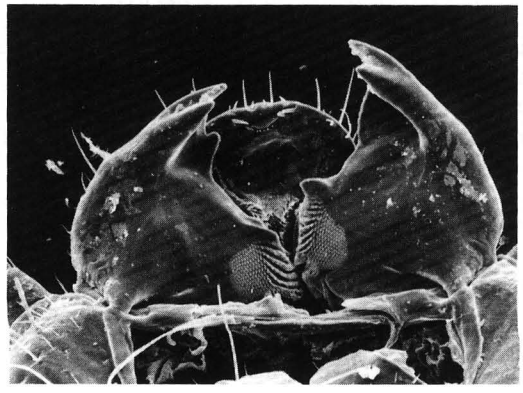


Figure 34.632

Figures 34.632a-c. Mycetophagidae. *Mycetophagus punctatus* Say. Tyringham, Massachusetts. **a.** larva, lateral, length = 8.6 mm; **b.** larva, dorsal (plus details); **c.** anterior part of head capsule, with ventral mouthparts removed, showing asymmetrical mandibles. (Figure 34.632b from Peterson, 1951)

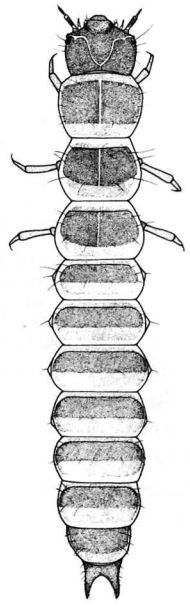


Figure 34.633

Figure 34.633. Mycetophagidae. *Litargus sexpunctatus* (Say). Savannah, Georgia. Larva, dorsal. Length = 4.7 mm.

have accessory processes on the urogomphi, a more ventrally-oriented, pygopod-like anal region, and longer accessory spiracular openings. The transverse and posteriorly oriented anal region of mycetophagids is also found in Archeocrypticidae and most members of the anthicid-scraptiid complex; the former group differs in having a distinct frontoclypeal suture and characteristic urogomphi, which are straight, posteriorly oriented, and lightly pigmented, while the latter usually have reduced mandibular molae, a dome-like antennal sensorium, or a median endocarina.

Biology and Ecology: Almost all mycetophagids are mycophagous, feeding on the softer and often rotting tissue of various hymenomycete fruiting bodies or the spores and sterile tissue of molds and xylariaceous Ascomycetes. Species of *Triphyllus, Mycetophagus, Pseudotriphyllus,* and *Litargus* has been recorded from a variety of Hymenomycetes, including *Pleurotus ostreatus* (Tricholomataceae), *Fistulina hepatica* (Fistulinaceae), *Climacodon septentrionale* (Hydnaceae), *Polyporus squamosus, Piptoporus betulinus, Laetiporus sulphureus, Bjerkandera adusta, Daedaleopsis confragosa,* and *Fomes fomentarius* (Polyporaceae) (Crowson, 1960a; Donisthorpe, 1935; Matthewman and Pielou, 1971; Palm, 1959; Weiss and West, 1920). The European *Mycetophagus atomarius* Fabricius, at least 1 *Esarcus,* and a number of species of *Litargus* appear to prefer the fruiting bodies of Xylariaceae, such as *Hypoxylon, Daldinia,* or *Trichoderma* (conidial stage) (Crowson, 1960a; Dajoz, 1964; Hingley, 1971; Lawrence, 1977a; Palm, 1959). A number of mycetophagids are associated with molds, and may occur in hay stacks, decaying vegetation, or moldy fruits, grains, and cereal products in granaries, warehouses, or domestic premises. The most commonly encountered stored products species are *Litargus balteatus* LeConte, *Mycetophagus quadriguttatus* Müller, and *Typhaea stercorea* (Linnaeus) (Aitken, 1975; Crowson, 1960a; Hinton, 1945b).

Members of the genus *Berginus* have different habits from most of the family. *Berginus tamarisci* Wollaston has been collected in flowers of tamarisk (Tamaricaceae), is known to breed in the male cones of *Pinus maritimus,* and has been found feeding on pollen and stamens of pharmaceutical cactus flowers (*Cereus grandifloreus*) imported into Germany (Hinton, 1945b; Horion, 1961; Perris, 1862). *Berginus californicus* Pierce has been recorded from flowers of a dodder (*Cuscuta*) in California (Pierce, 1939), while *B. maindroni* Grouvelle is known to be a predator of the lac scale (*Tachardia*) in India (Imms and Chatterjee, 1915). Another unusual habit is found in a Chilean species presently placed in the genus *Mycetophagus* (*M. chilensis* Philippi); specimens from Juan Fernandez Island were collected on ferns, and fern spores were found in the gut.

Description: Mature larvae 1.5 to 8 mm. Body elongate, more or less parallel-sided, straight, slightly flattened. Head and all visible terga usually pigmented, brown or yellow in color; pleural areas sometimes with distinct sclerotized plates as well; surfaces smooth; vestiture consisting of long and short, fine, simple hairs, sometimes densely distributed.

Head: Protracted and prognathous, moderately broad, slightly flattened. Epicranial stem very short or absent; frontal arms lyriform and contiguous at base. Median endocarina absent. Stemmata 4 or 5 on each side. Antennae well-developed, 3-segmented, sometimes long, with segment 2 much longer than 1; sensorium sometimes dome-like. Frontoclypeal suture absent; labrum free. Mandibles asymmetrical, bidentate, without accessory ventral process; mola well-developed, tuberculate or asperate, with tubercles or asperities extending onto ventral surface, left mola almost vertical, right oblique; prostheca absent. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and rounded mala which is not cleft at apex. Labium more or less free to base of mentum; ligula present; labial palps usually 2-segmented (1-segmented in *Thrimolus*). Hypopharyngeal sclerome a transverse bar. Hypostomal rods moderately long, subparallel or slightly diverging. Ventral epicranial ridges absent. Gula transverse.

Thorax and Abdomen: Legs moderately long, 5-segmented, usually somewhat spinose; tarsungulus with 2 setae lying side by side; coxae narrowly separated. Thoracic and abdominal segments sometimes with 1 or more pigmented pleurites. Tergum A9 usually with pair of well-developed, posteriorly oriented, slightly upturned, simple urogomphi (absent in *Thrimolus*); sternum A9 simple. Segment A10 transverse, posteriorly oriented.

Spiracles: Annular, annular-uniforous, or annular-biforous, with short accessory tubes.

Comments: The family includes 8 genera and about 200 species worldwide, with 5 genera and 26 species occurring in America north of Mexico (Parsons, 1975). The group may be divided into three subfamilies: Bergininae (*Berginus* with species in Europe, North Africa, Madagascar, India, Ceylon, North and Central America and the West Indies); Esarcinae (*Esarcus* with species from southern Europe and North Africa); and Mycetophaginae, including the remaining genera. The family occurs in most parts of the world, but the greatest diversity appears to be in the temperate parts of the Northern and Southern Hemispheres.

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Böving and Craighead 1931 (larvae of *Litargus balteatus, L. connexus* (Fourcroy), *L. sexpunctatus* (Say), *Mycetophagus obsoletus* (Melsheimer), *M. punctatus* Say, *Thrimolus duryi* Casey, and *Typhaea stercorea*).
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Weiss and West 1920 (fungus hosts).

ARCHEOCRYPTICIDAE (TENEBRIONOIDEA)

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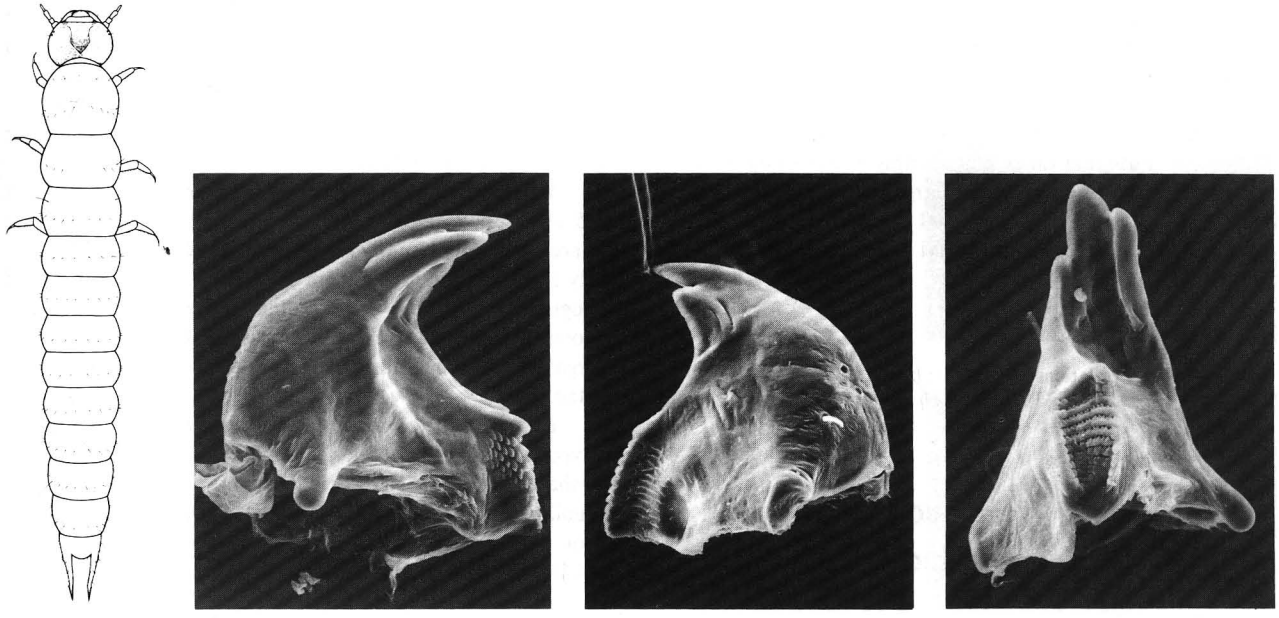
Figures 34.634a-d

Relationships and Diagnosis: The Archeocrypticidae were orignally included in the family Tenebrionidae. Kaszab (1964) proposed the tribe Archeocrypticini for their inclusion, and Watt (1974b) raised the taxon to family rank. The group belongs among the more primitive families of Tenebrionoidea and appears to be most closely related to Mycetophagidae and Pterogeniidae (Lawrence, 1977c; Lawrence and Newton, 1982). Archeocrypticid larvae resemble those of Mycetophagidae in general form, structure of the head and mouthparts, and form of the anal region, which is transverse and more or less posteriorly oriented, but the urogomphi are unique in being long, subparallel, lightly pigmented, and posteriorly oriented, and the frontoclypeal suture is distinct.

Biology and Ecology: Archeocrypticids are most commonly collected in leaf litter and other decaying plant material, but some of them feed in the softer fruiting bodies of certain Basidiomycetes. *Enneboeus caseyi* Kaszab has been collected in leaf litter, old pine cones, and rotting flowers. Several Australian species in the genera *Enneboeus* and *Enneboeopsis* have been found breeding in the fruiting bodies of *Piptoporus portentosus* and *Grifola berkeleyi;* the larvae are active like those of Mycetophagidae and are not adapted for boring into harder types of fungi.

Description: Mature larvae 2 to 6 mm. Body elongate, more or less parallel-sided, straight, slightly flattened. Dorsal surfaces lightly pigmented or with weakly developed, yellow tergal plates, smooth, with vestiture of longer and shorter, simple hairs, the latter sometimes densely distributed.

Head: Protracted and prognathous, moderately broad, slightly flattened. Epicranial stem short; frontal arms lyriform. Median endocarina absent. Stemmata 5 on each side. Antennae moderately long, 3-segmented, with short, conical sensorium. Frontoclypeal suture present; labrum free. Mandibles asymmetrical, bidentate or tridentate, without accessory ventral process; mola well-developed, tuberculate, with tubercles forming transverse ridges; left mola more vertical, produced into a tooth apically; prostheca absent. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and truncate mala which is not cleft. Labium free to base of mentum; ligula absent; labial palps 2-segmented and



Figures 34.634a-d. Archeocrypticidae. *Enneboeus caseyi* Kaszab. Barro Colorado Is., Canal Zone, Panama. **a.** larva, dorsal, length = 3.6 mm; **b.** right mandible, ventral; **c.** right mandible, dorsal; **d.** left mandible, mesal.

narrowly separated. Hypopharyngeal sclerome consisting of a tooth-like structure. Hypostomal rods very short and subparallel or slightly diverging. Ventral epicranial ridges absent. Gula transverse.

Thorax and Abdomen: Legs well-developed, 5-segmented; tarsungulus with 2 setae lying one distal to the other; coxae moderately narrowly separated. Tergum A9 with pair of posteriorly projecting, narrow, straight, lightly pigmented urogomphi which are widely separated, subparallel and acute at apex; sternum A9 simple. Segment A10 transverse, posteriorly oriented.

Spiracles: Annular-biforous.

Comments: The family contains 8 genera and 35 species worldwide with the single species *Enneboeus caseyi* Kaszab (= *Uloporus ovalis* Casey, not *Enneboeus ovalis* Waterhouse) occurring in America north of Mexico. The genus *Enneboeus,* as defined by Kaszab (1981), extends from the southern United States to Chile, and is also found in Australia. Other genera include the Neotropical *Pseudenneboeus, Archeocrypticus* from southern S. America and New Zealand, *Sivacrypticus* with a number of species in Africa and the Indomalayan Region, and the Australian genera *Enneboeopsis, Parenneboeus, Neboissianus,* and *Wattianus.*

Selected Bibliography

Kaszab 1964, 1969a, 1969b, 1979, 1981.
Lawrence 1977c (relationships), 1982c (larval characters).
Lawrence and Newton 1982 (relationships).
Triplehorn and Wheeler 1979 (relationships).
Watt 1974b (larval characters).

PTEROGENIIDAE (TENEBRIONOIDEA)

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This family includes 2 genera: *Pterogenius,* with 2 described species from Sri Lanka, and *Histanocerus,* with 6 described species and several undescribed, extending from Southeast Asia and the East Indies to New Guinea and the Solomon Islands. The group is considered to be among the more primitive heteromerous families, with relationships to Mycetophagidae, Tetratomidae, Ciidae, and Archeocrypticidae.

Larvae are elongate and subcylindrical, lightly sclerotized, except for the head and sometimes the last 2 terga, with smooth surfaces and a vestiture of long, simple setae. The head is subquadrate, as seen from above, with a long epicranial stem, bent to the left, and lyriform frontal arms, joined anteriorly by a transverse ecdysial line. There are 4 or 5 stemmata on each side, and the antennae are short and 3-segmented, with the sensorium as long as or longer than segment 3. The mandibles are highly asymmetrical, with large, transversely ridged molae and no prostheca. The ventral mouthparts are retracted, with a truncate mala, 3-segmented maxillary palps, 2-segmented labial palps, and a well-developed ligula. Hypostomal rods are short and divergent and ventral epicranial ridges are absent. The legs are close together and the tarsungulus is bisetose. Tergum A9 bears a pair of strongly upturned urogomphi, which may be simple or bifurcate; sternum A9 is simple. Segment A10 is transversely oval and posteroventrally oriented. The spiracles are

annular-biforous, with long accessory openings, and those on segment A8 are somewhat enlarged. Pupae have a peculiar spinose structure on the prothorax.

Pterogeniids live as larvae and adults on the more durable fruiting bodies of certain Polyporaceae (*Ganoderma, Trametes*). Pupation takes place within the fruiting bodies. Adults are dimorphic, and the enlarged and broadened head (*Pterogenius*) or enlarged antennal scape (*Histanocerus*) in the male is probably used in sexual combat.

Selected Bibliography

Crowson 1955.
Lawrence 1977c (relationships; habits; larvae of *Pterogenius nietneri* Candeze and *Histanocerus pubescens* Motschulsky; pupa of *H. pubescens*).

CIIDAE (TENEBRIONOIDEA)

(= CISIDAE, CIOIDAE)

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Minute Tree Fungus Beetles

Figures 34.635-639

Relationships and Diagnosis: The family Ciidae was traditionally placed in the Bostrichoidea or Cleroidea, based primarily on larval characters (presence of lacinia, reduction of maxillary articulating area, lack of true mandibular mola), but later authors have treated the group as either a member of the Cucujoidea (Crowson, 1955) or a primitive family of Tenebrionoidea (Crowson, 1960b; Lawrence, 1971, 1974b). The acute hyaline process at the base of the larval mandible and the inner (dorsal) lobe of the maxilla are difficult to interpret; the former may represent the cucujoid prostheca (unknown in other tenebrionoids) or a remnant of the mola (as in some Tetratomidae and Melandryidae), while the latter may be the true lacinia or a secondary development. When both adult and larval characters are taken into consideration, the most logical placement of the family is among the primitive Tenebrionoidea, near Tetratomidae and Mycetophagidae. Ciid larvae may be distinguished by the subcylindrical form and more or less hypognathous head, the lack of a true mola (several have anobiid-like pseudomolae), the long epicranial stem and V-shaped frontal arms, the dorsally situated laciniar lobe, and the reduced antennae which lack a third segment (except in *Sphindocis,* where segment 3 is shorter than the sensorium).

Biology and Ecology: Ciidae appear to feed almost exclusively on the fruiting bodies or vegetative hyphae of Basidiomycetes. Some ciids, such as species of *Orthocis,* may be associated with the primitive Auriculariales or found in rotten branches or vines, but the majority of species occur in the more durable fruiting bodies of the Polyporaceae and Hymenochaetaceae. Most species exhibit a certain degree of host preference, as has been shown by Lawrence (1973) and Paviour-Smith (1960a). Pupation usually occurs within the fungus, but pupae of *Sphindocis denticollis* Fall were found in the dry rotten wood of madrone (*Arbutus menziesii*) beneath the sporophores of *Trametes sepium.* At least 1 species, *Cis fuscipes* Mellié, is known to be parthenogenetic (thelytokous) (Lawrence, 1967a).

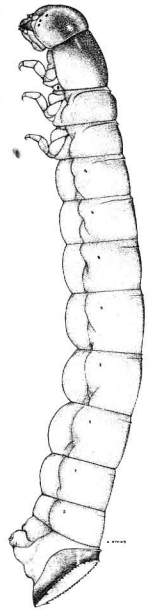
Description: Mature larvae 1 to 7 mm, usually less than 3.5 mm. Body elongate, parallel-sided, straight or slightly curved ventrally, usually subcylindrical. Dorsal surfaces usually lightly pigmented except for buccal region and tips of urogomphi or entire 9th abdominal tergum, sometimes with protergal plate and rarely with weak plates on remaining terga. Surfaces smooth and vestiture of scattered, long, simple setae.

Head: Protracted and moderately to strongly declined (hypognathous), globular. Epicranial stem long; frontal arms V-shaped. Median endocarina usually coincident with epicranial stem (absent in *Sphindocis*). Stemmata usually 3 to 5 on each side, sometimes 2, 1, or 0. Antennae very short, usually 2-segmented with long sensorium on apical segment; in *Sphindocis* 3-segmented with sensorium on segment 2 longer than segment 3. Frontoclypeal suture present; labrum free. Mandibles usually asymmetrical, broad and stout, bidentate, without accessory ventral process; mola usually absent, often replaced by narrow, acute, fixed, hyaline process on one or both mandibles; occasionally with well-developed pseudomola bearing transverse ridges. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, 3-segmented palp, and reduced articulating area (well-developed in *Sphindocis*); galea rounded or truncate; lacinia truncate, reduced, and subapical, not visible in ventral view, so that maxilla appears to have single mala. Labium free to base of mentum or partly connate with maxillae; ligula short, sometimes absent; labial palps 2-segmented, narrowly separated. Hypopharyngeal sclerome absent. Hypostomal rods absent. Ventral epicranial ridges present. Gula transverse.

Thorax and Abdomen: Legs relatively short and broad; tarsungulus with 2 setae lying side by side; coxae moderately close together. Tergum A9 usually with pair of small, upturned urogomphi, occasionally with single median process, more than 2 processes, or concave disc (*Sphindocis* and some *Cis*); sternum A9 usually simple, rarely (*Sphindocis*) with apical row of fine asperities. Segment A10 transversely oval, posteroventrally oriented.

Spiracles: Usually annular, rarely annular-uniforous or (*Sphindocis*) annular-biforous with long accessory tubes.

Comments: The family is presently divided into 2 subfamilies: Sphindociinae, with the single species *Sphindocis denticollis* from the northern coastal region of California, and the Ciinae, including about 40 genera and 550 species worldwide and 13 genera and 85 species in America north of Mexico (Lawrence, 1971, 1974b, 1982b). The Holarctic fauna is fairly well understood, but the group requires a world revision and many genera and species remain to be described from the Equatorial Region and Southern Hemisphere.



a

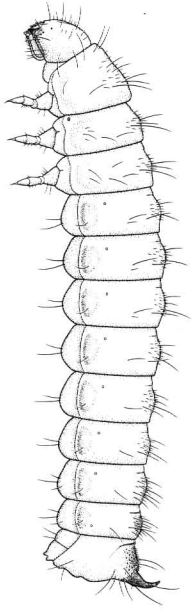
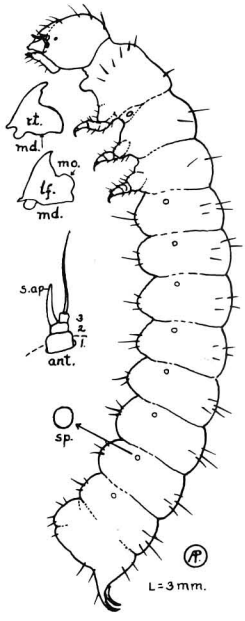


Figure 34.636



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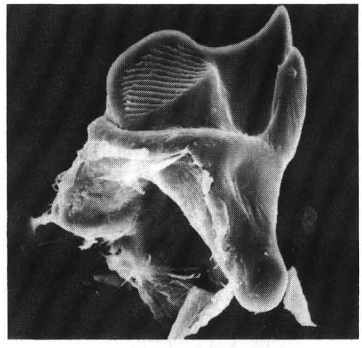

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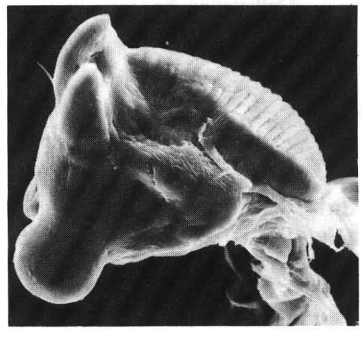

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Figure 34.637

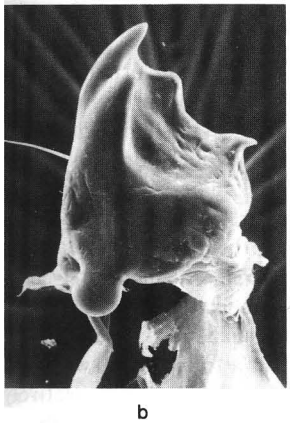

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Figure 34.635

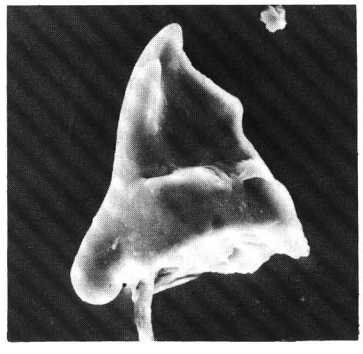
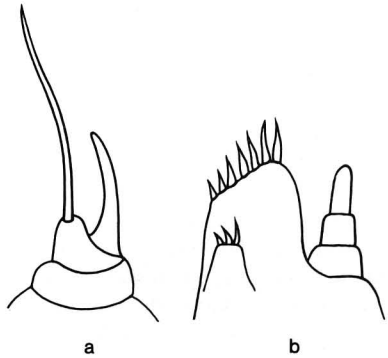


Figure 34.638



a b

Figure 34.639

Figures 34.635a,b. Ciidae. *Sphindocis denticollis* Fall. 4 mi. W. Forest Glen, Trinity Co., California. **a.** larva, lateral view, length = 7.6 mm; **b.** right mandible, ventral. Alpine Lake, Marin Co., California.

Figure 34.636. Ciidae. *Cis vitulus* Mannerheim. Big Sur, Monterey Co., California. Larva, lateral. Length = 3.9 mm.

Figures 34.637a-c. Ciidae. *Cis levettei* (Casey). **a.** larva, lateral (plus details). Length = 3 mm; **b.** left mandible, ventral; **c.** right mandible, ventral. Great Smoky Mts. National Park, Tennessee. (Figure 34.637a from Peterson, 1951)

Figure 34.638. Ciidae. *Malacocis brevicollis* (Casey). 3 mi. E Bloomingdale, New York. Right mandible, mesoventral.

Figures 34.639a,b. Ciidae. Ciinae. **a.** antenna; **b.** maxillary apex, dorsal.

Selected Bibliography

Böving and Craighead 1931 (larvae of *Cis fuscipes* and *Ceracis* sp., as *Ennearthron*).
Crowson 1955, 1960b.
Lawrence 1967a (parthenogenesis in *Cis fuscipes*), 1967b (*Ceracis*), 1971 (North America revision; larval characters), 1973 (fungus hosts; host preference), 1974a, 1974b (larva of *Sphindocis denticollis*), 1982b (North Amerian catalogue), 1982c (larval characters).
Paviour-Smith 1960a (fungus hosts: host preference), 1960b (*Cis bilamellatus* Fowler, introduction and spread in Britain).
Peterson 1951 (larva of *Cis levettei* (Casey)).
Saalas 1923 (larvae of *Cis bidentatus* (Olivier), *Cis jacquemarti* Mellié, *Cis quadridens* Mellié, *Cis punctulatus* Gyllenhal, *Ennearthron cornutum* (Gyllenhal). *Dolichocis laricinus* (Mellié), and *Rhopalodontus perforatus* (Gyllenhal)).
Verhoeff 1923 (larvae of *Cis boleti* (Scopoli) and *Sulucacis affinis* (Gyllenhal)).

TETRATOMIDAE (TENEBRIONOIDEA)

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Figures 34.640-642

Relationships and Diagnosis: The Tetratomidae were formerly included in the family Melandryidae (Arnett, 1968), but Crowson (1955, 1964c) placed them in a separate family, based on his studies of *Tetratoma* and *Penthe*. Miyatake (1960) added the tribe Pisenini and commented on the adult and larval similarities of this group to Mycetophagidae, while Hayashi (1975) and Viedma (1971) both noted the larval similarities between eustrophine Melandryidae and Tetratominae/Penthinae, suggesting that either the families be merged or the Eustrophinae be transferred to Tetratomidae. Larvae of *Pisenus* resemble those of both Mycetophagidae and Melandryidae-Hallomeninae in general body form, structure of the epicranial suture, and presence of a tuberculate mola, but they may be distinguished from either group by the presence of accessory teeth at the base of the urogomphi and from hallomenines by the absence of asperities at the base of sternum A9. Larvae of *Penthe* and Tetratominae, as well as *Eupisenus,* resemble those of Melandryidae-Eustrophinae in that the mandibular mola is absent, being replaced by a series of hyaline teeth and/or a membranous lobe. However, both groups differ from eustrophines in the form of the epicranial suture, in which the frontal arms appear to be forked at the apex, with one branch curving mesally and the other more or less straight. Tetratomine larvae also differ from eustrophines in having complex urogomphi (with accessory teeth), while the larva of *Penthe* has simple urogomphi but differs in lacking hypostomal rods and having a long, narrow ligula. The family Ciidae is also closely related to the Tetratomidae, but may be distinguished by the combination of more or less cylindrical body, globular head, long epicranial stem with V-shaped frontal arms, absence of a mola (sometimes replaced by a single hyaline process), and presence of a distinct laciniar lobe on the maxilla.

Biology and Ecology: Adult and larval Tetratomidae feed on the softer fruiting bodies of various Hymenomycetes, especially Polyporaceae and Tricholomataceae; adults generally feed on the surface, while larvae bore into the tissue of fresh or decaying sporophores. Adults of *Penthe* have been collected on *Grifola berkeleyi, Polyporus squamosus, Piptoporus betulinus, Fomitopsis pinicola, Phaeolus schweinitzii,* and several other polypores, while larvae have been found in an unidentified polypore, "tree fungi," and "watery fungus on chestnut stump" (Weiss and West, 1920; Hayashi, 1972). *Pisenus humeralis* (Kirby) is known to breed in *Tyromyces albellus, Laetiporus sulphureus,* and *Ischnoderma resinosum,* while larvae of *Eupisenus elongatus* (LeConte) are commonly found in *Laetiporus sulphureus. Tetratoma fungorum* (Fabricius) in England is known to breed in a number of fungi, including *Pleurotus ostreatus, Collybia velutipes,* and *Laetiporus sulphureus,* but its preferred habitat or "headquarters" appears to be *Piptoporus betulinus;* adults often feed on the surface at night, while larvae bore into fresh tissue, and pupation occurs in the soil (Paviour-Smith, 1964a, 1964b, 1964c). In North America, *Tetratoma concolor* LeConte has been collected in *Pleurotus ostreatus* and an unidentified mushroom, while *Incolia longipennis* Casey was found breeding in *Hapalopilus alboluteus* and *Tyromyces leucospongia.*

Description: Mature larvae 3 to 17 mm, usually 12 mm or less. Body elongate, parallel-sided or fusiform, straight or slightly curved ventrally, subcylindrical or slightly flattened. Head and all visible terga lightly sclerotized or with weakly developed, yellowish-brown, tergal plates; dorsal surfaces smooth; vestiture of longer and shorter, simple setae.

Head: Protracted and prognathous, moderately broad, somewhat flattened. Epicranial stem short to moderately long; frontal arms lyriform or characteristically forked, each with curved inner and straight outer branch. Median endocarina usually absent, occasionally (*Penthe*) coincident with epicranial stem. Stemmata 5 on each side. Antennae relatively short, 3-segmented. Frontoclypeal suture usually absent (present in Piseninae). Mandibles weakly to strongly asymmetrical, moderately stout, bidentate, without accessory ventral process; mola well-developed and transversely ridged in *Pisenus,* reduced and tuberculate in *Eupisenus,* replaced by group of acute hyaline processes in Tetratominae, and by a membranous lobe in *Penthe.* Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and blunt mala which may bear a single tooth at inner apical angle; dorsal surface of mala with brush of hairs on Tetratominae. Labium free to base of mentum; ligula usually short, long and narrow in *Penthe;* labial palps 2-segmented, usually narrowly separated. Hypopharyngeal sclerome usually absent or represented by transverse bar, tooth-like in *Pisenus.* Hypostomal rods usually short to moderately long and diverging, absent in *Penthe.* Ventral epicranial ridges absent. Gula transverse to almost as long as wide.

Thorax and Abdomen: Legs well developed, 5-segmented; tarsungulus with 2 setae, one distal to the other. Meso- and metatergum and abdominal terga 1–8 in *Penthe* with

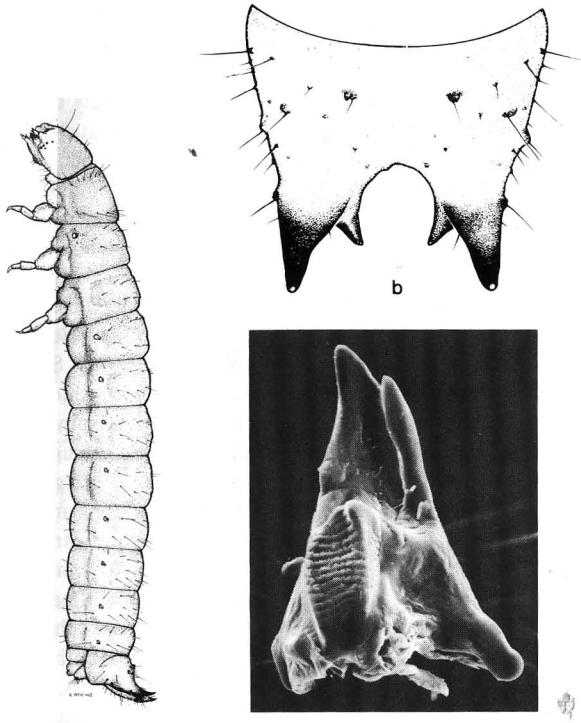

Figure 34.640

Figures 34.640a-c. Tetratomidae. *Pisenus humeralis* (Kirby). Florida Caverns State Park, Jackson Co., Florida. **a.** larva, lateral, length = 6 mm; **b.** abdominal apex, anterodorsal; **c.** left mandible, mesal.

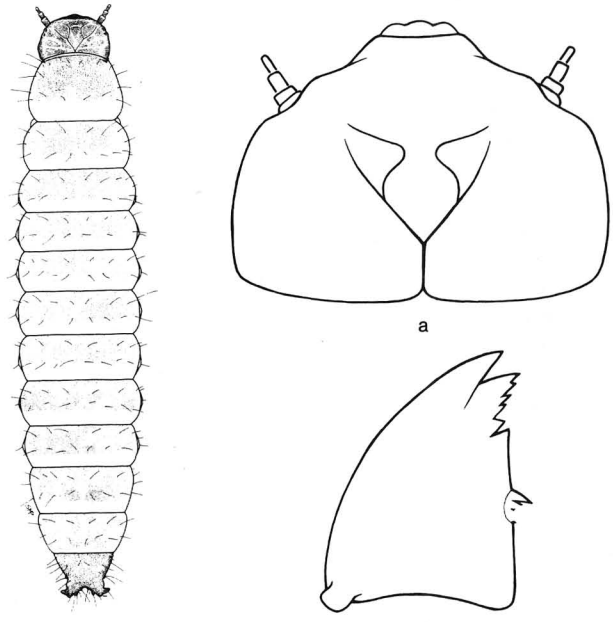

Figure 34.641

Figure 34.642

Figure 34.641. Tetratomidae. *Incolia longipennis* Casey. Paintbrush Canyon, Grand Teton Mts., Wyoming. Larva, dorsal. Length = 5 mm.

Figures 34.642a,b. Tetratomidae. *Tetratoma* sp. **a.** head, dorsal; **b.** right mandible, ventral.

patches or rows of asperities, in addition to maculations. Tergum A9 with pair of urogomphi, which are usually bifid, or with an accessory process at the base of each (simple in *Penthe*); sternum A9 simple. Segment A10 transversely oval, posteroventrally oriented.

Spiracles: Annular-biforous, with moderately long accessory tubes.

Comments: The family occurs throughout the Holarctic Region, with species of *Penthe* extending into India and the East Indies, and includes 6 genera and about 30 species. There are three recognized subfamilies: Piseninae (*Pisenus* and *Eupisenus*), Tetratominae (*Tetratoma, Abstrulia,* and *Incolia*), and Penthinae (*Penthe*). *Eupisenus* is only tentatively included in the first group, since both larvae and adults exhibit features more or less intermediate between Piseninae and Tetratominae.

Selected Bibliography

Arnett 1968.
Böving and Craighead 1931 (larva of *Penthe pimelia* (Fabricius)).
Crowson 1955, 1964c (larvae of *Tetratoma fungorum* and *T. desmaresti* Latreille).
Hayashi 1972 (larvae of *Pisenus rufitarsis* (Reitter), *P. insignis* (Reitter), and *Penthe japana* Marseul), 1975 (relationships).
Miyatake 1960 (relationships).
Paviour-Smith 1964a (biology of *Tetratoma fungorum;* habitat), 1964b (larva of *Tetratoma fungorum*), 1964c (biology of *T. fungorum*).
Viedma 1971 (relationships).

MELANDRYIDAE (TENEBRIONOIDEA)

(= SERROPALPIDAE)

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Figures 34.643-649

Relationships and Diagnosis: The family Melandryidae appears to be closely related to the Tetratomidae and the mordellid-rhipiphorid lineage, but the adult similarities between melandryids and anaspidine Scraptiidae (Crowson, 1966b) are probably a result of convergence, since anaspidine larvae are of an entirely different type. Larvae of the melandryid subfamilies Melandryinae and Osphyinae differ from those of Tetratomidae in lacking a mola or any other mesal structure at the base of the mandible, and usually by having a Y-shaped epicranial suture and an endocarina which extends beneath each frontal arm. Eustrophine larvae have a

membranous lobe and/or a series of hyaline teeth at the mandibular base as in larvae of Tetratominae and Penthinae, but they differ from the former in having simple urogomphi, from the latter in having hypostomal rods and a shorter ligula, and from both in having simple (lyriform) frontal arms which are not forked at the apex. Hallomenine larvae have a mandibular mola, and resemble larvae of Tetratomidae-Piseninae, but they differ in having a pair of asperities at the base of sternum A9. Larvae of *Rushia* and *Xylita*, because of the presence of a pit between the well-developed urogomphi, resemble a number of colydiid larvae; they differ from most colydiids, however, in having a more globular head with reduced or no stemmata, a long epicranial stem with an endocarina beneath it, no hypostomal rods, and no mandibular mola.

Biology and Ecology: Members of the Hallomeninae and Eustrophinae feed on the softer fruiting bodies of various Hymenomycetes. North American species of *Hallomenus* have been found as larvae in sporophores of *Laetiporus sulphureus, Dichomitus squalens, Osteina abducta,* and *Trametes serialis,* while the European *Mycetoma suturale* (Panzer) has been collected on *Ischnoderma resinosum. Eustrophinus* species have been found in a variety of bracket fungi (*Polyporus squamosus, Tyromyces albellus, Dichomitus squalens, Laetiporus sulphureus, Bjerkandera adusta, Inonotus munzii, I. vulpinus, Phellinus gilvus*) and wood-rotting mushrooms (*Pleurotus sapidus, Panus rudis, Lentinus lepideus*); *Synstrophus repandus* (Horn) has been collected on *Pleurotus ostreatus, Phaeolus schweinitzii,* and *Coriolus versicolor,* and *Eustrophus tomentosus* Say has been found in *Polyporus squamosus.* Larvae of Osphyinae and most Melandryinae occur in dead wood of varying consistency (relatively sound to soft and spongy), but often that which has been infested with a white rot fungus, such as *Coriolus versicolor, Hirschioporus abietinus,* or *Phellinus gilvus.* When they are associated with sporophores, the larvae feed in the rotting wood beneath; some species appear to prefer conifers or hardwoods, but this may be an artifact of collecting. Members of the tribe Orchesiini exhibit a wide variety of feeding habits, and some have been found in rotten wood, moss, and sooty molds, but a number *Orchesia* feed as larvae and pupate within relatively hard and durable polypore fruiting bodies. In eastern North America 3 species of *Orchesia* exhibit a definite preference for the type of sporophore in which they will breed: *O. castanea* (Melsheimer) prefers the thin, leathery, and light colored brackets of species of *Coriolus* and *Lenzites* (*sensu stricto*) (Polyporaceae); *O. gracilis* (Melsheimer) breeds in the hard, yellowish brown conks of the hymenochaetaceous fungus *Phellinus gilvus;* and *O. cultriformis* Laliberte occurs in the softer, dark brown fruiting bodies of *Inonotus* species (Hymenochaetaceae) (Dorn, 1936; Hayashi, 1975; Hoebeke and McCabe, 1977; Horion, 1956; Iablokoff, 1944; Viedma, 1966; Weiss, 1919; Weiss and West, 1920).

Description: Mature larvae 2.5 to 30 mm. Body elongate, more or less parallel-sided or slightly wider in middle, straight or slightly curved ventrally, subcylindrical to slightly flattened; usually very lightly sclerotized, except for buccal region and urogomphi, if present; occasionally with head and thoracic and abdominal tergal plates more heavily pigmented, brown in color; dorsal surfaces smooth; vestiture of scattered, simple hairs.

Head: Protracted and prognathous, moderately broad, slightly flattened, usually narrowed anteriorly so that clypeus and labrum are much narrower than frons. Epicranial stem usually moderately long (very short or absent in Eustrophinae, some Melandryinae, and Osphyinae); frontal arms usually V-shaped or U-shaped, lyriform in Eustrophinae and Hallomeninae, occasionally absent. Median endocarina usually coincident with epicranial stem and may extend beneath frontal arms as well (Y-shaped); occasionally (some Eustrophinae) extending anteriorly between frontal arms. Stemmata usually 5 on each side, occasionally 2 or 0. Antennae often very short, 3-segmented, or occasionally (Osphyinae) with only 2 apparent segments. Frontoclypeal suture usually absent (present in Eustrophinae); labrum free, emarginate apically in Eustrophinae. Mandibles more or less symmetrical, usually stout, unidentate or bidentate, rarely tridentate, without accessory ventral process; mola usually absent or represented by a few teeth or tubercles, sometimes replaced by a membranous lobe; well-developed and tuberculate in Hallomeninae; prostheca absent. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and rounded or truncate mala (cleft in Osphyinae). Labium usually with mentum and submentum fused (not so in Eustrophinae and Hallomeninae), usually free to base of mentum or postmentum; ligula usually present, often longer than labial palps, sclerotized in Osphyinae, absent or very short in Eustrophinae; labial palps 2-segmented and usually narrowly separated. Hypopharyngeal sclerome usually absent, represented by transverse bar in Eustrophinae, tooth-like in Hallomeninae. Hypostomal rods usually short to moderately long and diverging, 2 pairs present in Eustrophinae, absent in some Melandryinae (*Xylita, Rushia*). Ventral epicranial ridges absent. Gula usually transverse, longer than wide in Osphyinae.

Thorax and Abdomen: Meso- and metatergum and anterior abdominal terga and sterna sometimes with distinct ampullae. Legs well developed or short and broad, 5-segmented; tarsungulus with 1 or 2 setae. Tergum A9 usually without or with reduced urogomphi, sometimes with well-developed urogomphi (Eustrophinae, Hallomeninae, *Xylita, Rushia*), or with median process (Osphyinae); a pit present between urogomphi in *Xylita* and *Rushia.* Sternum A9 usually simple, with a single asperity on each side at base in Hallomeninae. Segment A10 transverse to almost circular, posteroventrally oriented.

Spiracles: Usually annular-biforous with very short accessory tubes, occasionally annular, annular-uniforous, or annular-biforous with long accessory tubes.

Comments: The family contains about 80 genera and 450 species worldwide, with 28 genera and about 70 species occurring in America north of Mexico. The subfamily Hallomeninae includes only the genera *Hallomenus* from N. America, Eurasia, and Africa, and *Mycetoma* from Europe. Eustrophinae includes several genera from N. America, tropical America, Eurasia, Africa, and Madagascar. Osphyinae

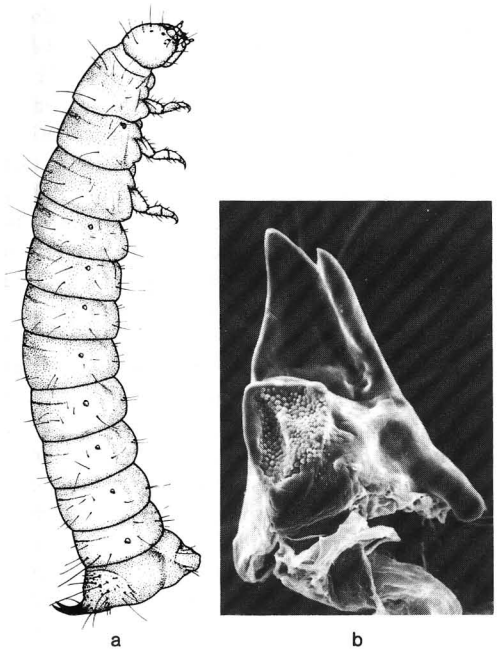

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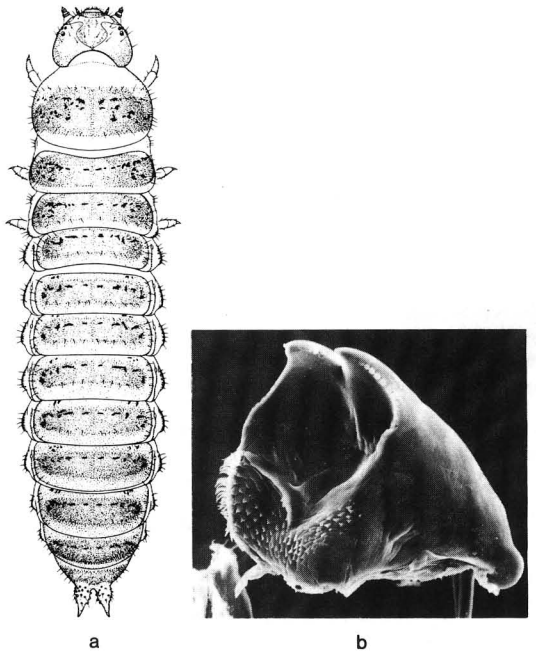
Figure 34.643



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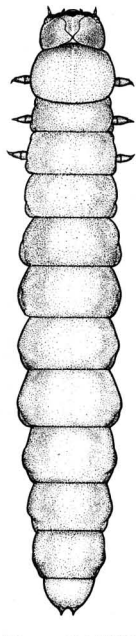

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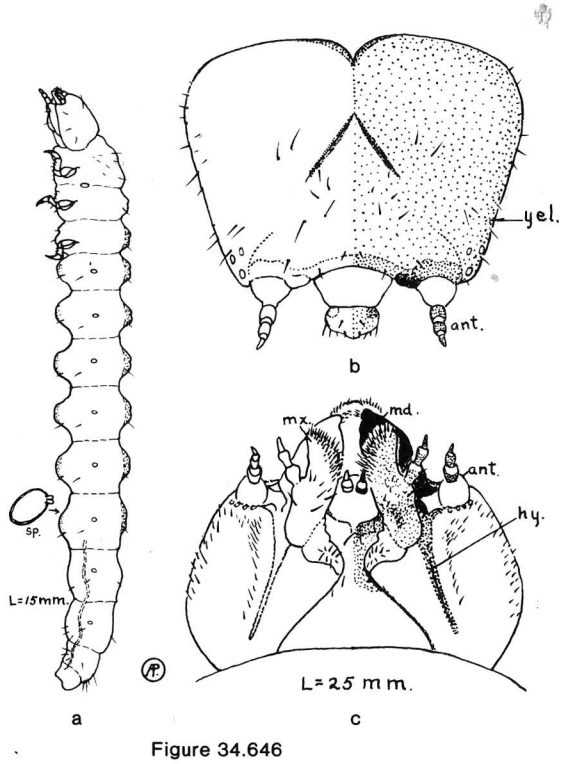

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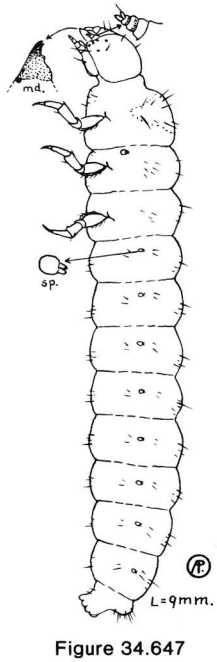

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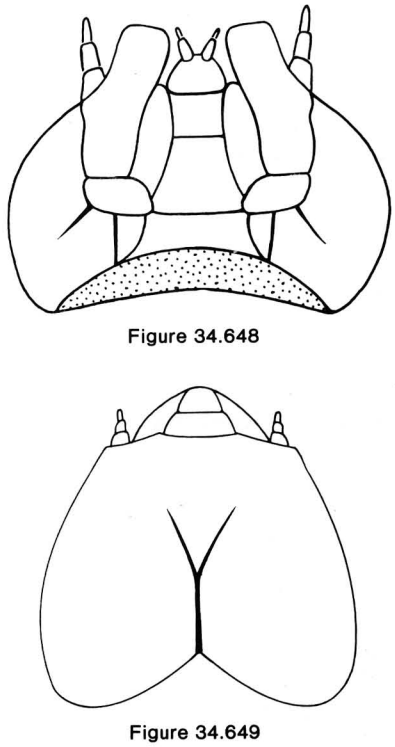

Figure 34.648

Figure 34.649

Figures 34.643a,b. Melandryidae. *Hallomenus* sp. Blue Hills, Norfolk Co., Massachusetts. **a.** larva, lateral, length = 6.9 mm; **b.** right mandible, mesal.

Figures 34.644a,b. Melandryidae. *Eustrophinus bicolor* (Fabricius). 2 mi. S Newbury, Essex Co., Massachusetts. **a.** larva, dorsal, length = 9.6 mm; **b.** left mandible, ventral.

Figure 34.645. Melandryidae. *Zilora occidentalis* Mank. Mt. Lemmon, Santa Catalina Mts., Arizona. Larva, dorsal. Length = 15 mm.

Figures 34.646a-c. Melandryidae. *Melandrya striata* Say. **a.** larva, lateral view, length = 15 mm; **b.** head, dorsal; **c.** head, ventral. (From Peterson, 1951)

Figure 34.647. Melandryidae. *Orchesia castanea* Melsheimer. Larva, lateral (plus details). Length = 9 mm. (From Peterson, 1951)

Figure 34.648. Melandryidae. (Eustrophinae). Head, ventral.

Figure 34.649. Melandryidae. (Melandryinae). Head, dorsal.

includes the Holarctic *Osphya*, the European *Conopalpus*, and 2 apparently related genera from Brazil. The remaining genera fall into the Melandryinae, which is usually divided into the tribes Orchesiini, Melandryini, Serropalpini, and Hypulini.

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Böving and Craighead 1931 (larvae of *Dircaea quadrimaculata* (Say), *Eustrophinus bicolor* (Fabricius), *Melandrya striata* Say, *Orchesia castanea*, *Osphya lutea* (Horn), and *Serropalpus barbatus* (Schaller)).
Crowson 1966b (relationships).
Dorn 1936 (fungus hosts).
Gressitt and Samuelson 1964b (larva of *Orchesia rennelli* Gressitt and Samuelson).
Hayashi 1975 (larvae of 14 species included in genera *Abdera*, *Euryzilora*, *Hypulus*, *Melandrya*, *Orchesia*, *Phloeotrya*, *Phryganophilus*, and *Serropalpus*), 1980 (same comments as Hayashi 1975).
Hoebeke and McCabe 1977 (larva of *Serropalpus coxalis* Mank).
Horion 1956.
Hudson 1934 (larva of *Mecorchesia brevicornis* Broun).
Iablokoff 1944 (fungus hosts).
Mamaev and Kompantzev 1978 (larva of *Euryzilora ussurica* Mamaev).
Peterson 1951 (larvae of *Melandrya striata*, *Melandrya* sp., and *Orchesia castanea*).
Viedma 1966 (larvae of many species included in genera *Abdera*, *Carida*, *Clinocara*, *Conopalpus*, *Hallomenus*, *Hypulus*, *Melandrya*, *Mycetoma*, *Osphya*, *Orchesia*, *Phloeotrya*, *Phyrganophilus*, *Serropalpus*, *Xylita*, and *Zilora*), 1971 (larva of *Eustrophinus bicolor* and relationships to Tetratomidae).
Weiss 1919b (fungus hosts).
Weiss and West 1920 (fungus hosts).

MORDELLIDAE (TENEBRIONOIDEA)

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Tumbling Flower Beetles

Figures 34.650–653

Relationships and Diagnosis: The family Mordellidae, with the exclusion of Anaspidinae (transferred to Scraptiidae by Crowson, 1955), forms a well-defined group, which is generally thought to belong to the complex including Melandryidae and Rhipiphoridae (Crowson, 1966b; Lawrence and Newton, 1982). Mordellid larvae may be distinguished by their more or less cylindrical form, hypognathous head, very short antennae (sometimes reduced to 1 or 2 segments), wedge-like mandibles, reduced legs which have only 3 or 4 indistinct segments, and usually the presence of a median, spine-like process on tergum A9.

Biology and Ecology: Adult mordellids are commonly found on flowers, where they apparently feed on nectar and pollen; the common name, tumbling flower beetles, is based on the habit of rapidly moving the hindlegs back and forth, when disturbed, causing the wedge-shaped body to tumble off its resting surface. Mordellid larvae are highly adapted for boring into relatively compact and often woody substrates. Many species feed in rotten wood, but some *Mordella* have been found breeding in the fruiting bodies of *Gloeophyllum saepiarium* and *G. trabeum* (Polyporaceae) (Weiss, 1920a), and most *Mordellistena* bore into stems of shrubs and herbaceous plants, causing damage to some cultivated species (Aguilar, 1962b; Crowson, 1955; Franciscolo, 1974).

Description: Mature larvae 3 to 18 mm, usualy 10 mm or less. Body elongate, more or less parallel-sided or slightly wider in middle, straight or slightly curved ventrally, subcylindrical. Very lightly sclerotized except for buccal region and sometimes apex of tergum A9; surfaces smooth; vestiture of fine, simple hairs, sometimes densely distributed.

Head: Protracted and prognathous, globular. Epicranial stem long; frontal arms absent. Median endocarina coincident with epicranial stem. Stemmata usually indistinct or absent, sometimes 1 to 3 on each side. Antennae very short, 1-, 2-, or 3-segmented. Frontoclypeal suture present; labrum free. Mandibles symmetrical, robust, more or less wedge-like with undivided apex and no accessory ventral process; mola absent; mesal surface of mandibular base simple. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, and rounded, simple mala; maxillary palp 2- or 3-segmented. Labium with mentum and submentum fused; ligula present, sometimes longer than labial palps, which are 2-segmented and narrowly separated. Hypopharyngeal sclerome absent. Hypostomal rods short to moderately long and diverging. Ventral epicranial ridges absent. Gular region absent so that labium is contiguous with thorax.

Thorax and Abdomen: Prothorax usually enlarged, sometimes with ridge or asperities on tergum. Legs very short, indistinctly 3- or 4-segmented, widely separated, without distinct tarsungulus. Abdominal segments 1–6 often with dorsal ampullae. Tergum A9 usually with median, spine-like process or pair of small, approximate urogomphi (occasionally without urogomphi or median process); sternum A9 simple. Segment A10 oval or almost circular, posteroventrally or ventrally oriented.

Spiracles: Annular.

Comments: The family includes about 100 genera and 1200 species worldwide, with 6 genera and about 200 species occurring in America north of Mexico. There are 2 subfamilies: Ctenidiinae, with the single South African species, *Ctenidia mordelloides* Castelnau, and Mordellinae with 5 tribes (Stenaliini, Reynoldiellini, Conaliini, Mordellini, Mordelistenini) containing the remainder of the species (Franciscolo, 1957). The group is widely distributed, and occurs in all major regions of the world.

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Ermisch 1956.
Franciscolo 1952, 1957, 1974 (larva of *Mordellistena ghanii* Franciscolo).
Hayashi 1980 (larvae of *Falsomordellistena katoi* Nomura, *Glipa fasciata* Kono, *Glipostena pelecotomidea* (Pic), *Hoshihananomia perlata* (Sulzer), and *Mordella truncatoptera* (Nomura)).
Lawrence and Newton 1982.
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Weiss 1920a (biology of *Mordella marginata* Melsheimer; fungus host).

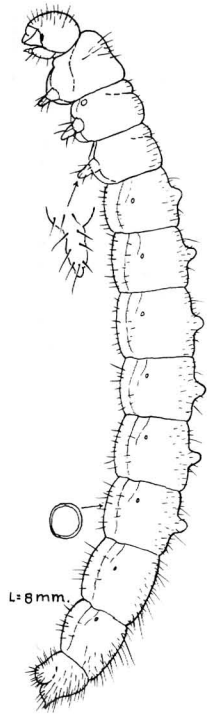
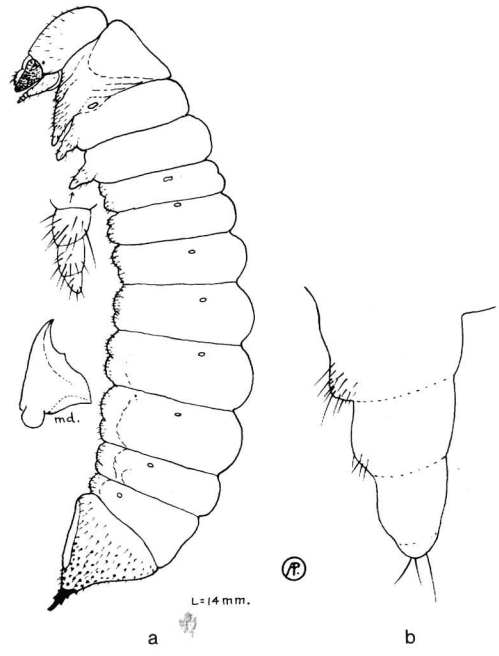


Figure 34.650



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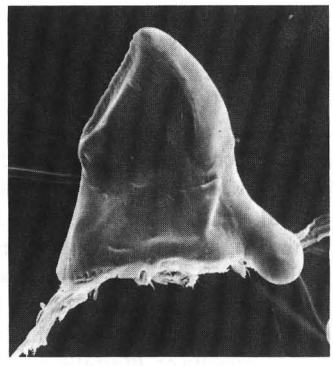

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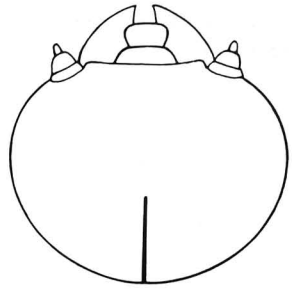

Figure 34.653

Figure 34.650. Mordellidae. *Mordellistena* sp. Larva, lateral (plus details). Length = 8 mm. (From Peterson, 1951)

Figures 34.651a,b. Mordellidae. *Tomoxia* sp. **a.** larva, lateral (plus details), length = 14 mm; **b.** metathoracic leg. (From Peterson, 1951)

Figure 34.652. Mordellidae. *Mordella* sp. Red Mountain, Colorado. Left mandible, ventral.

Figure 34.653. Mordellidae. Head, dorsal.

RHIPIPHORIDAE (TENEBRIONOIDEA)

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Rhipiphorid Beetles

Figures 34.654-657

Relationships and Diagnosis: Rhipiphorids are hypermetamorphic parasitoids of immature Hymenoptera and Blattodea. [Reports of attacks on scale insects (Peyerimhoff, 1942; Tucker, 1952) are of questionable validity.] Development involves both external and internal feeding stages. Because it is entomophagous and has a triungulin-type first instar larva, the family has been associated with the Meloidae and Stylopoidea (Strepsiptera) (Böving and Craighead, 1931; Arnett, 1968). However, evidence from adult anatomy indicates that the three groups are convergent (Crowson, 1955; Selander, 1957).

Rhipiphorid and meloid triungulins differ from those of the order Strepsiptera by having distinct antennae, mandibles, maxillary palpi, and trochanters and by the fact that the caudal setae arise from abdominal segment 9 (not 10). Triungulins of Rhipiphoridae and Meloidae are distinguished in the section on Meloidae. In later instars Rhipiphorinae become grotesque grubs feeding externally on wasp and bee larvae, whereas Rhipidiinae, feeding internally in cockroach larvae (nymphs), are degenerate, apodous, sac-like larvae initially, but later develop distinct appendages. There is no larval phase resembling the coarctate phase of Meloidae. Unlike Strepsiptera, both sexes of Rhipiphoridae abandon the host to pupate and are free-living as adults.

Biology and Ecology: No significant bionomic information is available for Nephritinae, Ptilophorinae, or Micholaeminae. In Pelecotominae the larva of *Rhipistena* has been described as an eruciform, apparently free-living predator of cerambycid larvae (*Prionoplus*), quite unlike other rhipiphorids (Hudson, 1934). In Rhipiphorinae the triungulin of *Macrosiagon* and *Metoecus* attaches to an adult wasp (Eumenidae, Scoliidae, Tiphiidae, Vespidae) and that of *Rhipiphorus* to an adult bee (Apidae, Halictidae) by grasping a body hair with the mandibles and is thereby carried to a provisioned nesting cell. After waiting, if necessary, for the host larva to hatch, the triungulin burrows into its thorax and eventually (sometimes after overwintering) becomes enormously distended (endophagous stage). When the host larva approaches maturity, the rhipiphorid makes an opening in the mesothorax and, after ecdysis, emerges to feed through 5 short instars by wrapping itself around the venter of the host's thorax (ectophagous stage). After devouring the host, the larva pupates in the cell. In Rhipidiinae (*Rhipidius, Rhipidioides,* and relatives) (fig. 34.656) the triungulin attaches

directly to a young cockroach (Blattellidae, Blattidae, Blaberidae) and inserts the head and part of the thorax through a membrane on the venter of the thorax, where it remains 2–3 weeks (ectophagous stage) before becoming an apodous 2nd instar larva (2nd phase) which initiates the endophagous stage by entering the host's body and migrating to the abdomen, where it may overwinter. Subsequently, there are several instars of rapid growth in which the larva has recognizable, although unsegmented, appendages (3rd phase). Ultimately, it develops segmented appendages, emerges from between the last tergites of the host's abdomen, and crawls away to pupate (4th phase). Except in *Rhipidius pectinicornis,* preying on *Blattella germanica,* larval development is completed before the host reaches the adult stage. A single cockroach may harbor more than 1 rhipidiine larva.

Eggs elongate, cylindrical, white, without sculpturing, laid in masses of a few to several hundred in flower buds (many *Macrosiagon* and *Rhipiphorus*), on leaves, in soil, or on wood (*Metoecus* and Rhipidiinae). Rhipidiine eggs are enmeshed in silk threads. Total number per female from 500–600 for *Macrosiagon tricuspidatum* to 2200 for *Rhipidius quadriceps.*

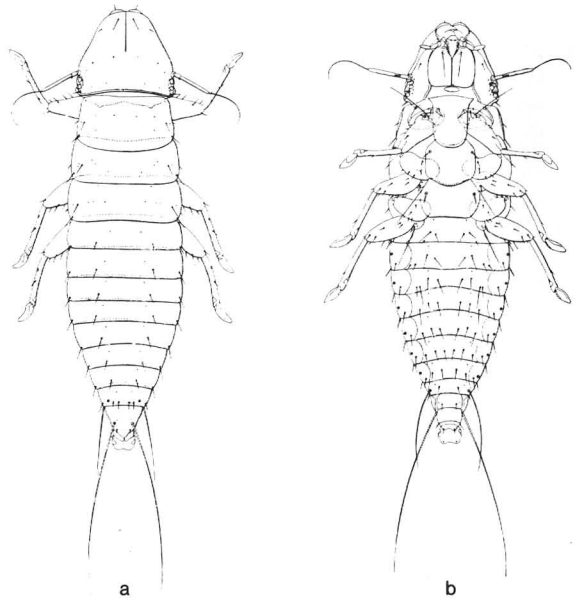
Pupa exarate in Rhipiphorinae, obtect and strongly dimorphic sexually in Rhipidiinae, females of which are larviform.

Description: Triungulin larva (1st instar): Length: .45–.95 mm. Body heavily sclerotized; form navicular before feeding, crescentic, with intersegmental membranes enormously enlarged when replete; spiracles on mesothorax and abdominal segments 1–8 (Macrosiagonini), 7–8 (Rhipidiinae), or 8 (Rhipiphorini); definite pattern of setae or setae and spinules (Rhipidiinae) on body (chaetotaxy sparser than in Meloidae); lacking line of dehiscence on body.

Head: Prognathous, rounded in front, with or without median dorsal cleft or anterior notch, with basal transverse ridge. Epicranial suture absent. Four (Rhipidiinae) or 5 stemmata on each side of head, behind antennal foramina, which are well behind middle of head. Antennae 2- (Rhipidiinae) or 3-segmented; segment 2 bifid in Rhipidiinae, with spiniform apical sensory appendix in Rhipiphorinae; last segment with long terminal seta. Labrum fused with frontoclypeus. Mandibles working more or less vertically, crossed in repose, falciform distally, smooth, with large basal lobe. Maxillae with stipes large and elongate or (Rhipidiinae) vestigial; cardo fused with stipes; palps 2- or 3-segmented, conspicuous; last segment with long terminal seta in Rhipidiinae. Labium much reduced; palps a pair of papillae.

Thorax and Abdomen: Thoracic nota well developed. Legs slender, elongate, 5-segmented; tibiae very long in Rhipidiinae; tarsungulus with 0–2 small claws and conspicuous pulvillus. Abdomen with 10 distinct segments; 10th tubular (may be subdivided in Rhipidiinae). Abdominal tergites and sternites well developed, with single transverse row of setae (or setae/spinules); pleurites distinct or not. Urogomphi absent; segment 9 generally with pair of enlarged caudal setae (shorter pair sometimes present on 8).

Later Instars: Rhipiphorinae (2nd–6th instars): Ectophagous. Body crescentic, lightly sclerotized, sparsely, minutely setate; spiracles on mesothorax and abdominal segments 1–7.



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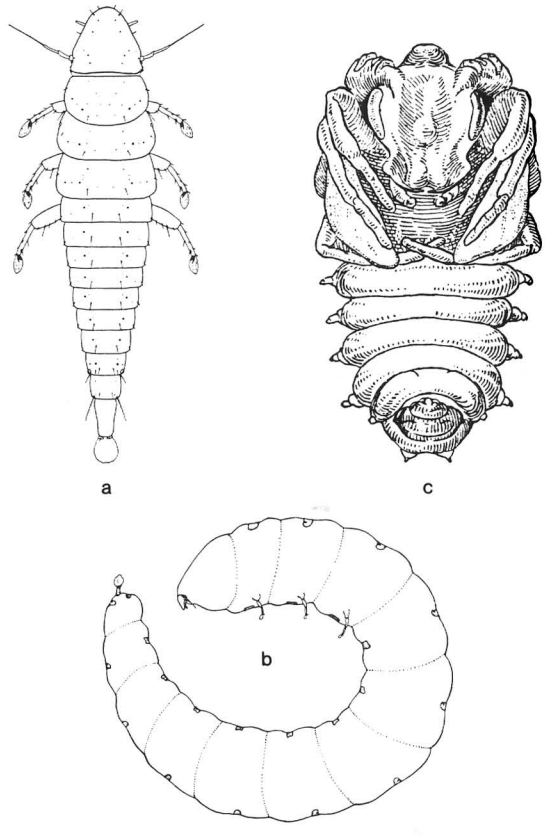
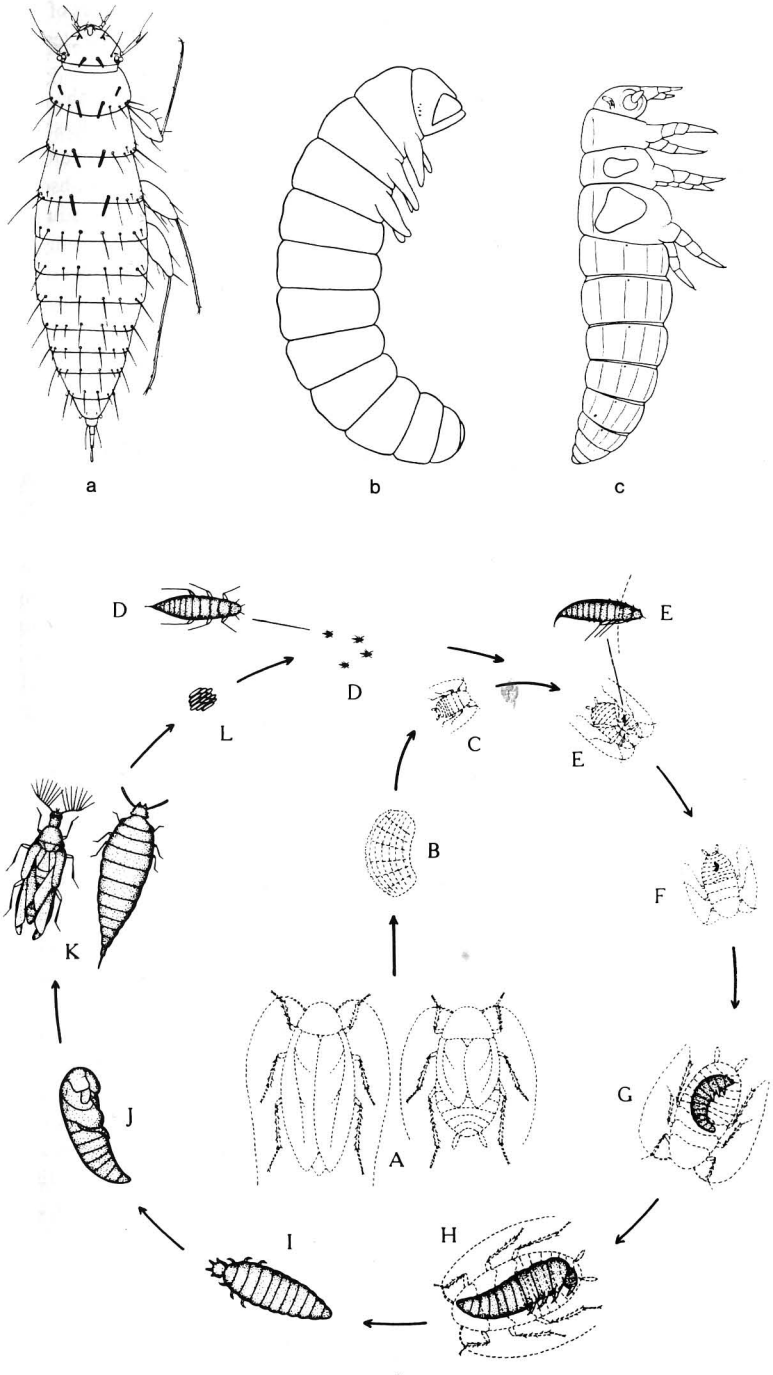


Figure 34.655

Figures 34.654a,b. Rhipiphoridae. *Macrosiagon ferrugineum flabellatum* Fabricius. **a.** triungulin, dorsal; **b.** ventral (after Grandi, 1936).

Figures 34.655a-c. Rhipiphoridae. *Rhipiphorus smithi* Linsley & MacSwain. **a.** triungulin, dorsal; **b.** replete triungulin, lateral; **c.** pupa, ventral (after Linsley *et al.,* 1952).



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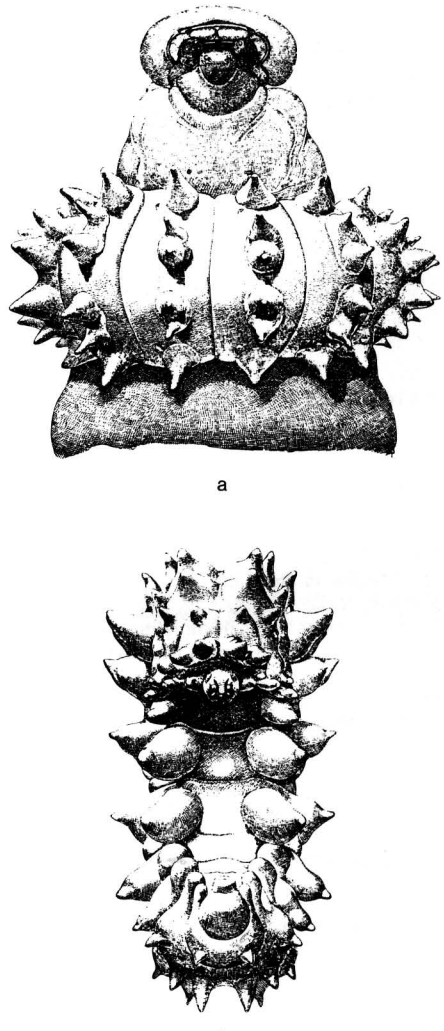

Figure 34.657

Figures 34.656a-d. Rhipiphoridae. *Rhipidius quadriceps* Abeille de Perrin. **a.** triungulin, dorsal; **b.** 3rd phase larva, lateral; **c.** 4th phase larva; **d.** life cycle. A, host cockroaches (*Ectobius*) adults; B, host oötheca; C, host larva; D, triungulin; E, triungulin attached to host; F, 2nd phase; G, 3rd phase; H, 4th phase, before emergence; I, 4th phase, emerged; J, pupa; K, adults; L, egg (after Besuchet, 1956).

Figures 34.657a,b. Rhipiphoridae. *Macrosiagon ferrugineum flabellatum.* **a.** ectophagous phase larva, on thorax of larval wasp; **b.** ventral view (after Grandi, 1936).

Head: Hypognathous. Epicranial suture, stemmata, and labial palps absent. Antennae vestigial. Labrum triangular, extending between mandibles. Mandibles with outer surface modified for cutting, toothed. Maxillary palps reduced to large mounds.

Thorax and Abdomen (segments 1–7). Each with several large, conical horns. Legs reduced, indistinctly segmented. Rhipidiinae: 2nd Phase (endophagous): apodous; spiracles, antennae, and mouthparts absent; 5 stemmata in line on each side of head. 3rd Phase (endophagous): pseudoeruciform; spiracles absent; antennae conical, unsegmented; maxillary palps and legs distinct, unsegmented. 4th Phase (emergent): pseudoeruciform; spiracles on mesothorax and abdominal segments 1–6; appendages well developed; antennae 2-segmented, maxillary palps 3-segmented, legs 5-segmented; tarsungulus falciform.

Spiracles: Annular. As indicated above, the number of abdominal spiracles varies among taxa and instars. All spiracles absent in intermediate instars of Rhipidiinae.

Comments: A poorly known family of about 300 species divided among 6 subfamilies and 38 genera (5 in North America). Hosts have been recorded for only 15% of the species. Among bionomic works that of Besuchet (1956a) is outstanding.

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COLYDIIDAE (TENEBRIONOIDEA)

(INCLUDING ADIMERIDAE, MONOEDIDAE)

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Figures 34.658-661

Relationships and Diagnosis: The constitution of the Colydiidae has been reviewed recently (Lawrence, 1980), and a number of taxa have been removed from the family, including the following groups listed in Arnett (1968): *Anchomma* (Tenebrionidae); *Aglenus* (Othniidae, Trogocryptinae); Deretaphrini and Bothriderini (Bothrideridae); Cerylonini, Euxestinae, and Murmidiinae (except *Eupsilobius*) (Cerylonidae); and *Eupsilobius* (= *Eidoreus*) (Endomychidae) (Sen Gupta and Crowson, 1973). The family is usually placed near the base of the Tenebrionoidea because of various "clavicorn" features of the adult, including abruptly clubbed antennae and reduced tarsal segmentation. Colydiids appear to be most closely related to members of the Zopheridae, and the division between them is not at all clearly defined.

Most colydiid larvae may be distinguished by the following combination of characters: (1) epicranial stem short or absent; (2) endocarinae absent; (3) 5 stemmata arranged in vertical rows of 3 and 2; (4) frontoclypeal suture absent; (5) molae symmetrical, either well-developed or reduced (sometimes with a few hyaline teeth only); (6) mala rounded or truncate and not cleft; (7) hypostomal rods present; (8) urogomphi with a pit between them; and (9) sternum A9 simple. The epicranial stem may be long in *Nematidium, Lasconotus,* and *Pycnomerus,* and in the last two a Y-shaped endocarina is present beneath it and the frontal arms; paired endocarinae are occasionally present (*Cicones*); stemmata and hypostomal rods may be absent (*Nematidium, Lasconotus,* Gempylodini); and urogomphal pits are sometimes absent (*Nematidium,* Gempylodini, *Colydium,* and some Pycnomerini, Coxelini, and Synchitini).

Biology and Ecology: Colydiidae are basically mycophagous, feeding on rotten plant material, fungal fruiting bodies, spores or hyphae, but some species may feed on living plant material, and predatory habits have evolved at least 3 times. Many of the fungus feeders occur in the stromata of, or on the conidial spore fields produced by species of Xylariaceae (Ascomycetes). Adults and larvae of *Bitoma quadricollis* Horn were found feeding on stromatal tissue of an *Hypoxylon; Cicones variegatus* (Hellwig) has been associated with *Hypoxylon deustum* and an *Ustulina; Synchita humeralis* (Fabricius) has been collected on *Daldinia tuberosa; Cicones pictus* Erichson and *Synchita angularis* Abeille are known from *Nummulariola bulliardii;* and *S. separanda* Reitter has been found on conidia of the *Tubercularia* type (Dajoz, 1966; Donisthorpe, 1935; Lawrence, 1977a; Palm, 1959). Various Synchitini, including species of *Bitoma, Colydodes, Namunaria,* and *Synchita* have been collected in the fruiting bodies of wood-rotting Basidiomycetes, but records usually consist of a few individuals, and known larvae occur in rotten wood or on ascomycete fungi. Rotten wood or cambial tissue is probably the main food source for *Aulonium* and *Colydium* (*see* below), the Pycnomerini, and various other colydiids as well. Members of the Coxelini and some of the Synchitini are often found in leaf litter and probably feed on decaying vegetation, while *Colobicus parilis* Pascoe attacks stored roots and fruits, and may transmit *Diplodia* (Coelomycetes) to sweet potatoes, yams, cassava, and *Citrus* (Hinton, 1945b). The European *Orthocerus clavicornis* (Linnaeus) occurs in sandy areas where it feeds on mosses or lichens growing on rocks, walls, and trees; it is especially common on the lichen *Peltigera canina* (Crowson, 1984a; Horion, 1961). Species of *Dryptops* occur on tree surfaces and may also be lichen feeders; they are peculiar in having an epicuticular growth of cryptogams, which gives the surface a green color (Samuelson, 1966). Other plant-associated colydiids include species of *Monoedus* whose larvae have been collected in the pith of stems (Craighead, 1920), and the Australian *Todima* which feed on the flower spikes of grass trees (*Xanthorrhoea*).

Almost all cases of predatory habits in the Colydiidae concern members of the Colydiini and Gempylodini and the synchitine genus *Lasconotus,* but it is possible that *Nematidium* is also predaceous. Members of the genus *Aulonium* are often abundant in the subcortical galleries of bark beetles, and are generally considered to be predators (Dajoz, 1977; Horion, 1961). Although larvae of *A. longum* LeConte have been observed feeding on larval *Dendroctonus* (Dahlsten, 1970), both *A. trisulcum* (Fourcroy) and *A. tuberculatum* Kraus have been reared entirely on plant material (Craighead, 1920; Marshall, 1978). Species of *Colydium* have also been recorded as bark beetle predators (Blackman and Stage, 1924; Dahlsten, 1970; Horion, 1961), but there is a lack of convincing evidence. A number of African gempylodines (*Aprostoma* and *Mecedanum*) have been reported to be predators in the galleries of ambrosia beetles (Platypodidae and *Xyleborus*) (Hinton, 1948c; Roberts, 1968; Schedl, 1962), as have species of *Pseudendestes* and *Munaria* in the Australian Region (Lawrence, 1980), and at least some of these records are based on detailed feeding observations. All known larvae of Colydiini and Gempylodini lack any obvious modifications usually associated with predaceous habits (molar reduction, loss of microtrichial patches on mandibles). Predatory behavior has been well established in the genus *Lasconotus,* and the larvae have highly modified mandibles. Hackwell (1973) noted that, although early instars fed primarily on fungi, third stage larvae of *L. subcostulatus* Kraus were aggressive predators on larvae and pupae of *Ips.*

Description: Mature larvae 2 to 20 mm, usually less than 10 mm. Body elongate, more or less parallel-sided, straight, and subcylindrical to slightly flattened. Usually lightly pigmented except for head and A9 tergum, sometimes with all visible terga pigmented; dorsal surfaces smooth; vestiture of scattered, simple setae.

Head: Protracted and prognathous, slightly flattened. Epicranial stem short to moderately long, sometimes absent; frontal arms lyriform or V-shaped, contiguous at base. Median endocarina usually absent, occasionally coincident with epicranial stem or with both stem and frontal arms. Paired endocarinae occasionally present beneath frontal arms. Stemmata usually 5 on each side, sometimes absent. Antennae usually well developed, occasionally very short, 3-segmented, with elongate, palpiform or conical sensorium. Frontoclypeal suture absent; labrum free. Mandibles symmetrical, usually bidentate, occasionally unidentate (*Lasconotus*) or tridentate, sometimes with serrate incisor edge, without accessory ventral process; mola either well-developed and tuberculate, asperate, or transversely ridged, or reduced, sometimes consisting of a few asperities or hyaline teeth only; prostheca absent. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and rounded or truncate mala, sometimes with tooth at inner apical angle. Labium usually free to base of mentum; ligula present (except in *Nematidium*); labial palps usually 2-segmented (1-segmented in *Nematidium* and Gempylodini). Hypopharyngeal sclerome usually present, variable. Hypostomal rods short to moderately long and diverging, sometimes absent. Ventral epicranial ridges absent. Gula usually transverse, occasionally longer than wide.

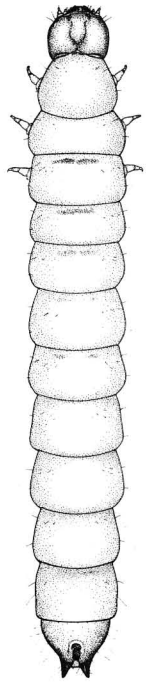


Figure 34.658

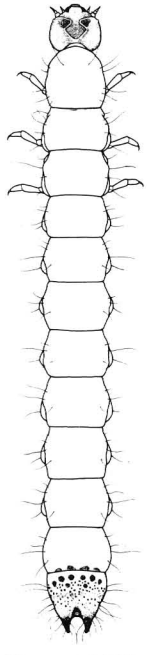


Figure 34.660

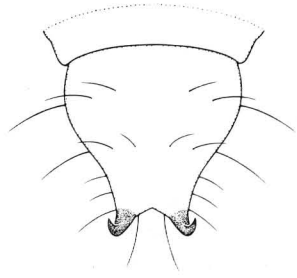
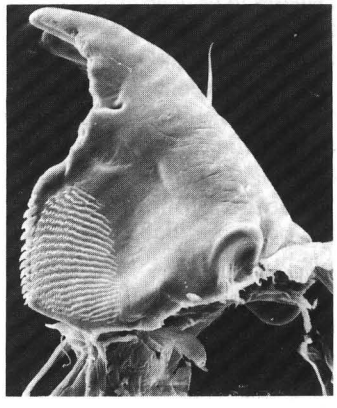


Figure 34.659



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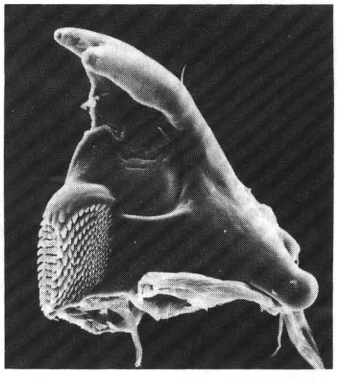

b

Figure 34.661

Figure 34.658. Colydiidae. *Pycnomerus* sp. Lake St. Clair, Tasmania. Larva, dorsal. Length = 8.7 mm.

Figure 34.659. Colydiidae. *Pycnomerus* sp. Monga State Forest, New South Wales. Abdominal apex, dorsal.

Figure 34.660. Colydiidae. *Namunaria pacifica* (Horn). Phoenix Lake, Marin Co., California. Larva, dorsal. Length = 7.5 mm.

Figures 34.661a,b. Colydiidae. *Aulonium longum* LeConte. Chuska Mts., Arizona. **a.** right mandible, dorsal; **b.** left mandible, ventral.

Thorax and Abdomen: Prothorax sometimes enlarged (*Lasconotus*). Legs well-developed, 5-segmented, moderately to widely separated; tarsungulus almost always with 2 setae lying side by side. Meso- and metatergum and anterior abdominal terga sometimes with rows or patches of asperities. Tergum A9 usually well-developed and sometimes variously pigmented and tuberculate, occasionally (*Nematidium* and Gempylodini) reduced, much shorter than tergum A8, almost always with paired, upturned, simple urogomphi, often with pit between them, rarely (*Cicones*) with median spine. Sternum A9 usually simple, sometimes with row of apical asperities. Segment A10 transversely oval, ventrally or posteroventrally oriented.

Spiracles: Usually annular-biforous with short accessory openings, sometimes apparently annular.

Comments: The family includes about 150 genera and 1000 species worldwide, with 18 genera and 75 species occurring in America north of Mexico. The Palearctic species have been reviewed recently (Dajoz, 1977), but much work remains to be done in establishing a worldwide tribal and generic classification. The tribes presently included in the family are Nematidiini, Gempylodini, Colydiini, Pycnomerini, Acropini, Monoedini, Synchitini, Coxelini (including Megataphrini), Diodesmini, Langelandiini, Rhopalocerini, and Orthocerini (including Corticini and Rhagoderini).

Selected Bibliography

Arnett 1968.
Blackman and Stage 1924.
Böving and Craighead 1931 (larvae of *Aulonium tuberculatum* LeConte, *Bitoma crenata* (Fabricius), *Nematidium filiforme* LeConte, *Phloeonemus catenulatus* Horn, and *Synchita fuliginosa* Melsheimer).
Craighead 1920 (same as Böving and Craighead 1931).
Crowson 1984a (association with Ascomycetes).
Dahlsten 1970.
Dajoz 1968 (larva of *Langelandia anophthalma* Aubé), 1971 (larva of *Pycnomerus fuliginosus* Erichson), 1977 (biology; Palaearctic revision).
Donisthorpe 1935 (fungus hosts).
Hackwell 1973 (biology of *Lasconotus subcostulatus* Kraus).
Hayashi 1972 (larvae of *Cicones hayashii* Sasaji, *Penthelispa vilis* (Sharp), and *Sympanotus pictus* Sharp).
Hinton 1945b (*Colobicus parilis* in stored products), 1948c (predators of ambrosia beetles).
Horion 1961.
Lawrence 1977a (association with Ascomycetes), 1980 (larva of *Pseudendestes robertsi* Lawrence).
Mamaev 1975.
Marshall 1978 (biology and larva of *Aulonium trisulcum* (Fourcroy)).
Nikitsky and Belov 1980a, 1980b (key to larvae of 19 species (16 genera); larvae of *Cicones pictus* Erichson, *Lastrema verrucollis* Reitter, *Niphopelta imperialis* Reitter, *Pycnomerus terebrans* Olivier, and *Synchita mediolanensis* Villa).
Palm 1959 (association with Ascomycetes).
Peterson 1951.
Roberts 1968 (predators of ambrosia beetles).
Samuelson 1966 (epizoic symbiosis).
Saalas 1923 (larvae of *Lasconotus jelskii* (Wankow), *Bitoma crenata* (Fabricius)).
Schedl 1962 (association with bark and ambrosia beetles).
Sen Gupta and Crowson 1973.
Verhoeff 1923 (larva of *Bitoma crenata*).

MONOMMIDAE (TENEBRIONOIDEA)

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Figures 34.662-664

Relationships and Diagnosis: The Monommidae are closely related to Colydiidae and Zopheridae, but their larvae differ from those of either group in having a reduced mandibular mola, paired endocarinae mesad of the frontal arms, and double rows of asperities forming incomplete transverse rings on abdominal terga 2 to 6 (Crowson, 1955, 1966b).

Biology and Ecology: Monommids feed on decaying plant material and are usually found in soft and highly decayed stems, but may also occur under bark of rotten logs, and have been found in yams and *Yucca* pods. *Hyporhagus gilensis* Horn was found in *Yucca* stems in Arizona, *Monomma brunneum* Thomson in papaya stems in India (Fletcher, 1916), and *Inscutomonomma hessei* Freude in the stems of *Euphorbia* in Africa (Freude, 1958). Pupation takes place in the soil (Freude, 1958).

Description: Mature larvae 5 to 15 mm, usually 10 mm or less. Body elongate, more or less parallel-sided, straight, slightly flattened. Dorsal surfaces lightly pigmented, smooth except for head and A9 tergum; vestiture of scattered, fine, simple setae.

Head: Protracted and prognathous, moderately broad, somewhat flattened. Epicranial stem absent; frontal arms lyriform and contiguous at base. Median endocarina absent; paired endocarinae located mesad of frontal arms. Stemmata 5 on each side. Antennae well developed, 3-segmented. Frontoclypeal suture absent; labrum free. Mandibles symmetrical, somewhat longer than wide, bidentate, without accessory ventral process; mola reduced and sub-basal, represented by a row of 10 or more hyaline teeth. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and truncate mala which is cleft at apex and has 2 teeth at inner apical angle. Labium free to base of mentum; ligula present; labial palps 2-segmented and moderately widely separated. Hypopharyngeal sclerome absent. Hypostomal rods moderately long and subparallel or slightly diverging (converging again at apex). Ventral epicranial ridges absent. Gula transverse.

Thorax and Abdomen: Metatergum and abdominal tergum 1 sometimes with transverse row of asperities (broken at midline). Legs short and spinose, 5-segmented, widely separated; tarsungulus with 2 setae lying side by side. Abdominal terga 2 to 6 each with double row of asperities forming transverse, complete or incomplete ring or with paired rings. Tergum A9 with pair of urogomphi, between which is a heavily sclerotized pit; sternum A9 simple. Segment A10 transversely oval, ventrally oriented.

Spiracles: Annular-biforous.

Comments: The family includes 12 genera and about 225 species worldwide, with *Apasthines* (1 species) and *Hyporhagus* (4 species) occurring in America north of Mexico. The group occurs in tropical and subtropical regions of both hemispheres, has its greatest diversity in Africa and Madagascar.

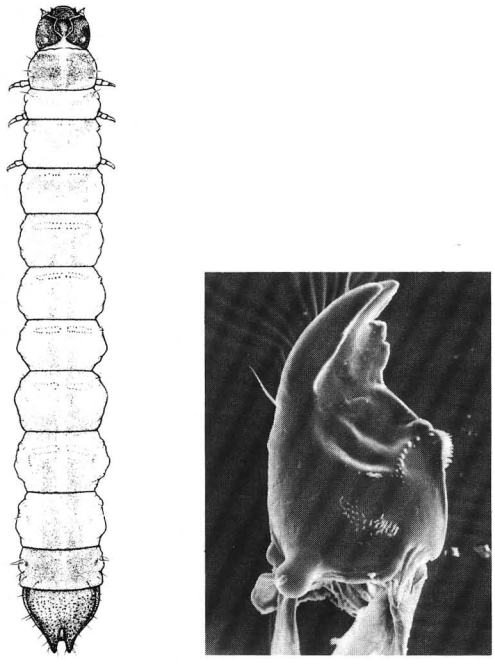

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Figure 34.662

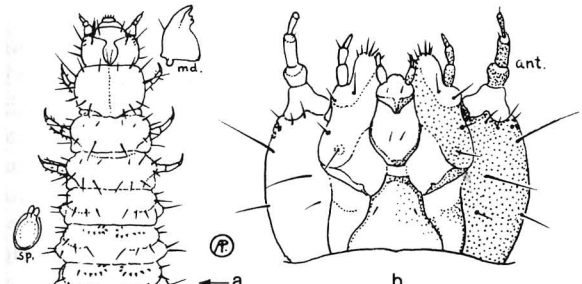

Figure 34.663

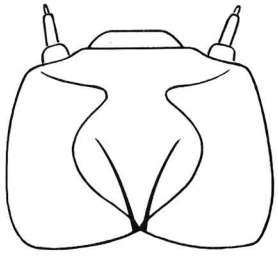

Figure 34.664

Figures 34.662a,b. Monommidae. *Hyporhagus gilensis* Horn. Vail, Pima Co., Arizona. **a.** larva, dorsal, length = 18.9 mm; **b.** right mandible, ventral.

Figures 34.663a,b. Monommidae. *Hyporhagus texanus* Linnell. El Paso, Texas. **a.** larva, dorsal (plus details), length = 9 mm; **b.** head, ventral. (From Peterson, 1951)

Figure 34.664. Monommidae. *Hyporhagus* sp. Head, dorsal.

Selected Bibliography

Crowson 1955, 1966b.
Fletcher 1916 (larva of *Monomma brunnea* Thomson).
Freude 1958 (larva of *Inscutomonomma hessei* Freude).
Peterson 1951 (larva of *Hyporhagus texanus* Linnell).

PROSTOMIDAE (TENEBRIONOIDEA)

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Figures 34.665-666

Relationships and Diagnosis: The composition of the Prostomidae is essentially that proposed by Böving and Craighead (1931) on the basis of critical examination of the larval stages. Crowson (1955) enumerated several characters of both larvae and adults which would support placement in the Heteromera, but treated it as a subfamily of Cucujidae until some years later (Crowson, 1967). The closest relative may be among the Inopeplidae, Salpingidae or Othniidae, all of which appear to be closely related. However, Lawrence (1977c) stated that the prostomids might also be derived from Crowson's (1966b) synchroid-zopherid-tenebrionid group. The asymmetrical cranium, with the right side larger than the left (fig. 34.665b), and transverse row of asperities on the distal margin of the ninth abdominal sternite (fig. 34.665c) characterize prostomid larvae.

Biology and Ecology: Larvae and adults are associated with dead, decaying trees. Typically, they are found within a characteristic mud- or clay-like material between layers of the decaying wood. Adult *Prostomis mandibularis* (Fabricius) have been collected beneath loose bark and within decaying wood of various conifers in western North America. Larvae of *P. mandibularis* and the Japanese *P. latoris* Reitter have been found beneath bark and within decaying wood of pines; in the case of *P. mandibularis,* the wood was in the red-rotten stage of decay (Hayashi, 1969b; Lawrence, Young, unpublished notes).

Description: Mature larvae attain lengths of 8–9 mm and widths of 1.3–2 mm. Body strongly flattened, smooth, lightly sclerotized, creamy white, widest slightly beyond the middle and narrowing posteriorly and anteriorly; vestiture sparse, consisting of short setae.

Head: (fig. 35.665b) Prognathous, exserted from prothorax, conspicuously asymmetrical with right side larger than left. Epicranial suture poorly defined, frontal arms lyriform, stem short or absent; endocarinae absent. Symmetrical labrum anterad of fused frons and clypeus. Stemmata absent. Antennal insertions fully exposed, antennae elongate, 3-segmented, sensorium of segment 2 conical, 0.5× length of apical segment. Mouthparts protracted, supported ventrally by well developed, posteriorly divergent hypostomal rods. Mandibles (figs. 34.666a,b) heavily sclerotized, movable, asymmetrical; left mandible with prominent molar tooth; apices of mandibles tridentate. Maxilla with 1-segmented cardo; undivided, pad-like maxillary articulating area; maxillary mala shallowly cleft subapically; 3-segmented palp. Labium free to base of mentum and possessing apically rounded ligula and 2-segmented palps. Hypopharyngeal sclerome transversely rectangular; gular sutures separate.

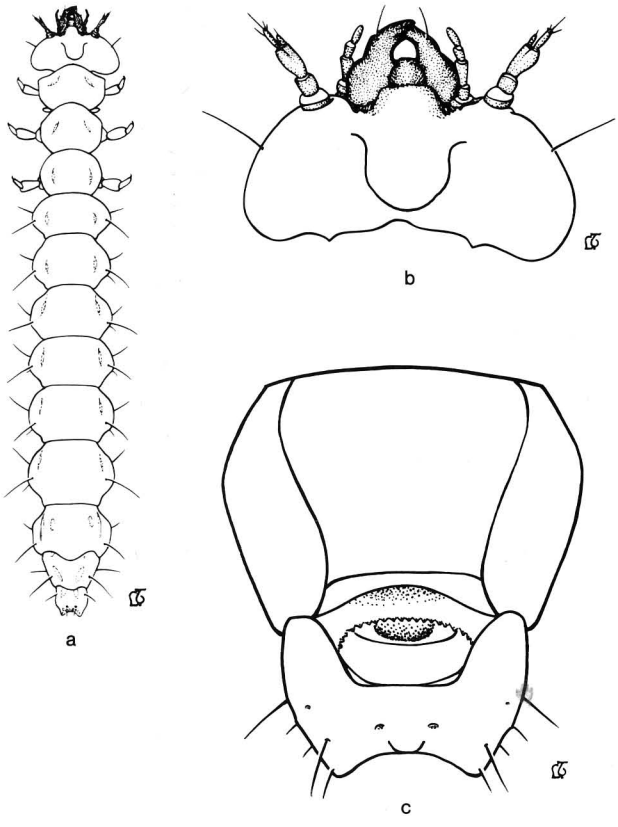

Figure 34.665

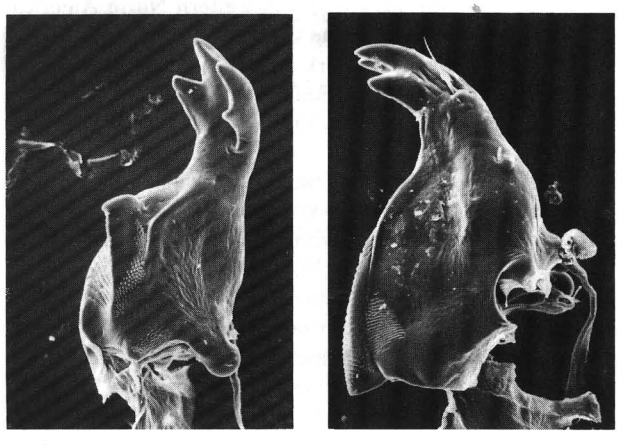

Figure 34.666

Figures 34.665a-c. Prostomidae. *Prostomis mandibularis* (Fabricius). Pacific House, El Dorado Co., California, elev. 3400 feet, under bark of red rotten pine. **a.** larva, dorsal; **b.** head capsule, dorsal; **c.** apex of abdomen, ventral.

Figures 34.666a,b. Prostomidae. *Prostomis* sp. East slope of Mt. McKinley, Mindanao, Philippine Islands. **a.** left mandible, oroventral view; **b.** right mandible, dorsal.

Thorax and Abdomen: Thorax elongate with prothorax slightly smaller than meso- or metathorax. Legs well developed, 5-segmented including tarsungulus. Legs similar in size and shape and bearing a number of spine-like setae. Abdomen strongly flattened, lightly sclerotized; 9th segment small; tergite 9 extended ventrally, bearing lightly sclerotized, paired, short, fixed urogomphi apically; urogomphal surface bearing numerous spinulae; sternite 9 (fig. 34.665c) partially enclosed by 8th sternite, bearing a transverse row of apical asperities. Segment 10 small, concealed from above by projection of 9th tergite; anal orifice oriented ventrally.

Spiracles: Thoracic and abdominal spiracles annular-biforous, those of thorax placed apically on well developed spiracular tubes.

Comments: This small and obscure family includes only 2 genera, *Dryocora* and *Prostomis,* with 20 species distributed throughout the world. The single species, *P. mandibularis* (Fabricius), occurs in the United States and Canada. Larvae of this species were figured by Böving and Craighead (1931) along with those of *D. howitti* Pascoe from New Zealand. Several additional *Prostomis* larvae have been described (Hayashi, 1969b, 1980; Hayashi, et al., 1959; Mamaev et al., 1977).

Selected Bibliography

Böving and Craighead 1931.
Crowson 1955, 1966b, 1967.
Hayashi 1969b, 1980.
Hayashi *et al.* 1959.
Lawrence 1977c.
Mamaev *et al.* 1977.

SYNCHROIDAE (TENEBRIONOIDEA)

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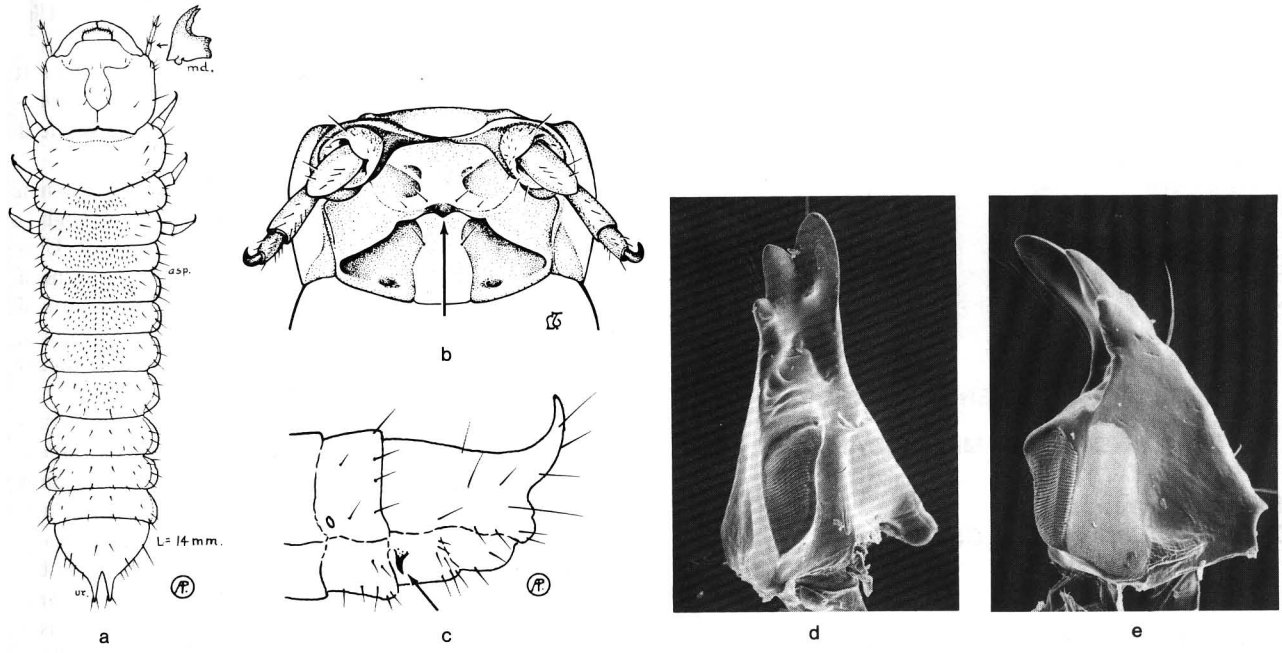
Figures 34.667a-e

Relationships and Diagnosis: Although long considered a member of the Melandryidae, *Synchroa* Newman was excluded on the basis of a critical examination of the larval stages, and proposed as the type genus of the family Synchroidae (Böving and Craighead, 1931). Viedma's (1966) analysis of melandryid larvae supported the removal, and Crowson (1966b) drew particular attention to the affinities between synchroids and the Zopheridae and Cephaloidae. The nearest relative may be found in the Cephaloidae. The presence of a single pair of asperities on the ninth abdominal sternite (fig. 34.667c) separates synchroid larvae from other Coleoptera larvae except for Pedilidae (*Pedilus, Pergetus*), Boridae (*Lecontia*), Salpingidae (*Aegialites, Rhinosimus*), Othniidae (*Aglenus*) and certain Melandryidae (e.g. *Hallomenus*). The urogomphi of synchroids, *Lecontia* and *Hallomenus* are simple; in those Pedilidae, Salpingidae, and Othniidae which have but a single pair of caudoventral asperities the urogomphi are branched. Other diagnostic features of synchroid larvae include the moderately long epicranial stem and small mesal dentiform process associated with the prothoracic sternum (fig. 34.667b).



Figures 34.667a-e. Synchroidae. *Synchroa punctata* Newman. Commonly collected in the Midwest and northeastern United States beneath somewhat loose bark of decaying hardwoods. **a.** larva, dorsal; **b.** prothorax, ventral; **c.** apex of abdomen, lateral; **d.** left mandible, oral; **e.** right mandible, dorsal. (Figures 34.667a,c from Peterson, 1951)

Biology and Ecology: Adults of *Synchroa punctata* Newman have been collected at lights and while running over the surfaces of dead deciduous trees at night. Larvae are associated with somewhat cool, moist conditions beneath slightly loose bark of decaying deciduous trees, especially wild cherry, *Prunus serotina*. Both woody and fungal materials have been extracted from the gut, but fungi appear to play a significant role in nutrition of larvae. From 1 to several years may be required for larval development depending upon the diet, and several instars commonly occur together beneath the bark of a given log. The pupal stage is spent beneath bark in a frass-walled ovate chamber prepared by the larva (Payne, 1931; Peterson, 1951; Young, unpublished notes).

Description: Mature larvae attain lengths of 15–18 mm and widths of 3–4 mm. Body orthosomatic and subcylindrical, subparallel throughout length, lightly sclerotized except for head and apices of urogomphi; vestiture of fine setae. Dorsum of meso- and metathorax and abdominal segments 1–5 beset with patches of small asperities, body otherwise generally smooth. Head and urogomphal apices yellowish-brown to piceous, remainder of body yellowish-white.

Head: Prognathous, exserted from prothorax. Epicranial suture with moderately elongate stem and lyriform frontal arms that are complete to near the antennal insertions; endocarinae absent. Labrum symmetrical, separated from fused frons and clypeus by suture. Stemmata on each side 5, 3 in anterior and 2 in posterior group. Antennal insertions fully exposed; antennae elongate, 3-segmented, small palpiform sensorium associated with segment 2. Mouthparts retracted. Mandibles (figs. 34.667d,e) heavily sclerotized, movable, asymmetrical, molar region of right mandible more prominent than that of left; apices of mandibles bidentate with single subapical tooth. Maxilla with cardo divided by internal fold and thus appearing 2-segmented, small pad-like maxillary articulating area; maxillary mala distinctly cleft subapically on adoral margin; 3-segmented palp. Labium free to base of mentum and possessing elongate, apically rounded ligula and 2-segmented palps. Hypopharyngeal sclerome molar-like with anterior surface concave, posterior rim provided with dense pile of stout, flattened setae. Mentum slightly wider than long with anterior margin shallowly emarginate; submentum rectangular, longer than wide; gular region transverse.

Thorax and Abdomen: Thorax elongate with sides subparallel; prosternum bearing a distinct mesal dentiform process (fig. 34.667b). Legs well developed, 5-segmented including tarsungulus. Legs similar in size and shape and bearing numerous stout, spine-like setae. Abdomen subcylindrical; tergite 9 extended ventrally, possessing single, shallow pit between bases of paired, heavily sclerotized, fixed urogomphi; urogomphal apices strongly curved upward; 9th sternite with single, stout asperity near each anterolateral margin (fig. 34.667c). Segment 10 more or less fused to 9th, visible ventrally surrounding anal orifice.

Spiracles: Thoracic and abdominal spiracles annular-biforous.

Comments: The 2 genera and 8 species have been found in Indonesia, Japan, and eastern North America. Worldwide, 7 species of *Synchroa* are currently recognized along with *Mallodrya subaenea* Horn. Two species, *M. subaenea* and *S. punctata* Newman, occur in North America. Larvae of *S.*

punctata and *S. melanotoides* Lewis have been described or illustrated (Böving and Craighead, 1931; Hayashi, 1980; Hayashi, *et al,* 1959; Peterson, 1951).

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ZOPHERIDAE (TENEBRIONOIDEA)

(INCLUDING MERYCIDAE)

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Ironclad Beetles

Figures 34.668-671

Relationships and Diagnosis: The Zopheridae was originally based on a few genera comprising the tenebrionid tribes Zopherini and Nosodermini (Böving and Craighead, 1931), but more recently the group has been expanded and redefined (Crowson, 1955; Doyen and Lawrence, 1979; Kamiya, 1963; Watt, 1967b, 1974a, 1974b). Possible sister groups include Synchroidae, Cephaloidae, Colydiidae-Monommidae, Perimylopidae, Chalcodryidae and Tenebrionidae (Crowson, 1966b; Doyen and Lawrence, 1979; Lawrence and Newton, 1982; Watt, 1967a, 1974a, 1974b). Although most zopherids were first described as tenebrionids, the group is easily distinguished from Tenebrionidae in both adult and larval stages. Larvae of Zopheridae differ from those of Tenebrionidae in having an internally divided cardo, cleft maxillary mala, annular-biforous spiracles (sometimes with highly reduced accessory openings), usually lyriform frontal arms, no frontoclypeal suture (occasionally vaguely indicated), and well-developed tenth abdominal segment without pygopods or spines. Larvae of *Phellopsis* are very similar to those of Synchroidae and stenotracheline Cephaloidae, from which they differ in having more or less symmetrical mandibles without transversely ridged molae and in lacking basal asperities on sternum A9 and a transverse groove on tergum A9. A cleft mala and divided cardines usually distinguish zopherid larvae from those of Colydiidae and Monommidae, and in addition zopherid mandibles resemble those of tenebrionids more than those of either group. The southern temperate family Perimylopidae differ from Zopheridae in having annular spiracles and a reduced mandibular mola.

Biology and Ecology: Adult Zopherinae and Usechinae have been recorded from the fruiting bodies of various fungi, but all known larvae appear to feed under bark or in dead, rotten wood, especially that which has been attacked by white rot (delignifying) fungi. Species of *Cotulades* in Australia are often found on lichen-covered surfaces at night, but their larvae also feed within white rotten wood. Among the Ulodinae, larvae of *Meryx* are common under the bark of fungusy logs, those of *Ulodes* and *Dipsaconia* feed in the soft fruiting bodies of *Pleurotus* or *Piptoporus,* those of *Brouniphylax* occur in woodier fungi. and those of *Syrphetodes* feed in rotten branches (Hudson, 1934).

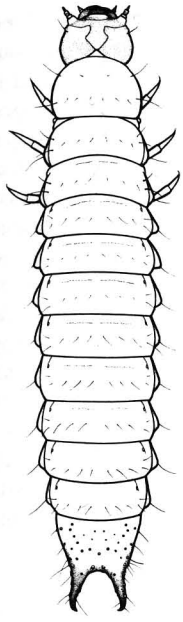
Description: Mature larvae 4 to 45 mm, usually 30 mm or less. Body elongate, more or less parallel-sided or slightly fusiform, straight, subcylindrical or slightly flattened. Usually lightly sclerotized except for buccal region and tips of urogomphi; occasionally (Ulodinae) with darker head and yellowish to dark brownish thoracic and abdominal tergites; dorsal surfaces usually smooth, occasionally (some Ulodinae) granulate; vestiture of scattered, simple setae.

Head: Protracted and prognathous, broad, slightly flattened, epicranial stem usually long (short or absent in *Phellopsis, Usechus,* and some Ulodinae); frontal arms V-shaped in Zopherinae and most Nosoderminae, lyriform in *Phellopsis, Usechus,* and Ulodinae. Median endocarina usually coincident with epicranial stem or Y-shaped, extending beneath frontal arms as well (absent in *Phellopsis, Usechus,* and *Meryx*). Stemmata on each side 5, 3 or 0. Antennae usually well-developed, 3-segmented, sometimes very short. Frontoclypeal suture usually absent (present in *Dipsaconia* and *Zopherus*); labrum free. Mandibles symmetrical or slightly asymmetrical, robust, bidentate or tridentate, without accessory ventral process; mola present, sometimes reduced in size, usually tuberculate or transversely ridged; prostheca absent. Ventral mouthparts retracted. Maxilla with transverse cardo, often distinctly divided, elongate stipes, well-developed articulating area, 3-segmented palp, and truncate mala, which is always cleft at apex and often has 1 or more teeth at inner apical angle. Labium more or less free to base of mentum; ligula present, sometimes longer than labial palps, which are 2-segmented and narrowly or broadly separated. Hypopharyngeal sclerome almost always tooth-like. Hypostomal rods absent in Zopherinae and most Nosoderminae, otherwise short to moderately long and diverging. Gula transverse.

Thorax and Abdomen: Legs well-developed, 5-segmented, sometimes short and spinose; tarsungulus usually with 2 setae lying side by side: coxae narrowly to widely separated. Meso- and metatergum and first 5 to 8 abdominal terga with patches, rows, or ridges of asperities. Tergum A9 with smooth surface and small, approximate urogomphi in Zopherinae and most Nosoderminae; *Phellopsis, Usechus* and Ulodinae with granulate and/or tuberculate 9th tergum and with larger urogomphi, which may have accessory processes (rare); sternum A9 simple. Segment A10 transverse, ventrally or posteroventrally oriented.

Spiracles: Annular-biforous, with long to very short accessory tubes (in the latter case appearing annular).

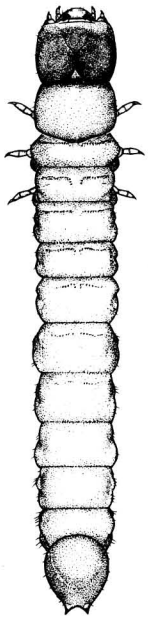
Comments: The family includes about 26 genera and 125 species worldwide, with 7 genera and 48 species in N. America. Three subfamilies are currently recognized (Doyen and Lawrence, 1979): Usechinae (*Usechus* and *Usechimorpha* from North America and Japan); Zopherinae (*Zopherus, Nosoderma, Phellopsis,* and 6 other genera from North, Central and South America, Africa, and Australia);



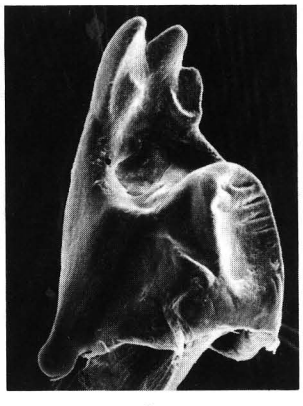
a

b

Figure 34.668



a



b

Figure 34.669

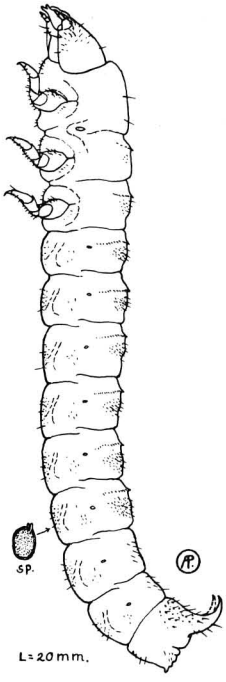


Figure 34.670

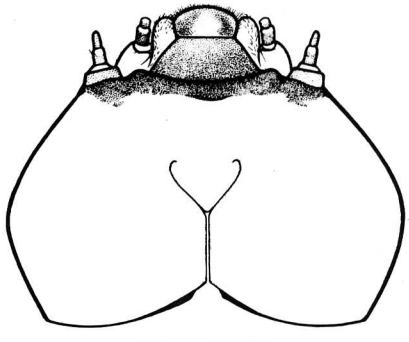


Figure 34.671

Figures 34.668a,b. Zopheridae. *Usechus lacerta* Motschulsky. Santa Clara Co., California. **a.** larva, dorsal, length = 8.5 mm; **b.** right mandible, mesoventral.

Figures 34.669a,b. Zopheridae. *Nosoderma* sp. 10 mi. S Las Vigas, Veracruz, Mexico. **a.** larva, dorsal, length = 15.5 mm; **b.** right mandible, mesoventral.

Figure 34.670. Zopheridae. *Phellopsis obcordata* (Kirby). Larva, lateral (plus details). Length = 20 mm. (From Peterson, 1951)

Figure 34.671. Zopheridae. *Zopherus nodulosus* Solier. Head, dorsal.

and Ulodinae (bulk of the genera from Chile, New Zealand, and Australia). The Australian genus *Meryx* is usually placed in a distinct family on the basis of adult features (Crowson, 1955); larvae of *Phellopsis* are quite distinct from other Zopherinae (Doyen and Lawrence, 1979); and the systematic position of several southern temperate groups is still uncertain.

Selected Bibliography

Böving and Craighead 1931 (larvae of *Phellopsis obcordata* (Kirby)).
Crowson 1955, 1966b.
Doyen 1976 (larva of *Phloeodes diabolicus* LeConte).
Doyen and Lawrence 1979 (larvae of *Brouniphylax varius* (Broun), *Dipsaconia pyritosa* Pascoe, *Meryx rugosa* Latreille, *Nosoderma* sp., *Syrphetodes punctatus* Broun, *Usechus lacerta* Motschulsky, *Zopherus granicollis* Horn, and *Z. nodulosus* Solier; key to New World genera).
Hudson 1934 (larvae of *Brouniphylax varius* and *Syrphetodes punctatus*).
Kamiya 1963.
Keleinikova and Mamaev 1971 (larva of *Phellopsis amurensis* Heyden).
Lawrence and Newton 1982.
Peterson 1951 (larva of *Phellopsis obcordata*).
Watt 1967b, 1974a, 1974b.

PERIMYLOPIDAE (TENEBRIONOIDEA)

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This family includes 4 genera and 8 species occurring in southern Patagonia and Tierra del Fuego (Argentina and Chile) (*Hydromedion* and *Chanopterus*), the Falkland Islands (*Darwiniella*), and South Georgia (*Hydromedion* and *Perimylops*). The group is closely related to Zopheridae.

Larvae are of moderate size (7–15 mm), elongate, parallel-sided, and slightly flattened, with moderately heavily sclerotized head and visible terga, and vestiture of simple setae. The head is slightly flattened, with a short epicranial stem, lyriform frontal arms, 5 stemmata on each side, and long antennae, with segments 1 and 2 subequal and the third reduced. Mandibles have 3 or 4 teeth at the apex, no mola or prostheca, and a few small, hyaline teeth at the base. The ventral mouthparts are retracted, with a rounded, cleft mala, 3-segmented maxillary palps, 2-segmented labial palps, and a well-developed ligula. Hypostomal rods and ventral epicranial ridges are absent. The legs are long, widely separated, with a bisetose tarsungulus. Tergum A9 bears a pair of complex urogomphi, each with an accessory process or pregomphus at the base. Segment A10 is transversely oval and posteroventrally oriented, with a sclerotized tergum. Spiracles are annular, those on the abdomen being subequal.

Perimylopids are usually collected under stones and moss and in tufts of tussock grass, but *Perimylops antarcticus* Müller has been taken in large numbers under carcasses. Larval gut contents of *Hydromedion* included fragments of grass leaves and inorganic matter.

Selected Bibliography

Doyen and Lawrence 1979 (relationships).
St. George 1939 (larva of *Perimylops antarcticus* Müller).
Watt 1967b (larva of *Hydromedion sparsutum* Müller; relationships), 1970 (larva of *Perimylops antarcticus*).

CHALCODRYIDAE (TENEBRIONOIDEA)

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This family includes the Tasmanian species *Sirrhas limbatus* Champion and 5 New Zealand species in the genera *Chalcodrya, Onysius,* and *Philpottia.* Adult chalcodryids have a number of features in common with Zopheridae and Perimylopidae, but the larvae resemble those of certain tenebrionids.

Larvae are moderately large (up to 30 mm), elongate, parallel-sided, and subcylindrical or slightly flattened, with a darkly pigmented head and lightly pigmented, brownish-yellow terga. The head is slightly flattened and evenly tuberculate, with a long epicranial stem, no median endocarina, V-shaped frontal arms, joined anteriorly by a transverse ecdysial line, 5 stemmata on each side, relatively short antennae, and a pair of sharp ridges extending anteriorly from the frontoclypeal region. The mandibles are bidentate, with a simple, concave mola and no prostheca. The ventral mouthparts are retracted, with a divided cardo, simple and rounded mala, 3-segmented maxillary palps and 2-segmented labial palps. Hypostomal rods and ventral epicranial ridges are absent, the legs are relatively long and slender, widely separated, with a bisetose tarsungulus. The meso- and metatergum and abdominal terga 1 to 8 each have a transverse ridge near the anterior edge, a transverse row of asperities near the posterior edge, and several more asperities of varying size on the disc. Tergum A9 is simple, without urogomphi, and segment A10 is transversely oval, more or less terminally oriented, with a sclerotized tergum and a pair of pygopods, each bearing a few lateral asperities. Spiracles are annular or annular-multiforous, larger and more elliptical anteriorly, smaller and more circular posteriorly.

Larvae of *Chalcodrya variegata* Redtenbacher have been collected in or beaten from dead twigs and branches, but they apparently emerge at night to feed on mosses and lichens.

Selected Bibliography

Watt 1974a (larva of *Chalcodrya* sp.; relationships).

TENEBRIONIDAE (TENEBRIONOIDEA)

(INCLUDING ALLECULIDAE, COSSYPHODIDAE, LAGRIIDAE, NILIONIDAE, RHYSOPAUSSIDAE, TENTYRIIDAE)

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Darkling Beetles, Mealworms, False Wireworms

Figures 34.672–693, and Figures 34,28, 34.45, 34.46

Relationships and Diagnosis: The limits of the family Tenebrionidae as used here conform to those of Watt (1967a) and Doyen and Lawrence (1979), with the inclusion of the Alleculidae, Lagriidae, Nilionidae, Cossyphodidae, and several genera, like *Myrmechixenus,* formerly placed in other families. The group is the largest in the superfamily, and is relatively easily distinguished in both larval and adult stages from other Tenebrionoidea. Diagnostic larval characters found in all members of the family include: the presence of a frontoclypeal suture, simple malar apex which is not cleft, simple 9th sternum, and annular or annular-multiforous spiracles; and the absence of an endocarina, mandibular prostheca, hypostomal rods, ventral prolegs, and patches or rows of tergal asperities. In addition, most species have a characteristic antennal sensorium, which is almost always flat and dome-like and usually C-shaped, so that it forms an incomplete ring around the terminal segment (or its fused remnant in species with 2-segmented antennae). Soil-dwelling tenebrionid larvae superficially resemble wireworms (larvae of many Elateridae) and have thus been called false wireworms; elaterid larvae are easily distinguished from those of Tenebrionidae,

however, by their more flattened head with a fused labrum, the presence of 1 large stemma on each side (or the absence of stemmata), the lack of a mandibular mola, and the presence of biforous spiracles with a distinct ecdysial scar. The phylogenetic relationships of Tenebrionidae are not clear, and possible related groups include Chalcodryidae, Perimylopidae, Zopheridae (and the related colydiid-monommid complex), Synchroidae, Cephaloidae, and Oedemeridae. Among these groups, a frontoclypeal suture is found only in Chalcodryidae, zopherine and a few ulodine Zopheridae, *Nematoplus* (Cephaloidae), and *Calopus* (Oedemeridae); most of these have a cleft or otherwise modified malar apex, *Nematoplus* has a highly asymmetrical head, *Calopus* has distinct ventral prolegs, and *Chalcodrya* has rows of tergal asperities and a transverse ecdysial line joining the frontal arms anteriorly. Annular-biforous spiracles will also distinguish all but Oedemeridae, Perimylopidae and Chalcodryidae.

Biology and Ecology: The majority of adult Tenebrionidae are relatively large, heavily sclerotized, dark in color, long-lived, and active at night, either on the ground or on the surfaces of logs or tree trunks. In some groups (Phrenapatini, some Pycnocerini, some Opatrini, Trachyscelini, Ulomini) the adults are adapted for burrowing into substrates, occupying the same habitats as their larvae; while in others (Lagriini, Cyphaleini, Alleculini, Cnodalonini, and Strongyliini) the adults are relatively soft-bodied, short-lived, and often diurnal and brightly colored. Brachyptery and aptery are common, and characterize almost all members of certain large taxa, like Tentyriinae and Adeliini. Many ground-inhabiting tenebrionids inhabit deserts and exhibit a number of morphological, physiological, and behavioral adaptations to arid, sandy environments (subelytral cavity, sand-walking and sand-swimming modifications, water catchment devices) (Cloudsley-Thompson, 1965; Dizer, 1955; Koch, 1962; Medvedev, 1965; Seely, 1976; Seely and Hamilton, 1976). A major feature of many adult tenebrionids is the presence of defense glands located near the abdominal apex and sometimes on the prothorax; the morphology of these glands, the chemistry of the secretions, and the types of defensive behavior (posturing, stridulation, distribution of secretions) associated with the gland system vary greatly and have been the subject of several recent studies (Eisner *et al.*, 1964, 1974; Kendall, 1968, 1974; Tschinkel, 1975a, 1975b, 1975c; Tschinkel and Doyen, 1980).

Tenebrionids are primarily saprophagous, feeding on a variety of dead plant and animal matter, including humus, leaf litter, rotten wood and cambium, wind-blown detritus, carrion, and dung; some soil-dwelling larvae, however, will feed on living plant roots or seedlings, while some forest-dwellers have become specialized fungus-feeders or facultative predators. Larvae may be divided into 2 groups according to major habitat: 1) xylophilous larvae, which occur in rotten wood and associated cambium and subcortical spaces, and 2) geophilous larvae, which occur in the soil and leaf litter. These will be discussed separately below.

Those larvae which bore directly into wood which has been softened and chemically altered by the action of various fungi include all or most Phrenapatini, Zolodinini, Tenebrionini, Cyphaleini, Amarygmini, Ulomini, Coelometopini, Cnodalonini, and Strongyliini, and some Adeliini, Diaperini, Gnathidiini, Alleculini, and Helopini. The tribes Alphitobiini, Triboliini, Hypophloeini, and Diaperini, include a number of smaller tenebrionids which occur under bark or in the galleries of bark beetles, ambrosia beetles, or wood borers, where they are primarily mycophagous. Larvae of the diaperine *Adelina plana* (Fabricius) have been found in a yeast-rich, fermenting tree wound along with larvae of *Anchorius* (Biphyllidae) and *Cryptarcha* (Nitidulidae). Species of *Corticeus* (Hypophloeini) are common under bark in the galleries of Scolytidae; although the majority are mycophagous, most will feed on larval, pupal or teneral bark beetles, and a few are normally predaceous, if not obligately so (Nikitsky, 1976b; Parker and Davis, 1971; Schedl, 1962; Struble, 1930). Species of *Lyphia* (Triboliini) occur in bamboo and palm fronds, where they prey on larvae of lyctine and dinoderine Bostrichidae (Hinton, 1948b); some *Tribolium* and *Palorus* have also been recorded as semipredators.

Those mycophagous Tenebrionidae which have become specialized for feeding on the reinforced hyphae comprising the relatively large and durable fruiting bodies of Basidiomycetes (especially Polyporaceae, Hymenochaetaceae, and Tricholomataceae) belong to the tribes Bolitophagini (including Rhipidandrini), Diaperini, Dysantini, and Toxicini. Most bolitophagines occur in the large conks of *Ganoderma* and *Fomes* species, but *Eleates* and *Megeleates* are commonly associated with *Fomitopsis pinicola,* a brown rot of conifers, while some species of *Rhipidandrus* and *Eledona* frequent dried mushrooms or smaller polypores. Within the diaperine genus *Platydema,* the degree of host preference varies, and species like *P. oregonense* LeConte and *P. americanum* Laporte and Brullé breed in a variety of fungal types, while *P. neglectum* Triplehorn is restricted to *Cryptoporus volvatus,* a peculiar polypore on conifers, and *P. ellipticum* (Fabricius) breeds only in *Phellinus gilvus* and related Hymenochaetaceae. The 2 species of *Neomida* in N. America appear to have nonoverlapping niches, in that *N. ferruginea* (LeConte) occurs in the larger, brownish fruiting bodies of *Ganoderma* and *Fomes* species, while *N. bicornis* (Fabricius) prefers the smaller, light-colored brackets of *Coriolus versicolor, Lenzites betulina,* and related forms. Other fungus-feeding Diaperini include *Alpitophagus bifasciatus* (Say) and species of *Diaperis, Pentaphyllus,* and *Ceropria.*

Surface-grazing on algae, lichens, and mosses growing on wood, bark, and occasionally rock surfaces, has been described for *Cylindronotus laevioctostriatus* (Goeze) (Helopini) (Brendell, 1975) but is probably of much wider occurrence within the family. The habit is not common in larvae, but it has been observed in Nilionini, Leiochrini, *Titaena* (Cyphaleini), and a species of *Amarygmus* (Amarygmini) (Jorge, 1974; Watt, 1974b).

Various xylophilous tenebrionids have come to inhabit the nests of birds, ants, or termites, and often the same groups have become stored products pests. Termitophily is known in the Rhysopaussini (probably a specialized group of Amarygmini) and in *Pseudeba novica* Blackburn; myrmecophily occurs in *Tribolium myrmecophilum* Lea; various *Tribolium* are known to inhabit the nests of wild bees; and species of *Tenebrio, Alphitobius,* and *Palembus* have been recorded

from bird nests. Other invasions of these habitats have involved geophilous species (*see* below). All of the important stored products pests in this family have been derived from xylophilous members of the tribes Tenebrionini, Triboliini, Alphitobiini, and Diaperini; these are listed under *Comments* below.

The geophilous Tenebrionidae include the assemblage of tribes (Tentyriini, Asidini, Pimeliini, etc.) often forming the subfamily Tentyriinae, the Goniaderini, most Adeliini and Lagriini, Phaleriini, most Helaeini and Nyctozoilini, Scaurini, Blaptini and Eleodini, Opatrini (in the broad sense), Trachyscelini, Crypticini, Apocryphini, some Alleculini and some Helopini. The group may be further divided into the surface and litter inhabitants, like Adeliini, Lagriini, Goniaderini, some Opatrini and Apocryphini, and those whose larvae burrow through the soil. Many of the latter group occur in the steppes and deserts, and some, like Phaleriini, Trachyscelini, and some Opatrini, are restricted to littoral regions, where they occur in the soil beneath dune plants or in seaweed, carrion, or other organic debris. Some members of this group, like the Stenosini, Cossyphodini, and some Opatrini (*Scleron, Notibius*) have become associated with ants, while others (some Opatrini) may inhabit nests of ground-nesting birds. Some members of the Eleodini (*Embaphion*) and the Australian helaeine group (*Pterohelaeus* and *Brises*) have invaded caves and probably feed on bat guano. Crop pests in Europe and America occur mainly in the tribes Opatrini, Eleodini, Blaptini, and Alleculini (*see Comments*).

Description: Mature larvae 5 to 70 mm. Body usually elongate and cylindrical to slightly flattened, occasionally short and broad, fusiform, or strongly flattened. Head and all trunk segments usually evenly, lightly to heavily sclerotized, occasionally with head and 9th tergum more heavily sclerotized than rest of body. Surfaces usually smooth, without patches or rows of asperities, sometimes with large, flat-bottomed punctures, occasionally with transverse carinae; abdominal apex sometimes more heavily sculptured; vestiture usually consisting of scattered short and/or long setae (body densely setose in Lagriini, Nilionini, and some groups of Tentyriinae).

Head: Protracted and prognathous to slightly declined, globular or slightly flattened. Epicranial stem usually long, occasionally short, and rarely absent; frontal arms almost always V- or U-shaped. Median endocarina absent. Stemmata 5 or fewer on each side, often inconspicuous or absent. Antennae usually 3-segmented, with elongate 2nd segment and with segment 3 small and much narrower than 2; sometimes with segment 3 highly reduced or absent, so that antennae are only 2-segmented (Lagriinae); rarely with basal segment also reduced, so that only a single segment is apparent (some Leiochrini). Sensorium usually flattened and dome-like, often forming an incomplete ring around the base of segment 3, occasionally elongate and conical or complex (sinuous or subdivided). Antennal insertions lateral, usually adjacent to the mandibular articulations, separated from them by a narrow strip of membrane; sometimes separated by a sclerotized bar which may be broad (Leiochrini, Nilionini). Frontoclypeal suture distinct. Labrum usually transverse, with few to many setae; tormae usually with transverse mesal arms which may be united at midline. Epipharynx usually with an anterior, subanterior, and posterior group of sensilla, a centrally located pair of short setae, an asymmetrical pair of posterior plates, and lateral setose patches. Mandibles usually more or less asymmetrical, short, stout, and subtriangular, with 1 to 3 apical teeth and a sharp incisor edge, sometimes bearing an additional tooth; molae well-developed and usually concave, irregularly tuberculate, or coarsely ridged, sometimes finely transversely ridged, the left one often with a projecting premolar lobe or tooth; prostheca and accessory ventral process absent; basolateral portion of dorsal surface sometimes with an elevated, setose, membranous area; outer edge occasionally carinate. Ventral mouthparts retracted; maxilla with transverse, subtriangular, undivided cardo, slightly elongate stipes, well-developed articulating area, 3-segmented palp, and rounded or truncate mala, which is not cleft, but sometimes slightly notched and only rarely with an uncus at the inner apical angle. Labium almost always with distinct mentum and submentum and usually with the latter separated by a suture from the gula; labial palps 2-segmented, broadly separated to subcontiguous; ligula usually present. Hypopharyngeal bracon present; hypopharyngeal sclerome well-developed, often bicuspidate or tricuspidate, often with setose, membranous elevation in front of it. Hypostomal rods always absent, ventral epicranial ridges rarely present (Toxicini). Gula well-developed, usually subquadrate to elongate (rarely transverse or undifferentiated).

Thorax and Abdomen: Prothorax usually slightly larger than meso- or metathorax. Legs well-developed, 5-segmented; prothoracic legs often much stouter and/or longer, with larger and denser setae or spines; legs usually more or less contiguous, but sometimes moderately widely separated; tarsungulus, especially that of prothoracic leg, sometimes very large and heavily sclerotized, and occasionally divided into 2 parts; 2 tarsungular setae usually unequal in length. Thoracic and abdominal terga usually simple (except for median ecdysial line) or occasionally with transverse carinae, tergum A8 sometimes with well-developed carina or 2 posteriorly-projecting tubercles. Thoracic and abdominal segments sometimes with paired or occasionally median gland openings located on terga or sterna. Tergum A9 usually terminal, extending onto ventral surface, its armature diagnostic at various levels; apex of tergum A9 simple and rounded, triangular, or bearing an acute median process, pair of urogomphi, concave plate or more complex armature; tergum A9 more rarely restricted to dorsal surface so that segment A10 is terminal. Sternum A9 long to very short, and sometimes highly reduced and not clearly separated from segment A10, almost always simple, without asperities. Segment A10 reduced, posteriorly to ventrally located, often with a pair of projecting pygopods, which may be spinose; sternum A9 and segment A10 occasionally concealed beneath the abutting edges of sternum A8 and tergum A9.

Spiracles: Annular, with circular or oval peritreme, which may be crenulate or lined with very small accessory chambers.

Comments: The family includes about 1700 genera and 18,000 species worldwide, with about 200 genera and 1550 species occurring in America north of Mexico. The subfamily and tribal classification has been the subject of recent studies (Doyen, 1972, 1984, 1985; Doyen and Lawrence, 1979; Doyen and Tschinkel, 1982; Watt, 1974b) and is undergoing further revision. Since the subfamilial and tribal concepts used in the discussions above are based on these recent studies, they do not correspond to those given in Arnett (1968). The Lagriinae refers to the family Lagriidae plus the genera *Anaedus, Paratenetus* and *Prateus* in N. America. Tentyriinae includes the tribes usually placed in Tentyriinae and Asidinae plus the Coniontini (*sensu* Doyen, 1972), *Alaephus, Eupsophulus, Alaudes,* and *Cnemeplatia.* Opatrini is used in the broad sense to include most of the Opatrini and Pedinini. Ulomini is restricted to *Uloma* and related genera, such as *Eutochia* and *Ulosonia,* while the rest of the ulomine genera listed in Arnett are placed in Alphitobiini (*Alphitobius*), Triboliini (*Tribolium, Lyphia, Latheticus, Palorus, Mycotrogus,* and *Tharsus*), Diaperini (*Gnatocerus, Cyaneus, Sitophagus, Adelina* (= *Doliema*), and *Doliopines*), or Hypophloeini (*Corticeus*). Goniaderini includes only *Anaedus* in the N. American fauna. The Tenebrionini, as understood here, includes *Tenebrio, Neatus, Zophobas, Scotobaenus, Centronopus,* and *Bius,* while the rest of the genera usually included in that tribe are placed in Coelometopini.

The Tenebrionidae include a number of economically important species which damage crops or more commonly stored products. Those larvae living in the soil and damaging cultivated plants are usually called false wireworms; they include *Eleodes* species in North America, species of *Blaps* (Blaptini), *Opatrum* and *Gonocephalum* (Opatrini), and *Omophlus* and *Podonta* (Alleculini) in Eurasia and North Africa, and species of *Pterohelaeus* (Helaeini) and *Gonocephalum* in Australia. Those species occurring in stored products are secondary pests of varying importance primarily in grains and cereal products. They include: the broad-horned flour beetle, *Gnatocerus cornutus* (Fabricius); slender-horned flour beetle, *G. maxillosus* (Fabricius); *Sitophagus hololeptoides* (Laporte); large black flour beetle, *Cyaneus angustus* (LeConte); 2-banded fungus beetle, *Alphitophagus bifasciatus* (Say); *Palembus ocularis* Casey; yellow mealworm, *Tenebrio molitor* L.; dark mealworm, *T. obscurus* Fabricius; confused flour beetle, *Tribolium confusum* Jacquelin duVal; red flour beetle, *T. castaneum* (Herbst); black flour beetle, *T. audax* Halstead; long-headed flour beetle, *Latheticus oryzae* Waterhouse; depressed flour beetle, *Palorus subdepressus* (Wollaston); small-eyed flour beetle, *P. ratzeburgi* (Wissmann); lesser mealworm, *Alphitobius diaperinus* (Panzer); and black fungus beetle, *A. laevigatus* (Fabricius). Some of these, such as *Tenebrio molitor* and *Alphitobius diaperinus* occur on a wide variety of plant and animal materials, and the latter is commonly found breeding in poultry manure; others like the species of *Gnatocerus, Palorus, Tribolium,* and *Latheticus* are most important as grain pests. Species of *Tribolium* are probably second only to those of *Drosophila* in their importance as study animals in genetics and population ecology.

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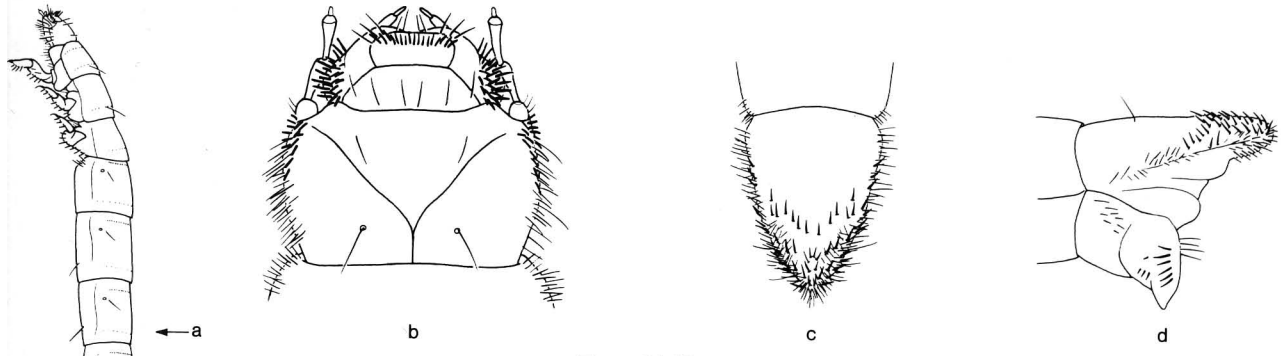


Figure 34.672

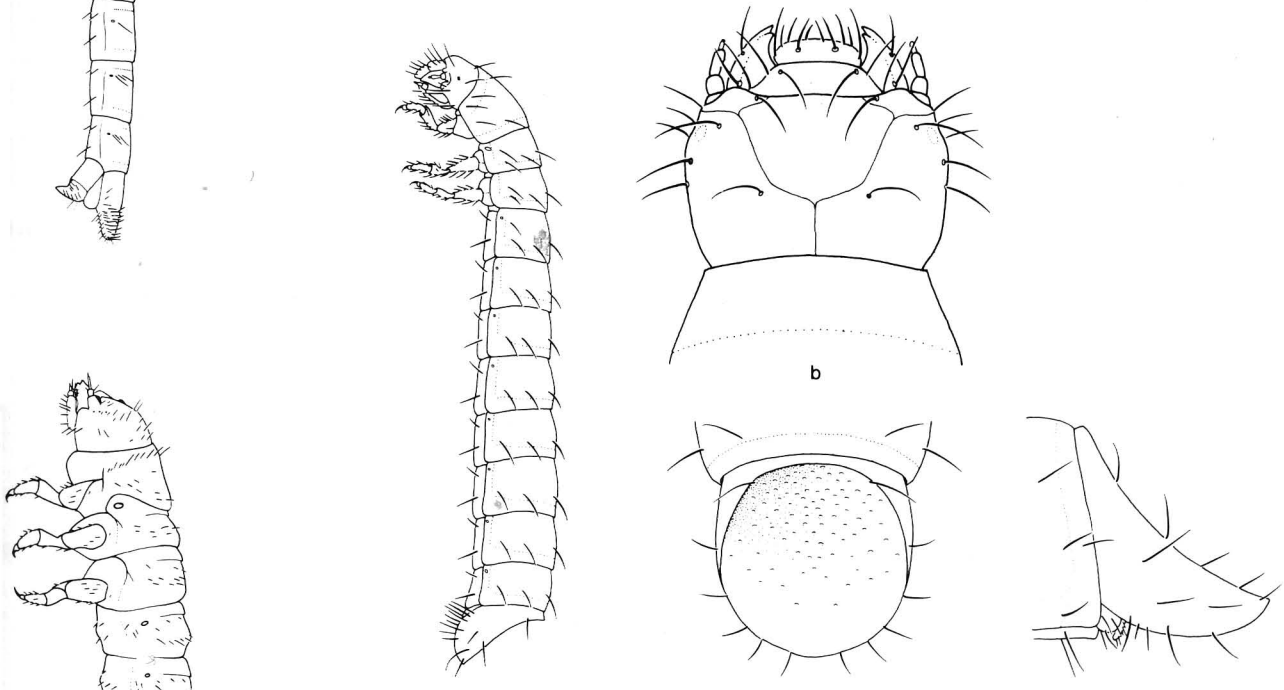


Figure 34.673

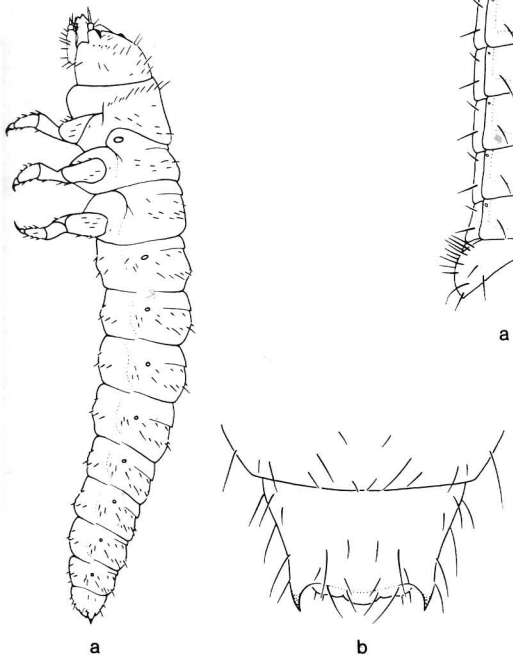
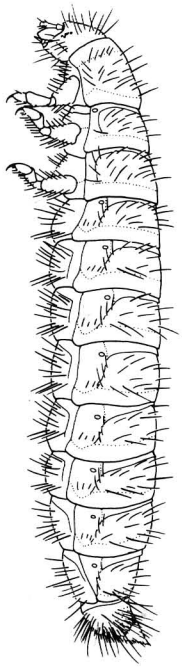


Figure 34.674

Figures 34.672a-d. Tenebrionidae. *Epitragus* sp. (Tentyriini). **a.** larva, lateral; **b.** head, dorsal; **c,d.** abdominal apex, dorsal and lateral.

Figures 34.673a-d. Tenebrionidae. *Meracantha contracta* (Beauvois) (Amarygmini). **a.** larva, lateral; **b.** head, dorsal; **c,d.** abdominal apex, dorsal and lateral.

Figures 34.674a,b. Tenebrionidae. *Bolitotherus cornutus* (Panzer) (Bolitophagini). **a.** larva, lateral; **b.** abdominal apex, dorsal. Also *see* figure 34.28 for anterior view of head. Feeds in bracket fungi.



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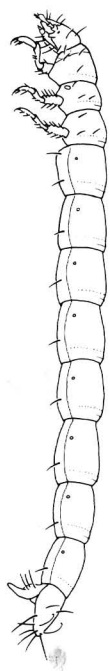

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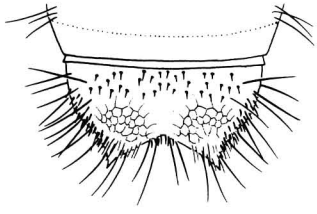

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Figure 34.675

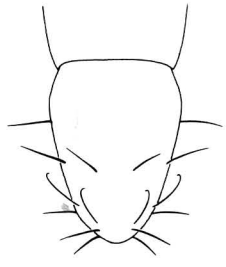

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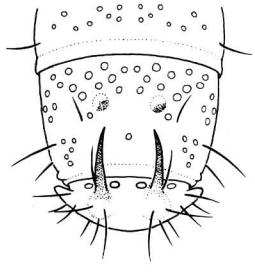
Figure 34.676



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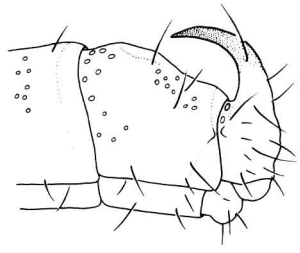

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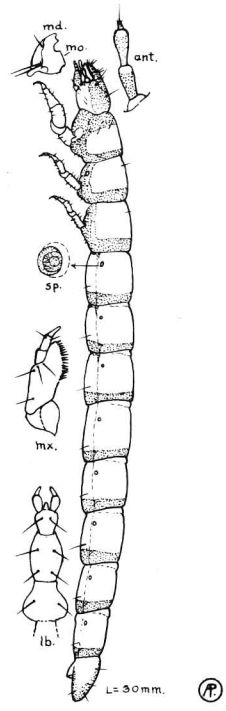
Figure 34.679



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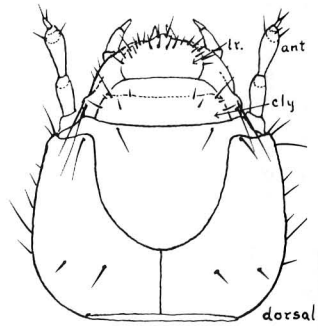

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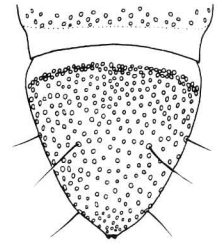
Figure 34.677



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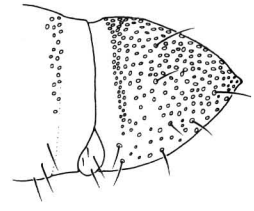

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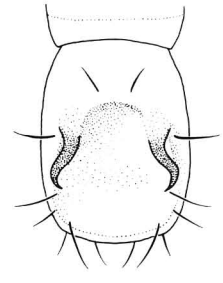
Figure 34.678



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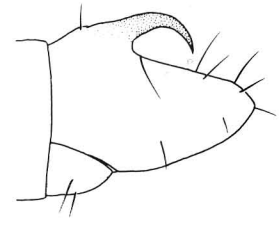


b

Figure 34.680

Figures 34.675a,b. Tenebrionidae. *Arthromacra aenea* (Say) (Lagriini). **a.** larva, lateral; **b.** abdominal apex, dorsal.

Figures 34.676a,b. Tenebrionidae. *Hymenorus niger* (Melsheimer) (Alleculini). **a.** larva, lateral; **b.** abdominal apex, dorsal.

Figures 34.677a,b. Tenebrionidae. *Capnochroa fuliginosa* Melsheimer (Alleculini). **a.** larva, lateral. Length = 30 mm; **b.** head, dorsal. Under bark of dead or dying trees and in decayed vegetation. (From Peterson, 1951)

Figures 34.678a,b. Tenebrionidae. *Uloma imberbis* LeConte (Ulomini). Abdominal apex, dorsal and lateral.

Figures 34.679a,b. Tenebrionidae. *Helops pernitens* LeConte (Helopini). Abdominal apex, dorsal and lateral.

Figures 34.680a,b. Tenebrionidae. *Dioedus punctatus* LeConte (Phrenapatini). Abdominal apex, dorsal and lateral.

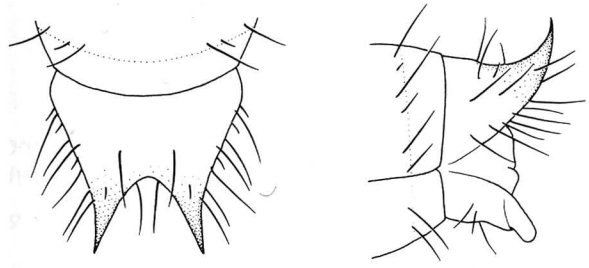


Figure 34.681

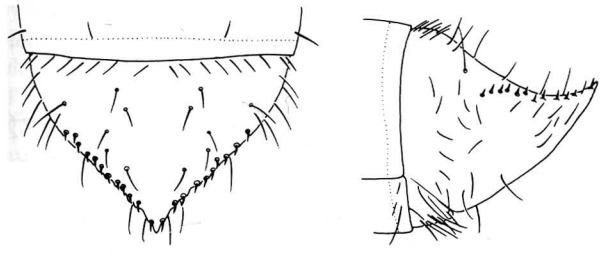


Figure 34.683

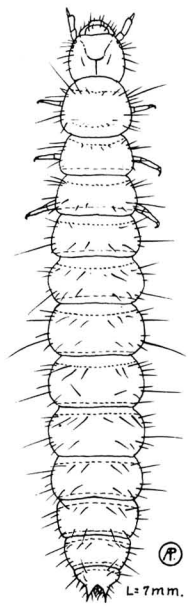
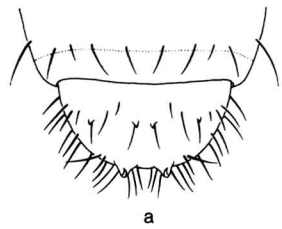


Figure 34.682



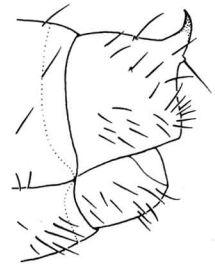


Figure 34.684

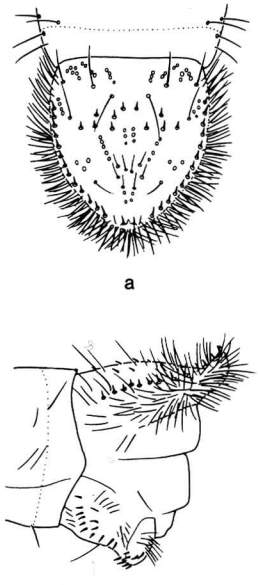
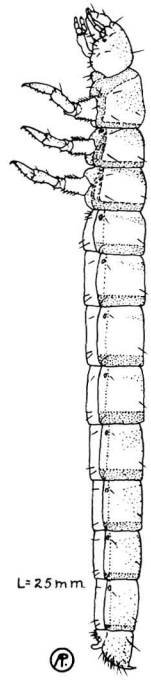
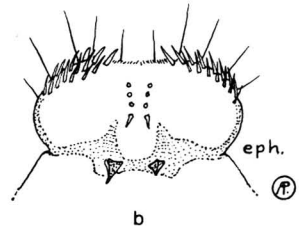
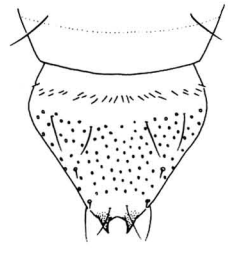


Figure 34.685







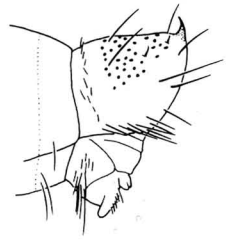


Figure 34.686

Figures 34.681a,b. Tenebrionidae. *Tribolium castaneum* (Herbst), red flour beetle (Triboliini). Abdominal apex, dorsal and lateral. Habits similar to *T. confusum* (see below).

Figure 34.682. Tenebrionidae. *Tribolium confusum* (Olivier), confused flour beetle. Larva, dorsal. Length = 7 mm. A common pest worldwide in grains, grain products and a variety of other dried foods. (from Peterson 1951)

Figures 34.683a,b. Tenebrionidae. *Asidopsis polita* (Say) (Asidini). Abdominal apex, dorsal and lateral.

Figures 34.684a,b. Tenebrionidae. *Alobates pennsylvanica* (De Geer) (Coelometopini). Abdominal apex, dorsal and lateral.

Figures 34.685a,b. Tenebrionidae. *Coniontis nemoralis* Eschscholtz (Coniontini). Abdominal apex, dorsal and lateral.

Figures 34.686a-d. Tenebrionidae. *Tenebrio molitor* L., yellow mealworm. (Tenebrionini) **a.** larva, lateral, length = 25 mm; **b.** epipharynx, **c,d.** abdominal apex, dorsal and lateral. Yellowish-brown, with dorsum, especially head and caudal segments, more reddish-brown; epipharynx with 12 ± setae near laterocephalic margin of each lateral half; ninth segment cone-shaped and terminating in 2 prominent, curved, sharp-pointed urogomphi which project dorsad. Infests refuse grain, coarse cereal bran, and mill products, especially if somewhat moist. Commonly reared for fish bait and pet food. (Figures a,b from Peterson, 1951)

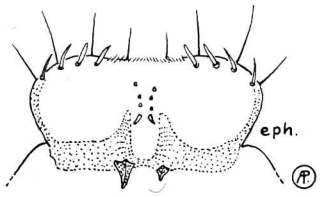


Figure 34.687

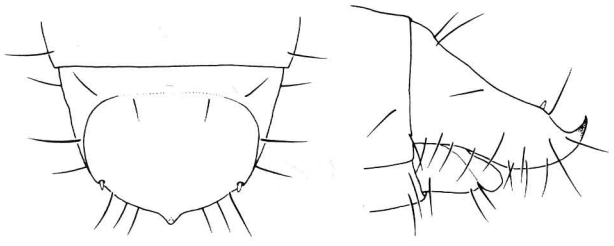


Figure 34.688

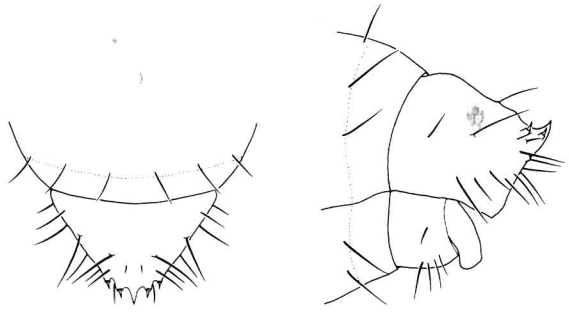


Figure 34.690

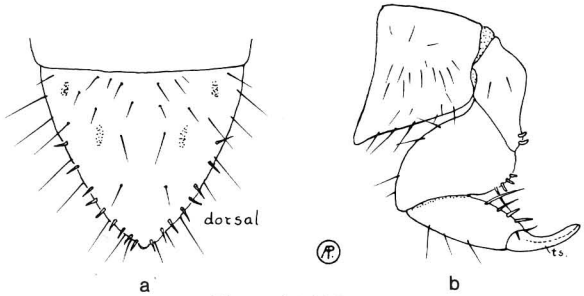


Figure 34.692

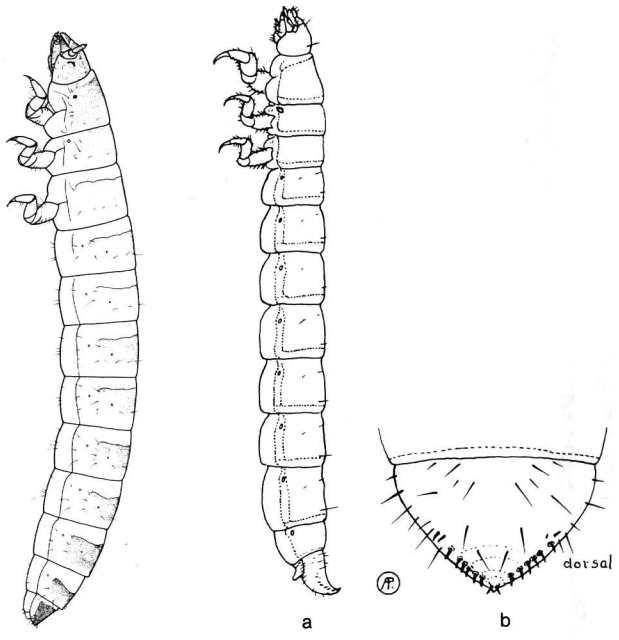


Figure 34.689

Figure 34.691

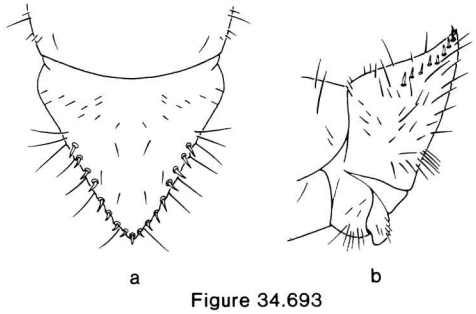


Figure 34.693

Figure 34.687. Tenebrionidae. *Tenebrio obscurus* Fabricius, dark mealworm. (Tenebrionini) Epipharynx with 4–5 spine-like setae on each half near cephalolateral margin; cone-shaped ninth segment projects caudad and terminates in 2 short, pointed urogomphi which project caudodorsad; also possesses two short spines on each lateral aspect cephalad of the urogomphi. Food habits similar to *T. molitor* L. (From Peterson, 1951)

Figures 34.688a,b. Tenebrionidae. *Phaleria rotundata* LeConte (Phaleriini). Abdominal apex, dorsal and lateral.

Figure 34.689. Tenebrionidae. *Corticeus praetermissus* (Fall) (Hypophleoini). Larva, lateral. (From Doyen and Lawrence, 1979).

Figures 34.690a,b. Tenebrionidae. *Platydema ellipticum* (Fabricius) (Diaperini). Abdominal apex, dorsal and lateral. *See* also figure 34.46, anterior part of head, dorsal, with frontoclypeal region, labrum-epipharynx, and mandibles removed, showing hypopharyngeal sclerome, and figure 34.45, right mandible, ventral.

Figures 34.691a,b. Tenebrionidae. *Eleodes suturalis* Say, false wireworm. (Eleodini) **a.** larva, lateral, length = 24 mm; **b.** abdominal apex, dorsal. Surface corneous and yellowish brown with head and distal portions of legs darker; frons V-shaped with epicranial suture .25 length of head capsule; epipharynx with broad, caudal, transverse, sclerotized band possessing 1 pair of stub-like, short, teeth near meson; prothoracic legs distinctly larger than others; lateral margins of upturned abdominal apex with 7 to 9 short spine-like setae. Infests soil planted to wheat or other small grains west of Mississippi River. (From Peterson, 1951)

Figures 34.692a,b. Tenebrionidae. *Eleodes opacus* (Say), plains false wireworm. (Eleodini) **a.** abdominal apex, dorsal. **b.** prothoracic leg. Yellowish with surface glabrous except ventral surface of head and thorax, legs and pygidium; prothoracic legs almost spineless but others spinose; abdominal apex bearing 2 small spines and lateral margins with 6 or 7 blunt spines. Found in soil of wheat west of Mississippi River. (From Peterson, 1951)

Figures 34.693a,b. Tenebrionidae. *Eleodes obsoletus* (Say) (Eleodini). Abdominal apex, dorsal and lateral.

CEPHALOIDAE (TENEBRIONOIDEA)

(INCLUDING NEMATOPLIDAE, STENOTRACHELIDAE)

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Figures 34.695-697

Relationships and Diagnosis: The limits of the family are still in dispute, and the inclusion of Stenotrachelinae by Crowson (1955, 1966b) and Arnett (1968) has been rejected by Mamaev (1973), who considered this group and also *Nematoplus* to be in separate families, and by Hayashi (1963) who placed *Stenocephaloon* in the Melandryidae. The larvae of *Stenotrachelus* and *Stenocephaloon* closely resemble those of *Synchroa* (Synchroidae) and *Phellopsis* (Zopheridae); the former differ in having a pair of basal asperities on sternum A9 and a median tooth on the prosternum, while the latter differ in having more symmetrical mandibles and no transverse groove on tergum A9. Larvae of *Nematoplus* and *Cephaloon* bear a strong resemblance to those of Oedemeridae and bolitophagine Tenebrionidae in the lightly sclerotized body, asymmetrical head capsule, and highly asymmetrical, transversely ridged, mandibular molae, and both groups have been considered likely relatives (Lawrence and Newton, 1982; Mamaev, 1973). Oedemerid larvae differ from those of cephaloids in having either abdominal "prolegs" (asperity-bearing ampullae) or patches of tergal asperities, while bolitophagine tenebrionids have annular spiracles. The family Meloidae has also been considered close to Cephaloidae (Abdullah, 1965; Lawrence and Newton, 1982), but all meloid larvae lack a mandibular mola.

Biology and Ecology: Little is known about the habits of adult cephaloids, but they are relatively rare and probably short-lived. Some have been collected from flowers (Arnett, 1968) and the mouthparts are consistent with pollen- or nectar-feeding, but Mamaev (1973) suggested that adult feeding in *Nematoplus* might not be necessary for egg maturation. Larvae of all species feed on decaying wood. Those of *Stenotrachelus aeneus* Paykull are found under bark or in the wood of dead angiosperms, including *Salix, Populus, Alnus,* and *Betula,* and are only rarely associated with conifers (Palm, 1959; Saalas, 1913). *Nematoplus* larvae feed in highly decomposed wood of stumps or logs which are infested with brown rots (fungi which selectively destroy cellulose); the wood is usually somewhat reddish and may be referred to as being in the red rot stage. At least some species of *Cephaloon,* like *C. variabilis* Motschulsky and *C. ungulare* (LeConte), have similar habits, but according to Mamaev (1973), *C. pallens* Motschulsky is usually found in large branches of deciduous trees.

Description: Mature larvae 10 to 25 mm. Body elongate, more or less parallel-sided, straight, subcylindrical to slightly flattened, lightly sclerotized except for buccal region and occasionally (Stenotrachelinae) tips of urogomphi; dorsal surfaces usually smooth; vestiture of scattered, simple, setae.

Head: Protracted and prognathous, broad, usually asymmetrical, sometimes broader than thorax, slightly flattened. Epicranial stem long and frontal arms V-shaped in *Cephaloon* and *Nematoplus;* epicranial stem absent and frontal arms lyriform and contiguous at base in Stenotrachelinae. Median endocarina usually Y-shaped, coincident with epicranial stem and frontal arms (absent in Stenotrachelinae). Stemmata 5 or 6 on each side, sometimes absent. Antennae well-developed, 3-segmented. Frontoclypeal suture present in *Nematoplus* only. Mandibles strongly asymmetrical, tridentate, without accessory ventral process; molae large and transversely ridged, the left one more or less parallel to long axis and produced at apical end, the right one strongly oblique; prostheca absent. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, and rounded or truncate mala, which may be weakly emarginate at apex and may bear 1 or more teeth at inner apical angle. Labium free to base of mentum; ligula well-developed; labial palps 2-segmented. Hypopharyngeal sclerome tooth-like. Hypostomal rods absent in *Cephaloon* and *Nematoplus,* short and diverging in Stenotrachelinae. Gula transverse.

Thorax and Abdomen: Legs well-developed, 5-segmented; tarsungulus with 2 setae lying side by side. Meso- and metatergum and abdominal terga 1–6 with rows and patches of asperities in Stenotrachelinae. Tergum A9 granulate or tuberculate in Stenotrachelinae and bearing a pair of upturned urogomphi, sclerotized at apex; tergum A9 smooth in *Cephaloon* and *Nematoplus,* the former with a pair of posteriorly projecting, straight, lightly sclerotized urogomphi, and the latter without urogomphi; sternum A9 simple. Segment A10 transverse, more or less posteriorly oriented in *Cephaloon* and *Nematoplus,* ventrally or posteroventrally oriented in Stenotrachelinae.

Spiracles: Annular-biforous, with long or short accessory tubes.

Comments: The family is a small one, containing about 20 species and 7 genera restricted to the cooler parts of the Holarctic Region; the N. American fauna consists of 4 genera and 10 species. Three distinct subfamilies are recognized: Cephaloinae (*Cephaloon*), Nematoplinae (*Nematoplus, Pedilocephaloon*), and Stenotrachelinae (*Stenotrachelus, Stenocephaloon, Anelpistus,* and *Scotodes*).

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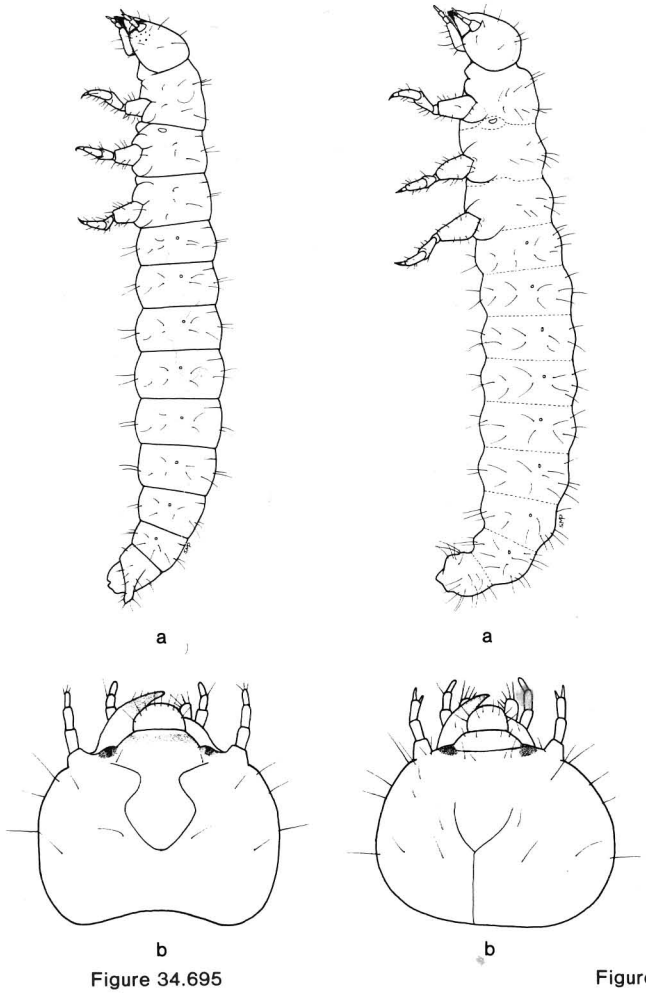


Figure 34.695

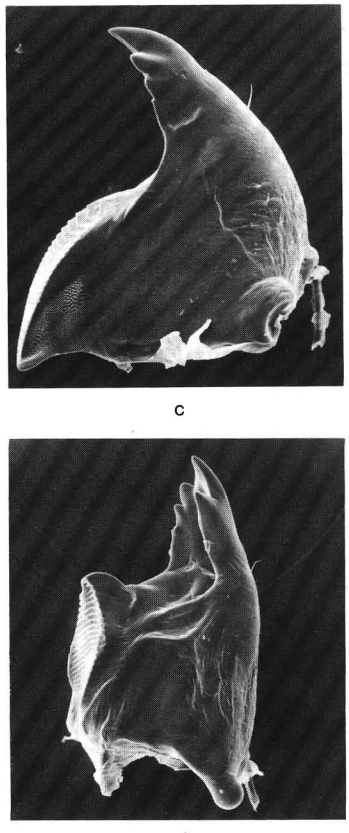


Figure 34.696

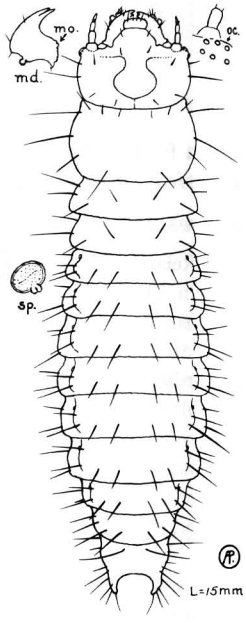


Figure 34.697

Figures 34.695a,b. Cephaloidae. *Cephaloon ungulare* (LeConte). Jefferson Notch, Coos Co., New Hampshire. **a.** larva, lateral, length = 22.6 mm; **b.** head, dorsal.

Figures 34.696a-d. *Cephaloidae. Nematoplus collaris* LeConte. Jefferson Notch, Coos Co., New Hampshire. **a.** larva, lateral, length = 17.4 mm; **b.** head, dorsal; **c.** right mandible, dorsal; **d.** left mandible, ventral.

Figure 34.697. *Cephaloidae. Cephaloon* sp. Larva, dorsal (plus details). Length = 15 mm. (From Peterson, 1951)

MELOIDAE (TENEBRIONOIDEA)

Richard B. Selander, *University of Illinois*

Blister Beetles, Oil Beetles

Figures 34.698-709

Relationships and Diagnosis: The Meloidae and Rhipiphoridae were isolated from other Heteromera (= Tenebrionoidea) as Meloidea by Böving and Craighead (1931) because of anatomical and behavioral similarities in the first larval instar; some authors would add the Stylopoidea (= Strepsiptera). Meloid larvae are specialized predators of insect eggs, larvae and provisions, whereas rhipiphorid and stylopoid larvae are parasitoids, each attacking a single insect host and spending at least part of the feeding period within its body. Moreover, on the basis of adult anatomy, the meloids and rhipiphorids are more similar to "non-parasitic" Anthicidae and Mordellidae-Scraptiidae, respectively, than to each other, and the Stylopoidea are distinctive enough to warrant assignment to a separate superfamily (Crowson, 1955; Selander, 1964) or an independent order Strepsiptera as is done here (Lawrence and Newton, 1982).

Meloidae exhibit hypermetamorphosis, the larva typically passing through 4 phases (fig. 34.698): triungulin (T), first grub (FG), coarctate (C), and second grub (SG). T larvae are campodeiform or navicular, heavily sclerotized, and active. Phoretic triungulins, in particular, may be confused with first instar rhipiphorids but have 1 or 2 (rather than several) stemmata on each side of the head, well developed labial palpi (except in *Tetraonyx*), a line of dehiscence on the thorax, and lack pulvilli. FG larvae superficially resemble larval Scarabaeidae, from which they differ in having the antennae

3-segmented, the mandibles similar to each other and lacking a definite molar area, the tarsungulus with 2 (1 in *Tetraonyx*) setae, and the abdomen 9-segmented and lacking a raster. C larvae, which are heavily sclerotized and immobile and have the mouthparts and legs reduced to stubs, are more likely to be mistaken for Diptera puparia than for beetle larvae. SG larvae are generally similar to FG larvae (*see* below).

Biology and Ecology: So far as known (Eleticinae have not been studied), larval meloids are predatory. Most Meloinae and all Nemognathinae attack the nesting cells of bees, where they consume both the immature host and the provisions in 1 or more cells. Most species of the subtribes Epicautina and Mylabrina (Meloinae) prey on grasshopper eggs. Some Epicautina, at least, are evidently predators of meloid eggs (Selander, 1981). Phoresy of T larvae on adult bees is characteristic of the Meloini (in the Meloinae) and all Nemognathinae.

The ontogenetic cycle of Meloidae is diagrammed in fig. 34.698. Typically, the larva, after beginning to feed in the first instar, grows rapidly through 4 instars of the FG phase (FG_{2-5}), passes a more or less extended period of inactivity in the C phase (C_6), and finally reverts to a grublike form (SG_7) before becoming a pupa. In most Meloinae the C larva and pupa occupy chambers in the soil excavated during the preceding instar. In Nemognathinae the FG_5 and C_6 exuviae are not cast off by the larva but rather encapsulate it.

In response to high temperature, many *Epicauta* develop directly from the FG phase to the pupal stage. In addition, larvae of this genus may have an extra instar (FG_6) in the FG phase. Presumably in response to adverse conditions, larvae of some Lyttini may revert to the C phase after reaching the SG phase. Rarely, some of the subtribe Lyttina skip the SG phase. Most meloids pass the winter or dry season as C larvae but a few do so by diapausing in the egg, T larval phase, or adult stage.

Eggs cylindrical, white to orange, without sculpturing, laid in masses of a few score to a few thousand in soil (Meloinae), on plants (especially bracts) (most Nemognathinae), or near or in nests of host bees (degenerate nemognathines such as *Tricrania* and *Hornia*).

Pupa typical coleopteran, with (Meloinae, fig. 34.709) or without bracing spines on dorsum.

Description: The larval phases are so distinctive that it is convenient to treat them separately.

T Phase: (figs. 34.699–34.705) Length 0.6–4.5 mm. Body heavily sclerotized, campodeiform or (Nemognathinae) navicular, with conspicuous spiracles on mesothorax and abdominal segments 1–5 (Tetraonycini) or 1–8, a definite pattern of setae on body and legs, and generally a line of dehiscence on thorax, often extending onto abdomen.

Head: Prognathous, often with a basal transverse ridge in phoretic larvae. Epicranial suture well developed, with frontal sutures shortened, reduced to coronal suture, or entirely absent. Gula well developed, with 2 setae (in Meloinae). One or (Nemognathini) 2 stemmata on each side of head. Antennae 3-segmented, inserted before middle of head, with sensory organ (often cone-shaped) at apex of segment 2; segment 3 with long terminal seta. Labrum distinct, closely applied ventrally to head capsule (subtribe Pyrotina), or fused with frontoclypeus to form a nasale (Nemognathinae). Mandibles working horizontally in non-phoretic larvae, more or less vertically in phoretic ones, smooth, dentate, or (many Nemognathinae) with transverse ridges. Maxillae with stipes large, cardo distinct or not; palps 3-segmented, conspicuous. Labium with mentum (1st and 2nd prementa) weakly sclerotized; palps 2-segmented (absent in Tetraonycini).

Thorax: Nota well sclerotized, sterna weakly so in most Meloinae, strongly so in Nemognathinae. Legs slender, elongate, 5-segmented; tarsungulus conical, set with 1 (Tetraonycini), 2, or several (some of the subtribe Mylabrina) slender setae, or spatulate and with 2 spatulate setae, forming a trident (*e.g.*, many *Meloe*, fig. 34.701). Pulvilli absent.

Abdomen: With 9 segments of more or less uniform length and a much reduced tenth segment; terga heavily sclerotized, sterna variably so; tergites with an anterior median group of minute setae and median transverse and posterior marginal rows of setae; pleurites distinct or not. Spiracles of segment 8 on hooklike elevations in Nemognathini, those of segment 1 on large lateral extensions in Tetraonycini. Urogomphi absent; end of abdomen with a pair of large caudal setae except in Nemognathini.

FG Phase: (figs. 34.706, 34.707a) Maximum length 5–25 mm. Differs from T phase as follows: Thorax and abdomen membranous, pale, the body progressively more scarabaeiform with growth. Body setae often numerous in later instars. Spiracles present on mesothorax, metathorax, and abdominal segments 1–8, often dorsal in position in early instars.

Head: Initially prognathous, becoming hypognathous with growth. Epicranial suture well developed, fine. Stemmata replaced by subcuticular black eye spots. Antennae with sensory organ small; segment 3 becoming shorter in successive instars, lacking a long terminal seta. Labrum fleshy, exposed. Mandibles massive, dentate or not. Labial palps always present, 1 or 2-segmented.

Thorax: Pronotal and prosternal plates present in later instars. Tarsungulus conical, bearing 2 short setae.

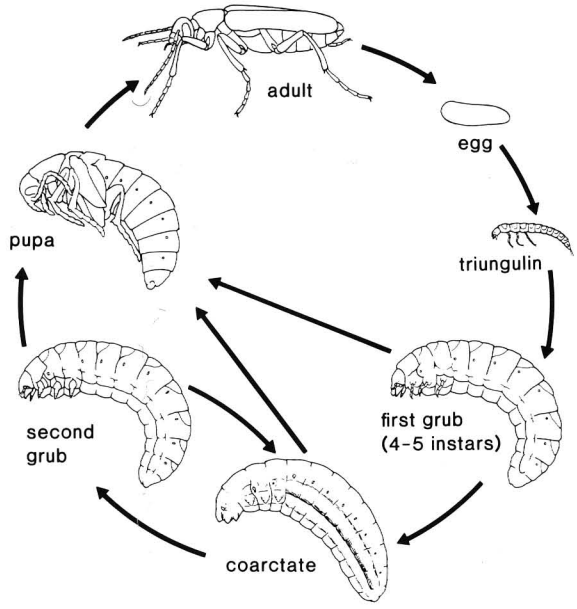
Abdomen: Segments lobed, with a distinct ridge lateroventrally. Spiracles small, round.

C Phase: (figs. 34.707b, 34.708) Body less C-shaped than in late instar FG larva; cuticle thick, very heavily sclerotized, leathery, brown, glabrous. Body segments fused. Appendages reduced to unsegmented stubs, fused to body. Spiracles normally oval, elevated, those on abdominal segment 8 vestigial in Nemognathinae. Oral cavity and anus closed. Musculature vestigial.

SG Phase: (fig. 34.707c) Much like late-instar FG larva, but with body setae shorter and somewhat sparser, head less strongly sclerotized, labial palps often vestigial, legs shorter and thicker, tarsungulus vestigial or absent, and spiracles oval.

Spiracles: See each phase above.

Comments: A large family (about 2500 species) of considerable ecological importance because of its larval biology. In addition, adults of some species (especially of *Epicauta* and *Mylabris*) are crop pests. T (triungulin) anatomy is extensively employed taxonomically, due largely to the pioneering work of Cros (1940) and MacSwain (1956); other larval phases have been largely neglected in this regard.



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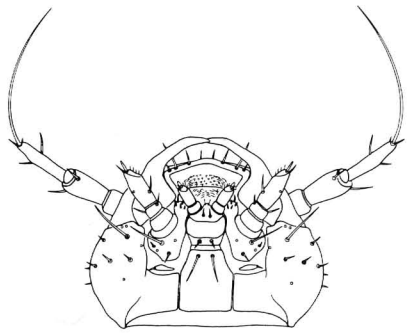

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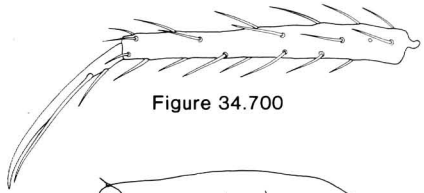

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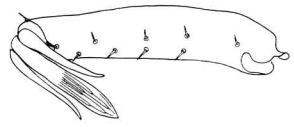

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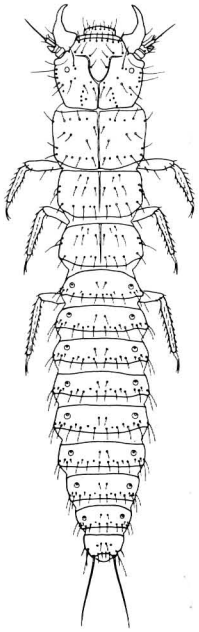

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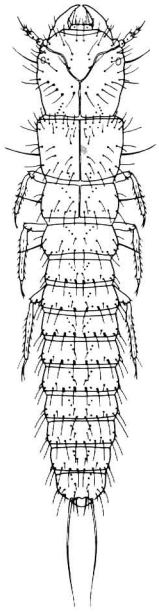

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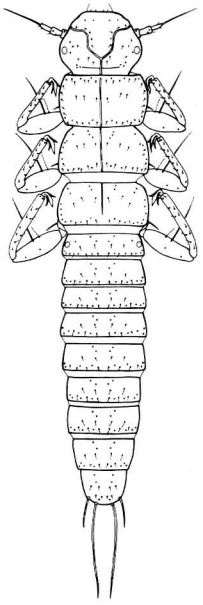

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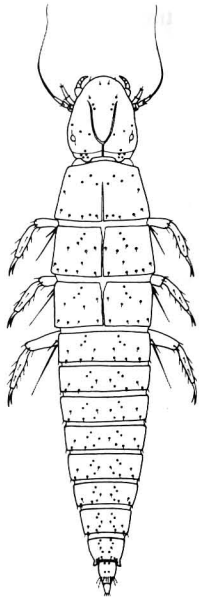


Figure 34.705

Figures 34.698–34.705. Meloidae.

Figure 34.698. Ontogenetic cycle. (Redrawn from Selander & Weddle, 1969, reprinted with permission from the Entomological Society of America.)

Figure 34.699. *Meloe americanus* Leach, T_1, head, ventral (after Pinto & Selander, 1970). © 1970, reprinted with permission of the Board of Trustees, University of Illinois.

Figure 34.700. *Megetra cancellata* (Brandt & Erichson), T_1, hind tibia and tarsungulus.

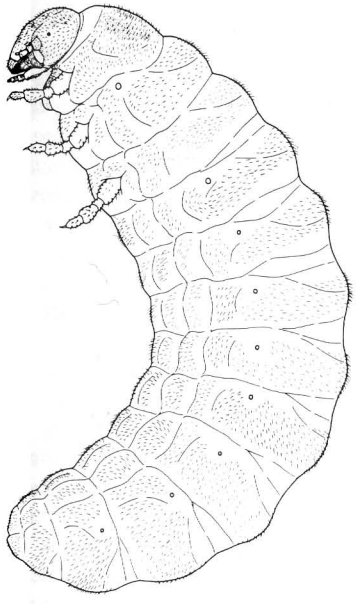
Figure 34.701. *Meloe angusticollis* Say, T_1, hind tibia and tarsungulus. Note the "3-clawed" (triungulin) appearance.

Figure 34.702. *Lytta mutilata* Horn, T_1.

Figure 34.703. *Epicauta segmenta* (Say), T_1.

Figure 34.704. *Meloe dianella* Pinto & Selander, T_1.

Figure 34.705. *Nemognatha piezata* (Fabricius), T_1.



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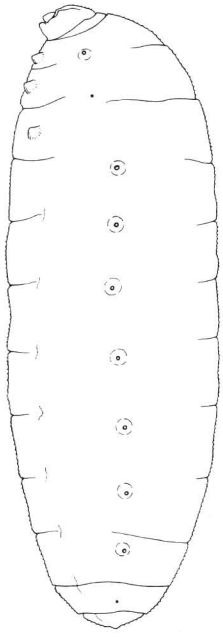

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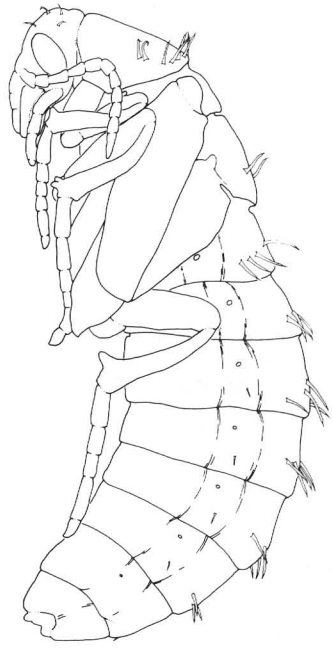

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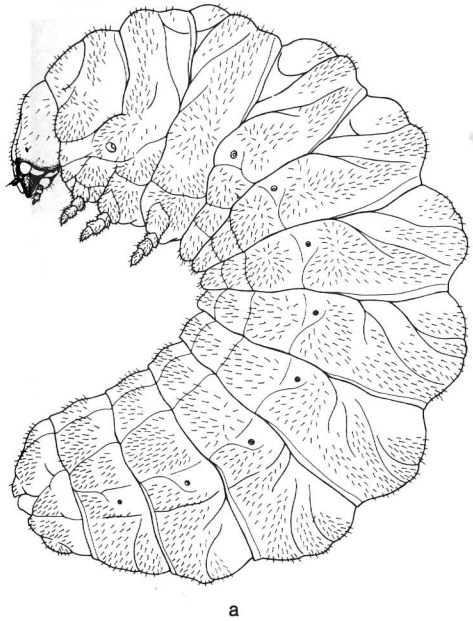

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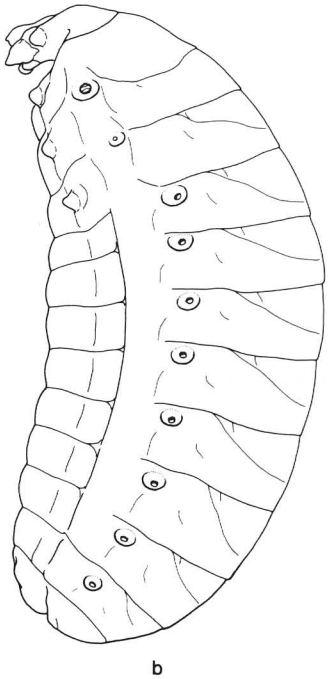

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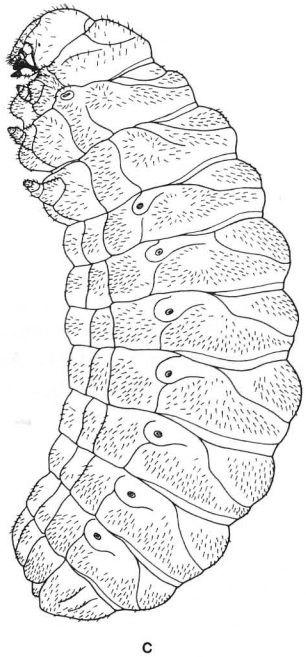

c

Figure 34.707

Figure 34.706. Meloidae. *Meloe dianella,* FG_5 (after Pinto & Selander, 1970). © 1970, reprinted with permission of the Board of Trustees, University of Illinois.

Figures 34.707a-c. Meloidae. *Epicauta segmenta,* **a.** FG_5; **b.** C_6; **c.** SG_7.

Figure 34.708. Meloidae. *Nemognatha lutea* LeConte, C_6.

Figure 34.709. Meloidae. *Pyrota palpalis* Champion, pupa (after Selander & Mathieu, 1964).

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OEDEMERIDAE (TENEBRIONOIDEA)

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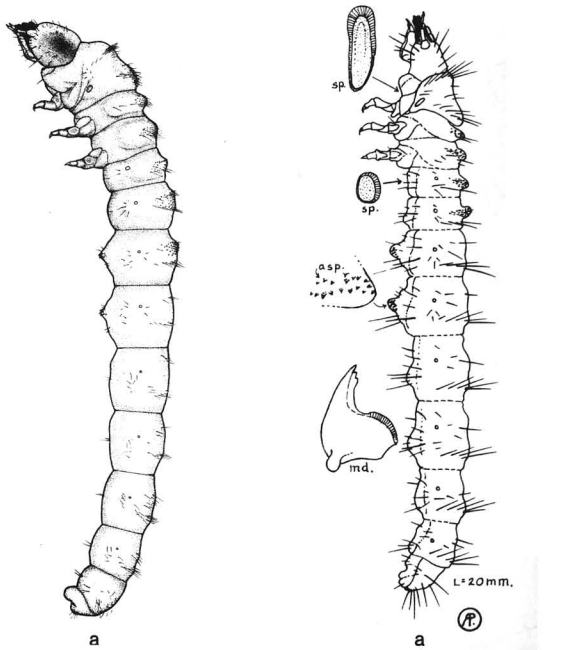
Division of Entomology, CSIRO

Figures 34.710-712

Relationships and Diagnosis: The Oedemeridae are a distinctive group of tenebrionoid beetles, whose closest relatives are probably to be found among the Cephaloidae, Synchroidae, and Zopheridae (Hayashi, 1975; Lawrence and Newton, 1982; Mamaev, 1973; Rozen, 1960). Most oedemerid larvae differ from those of other Coleoptera in having asperity-bearing ampullae on the anterior abdominal terga and sterna, with those on the sterna resembling the prolegs of Lepidoptera; other characters include the relatively large head and highly asymmetrical mandibular molae, the usual absence of urogomphi, lack of frontoclypeal suture and hypostomal rods (both present in *Calopus*), and presence of a well-developed and usually columnar prehypopharynx in front of the hypopharyngeal sclerome. The only oedemerids lacking the abdominal ampullae are the Old World Oedemerini, which are typical in all other respects.

Biology and Ecology: Adult Oedemeridae are often found on flowers, where they feed on nectar and pollen. Most oedemerid larvae feed in dead wood, especially that which is relatively soft and rotten, but many of the Oedemerini occur in the stems or roots of shrubs or herbaceous plants, and *Calopus* has been reported damaging living trees. Larvae may be associated with both white and brown rots, and some have been found in rotten structural timber. Many occur in driftwood, which may be intermittently submerged in fresh or salt water. *Nacerdes melanura* (L.) may cause damage to wharves or pilings, while the Oedemerini are possible agricultural or horticultural pests because of their stem and root boring habits (Arnett, 1968; Burke, 1906; Horion, 1956; Rozen, 1958, 1960).

Description: Mature larvae 10 to 40 mm, usually 25 mm or less. Body elongate, parallel-sided, straight or slightly curved ventrally, and subcylindrical, always very lightly pigmented, except for buccal region and occasionally tips of urogomphi, color nearly white: surface smooth and vestiture of scattered, simple setae.



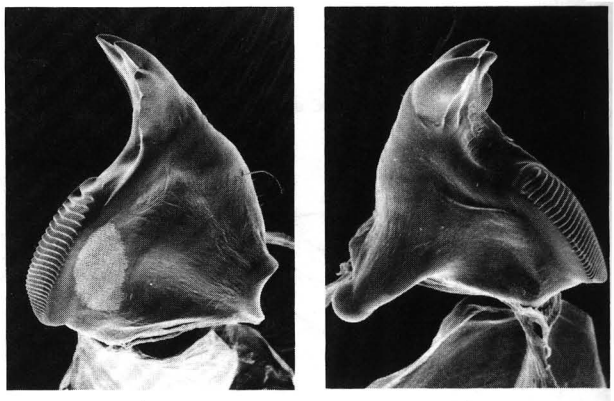


Figure 34.710

Figure 34.711

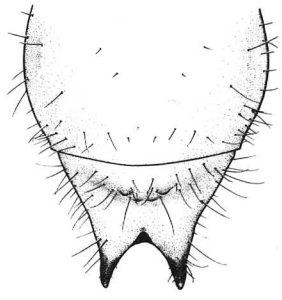


Figure 34.712

Figures 34.710a,b. Oedemeridae. *Ditylus* sp. Edge of Deep Lake, Vernon, British Columbia. **a.** larva, lateral, length = 38.6 mm; **b.** right mandible, dorsal.

Figures 34.711a,b. Oedemeridae. *Nacerdes melanura* (L.). **a.** larva, lateral view (plus details), length = 20 mm; **b.** right mandible, ventral. St. John, New Brunswick. (Figure 34.711a from Peterson, 1951)

Figure 34.712. Oedemeridae. *Calopus angustus* LeConte. Vancouver, British Columbia. Abdominal apex, dorsal.

Head: Protracted and prognathous, broad, sometimes asymmetrical, slightly flattened. Epicranial stem moderately to very long; frontal arms usually V-shaped (lyriform in *Calopus*). Median endocarina Y-shaped, coincident with epicranial stem and frontal arms. Stemmata usually absent, sometimes 2 or 5 on each side. Antennae well developed, 3-segmented, with reduced 3rd segment. Frontoclypeal suture usually absent (present in *Calopus*); labrum free. Mandibles strongly asymmetrical, bidentate or tridentate, without accessory ventral process; molae large and transversely ridged, the left one more or less parallel to long axis and produced apically, the right one strongly oblique; prostheca absent. Ventral mouthparts retracted. Maxilla with transverse cardo, sometimes distinctly divided, elongate stipes, well-developed articulating area, 3-segmented palp, and rounded mala which is sometimes broadly emarginate at apex and usually has a single tooth at inner apical angle (2 or 3 teeth in *Calopus*). Labium free to base of mentum; ligula well developed or sometimes reduced; labial palps 2-segmented. Hypopharyngeal sclerome a distinct tooth-like structure, in front of which is a distinct and usually columnar prehypopharynx. Hypostomal rods usually absent (moderately long and slightly diverging, but not well sclerotized in *Calopus*). Ventral epicranial ridges absent. Gula transverse.

Thorax and Abdomen: Thorax relatively short, but usually somewhat wider than abdomen. Legs short, moderately to widely separated; tarsungulus with 2 setae lying side by side. Thorax usually with paired patches of asperities on all terga, occasionally absent or present on meso- and metatergum only. Meso- and metatergum and abdominal terga 1–2 or 1–3 (1–5 in *Calopus*) with asperity-bearing ampullae (absent in Oedemerini). Abdominal sterna 2–3, 3–4 or 2–4 usually with paired, asperity-bearing ampullae (on 2–5 in *Calopus,* absent in Oedemerini). Tergum A9 usually without urogomphi or with a very small, lightly sclerotized pair; in *Calopus* with well-developed, upturned urogomphi with pit between them; sternite A9 usually simple, in *Calopus* with 3–4 asperities on each side at base. Segment A10 transverse, posteriorly or posteroventrally oriented.

Spiracles: Annular or annular-multiforous.

Comments: The family contains about 100 genera and 1500 species worldwide, with 17 genera and about 75 species occurring in America north of Mexico. Three subfamilies are usually recognized: Calopodinae (*Calopus, Sparedrus, Sparedropsis,* and *Ocularium*), distributed throughout the Holarctic Region, and extending into southeast Asia and Central America; Nacerdinae (*Nacerdes, Xanthochroa,* and a few other genera); and Oedemerinae, which is further divided into the tribes Ditylini, Asclerini, and Oedemerini (Arnett, 1951, 1961, 1968; Rozen, 1960). This classification is badly in need of world revision.

Selected Bibliography

Arnett 1951, 1961, 1968.
Burke 1906 (larva of *Calopus angustus* LeConte).
Böving and Craighead 1931 (larvae of *Calopus angustus, Copidita thoracica* (Fabricius), and *Alloxacis dorsalis* (Melsheimer)).
Duffy 1952b (larvae of *Sessinia livida* (Fabricius)).
Gardner 1929.
Hayashi 1980 (larvae of *Asclera nigrocyanea* Lewis, *Eobia cinereipennis* Motschulsky, and *Xanthochroa* sp.).
Horion 1956.
Hudson 1975 (larval characters).
Lawrence and Newton 1982.
Liebenow 1978.
Mamaev 1973 (larvae of *Calopus serraticornis* (Linnaeus), *Oedemera virescens* (L.), and *Chrysanthia viridissima* (Linnaeus)).
Peterson 1951 (larva of *Nacerdes melanura*).
Rozen 1958 (larva of *Nacerdes melanura*); 1959 (pupae representing 8 genera); 1960 (larval key; larvae of many species representing 19 genera).

MYCTERIDAE (TENEBRIONOIDEA) (INCLUDING HEMIPEPLIDAE)

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Figures 34.713–714

Relationships and Diagnosis: The Mycterinae and Laconotinae, traditionally placed in a broadly defined Salpingidae or Pythidae (Arnett, 1968; Seidlitz, 1920; Spilman, 1952), and the Hemipeplinae, formerly treated as a separate family (Arrow, 1930) or a subfamily of Cucujidae (Arnett, 1968), were combined into a single heteromerous family by Crowson and Viedma (1964), following an earlier suggestion by van Emden (1942b). The family appears to be most closely related to the Boridae and to the complex of tenebrionoid families including Pythidae, Pyrochroidae, Inopeplidae, Othniidae, and Salpingidae. Mycterid larvae may be distinguished from those of most other Coleoptera by the unique structure of the abdominal apex, in which the 9th tergum forms a hinged, terminal plate, the 10th segment is partly enclosed by the U-shaped 9th sternum, and the latter is partly contained within an emargination of sternum 8. Larvae of Boridae have a similar anal region, but they differ from mycterid larvae in having more strongly retracted ventral mouthparts, a well-developed articulating area, well-developed, asymmetrical mandibular molae, and no median endocarina; among the Mycteridae, the mandibular molae are reduced in all forms except Hemipeplinae which have a median endocarina.

Biology and Ecology: Adults of *Mycterus* are commonly collected on flowers; *M. curculionoides* has been taken on *Cistus* in Europe, *M. canescens* Horn and *M. concolor* LeConte both occur on *Ceanothus* blossoms, and *M. quadricollis* Horn is known to frequent flowers of *Yucca* in the American Southwest (Banks, 1912; Crowson and Viedma, 1964; Hopping, 1935). Some mycterids have been recorded as adults from various palms; *Mycteromimus insularis* Champion is known only from *Phoenicophorium,* while *Hemipeplus marginipennis* (LeConte) occurs on *Sabal palmetto* in the southeastern United States (Schwarz, 1878; Scott, 1933). Mycterid larvae occur under bark or in the leaf axils or dead fronds of monocotyledonous plants; they are phytophagous, and plant material has been found in the gut of several species. Larvae of *Mycterus curculionoides* were

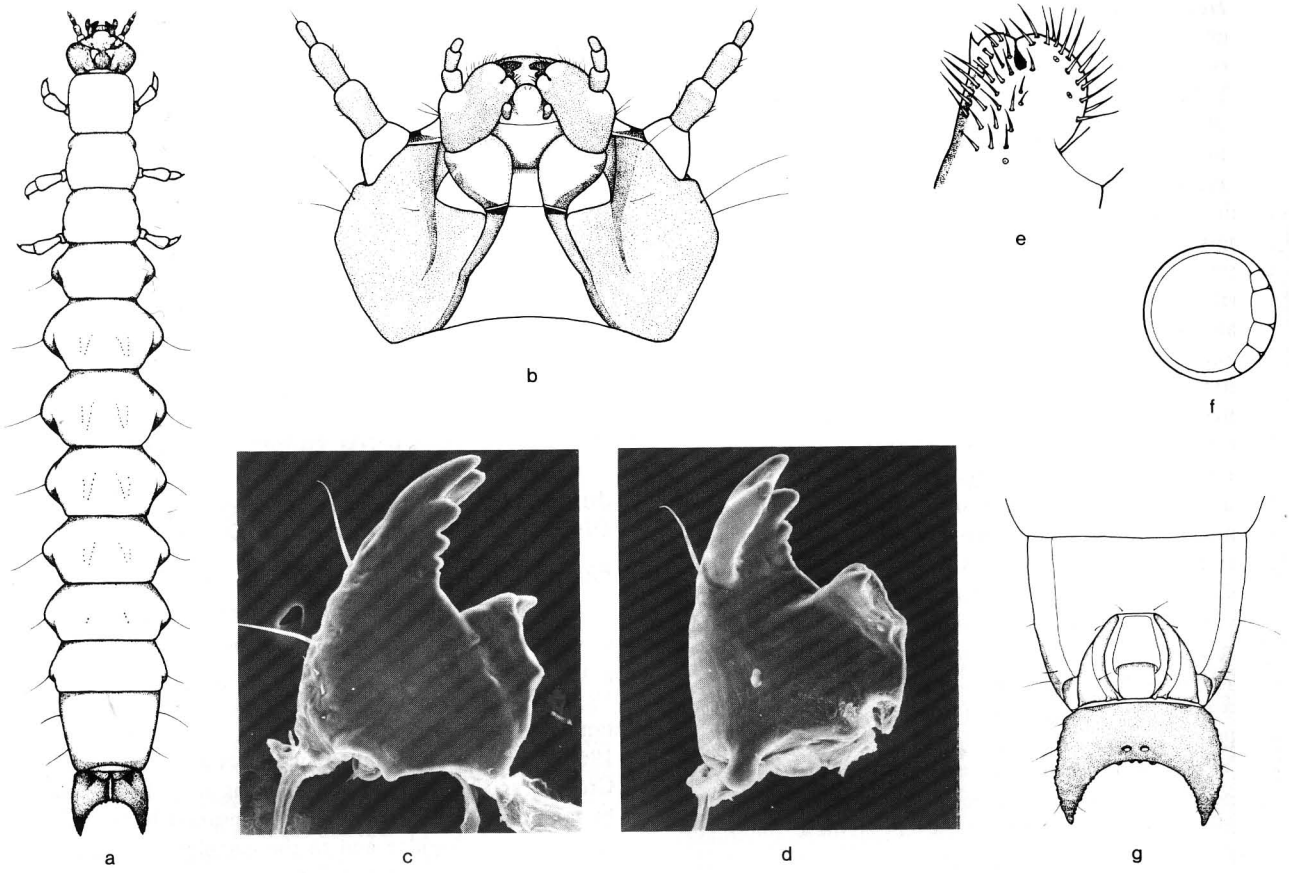

Figure 34.713

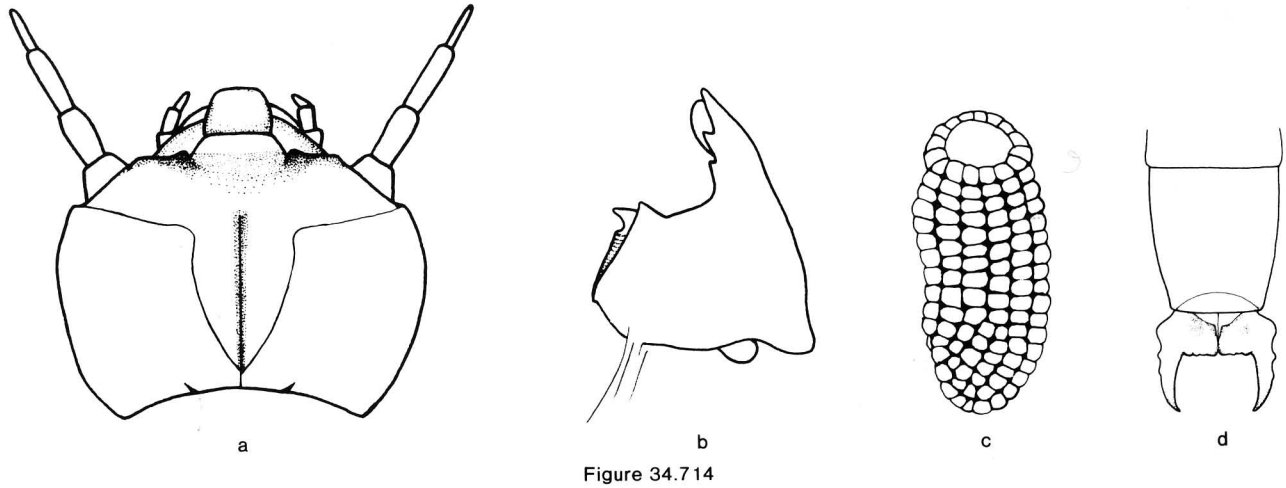

Figure 34.714

Figures 34.713a-g. Mycteridae. *Lacconotus pinicola* Horn. Chuska Mts., Apache Co., Arizona. **a.** larva, dorsal, length = 18 mm; **b.** head, ventral; **c.** left mandible, dorsal; **d.** right mandible, ventral; **e.** apex of maxillary mala, ventral; **f.** abdominal spiracle; **g.** abdominal apex, ventral.

Figures 34.714a-d. Mycteridae. *Hemipeplus marginipennis* (LeConte). Indian River, Florida. **a.** head, dorsal; **b.** right mandible, dorsal; **c.** abdominal spiracle; **d.** abdominal apex, dorsal.

taken under the bark of *Pinus,* those of *Lacconotus pinicola* Horn were found under bark of *Abies* and *Populus,* and larvae thought to be *L. pallidus* Van Dyke were found under *Quercus* bark (Crowson and Viedma, 1964). Larvae of *Eurypus muelleri* Seidlitz were collected in dead palm leaves, while those of *Eurypus rubens* Kirby and *Hemipeplus nuciferae* Arrow represent minor pests of the coconut palm; *E. rubens* was found in leaf axils and formed a pupal case from the fibrous material of the leaf, while *H. nuciferae* was observed feeding on young, unexpanded coconut leaves (Arrow, 1930; Bondar, 1940a; Costa and Vanin, 1977).

Description: Mature larvae 5 to 30 mm, usually 20 mm or less. Body elongate, more or less parallel-sided, straight, and strongly flattened. Lightly sclerotized except for head and tergum A9; surfaces smooth; vestiture of scattered, simple setae.

Head: Protracted and prognathous, broad, transversely oval, flattened. Epicranial stem short or absent; frontal arms lyriform and contiguous at base. Median endocarina usually absent, extending anterad of epicranial stem in Hemipeplinae. Stemmata 5 or 2 on each side. Antennae well developed, 3-segmented, usually with a short, dome-like sensorium. Frontoclypeal suture absent; labrum free. Mandibles symmetrical or weakly asymmetrical, bidentate or tridentate, without accessory ventral process; mola usually reduced and tuberculate or simple (well developed and transversely ridged in Hemipeplinae); prostheca absent. Ventral mouthparts slightly retracted. Maxilla with more or less longitudinally oblique cardo, short and broad stipes, well-developed articulating area, 3-segmented palp, and rounded mala, which is cleft at apex, sometimes with a tooth at inner apical angle. Labium free to base of mentum; ligula longer than labial palps, which are usually 1-segmented (2-segmented in *Mycterus*). Hypopharyngeal sclerome a transverse bar. Hypostomal rods long and diverging. Gula transverse.

Thorax and Abdomen: Thorax usually somewhat narrower than abdomen. Legs relatively short, 5-segmented, widely separated; tarsungulus usually with 2 setae lying side by side (2 setae lying one distal to the other in Hemipeplinae). Abdominal terga and sterna 2–6 each with paired rows of asperities forming incomplete rings which are longitudinally oriented. Segment A8 much longer than A7; segment A9 short. Tergum A9 heavily sclerotized and forming an articulated plate, bearing a pair of urogomphi, sometimes with median process or 2 posteriorly oriented pits between them; tergum A9 often longitudinally divided. Sternum A8 posteriorly excavated and partly enclosing sternum A9. Sternum A9 deeply excavate, forming U-shaped sclerite (or combination of sclerites), which encloses segment A10 and bears 1 to 3 asperities or teeth at each end. Segment A10 transversely oval or circular, ventrally oriented.

Spiracles: Annular-multiforous, with a series of accessory openings around peritreme or clustered at one end.

Comments: The family includes 30 genera and about 160 species worldwide, with 5 *Mycterus,* 3 *Lacconotus,* and 2 *Hemipeplus* species occurring in America north of Mexico. Mycterinae occur primarily in the drier parts of N. America, Eurasia, and North Africa, while Lacconotinae and Hemipeplinae are widespread but most diverse in the tropics.

Selected Bibliography

Arnett 1968.
Arrow 1930.
Banks 1912.
Böving and Craighead 1931 (larva of *Hemipeplus* sp.).
Bondar 1940a (larva of *Eurypus rubens* Kirby).
Costa and Vanin 1977 (larva of *Eurypus muelleri* Seidlitz), 1984b.
Crowson and Viedma 1964 (relationships; larva of *Mycterus curculioides* (Fabricius)).
Emden 1942c (larval characters of *Hemipeplus*).
Hopping 1935.
Schwarz 1878.
Scott 1933.
Seidlitz 1920.
Spilman 1952.
Thomas 1985.

BORIDAE (TENEBRIONOIDEA)

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Figures 34.715–716

Relationships and Diagnosis: Except for the addition of *Lecontia* (Young, 1985b), the scope of the Boridae is essentially the same as that outlined by Crowson (1955). There is little doubt that the closest relatives are the Mycteridae and Pythidae, even though early classifications based upon adults associated *Boros* Herbst with the Tenebrionidae as well as the Pythidae. Larvae and adults of lacconotine mycterids bear numerous similarities to the borids. The structure of abdominal segment 9 distinguishes borid larvae from those of most other Coleoptera. The ninth tergite forms a hinged plate similar to that of Inopeplidae, Mycteridae, Prostomidae and Pyrochroidae. Additional diagnostic features include the well developed, pad-like maxillary articulating areas, a pair of posteriorly directed, dentiform structures along the posteromesal margin of the pronotum (*Lecontia*) or anteromesal aspect of the mesonotum (*Boros*), and the presence of 2 urogomphal pits. Larvae of Pyrochroidae and Pedilidae (*Cononotus, Pedilus*) also have 2 urogomphal pits, but lack dentiform processes on the thorax. Mycteridae usually lack urogomphal pits and have a reduced maxillary articulating area. Structures similar to the dentiform processes on the dorsum of the pro- and mesothorax of Boridae also occur in the Pythidae, but pythids generally have 0–1 urogomphal pits; they also possess a series of 12 or more preanal asperities along the anterior margin of sternite 9.

Biology and Ecology: Adults of *Boros unicolor* Say and *Lecontia discicollis* (LeConte) have been collected from beneath bark of conifers and by sifting through forest litter. Larvae of *B. unicolor* and the European *B. schneideri* (Panzer) have been collected from beneath the somewhat loose bark of dead pines (St. George, 1931, 1940).

Description: Mature larvae attain lengths of 17–23 mm (*Boros*) or 38–45 mm (*Lecontia*) and widths of 2–2.5 mm (*Boros*) or 3.7–5.5 mm (*Lecontia*). Body strongly flattened, subparallel throughout, lightly sclerotized except for head and abdominal segment 9. Sinuate parabasal ridges associated with thoracic and abdominal tergites; vestiture consisting of

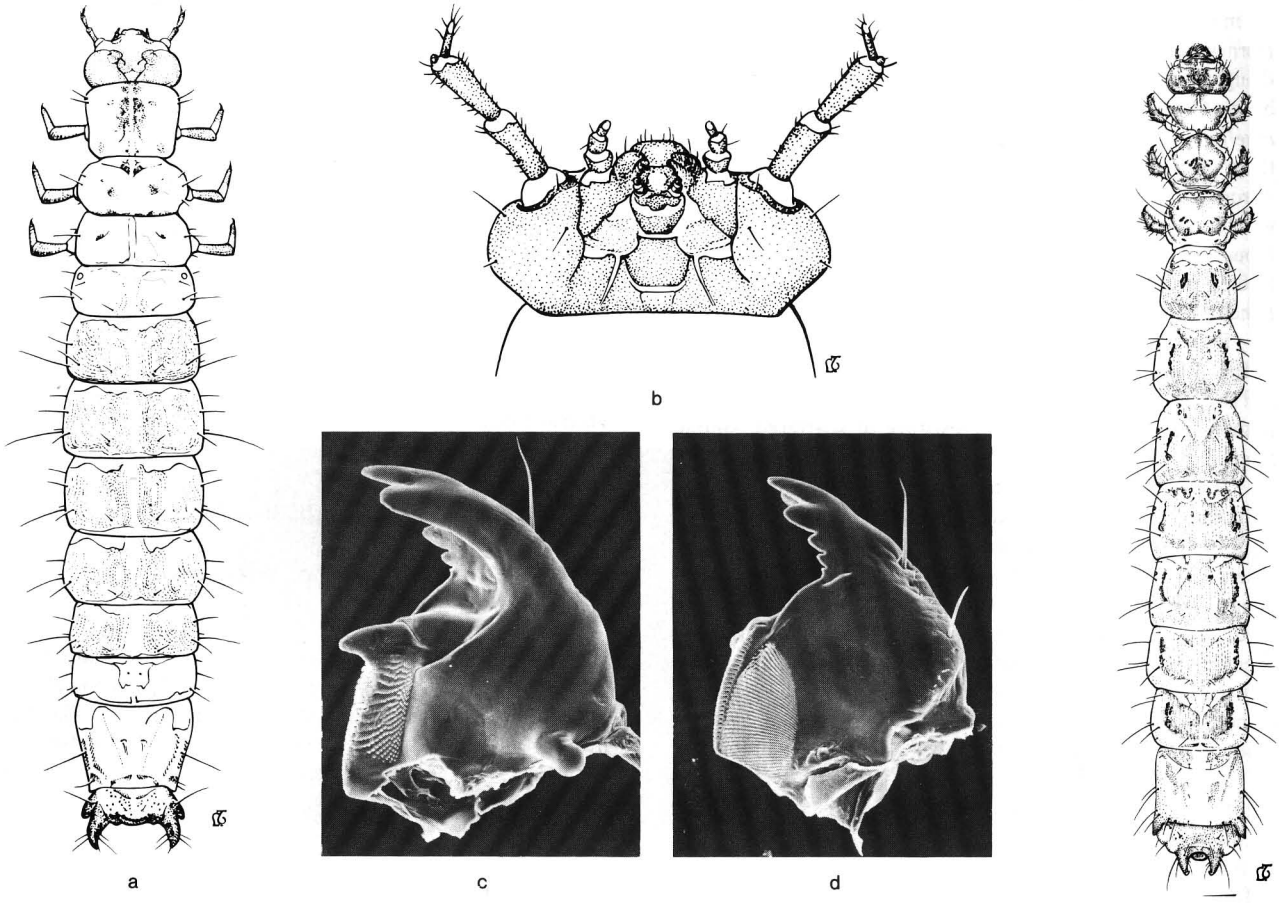

Figure 34.715

Figures 34.715a-d. Boridae. *Boros unicolor* Say. Figures **a,b:** Grayling, Crawford Co., Michigan, beneath bark of *Pinus;* Figures **c,d:** Miles Standish Forest, Massachusetts. **a.** larva, dorsal; **b.** head capsule, ventral; **c.** left mandible, ventral; **d.** right mandible, dorsal.

Figure 34.716

Figure 34.716. Boridae. *Lecontia discicollis* (LeConte). Chippewa Co., Michigan. Larva, dorsal.

scattered setae; surface of body otherwise generally smooth. Dorsum of body yellowish-brown, venter yellowish; head and abdominal segment 9 reddish-brown to nearly black.

Head: Prognathous, exserted from prothorax. Epicranial suture with stem short, anterior arms lyriform and complete to posterior margins of antennal insertions; endocarinae absent. Symmetrical labrum anterad of fused frons and clypeus. Stemmata on each side 5, 3 in anterior and 2 in posterior group (*Boros*) or entirely lacking (*Lecontia*). Antennal insertions fully exposed, antennae elongate, 3-segmented, a small conical sensorium associated with segment 2. Mouthparts retracted, supported ventrally by well developed, posteriorly divergent hypostomal rods (fig. 34.715b). Mandibles (figs. 34.715c,d) heavily sclerotized, movable, asymmetrical; left mandible bearing prominent molar tooth; apices of mandibles tridentate. Maxilla with cardo divided by internal fold and thus appearing 2-segmented, also with well developed, pad-like maxillary articulating area, undivided maxillary mala, and 3-segmented palp. Labium free to base of mentum, possessing elongate, distally rounded ligula and 2-segmented palps. Hypopharyngeal sclerome transversely rectangular. Mentum slightly wider than long with anterior margin shallowly emarginate; submentum trapezoidal (*Boros*) or quadrate (*Lecontia*), gular region transverse.

Thorax and Abdomen: Thorax elongate with sides subparallel, cervicosternum divided into 3 plates, posterior margin of pronotum (*Lecontia*) or anterior margin of mesonotum (*Boros*) bearing 2 posteriorly directed, flat, dentiform processes along meson. Legs well developed, 5-segmented including tarsungulus, legs similar in size and shape, bearing numerous fine setae. Abdomen strongly flattened; tergite 9 heavily sclerotized, hinged, extending ventrally to form the entire terminal region or urogomphal plate; ventral aspect divided along meson by longitudinal suture (*Boros*) or deep, wide sulcus (*Lecontia*); caudoventral margin bearing 2 shallow urogomphal pits between the paired, fixed urogomphi; 9th sternite broadly U-shaped (*Boros*) or transversely rectangular (*Lecontia*) and recessed into emargination of 8th sternite, produced distolaterally into a series of small,

apically dentiform plates (*Boros*) or simple and bearing a single asperity on each side (*Lecontia*). Segment A10 reduced, visible ventrally surrounding anal orifice.

Spiracles: Thoracic spiracle annular-biforous (*Boros*) or ovate with peritreme partially crenulated (*Lecontia*); abdominal spiracles annular or annular-biforous.

Comments: The Boridae contains 2–3 Holarctic genera and 5–6 species inhabiting coniferous forests. In N. America, borids are represented by *Boros unicolor* Say and *Lecontia discicollis* (LeConte). Larvae have been described or illustrated for *Boros* (Böving and Craighead, 1931; Hayashi, 1980; Mamaev *et al,* 1977; St. George, 1931, 1940) and *Lecontia* (Young, 1985b).

Selected Bibliography

Böving and Craighead 1931.
Crowson 1955.
Hayashi 1980.
Mamaev *et al.* 1977.
St. George 1931, 1940.
Young 1985b.

TRICTENOTOMIDAE (TENEBRIONOIDEA)

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This family includes 2 genera: *Autocrates* with 2 species in western China and the Himalayas, and *Trictenotoma,* with 10 species distributed from central China and India to Sri Lanka and the East Indies. The group is thought to be closely related to the family Pythidae.

Larvae are very large (over 100 mm), elongate and parallel-sided and slightly flattened, yellowish-white, with a darker head. The head is large and slightly flattened, with a short epicranial stem, lyriform frontal arms, no stemmata or median endocarina, and relatively long antennae, with a reduced third segment. The mandibles are large, asymmetrical, and tridentate, with a coarsely ridged mola and no prostheca. Ventral mouthparts are retracted, with a truncate mala, broadly excavate at apex and with a distinct uncus at the inner edge; maxillary palps are 3-segmented and labial palps 2-segmented. Hypostomal rods are absent and ventral epicranial ridges are present. The thorax is very short and broad, the legs are short, stout, and widely separated. The mesotergum, metatergum, and abdominal terga 1 to 7 bear a series of short, irregular, longitudinal ridges, which form obliquely transverse rows on thorax and longitudinal rows on abdomen. Sterna A2–8 with short, longitudinal ridges arranged in transverse rows. Tergum A9 with a pair of approximate, posteriorly projecting urogomphi, turned up at the apex; ventral portion of tergum A9 divided into plates; sternum A9 with a continuous row of asperities at the base. Segment A10 transverse and ventrally oriented. Spiracles are annular, with an elliptical peritreme.

Trictenotomid larvae live in rotten wood.

Selected Bibliography

Crowson 1955.
Gahan 1908 (larva of *Trictenotoma childreni* Gray).

PYTHIDAE (TENEBRIONOIDEA)

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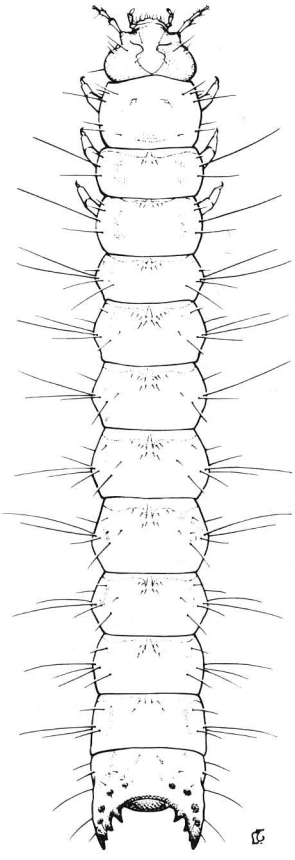
Figures 34.717–719

Relationships and Diagnosis: As defined here, the North American Pythidae conform well with Arnett's (1968) salpingine tribe Pythini, with the addition of *Sphalma* Horn (as suggested by Young, 1976b) and the exclusion of *Boros* Herbst and *Lecontia* which are referred to the closely related family Boridae. Possible affinities of the monotypic *Trimitomerus* Horn with the family Trictenotomidae were alluded to by Crowson (1955), and discovery of the larva of *T. riversi* Horn could provide meaningful insight into its systematic position. A number of genera related to the Chilean *Pilipalpus* Fairmaire and Australian *Techmessa* Bates have been variously associated with Anthicidae or Pyrochroidae (Abdullah, 1964 and Paulus, 1971). While the pilipalpines appear to be better placed in the Pythidae, there is good evidence to support the contention that pythids and pyrochroids are closely related. The Pythidae also appear to be fairly closely related to the Mycteridae by way of the Boridae. The series of 12 or more preanal asperities along the anterior margin of the ninth abdominal sternite (figs. 34.717d, 34.719b) distinguishes pythid larvae from those of most other families. Asperities in pyrochroid larvae form a single, continuous arch, while pythids and othniids have a double arch. The double arch is nearly continuous mesally in Pythidae, whereas in othniids it is broadly discontinuous along the meson, with the distance between arches greater than twice that between adjacent asperities of a single arch. Larvae of Prostomidae also possess a row of asperities on the ninth sternite, but it is located near the posterior margin.

Biology and Ecology: Adults are found on and beneath the bark of dead logs or by sweeping foliage. Larvae are associated with dead logs; those of *Pytho* are typically found beneath somewhat loose bark of conifers where they feed on the decaying cambial-phloem layer; *Priognathus* larvae are usually found within decaying wood of conifers, and larvae of *Sphalma quadricollis* Horn have been collected from beneath bark of decaying black cottonwood, *Populus trichocarpa.* Larvae of the aberrant *Trimitomerus riversi* Horn are unknown; adults have been taken at lights in Arizona (Anderson and Nilssen, 1978; Hatch, 1965; Hayashi, 1969b; Peterson, 1951; Smith and Sears, 1982; Young, 1976b, unpublished notes).

Description: Mature larvae attain lengths of 8.5–30 mm and widths of 1.5–4 mm. Body orthosomatic and subcylindrical to slightly flattened (*Priognathus, Sphalma*) or strongly flattened (*Pytho*), creamy-yellow to yellowish-brown, lightly sclerotized except for head and abdominal segment 9; sides



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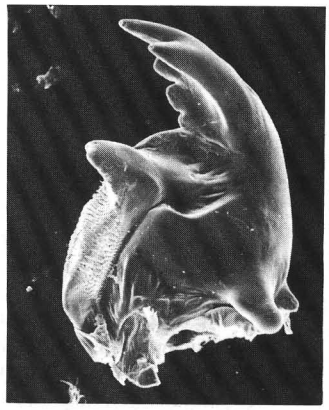

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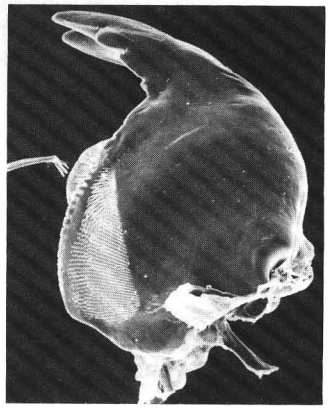

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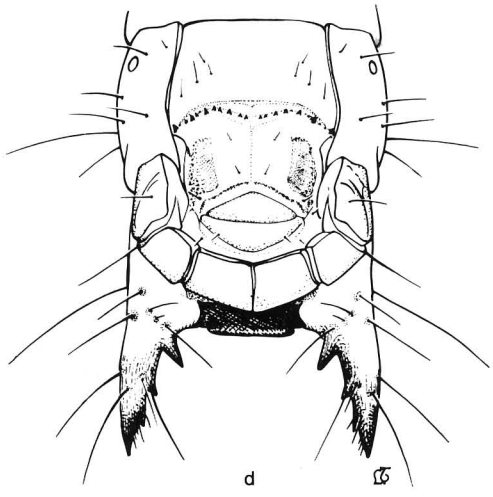


d

Figure 34.717

Figures 34.717a-d. Pythidae. *Pytho* sp. Figures **a,d:** Van Riper State Park, Marquette Co., Michigan, beneath moist bark of *Pinus;* Figures **b,c:** Jefferson Notch, New Hampshire. **a.** larva, dorsal; **b.** left mandible, ventral; **c.** right mandible, dorsal; **d.** apex of abdomen, ventral.

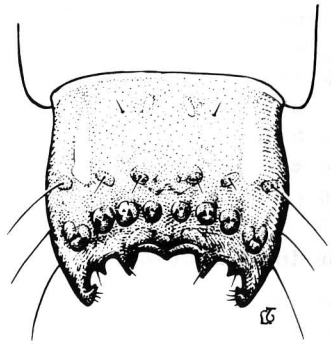
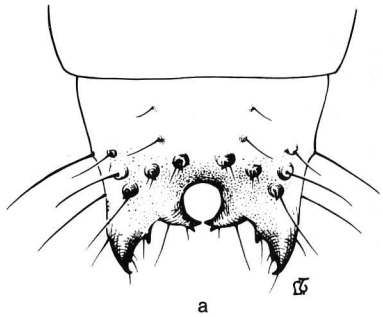


Figure 34.718

Figure 34.718. Pythidae. *Priognathus monilicornis* (Randall). Grayling, Crawford Co., Michigan, from dead log. Urogomphal plate, dorsal.



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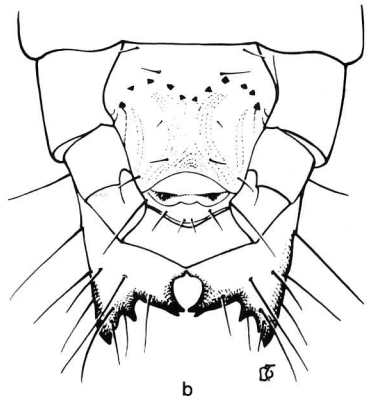

b

Figure 34.719

Figures 34.719a,b. Pythidae. *Sphalma quadricollis* Horn. Summerdale Campground, Sierra National Forest, Mariposa Co., California, from beneath bark of *Populus trichocarpa,* primarily on underside of log adjacent to soil. **a.** urogomphal plate, dorsal; **b.** apex of abdomen, ventral.