192'. Abdomen with 6 or more pairs of pleurites (fig. 150); mesal surface of mandibular base usually with articulated, pubescent process, as well as brush of hairs (fig. 67); stemmata forming tight cluster; cardo distinct and sclerotized. On rocks, submerged wood, debris in streams, sometimes in lakes or pools ..... ***Elmidae*** p. 404

193(115'). Median endocarina absent or coincident with epicranial stem (fig. 19) 194

193'. Median endocarina Y-shaped, coincident with epicranial stem and frontal arms (fig. 23) **(see 3rd and 4th choices)** 231

193[2]. Median endocarina extending anterad of epicranial stem (fig. 20) 232

193[3]. Median endocarina located between frontal arms (fig. 22); epicranial stem absent 238

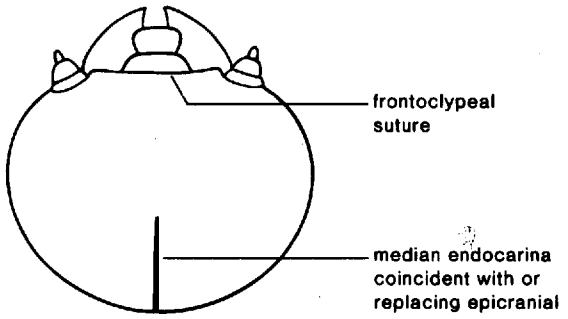


Figure 19

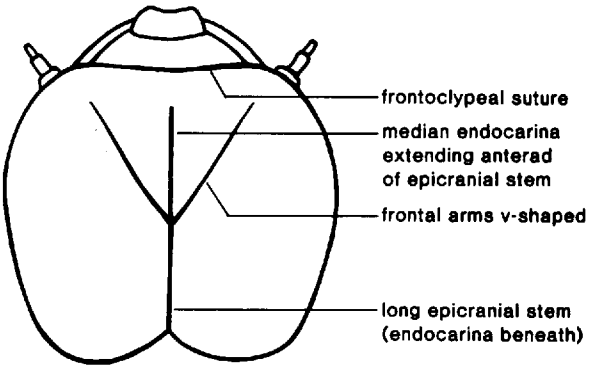


Figure 20

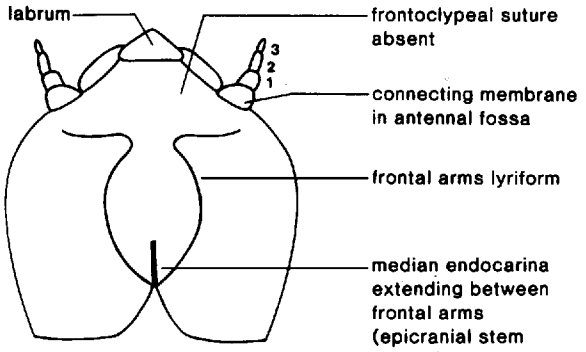


Figure 22

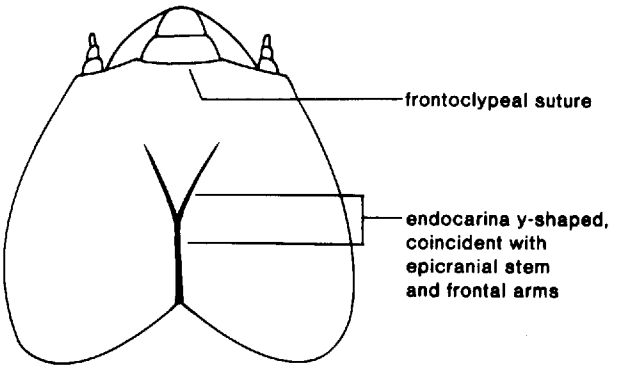


Figure 23

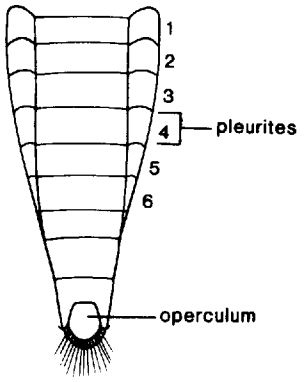


Figure 150

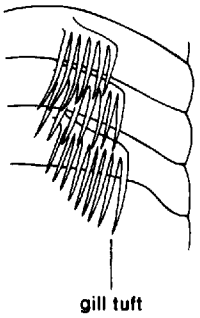


Figure 151

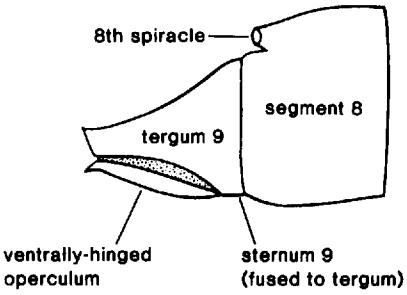


Figure 187

194(193). Abdominal apex without hinged operculum 195
194'. Abdominal apex with ventrally hinged operculum (fig. 187) 230
195(194). Mesal surface of mandibular base simple or slightly expanded (figs. 44, 46, 47) 196
195'. Mesal surface of mandibular base with brush of hairs (penicillus) (fig. 53) (**see next 4 choices**) 208
195². Mesal surface of mandibular base with *articulated,* pubescent process (fig. 67); paired ventral abdominal gill tufts (fig. 151) on segments A1–7. In debris or soil on river or stream bottoms. California ..... ***Eulichadidae*** p. 390
195³. Mesal surface of mandibular base with *fixed,* rigid, hyaline process, sometimes partly sclerotized (figs. 58, 61, 82) 209
195⁴. Mesal surface of mandibular base with 2 to 5 hyaline processes, sometimes joined basally (figs. 59, 60) 216
195⁵. Mesal surface of mandibular base with membranous lobe (fig. 64) 226

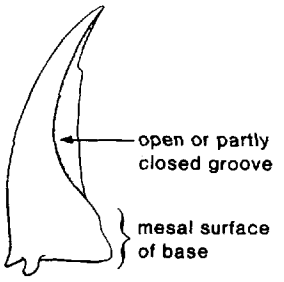


Figure 44

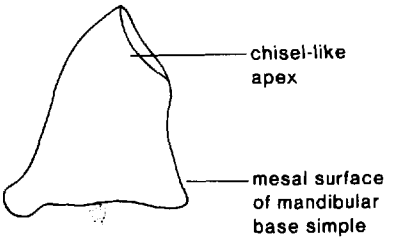


Figure 46

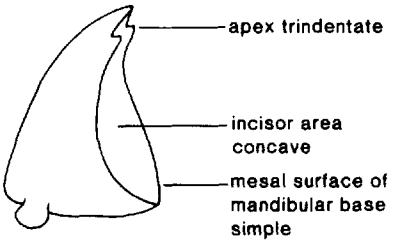


Figure 47

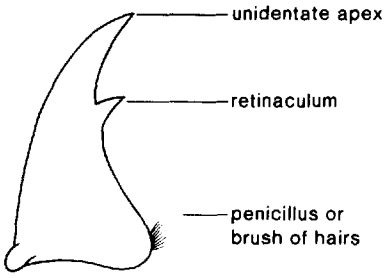


Figure 53

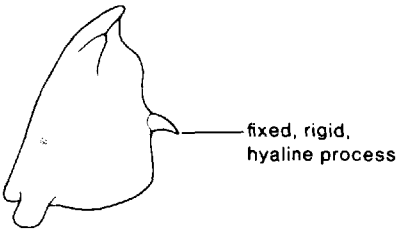


Figure 58

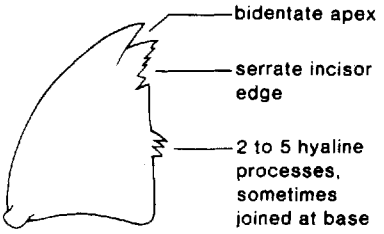


Figure 59

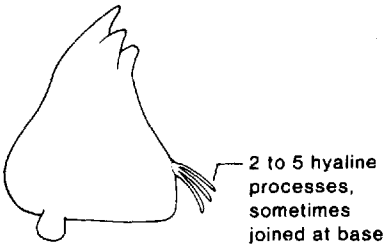


Figure 60

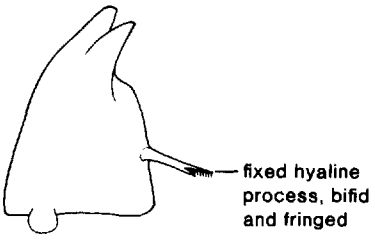


Figure 61

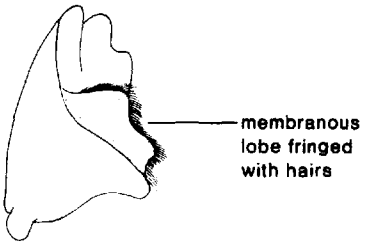


Figure 64

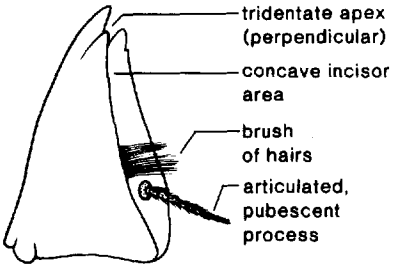


Figure 67

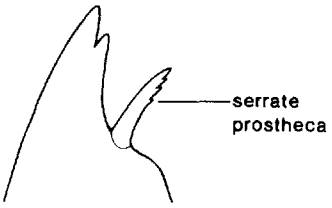


Figure 82

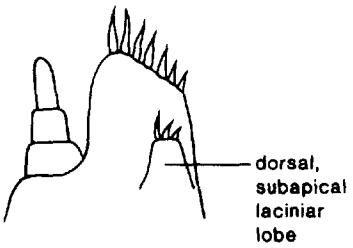


Figure 110

196(195). Apex of mala or galea rounded or truncate (figs. 88, 109, 110) 197

196′. Apex of mala or galea falciform (figs. 89, 105, 111) or stylet-like (fig. 104); urogomphi usually articulated at base (figs. 162, 163) **(see 3rd choice)** 205

196². Apex of mala trilobed (fig. 107); urogomphi articulated at base (fig. 162); labrum more or less fused to clypeus, but with vague indication of clypeolabral suture (fig. 14). In rotten mushrooms ..... (*Oxyporus*) **(Oxyporinae)** ***Staphylinidae*** p. 341

197(196). Antennal segments 1 or 2; body elongate and subcylindrical, lightly sclerotized; head moderately to strongly declined (hypognathous) (fig. 10) 198

197′. Antennal segments 3 **(see 3rd choice)** 199

197². Antennal segments 4; urogomphi articulated at base (fig. 162). In leaf litter, rotten wood, carrion, dung, under bark ..... (part) ***Staphylinidae*** p. 341

198(197). Segments in T2 leg 3 or 4, the segments indistinctly separated (fig. 128); ventral epicranial ridges absent; antennal sensorium not or only slightly longer than terminal antennal segment. In rotten wood, stems, fungus fruiting bodies ..... (part) ***Mordellidae*** p. 508

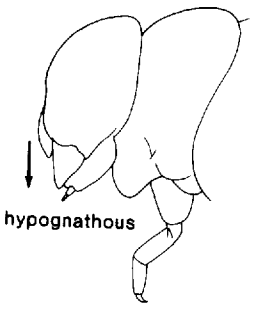


Figure 10

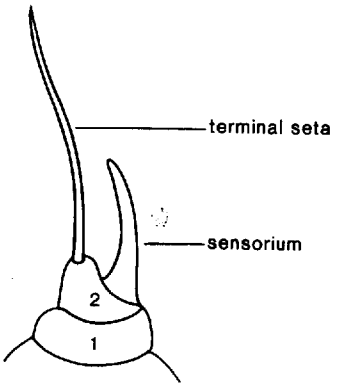


Figure 32

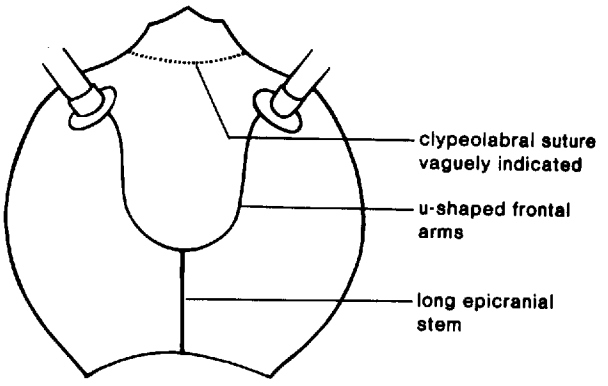


Figure 14

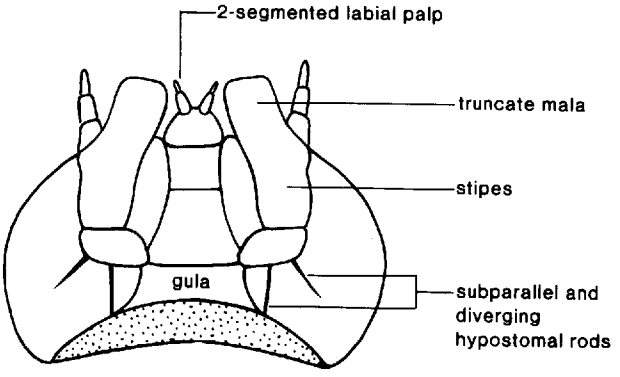
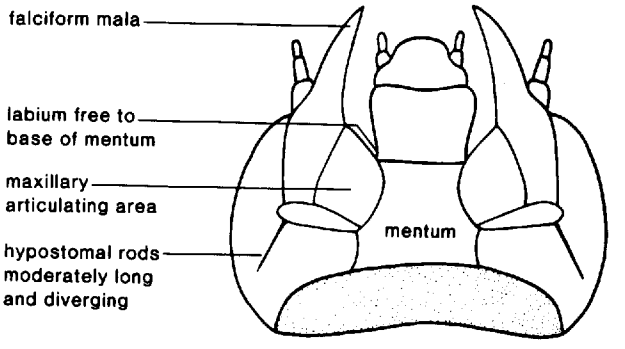
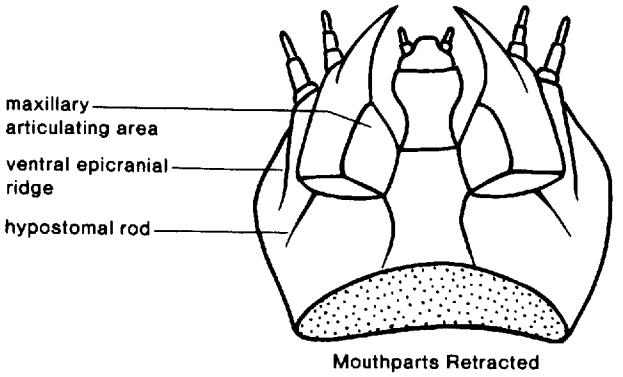


Figure 88



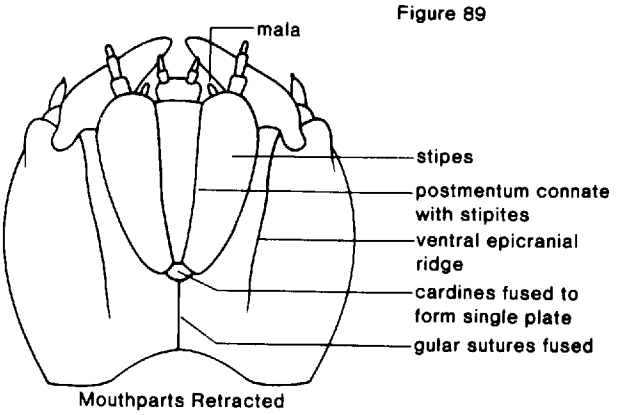
Mouthparts Retracted

Figure 89



Mouthparts Retracted

Figure 90



Mouthparts Retracted

Figure 93

198'. Segments in T2 leg 5 including tarsungulus (fig. 126); ventral epicranial ridges present (figs. 90, 93); antennal sensorium much longer than terminal (2nd) antennal segment (fig. 32). In fungus fruiting bodies ..... (**Ciinae** part) ***Ciidae*** p. 502

199(197'). Maxilla with single mala (figs. 88, 89) 200

199'. Maxilla with separate galea and lacinia (figs. 109, 111) 204

200(199). Apex of mandible truncate and lined with rows of spines (fig. 55); body somewhat flattened and lightly sclerotized; urogomphi fixed at base. On fungus covered logs ..... ***Dasyceridae*** p. 335

200'. Apex of mandible not truncate or lined with rows of spines 201

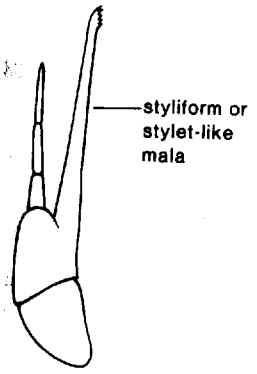


Figure 104

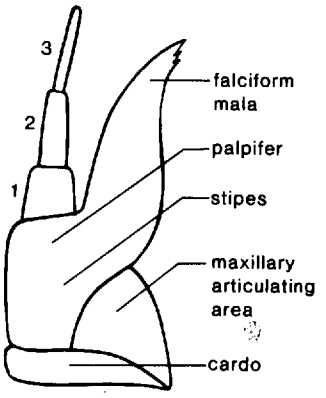


Figure 105

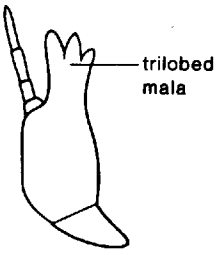


Figure 107

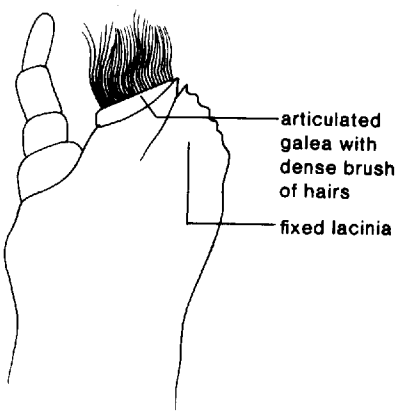


Figure 109

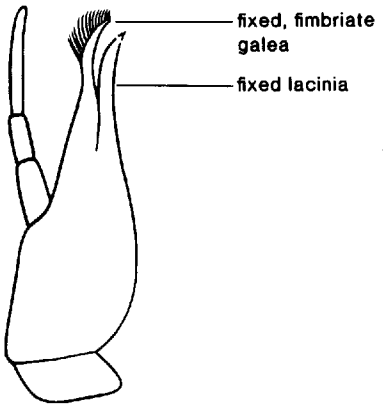


Figure 111

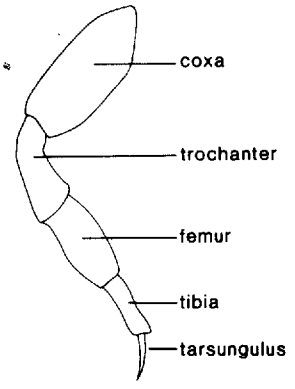


Figure 126

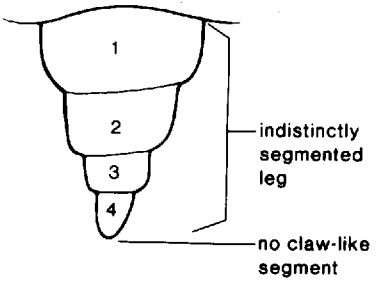


Figure 128

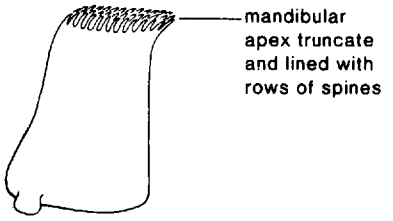


Figure 55

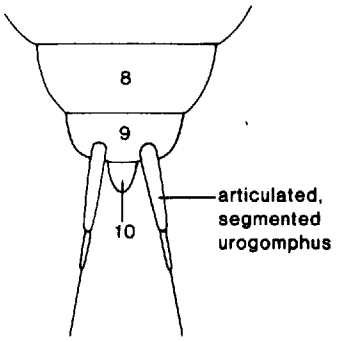


Figure 162

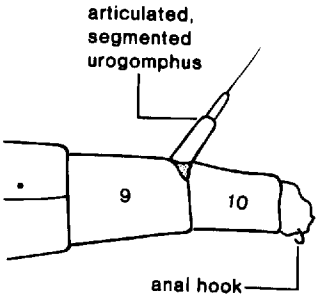


Figure 163

201(200'). Apex of antennal segment 2 oblique, so that sensorium arises proximad of segment 3 (fig. 30); frontoclypeal suture absent; hypostomal rods absent; segment A10 distinct and usually visible from above (fig. 162); urogomphi often articulated at base (fig. 162); abdominal terga usually bearing distinct plates, which are set off from those on sterna and are never asperate. In leaf litter, rotten wood, carrion, dung, under bark ..... (part) ***Staphylinidae*** p. 341

201'. Apex of antennal segment 2 truncate, so that sensorium and segment 3 arise together (fig. 29); frontoclypeal suture (figs. 13, 19) and hypostomal rods (fig. 89) present, OR abdominal terga with patches or rows of asperities; segment A10 reduced, not visible from above; urogomphi fixed at base; abdominal terga and sterna not forming distinct plates 202

202(201'). Head moderately to strongly declined (hypognathous) (fig. 10); gular region absent (labium contiguous with thoracic membrane) (fig. 96); segments in T2 leg 3 or 4, the segments indistinctly separated (fig. 128); body elongate and cylindrical, lightly sclerotized. In rotten wood, stems, fungus fruiting bodies ..... (part) ***Mordellidae*** p. 508

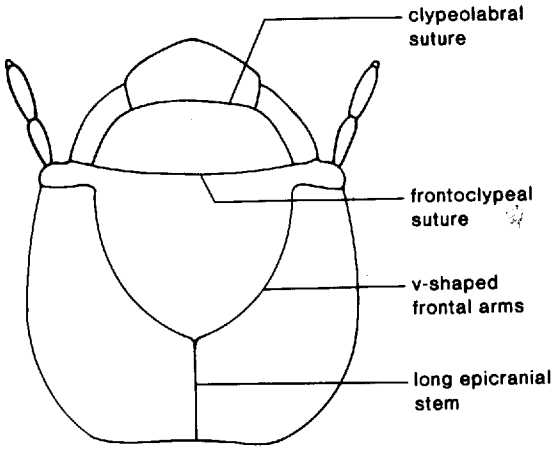


Figure 13

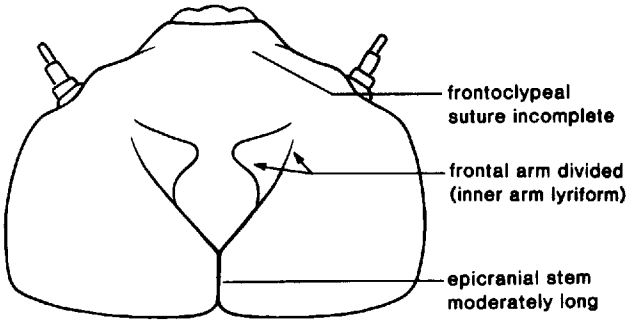


Figure 18

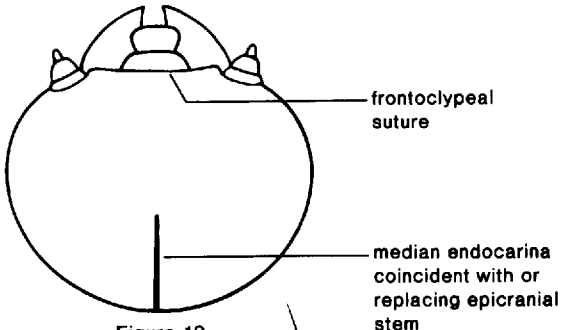


Figure 19

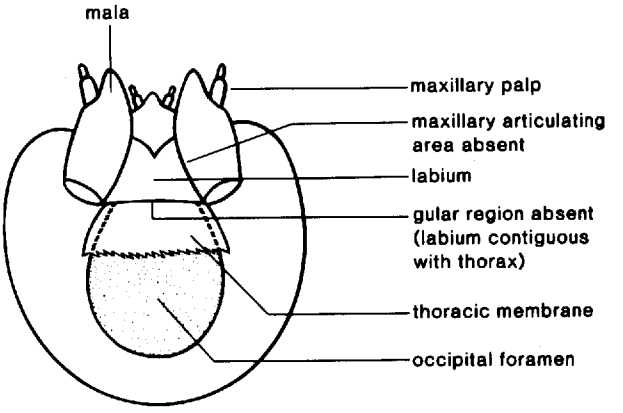


Figure 96

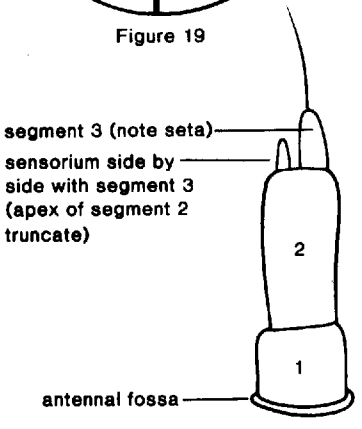


Figure 29

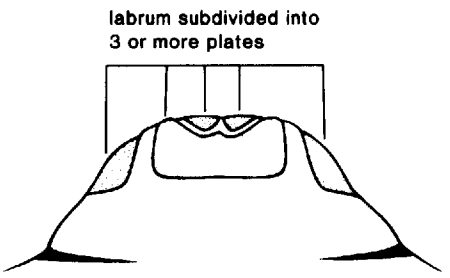


Figure 39

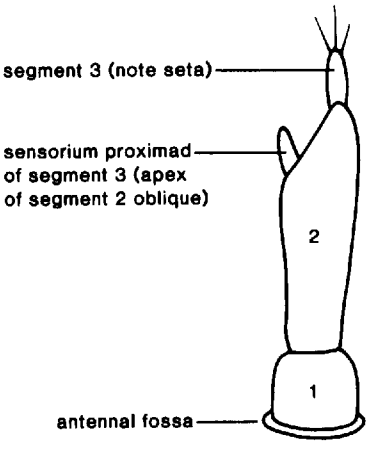


Figure 30

202'. Head prognathous or slightly declined; gular region present (separating labium from thorax) (fig. 85); segments in T2 leg 5, including tarsungulus (fig. 126) 203

203(202'). Frontoclypeal suture present (figs. 13, 19); hypostomal rods almost always present (fig. 89); mesocoxae almost always separated by more than 2 coxal diameters; dorsal surfaces very lightly pigmented and without asperities. In rotten wood, fungus fruiting bodies ..... (**Melandryinae** part) ***Melandryidae*** p. 505

203'. Frontoclypeal suture absent (fig. 18); hypostomal rods absent; mesocoxae separated by 1 to 2 coxal diameters; dorsal surfaces with pigmented maculae and rows or patches of asperities. Under bark, in soft fungi .... (*Penthe* part) (**Penthinae**) ***Tetratomidae*** p. 504

204(199'). Epicranial stem absent or very short; mandibles broad at base, not falcate; labrum not subdivided; abdominal segments without lateral plates or spine-like processes; galea without large, dense brush of hairs, but often fimbriate (with fringe of setae) (fig. 111). In leaf litter, carrion, fungi ..... (part) ***Leiodidae*** p. 327

204'. Epicranial stem moderately long (fig. 14); mandibles narrow and falcate (fig. 44); labrum subdivided into 3 or more sclerites (fig. 39); abdominal segments produced laterally forming tergal plates or spine-like processes; galea with large, dense brush of hairs (fig. 109). In carrion, decaying vegetation ..... ***Silphidae*** p. 339

205(196'). Epicranial stem absent or very short; maxilla with separate galea and lacinia (fig. 111) 206

205'. Epicranial stem moderately long (fig. 14); maxilla with single mala (fig. 105) 207

206(205). Head prognathous or slightly declined; segments in T2 leg 5 including tarsungulus (fig. 126); urogomphi articulated at base (fig. 162); dorsal surfaces generally smooth; thoracic and abdominal segments without lateral tergal processes; mandible without subapical pseudomola. In leaf litter, carrion, fungi ..... (part) ***Leiodidae*** p. 327

206'. Head moderately to strongly declined (hypognathous) (fig. 10); segments in T2 leg 3 or 4; urogomphi fixed at base; dorsal surfaces generally spinose or complexly sculptured; thoracic and abdominal segments each with 1 or 2 pairs of lateral tergal processes; mandible with subapical pseudomola consisting of several spines or teeth (fig. 54). In decaying vegetation ..... ***Micropeplidae*** p. 334

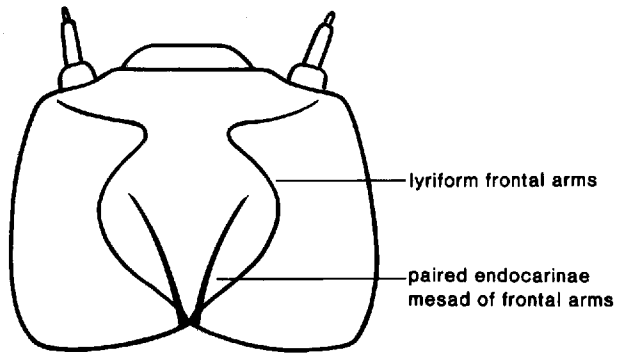


Figure 25

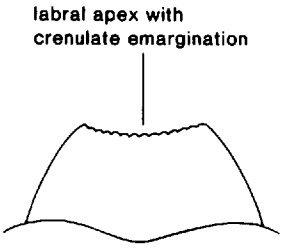


Figure 37

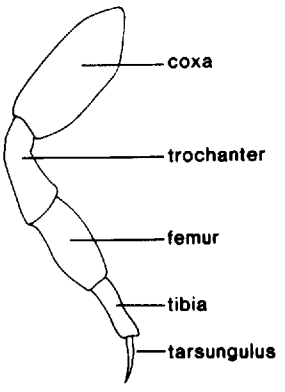


Figure 126

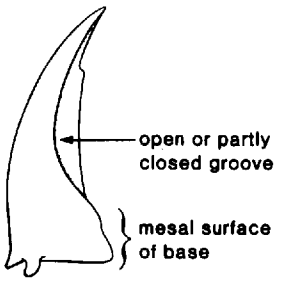


Figure 44

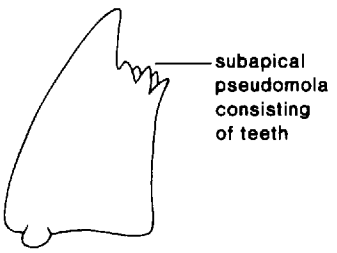


Figure 54

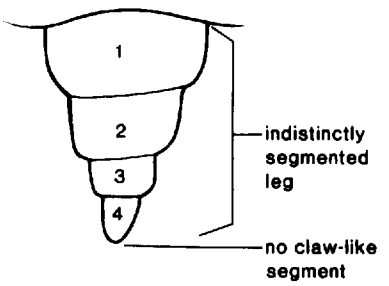


Figure 128

207(205'). Labrum with crenulate emargination (fig. 37). On surfaces of fungi and bark, in leaf litter ..... ***Scaphidiidae*** p. 337

207'. Labrum without crenulate emargination. In leaf litter, rotten wood, carrion, dung, under bark ..... (part) ***Staphylinidae*** p. 341

208(195'). Mentum or postmentum not divided longitudinally; paired endocarinae located mesad of frontal arms (fig. 25); maxilla with single mala (fig. 88); segments in maxillary palp 3; ventral epicranial ridges absent; maxillary articulating area exposed (fig. 85); anal region without hooks or papillae. Under bark, in rotting stems ..... (part) ***Monommidae*** p. 514

208'. Mentum or postmentum divided longitudinally into 3 parts (fig. 98); paired endocarinae absent; maxilla with separate galea and lacinia (fig. 98); segments in maxillary palp 4; ventral epicranial ridges present (fig. 93); maxillary articulating area concealed behind expanded mentum (fig. 98); anal region with several pairs of hooks and 1 or more papillae (fig. 189). In plant debris in or near streams ..... (**Anchytarsinae** part) ***Ptilodactylidae*** p. 391

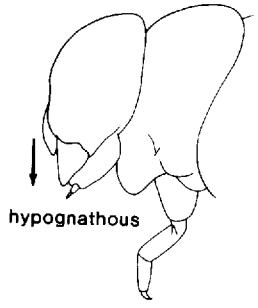


Figure 10


Figure 4

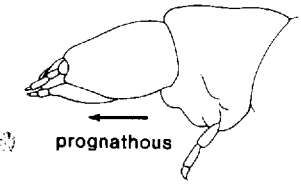


Figure 8

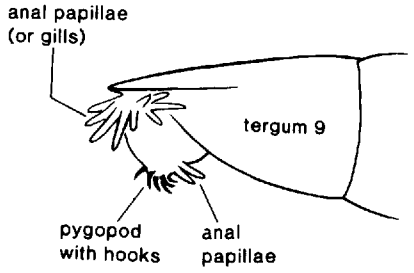


Figure 189

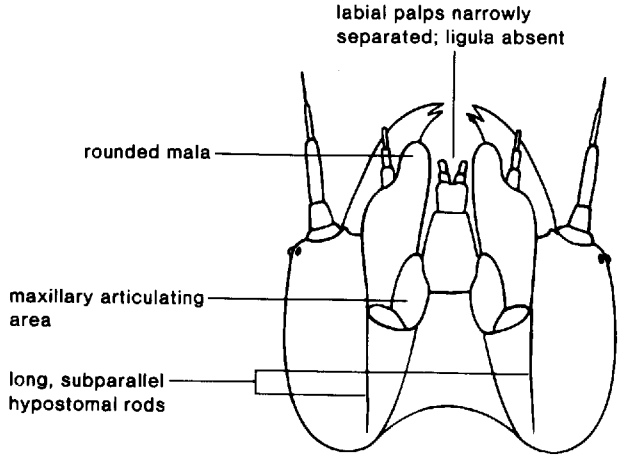
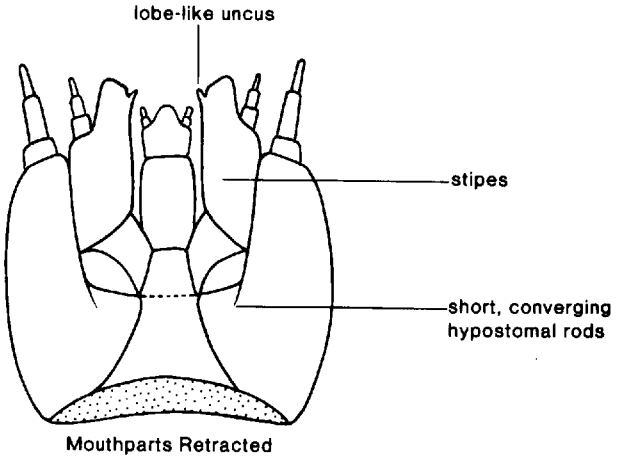


Figure 86



Mouthparts Retracted
Figure 87

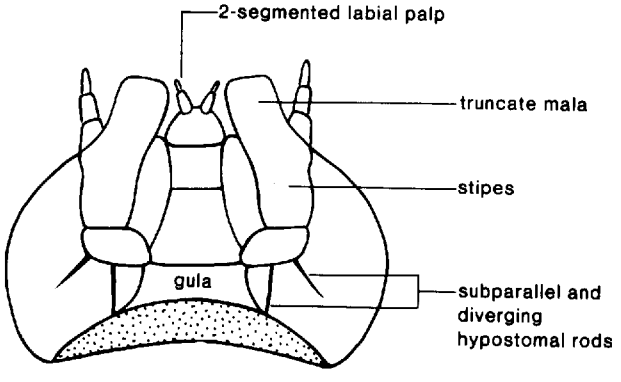
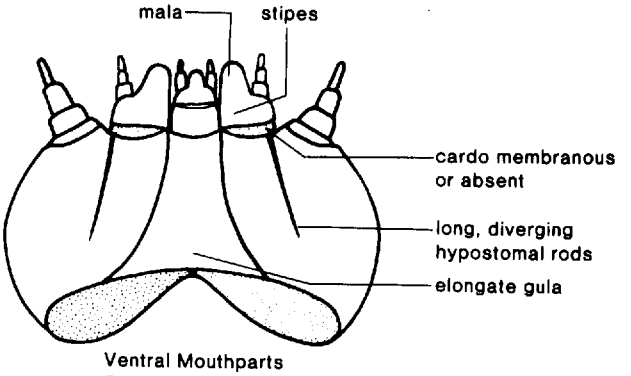


Figure 88



Ventral Mouthparts
Strongly Protracted
Figure 92

209(195[3]). Antennal segments 2 210

209′. Antennal segments 3 212

210(209). Head prognathous or slightly declined (fig. 8); epicranial stem absent; labial palps separated by more than width of first palpal segment; ventral epicranial ridges absent; body with enlarged abdomen (physogastric). Usually in tunnels of woodboring insects (ectoparasitic) 211

210′. Head moderately to strongly declined (hypognathous) (fig. 10); epicranial stem moderately long; labial palps contiguous or separated by less than width of first palpal segment; ventral epicranial ridges present (fig. 93); body subcylindrical or slightly flattened, without enlarged abdomen. In fungus fruiting bodies ..... (**Ciinae** part) ***Ciidae*** p. 502

211(210). Ventral mouthparts strongly protracted (fig. 92); hypostomal rods distinct, diverging (fig. 92) ..... (**Passandrinae** part) ***Cucujidae*** p. 463

211′. Ventral mouthparts retracted (fig. 87); hypostomal rods absent ..... (**Bothriderinae** part) ***Bothrideridae*** p. 477

212(209′). Head prognathous or slightly declined (fig. 8); maxilla with single mala (figs. 86, 92, 104); stemmata present 213

212′. Head moderately to strongly declined (hypognathous) (fig. 10); maxilla with separate galea and lacinia (fig. 215); stemmata absent. In leaf litter, stored products, ant nests ..... (**Thorictinae**) ***Dermestidae*** p. 434

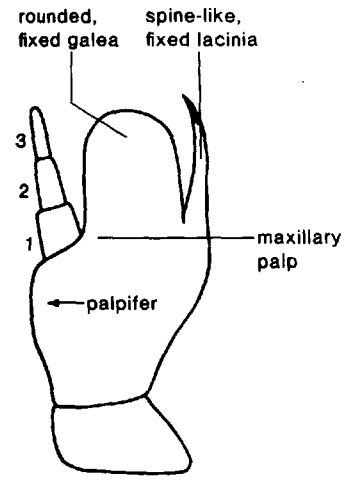
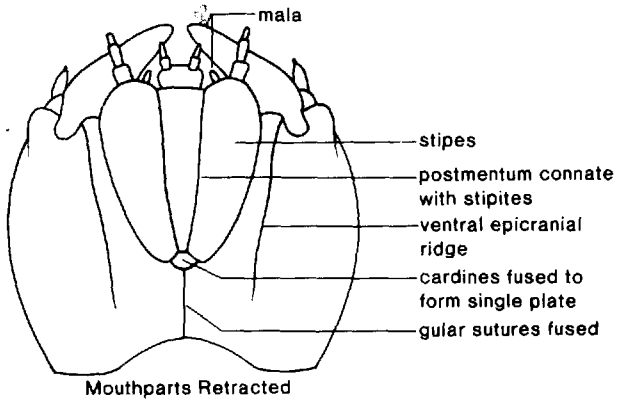


Figure 215



Mouthparts Retracted

Figure 93

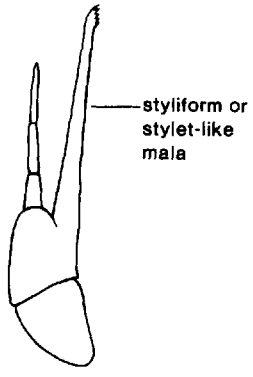
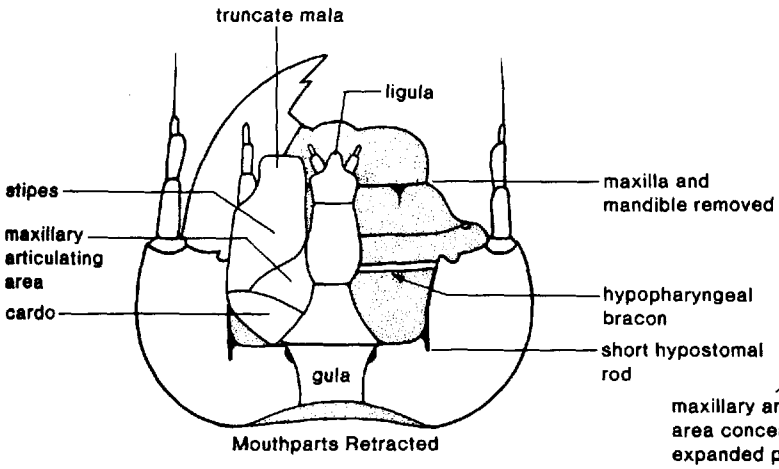


Figure 104



Mouthparts Retracted

Figure 85

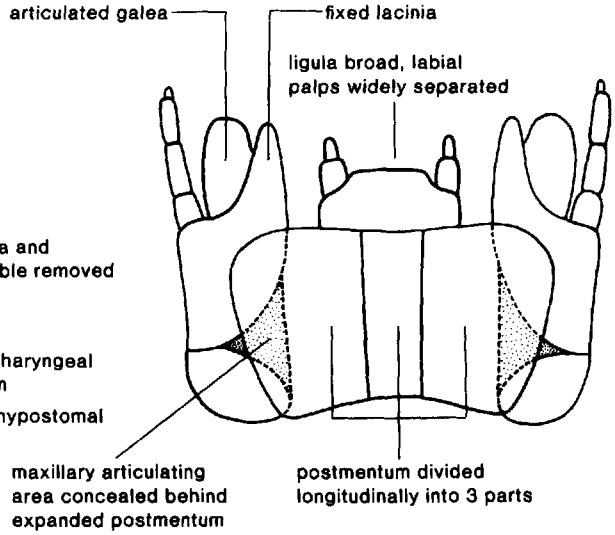


Figure 98

213(212). Urogomphi articulated at base (fig. 162); mala stylet-like (fig. 104); vestiture including frayed setae (fig. 4); stemmata on each side 3 or 6. In leaf litter ..... (**Proteininae**) ***Staphylinidae*** p. 341

213′. Urogomphi fixed at base; mala rounded or truncate (figs. 86, 92); vestiture consisting of simple setae 214

214(213′). Epicranial stem absent and frontal arms lyriform (fig. 22); posterior edge of head capsule distinctly emarginate dorsally; body strongly flattened. Under bark, in rotten wood ..... (part) ***Inopeplidae*** p. 551

214′. Epicranial stem moderately long and frontal arms V- or U-shaped (fig. 20); posterior edge of head capsule not or slightly emarginate dorsally; body not or only slightly flattened 215

215(214′). Hypostomal rods well-developed and extending almost to posterior edge of head (fig. 86); stemmata on each side 6; paired dorsal abdominal glands absent. In sand dunes. Exotic (Australia, New Zealand, New Caledonia) ..... ***Phycosecidae*** p. 452

215′. Hypostomal rods absent; stemmata on each side 5 or fewer; abdominal segments with 1 or more pairs of dorsal glands (fig. 140). In leaf litter, soil, on ground, under bark, in stems ..... ***Melyridae*** p. 453

216(195[4]). Epicranial stem absent 217

216′. Epicranial stem moderately long (fig. 18) 224

217(216). Ventral mouthparts strongly protracted; stipes wider than long (fig. 92); frontal arms distant at base (fig. 16); terga A1–8 never with sclerotized plates 218

217′. Ventral mouthparts retracted; stipes longer than wide (fig. 89); if frontal arms distant at base, terga A1–8 each with a sclerotized plate 219

218(217). Tergum A9 forming articulated plate (fig. 165); paired endocarinae located beneath frontal arms; body elongate and strongly flattened, without sclerotized plates on thoracic terga. Under bark, on surfaces of wood or fungi, in stored products ..... (**Laemophloeinae**) ***Cucujidae*** p. 463

218′. Tergum A9 not forming articulated plate; paired endocarinae absent; body not strongly flattened; sclerotized plate present on protergum and paired plates usually present on meso- and metaterga. Under bark, in leaf litter or rotten wood ..... (**Phyllobaeninae** part) ***Cleridae*** p. 450

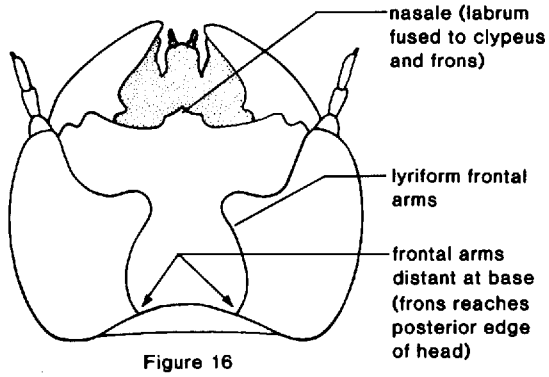


Figure 16

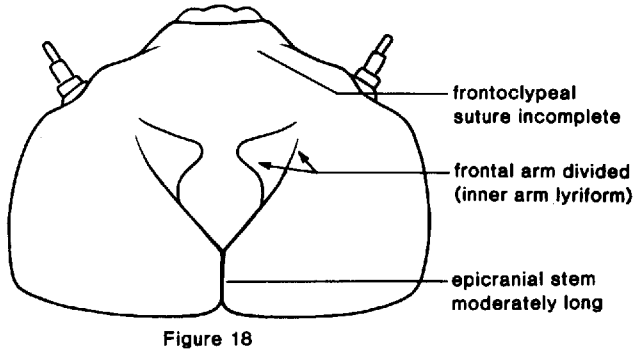


Figure 18

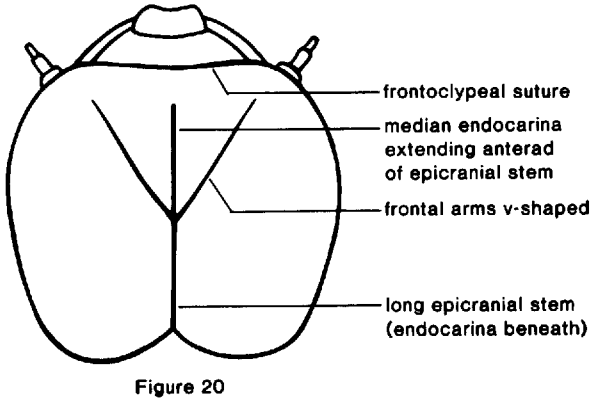


Figure 20

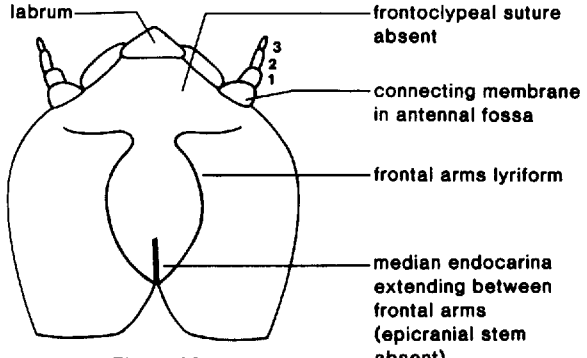


Figure 22

Figs. 4, 86, 87, 92, 104

219(217′). Paired endocarinae absent; frontal arms distant at base; mesal surface of mandibular base with 2 hyaline processes, one acute and the other rounded and pubescent; thoracic terga and abdominal terga A1–9 each with a distinct, pigmented plate. In bird nests. Exotic (South temperate regions) ..... (part) ***Cavognathidae*** p. 469

219′. Paired endocarinae present and frontal arms contiguous at base (figs. 24, 25); basal mandibular processes different; without pigmented plates on all thoracic and abdominal terga 220

220(219′). Paired endocarinae coincident with frontal arms (fig. 24); abdominal spiracles annular 221

220′. Paired endocarinae located mesad of frontal arms (fig. 25); abdominal spiracles annular-biforous (fig. 197) 223

221(220). Labial palps contiguous or separated by less than width of first palpal segment; hypostomal rods present (figs. 86, 89); spiracles not on sclerotized plates 222

221′. Labial palps separated by more than width of first palpal segment; hypostomal rods absent; spiracles located on sclerotized plates. In cracks on intertidal rocks (western North America) ..... (*Aegialites*) (**Aegialitinae**) ***Salpingidae*** p. 549

222(221). Ratio of antennal length to head width less than .15; hypostomal rods diverging and moderately long (fig. 89); urogomphi simple (fig. 170). In rotten wood, fungus fruiting bodies ..... (**Melandryinae** part) ***Melandryidae*** p. 505

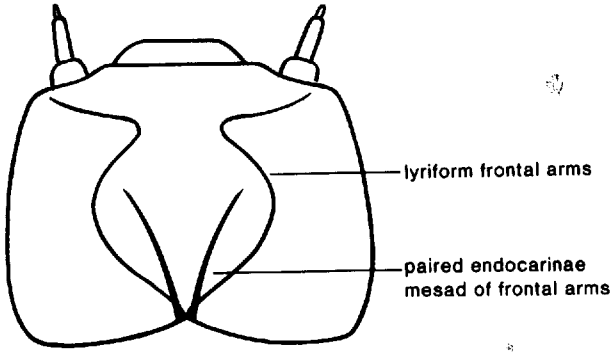


Figure 25

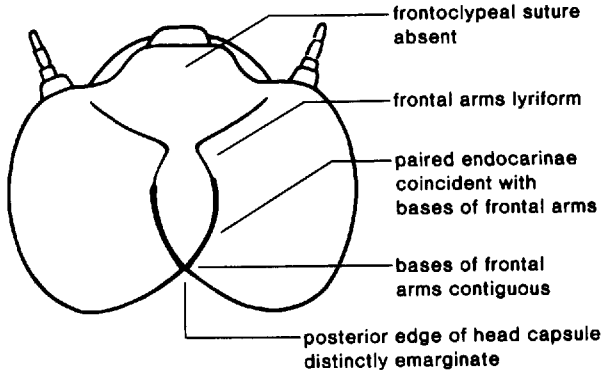


Figure 24

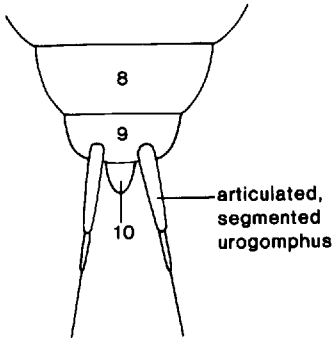
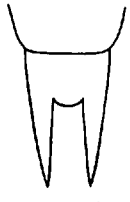
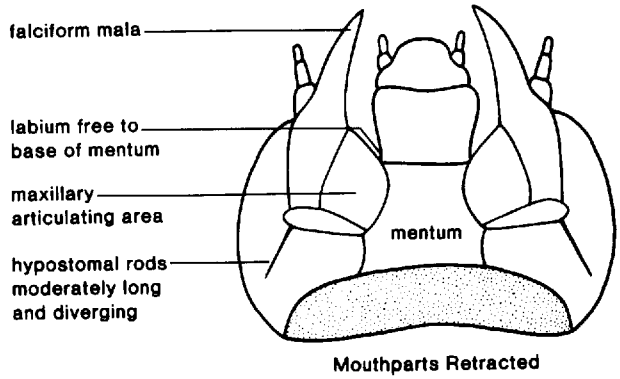


Figure 162


Dorsal
Figure 170



Mouthparts Retracted
Figure 89

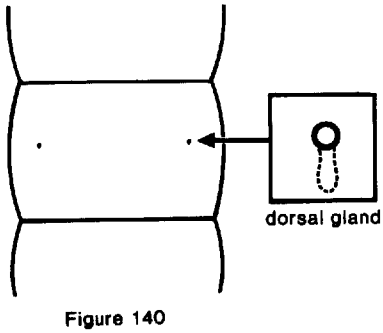
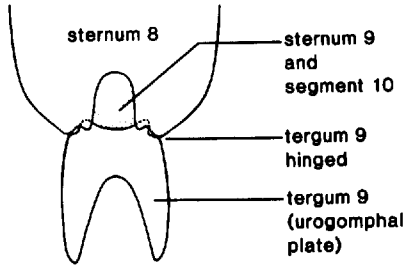
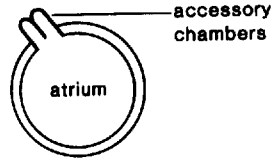


Figure 140



Ventral
Figure 165



Annular Biforous
Figure 197

Fig. 86 ⟶

222′. Ratio of antennal length to head width .15 to .5; hypostomal rods subparallel and extending almost to posterior edge of head (fig. 86); urogomphi bifurcate (fig. 184). Under bark, in rotten stems, leaf litter ..... (**Salpinginae** part) ***Salpingidae*** p. 549

223(220′). Frontal arms lyriform (fig. 25); ratio of antennal length to head width .15 to .5; labial palps separated by more than width of first palpal segment; hypostomal rods converging posteriorly (fig. 87); abdominal terga with paired rows of asperities forming open or closed rings (fig. 145); urogomphi simple with pit between them (fig. 173). Under bark, in rotting stems ..... (part) ***Monommidae*** p. 514

223′. Frontal arms V- or U-shaped (fig. 12); ratio of antennal length to head width less than .15; labial palps contiguous or separated by less than width of first palpal segment; hypostomal rods subparallel (fig. 86); dorsal surfaces without asperities; urogomphi complex, with accessory processes (fig. 169) and without pit between them. In fungus fruiting bodies ..... (*Thymalus*) (**Peltinae**) ***Trogossitidae*** p. 448

224(216′). Ratio of antennal length to head width .15 to .5; spiracles annular-biforous (fig. 197); setae on tarsungulus 2 225

224′. Ratio of antennal length to head width more than .5; spiracles annular; setae on tarsungulus 1; urogomphi with accessory processes (fig. 181). In tufts of tussock grass. Exotic (South temperate regions) ..... ***Perimylopidae*** p. 520

225(224). Hypostomal rods absent; apex of mandible with single lobe or tooth; mesocoxae separated by 1 to 2 basal coxal diameters; body more or less cylindrical and lightly sclerotized, with enlarged thorax; urogomphi simple. In rotten wood, under bark ..... (part) ***Colydiidae*** p. 512

225′. Hypostomal rods present (fig. 89); apex of mandible bilobed or bidentate; mesocoxae separated by less than 1 basal coxal diameter; body slightly flattened without enlarged thorax; urogomphi with accessory processes (fig. 169). In fungus fruiting bodies ..... (**Tetratominae**) ***Tetratomidae*** p. 504

226(195[5]). Urogomphi articulated at base (fig. 162); segment A10 distinct and visible from above (fig. 162); spiracles annular; antennal segment 2 oblique at apex so that sensorium arises proximad of segment 3 (fig. 30) 227

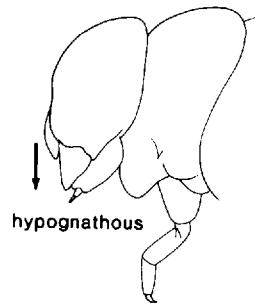


Figure 10

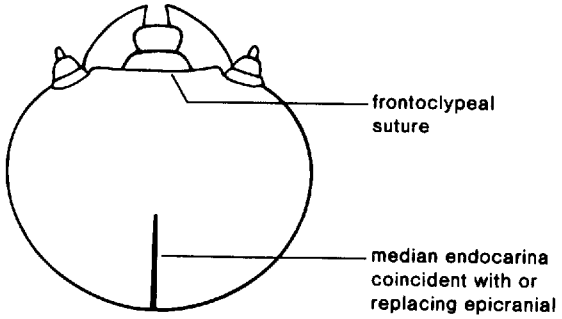


Figure 19

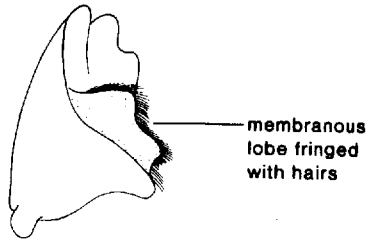


Figure 64

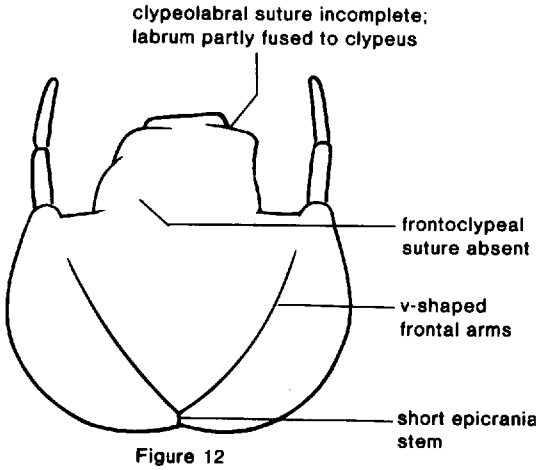


Figure 12

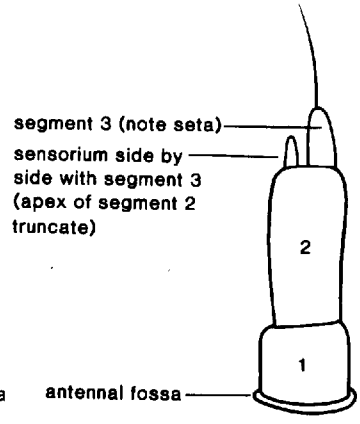


Figure 29

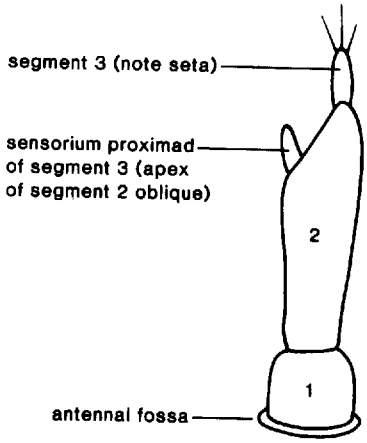


Figure 30

Figs. 25, 89, 162, 197

226'. Urogomphi fixed at base; segment A10 concealed from above; spiracles annular-biforous (fig. 19) or dorsal surfaces granulate or spinose; antennal segment 2 truncate at apex, so that sensorium and segment 3 arise together (fig. 29) 228

227(226). Maxillary articulating area absent; frontal arms absent; labium consisting of a single plate; head strongly transverse; urogomphi unsegmented. In beaver nests, on beaver pelts ..... (*Platypsyllus*) (**Platypsyllinae**) ***Leptinidae*** p. 330

227'. Maxillary articulating area present (fig. 85); frontal arms present; labium consisting of prementum, mentum, and submentum; head only slightly transverse; urogomphi segmented (fig. 162). In leaf litter, rotten wood, fungi ..... (part) ***Leiodidae*** p. 327

228(226'). Head moderately to strongly declined (hypognathous) (fig. 10); apex of mala usually cleft (fig. 106); mandible usually tridentate at apex (fig. 64); if spiracles annular-biforous, labial palps separated by more than width of first palpal segment. In or on surfaces of fungus fruiting bodies ..... (part) ***Erotylidae*** p. 473

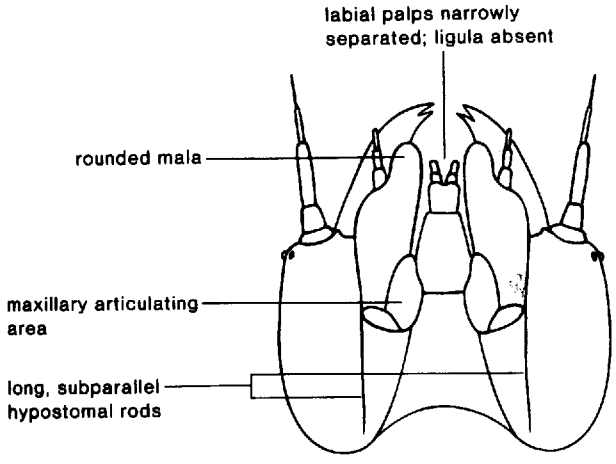


Figure 86

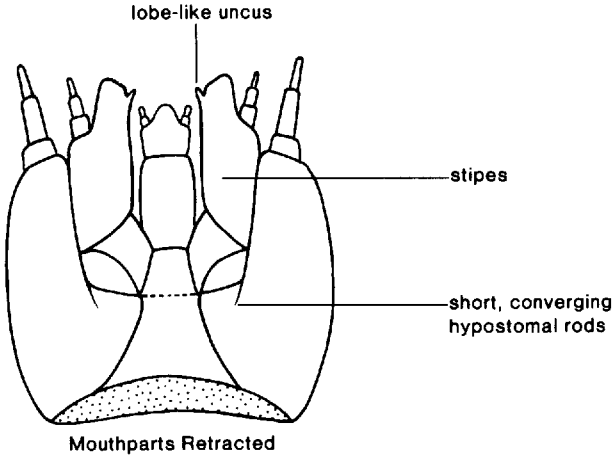


Figure 87

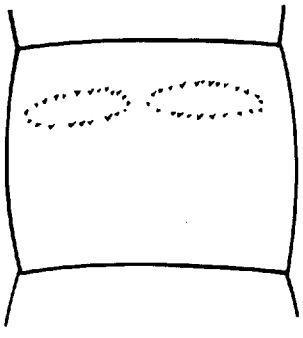


Figure 145

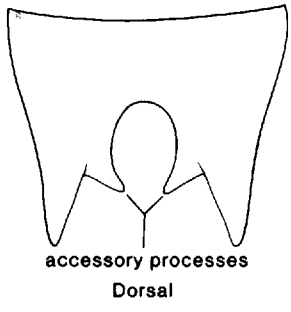


Figure 169

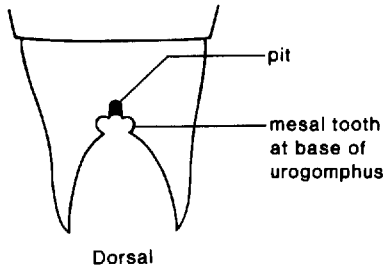


Figure 173

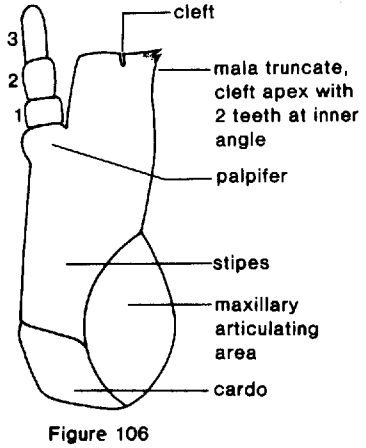


Figure 106

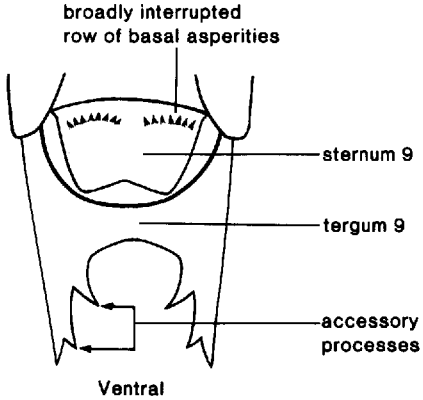


Figure 181

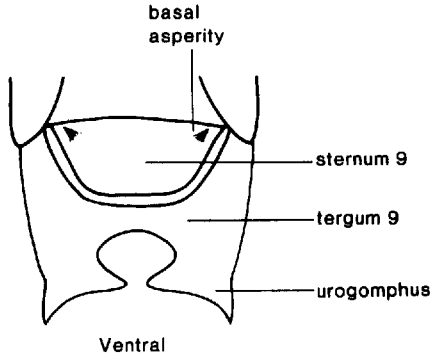


Figure 184

Fig. 85: See p. 252.

228′. Head prognathous or slightly declined; apex of mala not cleft; mandible bidentate at *apex* (fig. 62 (may have serrate edge below apex as in fig. 59)); spiracles annular-biforous (fig. 197); labial palps separated by less than width of first palpal segment 229

229(228′). Hypostomal rods present (2 pairs) (fig. 88); epicranial stem absent; ratio of antennal length to head width .15 to .5; abdominal terga without asperities. In fungus fruiting bodies, in rotten wood ..... (**Eustrophinae** part) ***Melandryidae*** p. 505

229′. Hypostomal rods absent; epicranial stem moderately long (fig. 18); ratio of antennal length to head width less than .15; abdominal terga with patches (fig. 142) or rows (fig. 144) of asperities. Under bark, in soft fungi .... (*Penthe* part) (**Penthinae**) ***Tetratomidae*** p. 504

230(194′). Epicranial stem absent or very short; maxilla with separate galea and lacinia (fig. 100); cardines separated from each other by labium; posterior edge of head capsule distinctly emarginate dorsally; ratio of antennal length to head width .15 to .5; spiracles A1–7 small and non-functional, partly surrounded by large plastron plates (fig. 213). In soil or gravel at edges of streams (western North America) ..... (*Araeopidius*) (**Araeopidiinae**) ***Ptilodactylidae*** p. 391

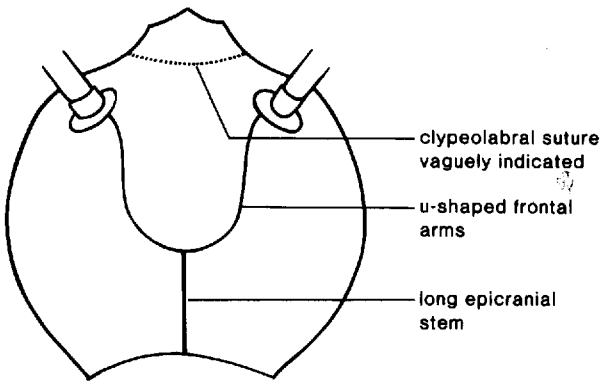


Figure 14

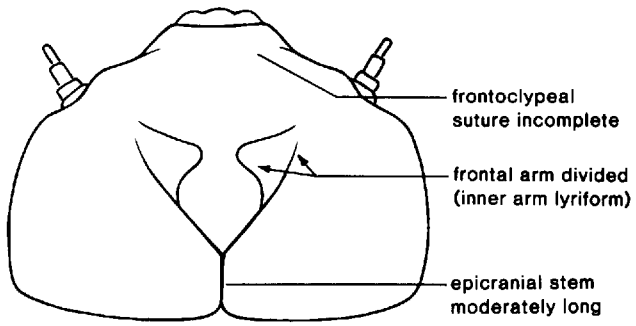


Figure 18

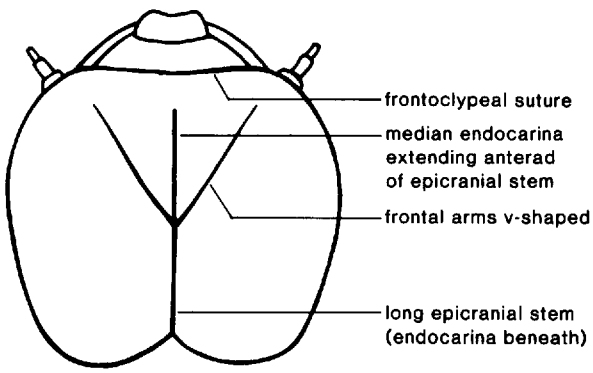


Figure 20

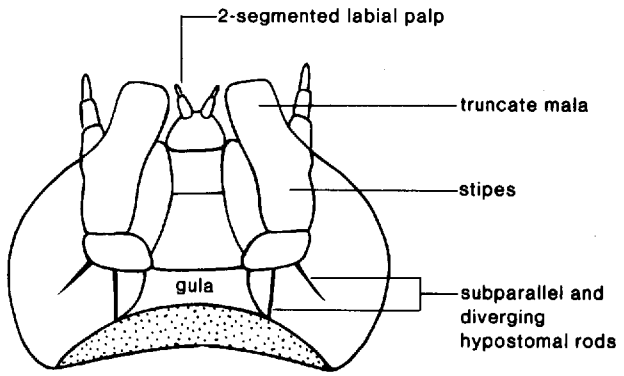


Figure 88

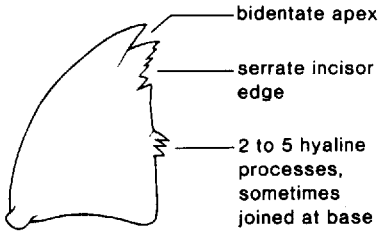


Figure 59

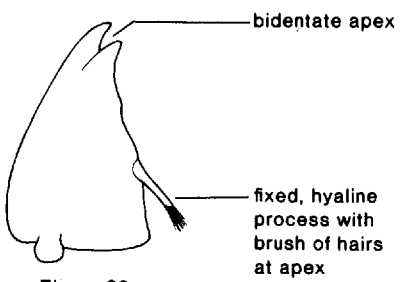
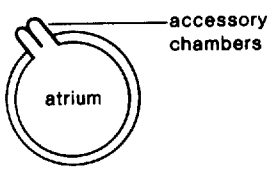


Figure 62



Annular Biforous
Figure 197

230'. Epicranial stem moderately long (fig. 20); maxilla with single mala (fig. 99); cardines completely fused forming single plate (fig. 97); posterior edge of head capsule not or only slightly emarginate dorsally; ratio of antennal length to head width less than .15; spiracles A1–7 undulate, placed at the ends of short lateral processes (fig. 209); plastron plates absent. In leaf litter, flood debris, ant refuse heaps ..... (part) ***Chelonariidae*** p. 394

231(193'). Epicranial stem moderately long (fig. 14); apex of mala falciform (fig. 105); urogomphi articulated at base (fig. 162); posterior edge of head capsule not or only slightly emarginate dorsally; ratio of antennal length to head width more than .5. In leaf litter, rotten wood, carrion, dung, under bark ..... (part) ***Staphylinidae*** p. 341

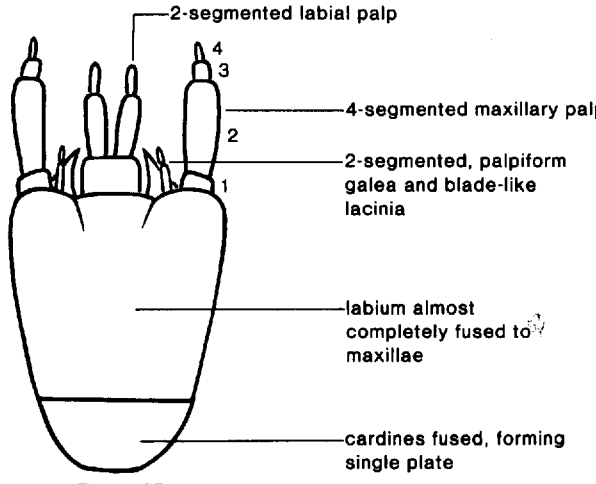


Figure 97

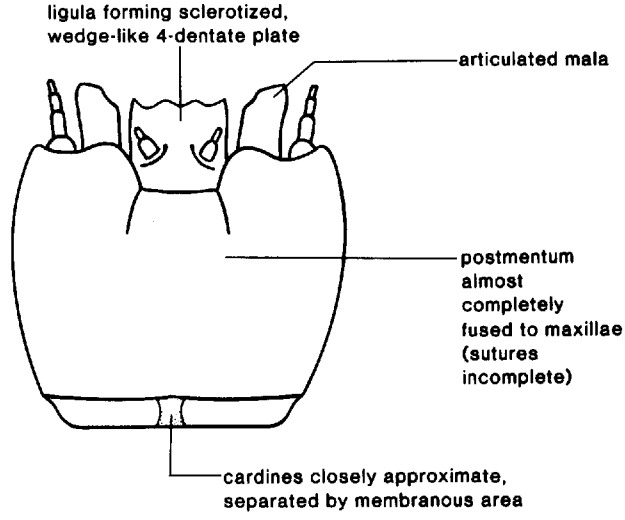


Figure 99

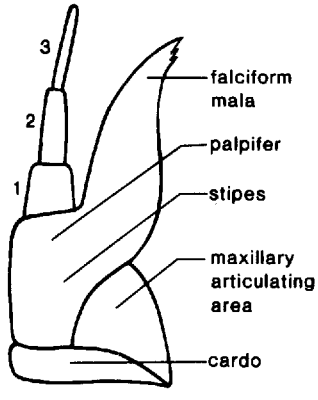


Figure 105

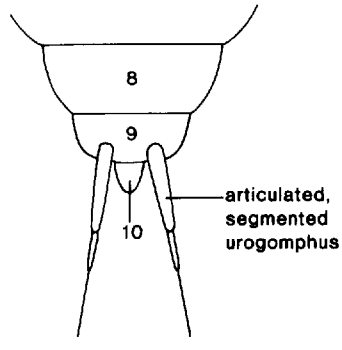


Figure 162

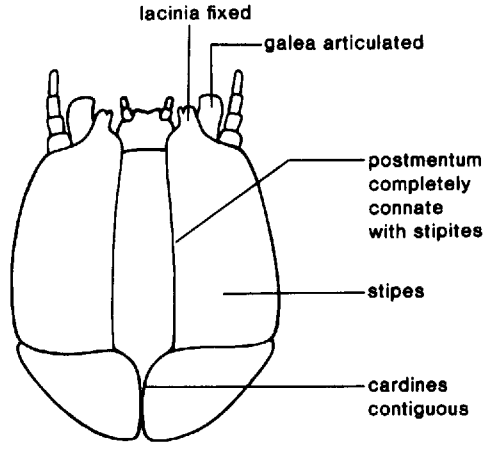


Figure 100

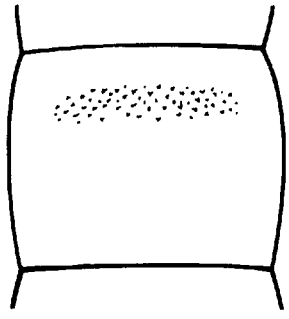


Figure 142

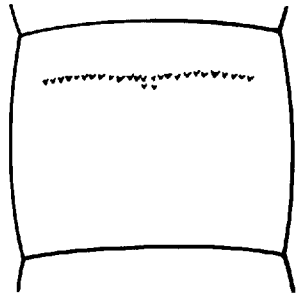


Figure 144

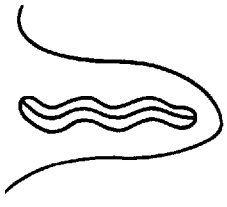


Figure 209

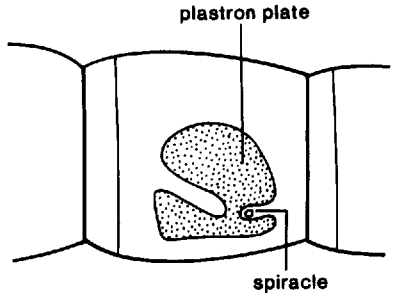


Figure 213

231'. Epicranial stem absent or very short; apex of mala rounded or truncate; urogomphi fixed at base; posterior edge of head capsule distinctly emarginate dorsally; ratio of antennal length to head width less than .15. In fungus fruiting bodies ..... (**Peltinae** part) ***Trogossitidae*** p. 448

232(193²). Legs more or less reduced with 4 segments or fewer; head strongly retracted (fig. 9) 233

232'. Legs not reduced, with 5 segments including tarsungulus (fig. 126); head protracted or slightly retracted (fig. 8) 235

233(232). Head distinctly longer than wide, narrower posteriorly; epicranial stem not located in broad furrow; cardines completely fused with labium. Under bark, in living or dead wood ..... (**Lamiinae** part) ***Cerambycidae*** p. 556

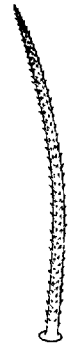


Figure 6

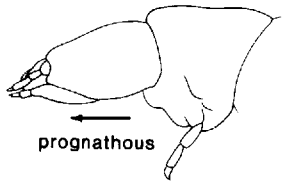


Figure 8

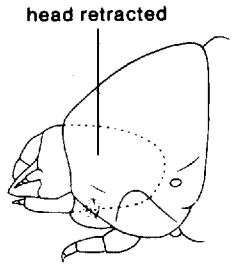


Figure 9

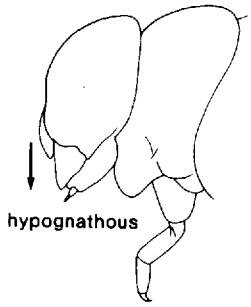


Figure 10

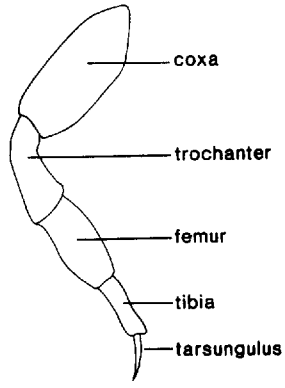


Figure 126

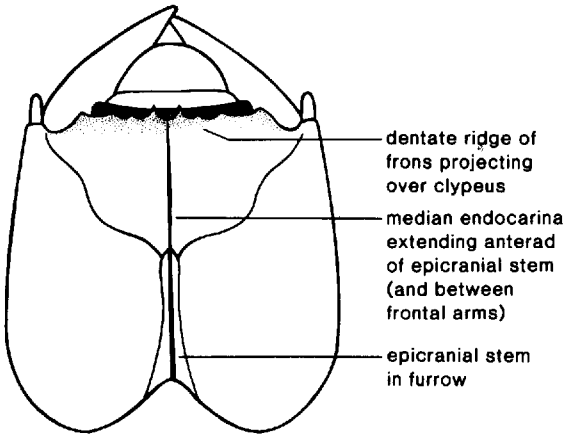


Figure 17

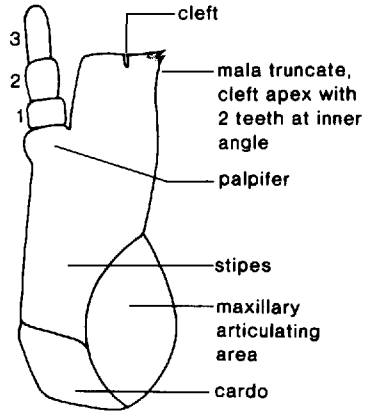


Figure 106

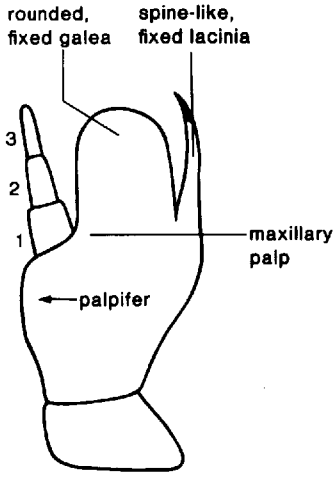
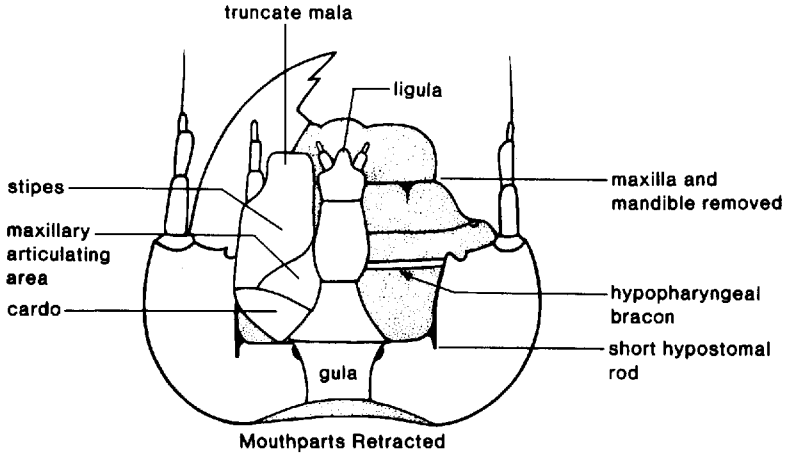
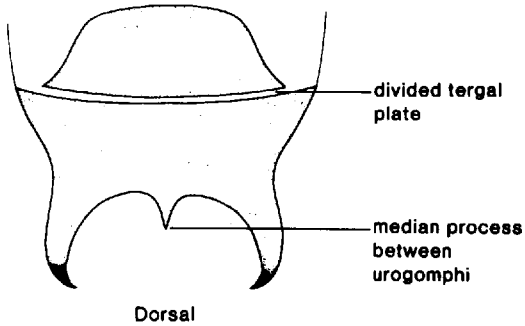


Figure 215



Mouthparts Retracted

Figure 85



Dorsal

Figure 172

233′. Head not or only slightly longer than wide, not narrowed posteriorly; epicranial stem located in broad furrow for attachment of retractor muscles (fig. 17); cardines separated from each other by labium (fig. 95) 234

234(233′). Occipital foramen not divided; apex of mandible parallel or oblique to plane of movement, its cutting edge straight and not gouge-like. In living or dead conifer wood ..... (**Aseminae**) ***Cerambycidae*** p. 556

234′. Occipital foramen divided into 2 parts by tentorial bridge (fig. 95); apex of mandible perpendicular to plane of movement, its cutting edge rounded and gouge-like (fig. 48). Under bark, in living or dead wood ..... (**Cerambycinae** part) ***Cerambycidae*** p. 556

235(232′). Head prognathous or slightly declined (fig. 8); ventral mouthparts protracted (fig. 92) or only slightly retracted; stipes wider than long; gula longer than wide (fig. 92); apex of mandible with single lobe or tooth; body surfaces smooth and vestiture consisting of simple setae or hairs 236

235′. Head moderately to strongly declined (hypognathous) (fig. 10); ventral mouthparts retracted (fig. 85); gula wider than long (fig. 85); apex of mandible trilobed or tridentate; dorsal surfaces of body granulate or tuberculate or vestiture including barbed hairs (spicisetae, fig. 6) 237

236(235). Hypostomal rods extending to posterior edge of head. In galleries of wood-boring insects. Exotic (New Zealand, Madagascar) ..... ***Chaetosomatidae*** p. 450

236′. Hypostomal rods, if present, not extending to posterior edge of head ..... (part) ***Cleridae*** p. 450

237(235′). Maxilla with single mala, sometimes cleft or with 1 or more teeth at inner apical angle (fig. 106); segments in maxillary palp 3; segment A10 concealed from above; vestiture consisting of fine hairs or setae only; anal region posteroventrally oriented; dorsal surfaces usually granulate or tuberculate. In fungus fruiting bodies ..... (part) ***Erotylidae*** p. 473

237′. Maxilla with separate galea and spine-like lacinia (as in fig. 215); segments in maxillary palp 4; segment A10 distinct and visible from above; vestiture including barbed hairs (spicisetae, fig. 6); anal region posteriorly or terminally oriented; dorsal surfaces smooth. On a variety of animal and plant products, including carrion ..... (**Dermestinae**) ***Dermestidae*** p. 434

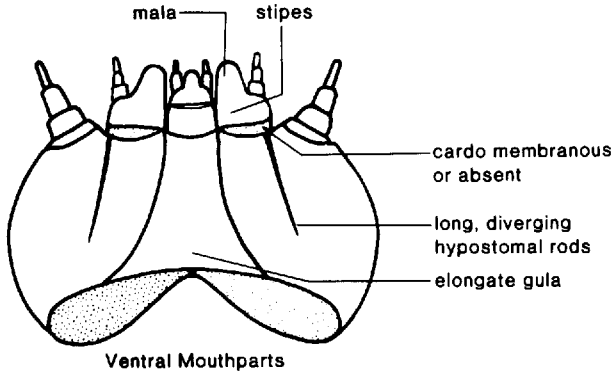
238(193[3]). Stipes longer than wide; ventral mouthparts retracted (fig. 87) 239

238′. Stipes wider than long; ventral mouthparts strongly protracted (fig. 92) 246

239(238). Tergum A9 without divided plate or median process between urogomphi 240

239′. Tergum A9 with transversely divided plate and median process between urogomphi (fig. 172); sclerotized plate on tergum A9 transversely divided (fig. 172). Under bark, in rotten wood, fungus fruiting bodies, stored products ..... (**Lophocaterinae**) ***Trogossitidae*** p. 448

240(239). Gular region absent (labium contiguous with thoracic membrane) (fig. 96); antennae very short, with sensorium on segment 2 much longer than reduced 3rd segment; apex of mandible multilobed or multidentate; stemmata on each side 1 ..... (**Orsodacninae**) ***Chrysomelidae*** p. 568



Ventral Mouthparts Strongly Protracted

Figure 92

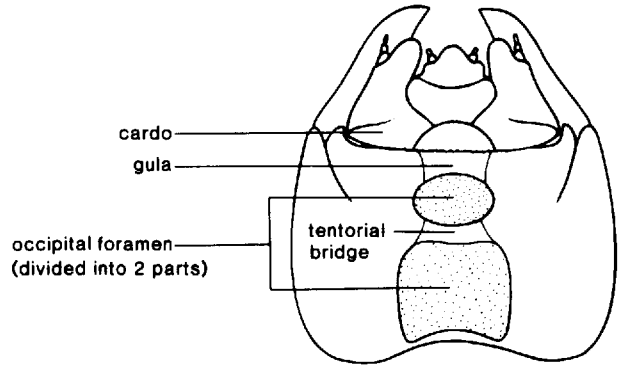


Figure 95

Figs. 48, 87, 96

240′. Gular region present (separating labium from thorax) (fig. 85); antennae longer, with segment 3 longer than sensorium; apex of mandible usually bidentate; stemmata on each side 4 or more 241

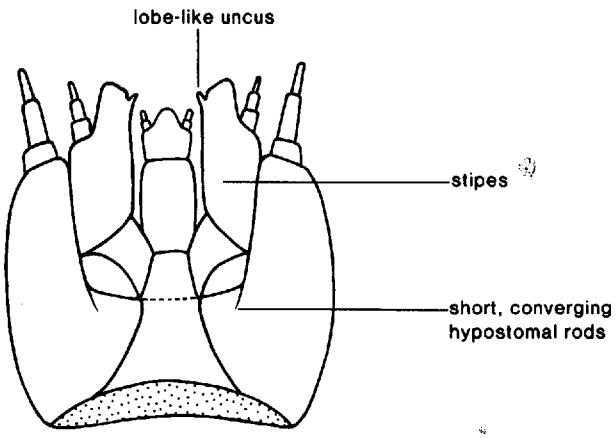
241(240′). Mesal surface of mandibular base with pubescent, membranous area (fig. 64); 2 pairs of hypostomal rods present, one subparallel and the other diverging (fig. 88); terga T1–3 and terga A1–9 each with distinct pigmented plate. In fungus fruiting bodies ..... (**Eustrophinae** part) ***Melandryidae*** p. 505

241′. Mesal surface of mandibular base with 1 or more hyaline processes (figs. 58–61); single pair of hypostomal rods present (fig. 89); thorax and abdomen with tergal plates on some segments only, and these usually paired 242

242(241′). Gula wider than long (fig. 85) 243

242′. Gula longer than wide (fig. 92) 245

243(242). Labial palps 1-segmented; mesal surface of mandibular base with single, acute, hyaline process (fig. 58); urogomphi approximate, arising from elevated common base. In leaf litter. Exotic (South temperate regions) ..... (**Rentoniinae**) ***Trogossitidae*** p. 448



Mouthparts Retracted

Figure 87

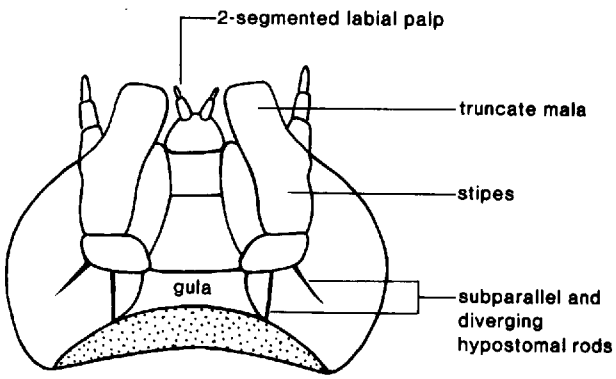
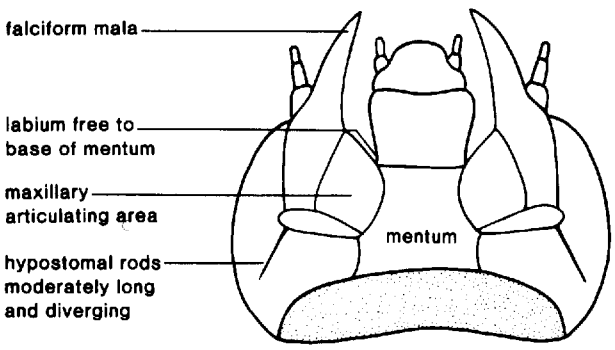


Figure 88



Mouthparts Retracted

Figure 89

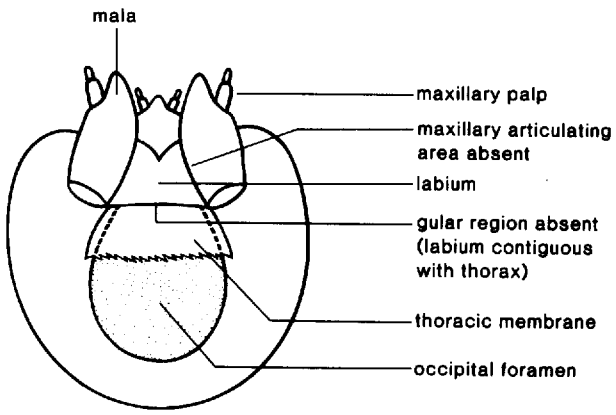


Figure 96

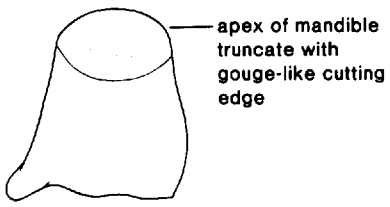


Figure 48

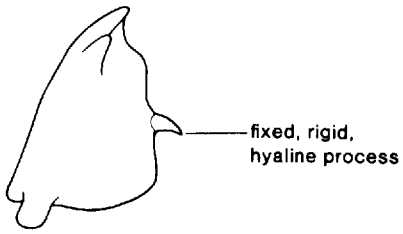


Figure 58

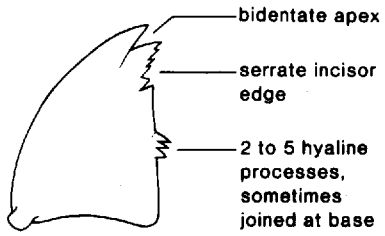


Figure 59

243′. Labial palps 2-segmented; mesal surface of mandibular base with 3 acute, hyaline processes (fig. 59); urogomphi distant at base, strongly curved, with apices slightly converging 244

244(243′). Frontal arms distinctly lyriform, each with an acute angle at middle (fig. 25); terga A6–8 without paired sclerotized plates. Under bark or in fungus fruiting bodies. Exotic (Europe) ..... ***Phloiophilidae*** p. 447

244′. Frontal arms only slightly, obtusely angulate at middle; terga A6–8 with paired, sclerotized plates. Under bark or in fungus fruiting bodies. Exotic (New Zealand) ..... (**Protopeltinae**) ***Trogossitidae*** p. 448

245(242′). Urogomphi with accessory processes (fig. 169); head transverse; tergal sclerites of mesothorax indistinct and separated by more than their width; sclerotized plate on tergum A9 with raised rim. Under bark, in rotten wood, fungus fruiting bodies ..... (*Calitys*) (**Calitinae**) ***Trogossitidae*** p. 448

245′. Urogomphi without accessory processes; head subquadrate or longer than wide; tergal sclerites of mesothorax distinct and separated by much less than their width; sclerotized plate on tergum A9 without raised rim. Under bark, in rotten wood, fungus fruiting bodies, stored products ..... (**Trogossitinae**) ***Trogossitidae*** p. 448

246(238′). Sternum A9 completely concealed beneath sternum A8 (fig. 164); hypostomal rods long and diverging (fig. 92); apex of mandible tridentate (fig. 60); mesal surface of mandibular base with 1 or more hyaline processes (fig. 60); A8 spiracles located at posterior end of segment and facing posteriorly (fig. 168). In flower heads, rotting wood, fungus fruiting bodies ..... (part) ***Phalacridae*** p. 466

246′. Sternum A9 partly or entirely exposed; hypostomal rods, if present, short or subparallel; apex of mandible with fewer than 3 teeth or lobes; A8 spiracles laterally placed and oriented 247

247(246′). Apex of mandible with single lobe or tooth; gula longer than wide (fig. 92); maxillary articulating area absent. Under bark, in dead wood, leaf litter, fungi ..... (part) ***Cleridae*** p. 450

247′. Apex of mandible bilobed or bidentate; gula wider than long (fig. 85); maxillary articulating area present (fig. 85). Under bark, in living or dead wood .... (**Lepturinae** part) ***Cerambycidae*** p. 556

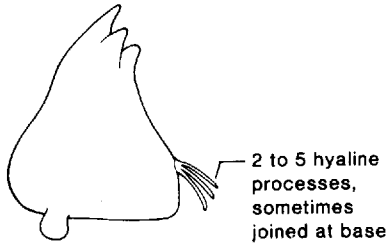


Figure 60

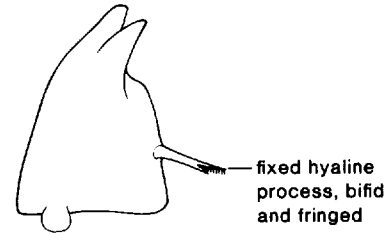


Figure 61

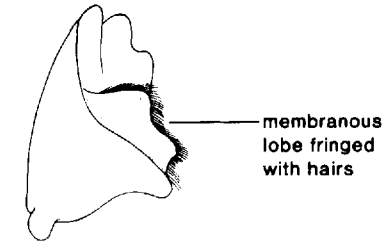


Figure 64

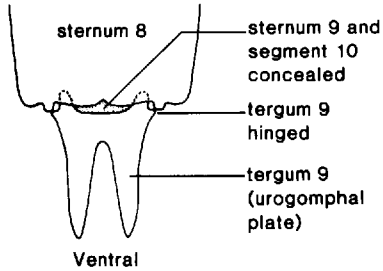


Figure 164

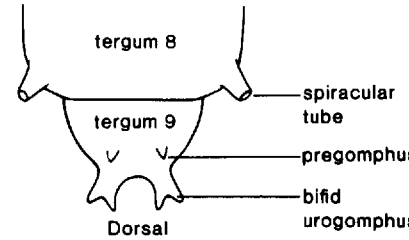


Figure 168

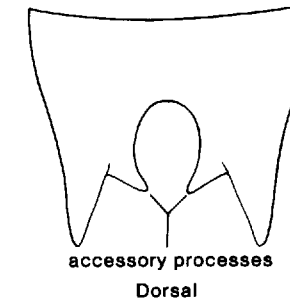


Figure 169

248(3′). Tergum A9 without paired processes (urogomphi) 249
248′. Tergum A9 with paired processes (urogomphi) (figs. 162, 166–185, 217) 311
249(248). Antennal segments 1 250
249′. Antennal segments 2 (**see 3rd and 4th choices**) 253
249². Antennal segments 3 (minute antennae may appear only 2-segmented) 261
249³. Antennal segments 4 or more 307
250(249). Abdominal terga without patches of asperities; frontal arms present (figs. 20, 22); segment A10 without oval lobes separated by longitudinal groove 251
250′. Abdominal terga with patches of asperities on 1 or more segments (fig. 142); frontal arms absent; segment A10 with pair of oval lobes separated by longitudinal groove (fig. 193). In fungus fruiting bodies, rotting wood, stems, vines ..... (part) ***Anobiidae*** p. 441
251(250). Legs distinctly 5-segmented (fig. 126); frontal arms lyriform (figs. 22, 25); molar surface with numerous, fine ridges (fig. 74); ratio of antennal length to head width greater than .15; body relatively straight or slightly curved ventrally, flattened, ovate, and heavily pigmented dorsally. On bark or rock surfaces, in moss. Exotic (Old World) ..... (Leiochrini) ***Tenebrionidae*** p. 520
251′. Legs with 4 segments or fewer (possibly with an additional coxal lobe); frontal arms, if present, V- or U-shaped (fig. 20); molar surface simple (fig. 69); ratio of antennal length to head width less than .15; body strongly curved ventrally (C-shaped), more or less elongate and lightly pigmented 252
252(251′). Legs 4-segmented; mandible with accessory ventral process (fig. 75). In flowers of *Delphinium* (Ranunculaceae). Exotic (Eurasia and northern Africa) ..... (*Nemonyx*) ***Nemonychidae*** p. 585
252′. Legs with 2 segments or fewer; mandible without accessory ventral process. In fungus fruiting bodies, dead wood, stems, vines, etc. ..... (part) ***Anthribidae*** p. 586
253(249′). Segments of T2 leg 6 including single claw (fig. 125); head with median endocarina extending anteriorly almost to edge of clypeus (fig. 21); ligula sclerotized and wedge-like (fig. 117). Probably in rotten wood .... (*Priacma*, first instar) ***Cupedidae*** p. 298

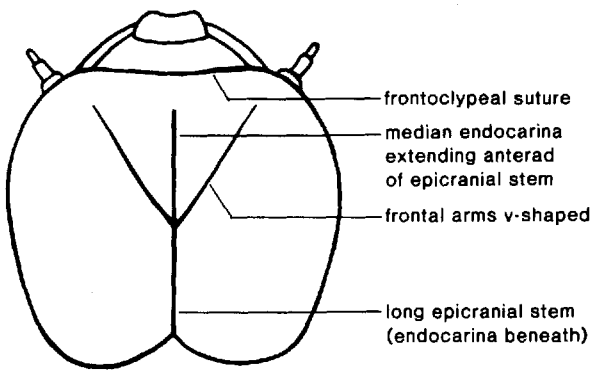


Figure 20

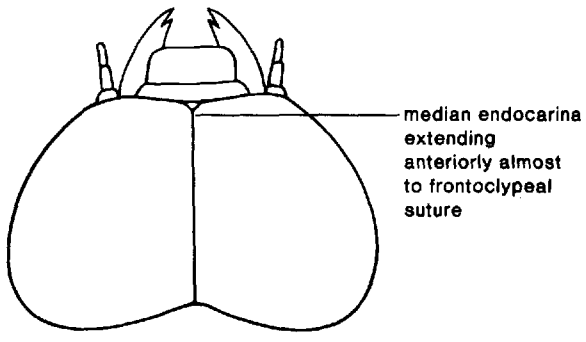


Figure 21

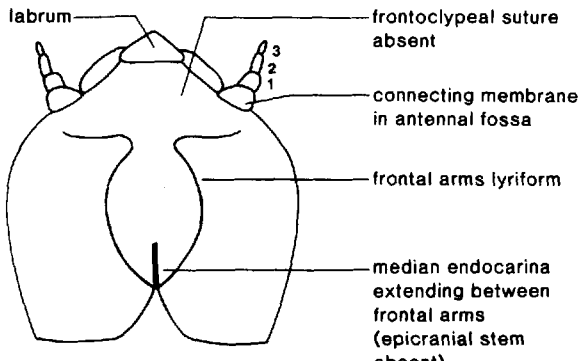


Figure 22

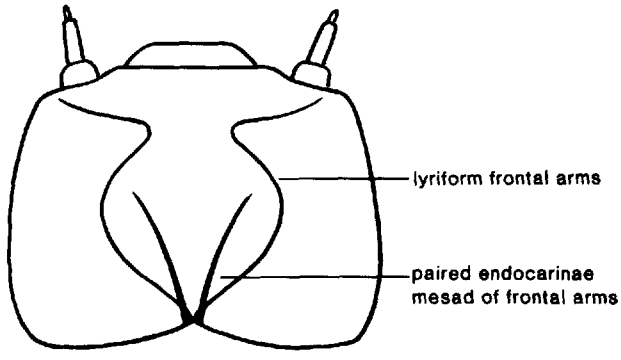


Figure 25

Figs. 166–185: See pages 249, 255, 265, 275

253'. Segments of T2 leg 5 including tarsungulus (fig. 126); median endocarina, if present, not extending far anteriorly; ligula not forming wedge-like sclerome 254

254(253'). Spiracular gills (transparent vesicles, gill tufts, or segmented, spiracle-bearing processes) present on abdomen or thorax and abdomen (figs. 152, 211, 212); length less than 3mm (2mm in North American forms); aquatic 255

254'. Spiracular gills absent; length usually more than 2mm; terrestrial 256

255(254). Segmented spiracular gills (fig. 152) on segments A1–8; ratio of antennal length to head width more than .2. On rocks in streams or near waterfalls. Exotic (Brazil, South Africa, Madagascar) ..... (part) ***Torridincolidae*** p. 302

255'. Vesicular spiracular gills (fig. 211) on raised spiracular tubes on A1–8; ratio of antennal length to head width more than .2. In sand, gravel, or mud at edges of streams (**see 3rd choice**) ..... (part) ***Microsporidae*** p. 302

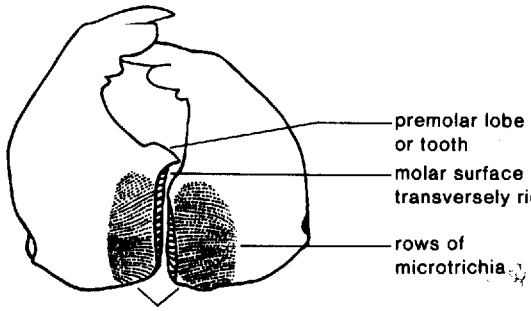


Figure 74

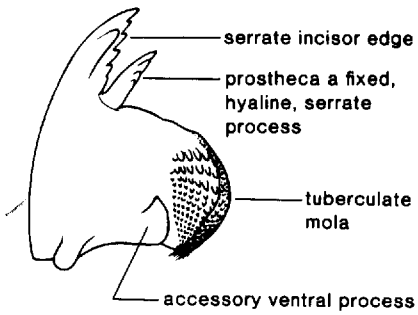


Figure 75

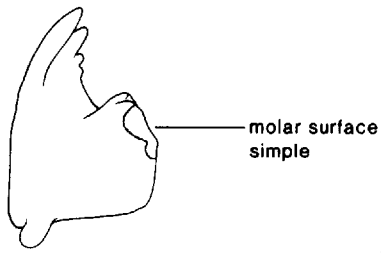


Figure 69

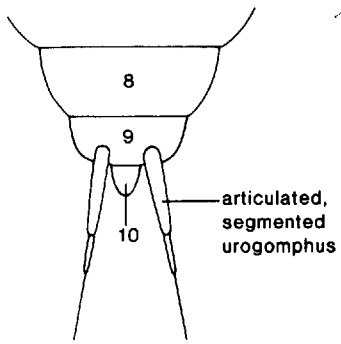


Figure 162

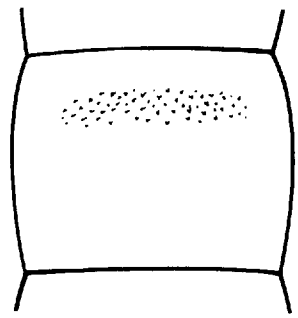


Figure 142

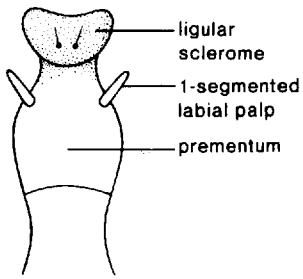


Figure 117

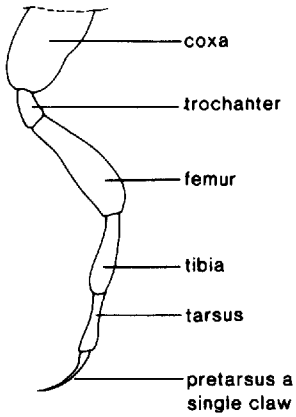


Figure 125

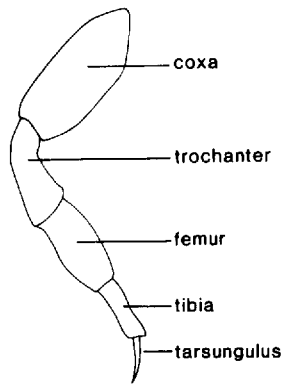


Figure 126

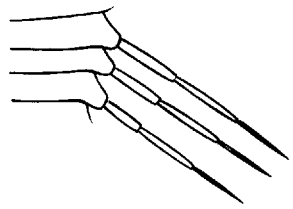


Figure 152

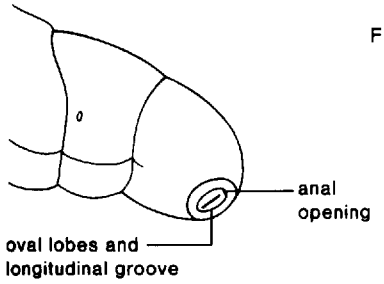


Figure 193

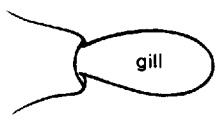


Figure 211

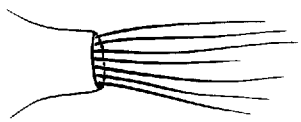


Figure 212

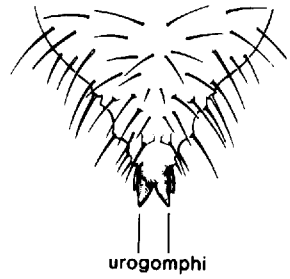


Figure 217

255[2]. Vesicular (fig. 211) or rarely tufted (fig. 212) gills present on raised spiracular tubes on T1, A1 and A8; spiracular tubes on segment A8 long and posteriorly projecting (fig. 161); ratio of antennal length to head width less than .15. On alga-covered rocks or in sand and mud in streams, pools, or hot springs ..... (part) ***Hydroscaphidae*** p. 303

256(254'). Body broadly ovate, strongly flattened, and disc-like (as in fig. 2); head concealed from above by T1; segments in maxillary palp 2. Under bark, in fungus fruiting bodies, in leaf litter. Exotic (Neotropical and Old World); possibly in southern United States ..... ***Discolomidae*** p. 481

256'. Body more or less elongate; head not concealed from above 257

257(256'). T3 leg reduced and 1-segmented (fig. 131); spiracles cribriform (fig. 208). In rotten wood ..... ***Passalidae*** p. 375

257'. T3 leg not reduced; spiracles not cribriform 258

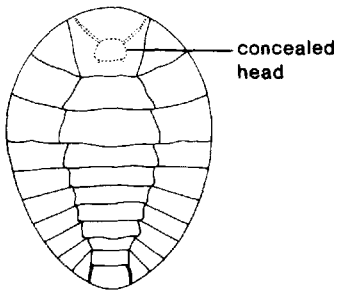


Figure 2


Figure 4

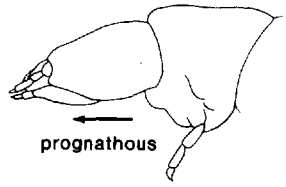


Figure 8

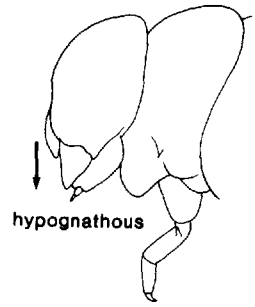


Figure 10

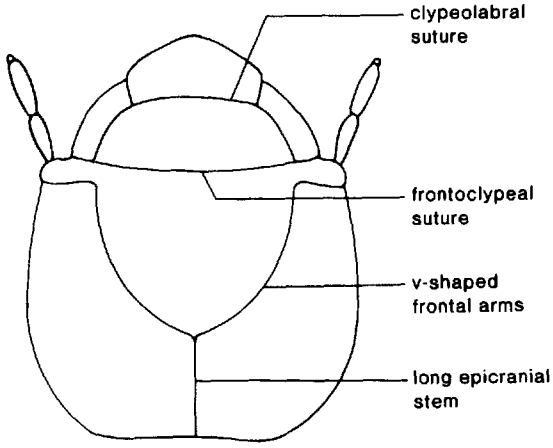


Figure 13

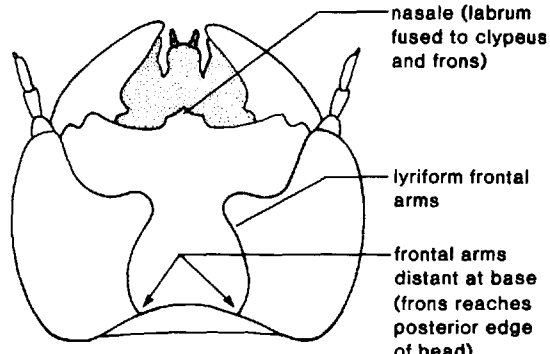


Figure 16

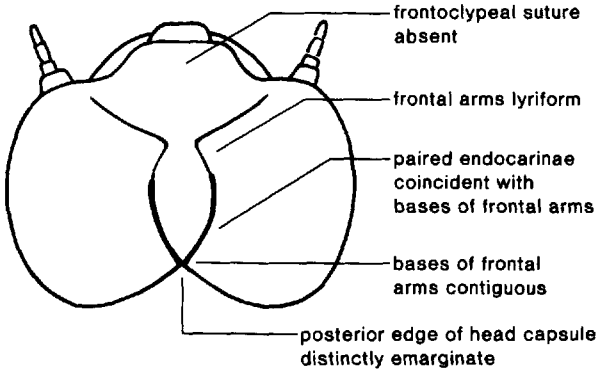


Figure 24

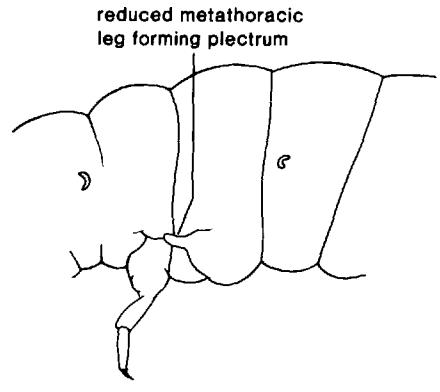


Figure 131

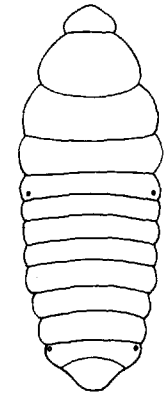


Figure 138

←— Figs. 75, 211, 212

258(257′). Head strongly declined (hypognathous) (fig. 10), globular; prothorax enlarged and swollen dorsally, forming a hood-like structure over head; ratio of antennal length to head width less than .15; body elongate and cylindrical. Tunneling in wood ..... (part) ***Lymexylidae*** p. 446

258′. Head prognathous or slightly declined (fig. 8); prothorax not enlarged and hood-like; ratio of antennal length to head width more than .15 259

259(258′). Frontoclypeal suture present (fig. 13); hypostomal rods absent. In rotten wood, fungus fruiting bodies, leaf litter ..... (part) ***Tenebrionidae*** p. 520

259′. Frontoclypeal suture absent (fig. 24); hypostomal rods long and diverging (figs. 89, 92) 260

260(259′). Frontal arms separated at base (fig. 16); mala rounded or truncate (fig. 92); large paired gland openings on terga A1 and A8 (fig. 138); body more or less oblong, fusiform, vestiture including expanded or clavate setae (fig. 4). In leaf litter, on surfaces of fungi and molds ..... (part) ***Corylophidae*** p. 495

260′. Frontal arms contiguous at base (fig. 24); mala falciform (fig. 89); abdomen without paired gland openings; body elongate and more or less parallel-sided; vestiture consisting of simple setae. Under bark, in leaf litter, in stored products ..... (Silvanini part) ***Cucujidae*** p. 463

261(249[2]). Prostheca absent 262

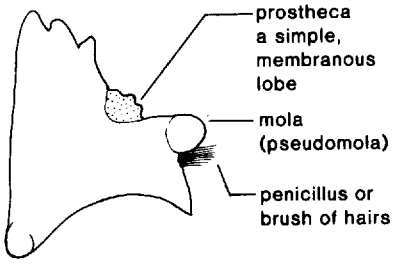


Figure 72

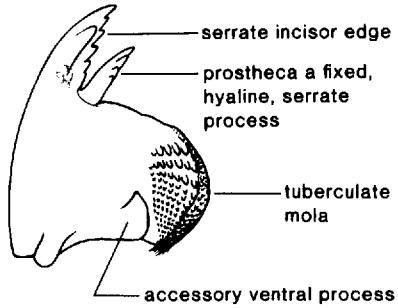


Figure 75

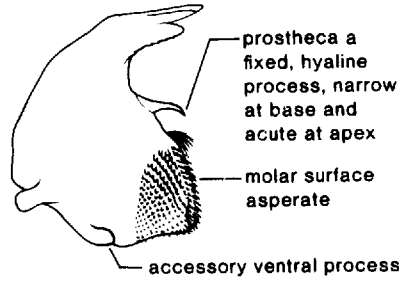


Figure 78

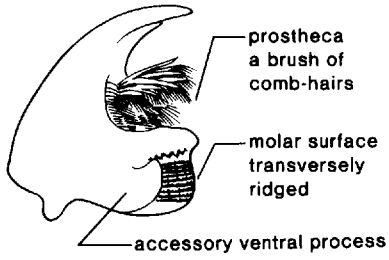


Figure 80

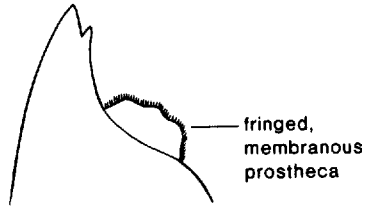


Figure 84

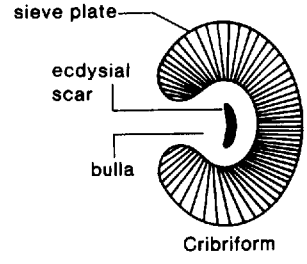
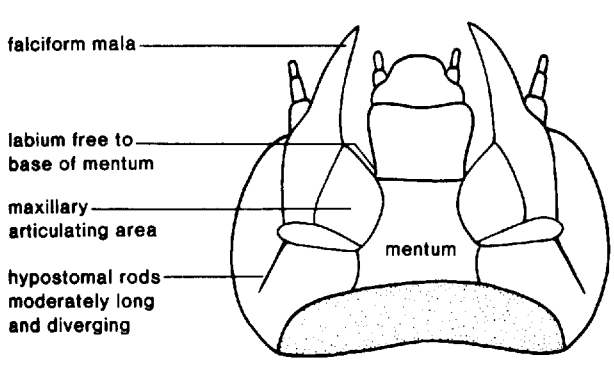
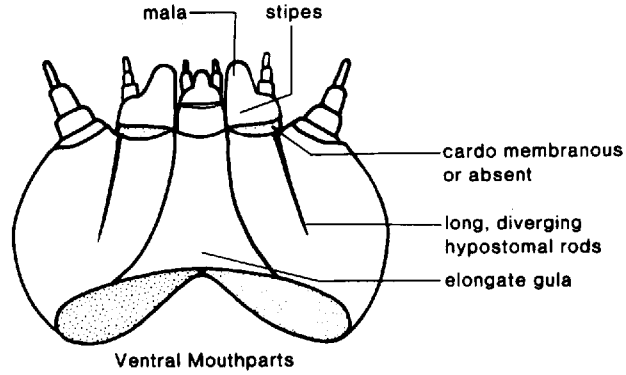


Figure 208



Mouthparts Retracted
Figure 89



Ventral Mouthparts
Strongly Protracted
Figure 92

261′. Prostheca a brush of simple or complex hairs (fig. 80) **(see 3rd thru 6th choices)** **286**

261^2. Prostheca a fixed, rigid, hyaline process (figs. 75, 78) sometimes partly sclerotized and sometimes appearing articulated **287**

261^3. Prostheca consisting of 2 hyaline processes; length less than 2.5mm; paired gland openings (fig. 139) on terga A1–7. In leaf litter, on surfaces of fungi ..... (part) ***Corylophidae*** p. 495

261^4. Prostheca a simple, membranous lobe (fig. 72) **303**

261^5. Prostheca a membranous lobe fringed with simple or complex hairs (fig. 84) **306**

262(261). Tergum A9 simple **265**

262′. Tergum A9 with median process (figs. 158, 159) **(see 3rd and 4th choices)** **281**

262^2. Tergum A9 with concave, terminal disc (fig. 160) **285**

262^3. Tergum A9 complex, with several sclerotized processes (fig. 180) **263**

263(262^3). Sternum A9 simple; frontoclypeal suture present (fig. 13). In rotten wood ..... (Strongyliini) ***Tenebrionidae*** p. 520

263′. Sternum A9 with asperities at base (figs. 180, 182); frontoclypeal suture absent (fig. 24) **264**

264(263′). Hypostomal rods present (fig. 85); sternum A9 with 2 basal asperities on each side. Exotic (Old World) ..... (**Trogocryptinae** part) ***Othniidae*** p. 547

264′. Hypostomal rods absent; sternum A9 with doubly curved row of basal asperities (fig. 180). In rotten wood ..... (**Pythinae** part) ***Pythidae*** p. 539

265(262). Maxilla with single mala (figs. 86, 106) **266**

265′. Maxilla with galea and lacinia (figs. 100, 111) **276**

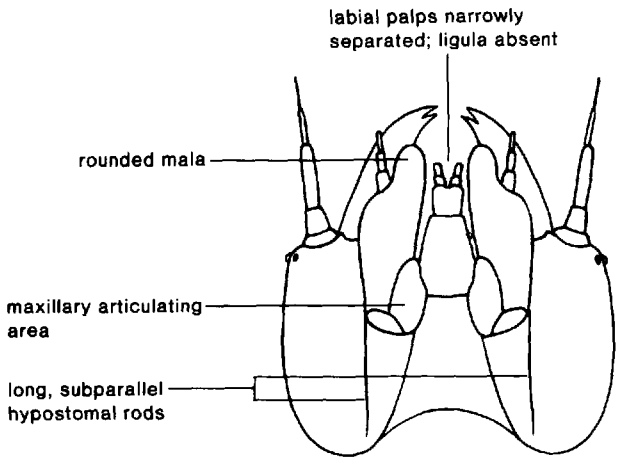


Figure 86

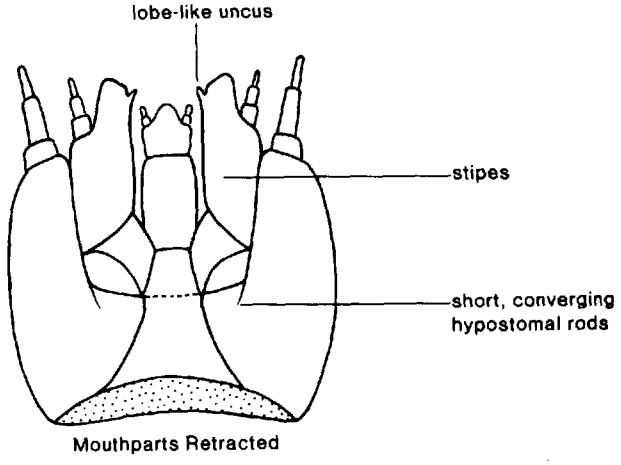


Figure 87

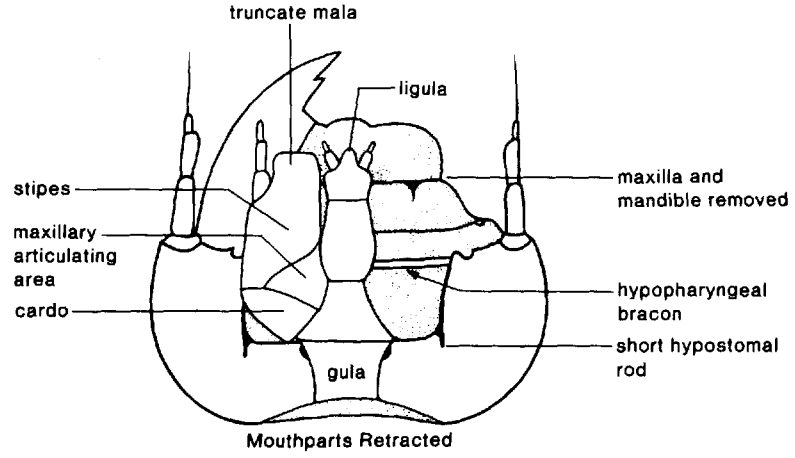


Figure 85

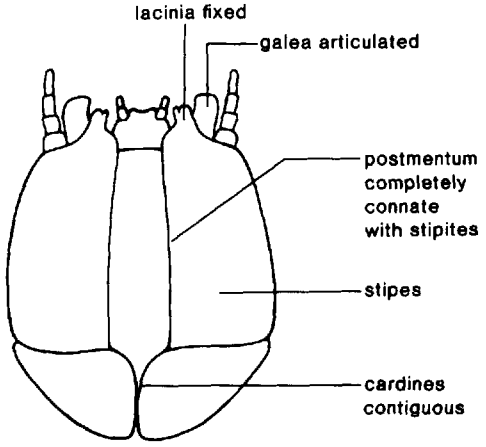


Figure 100

266(265). Head moderately to strongly declined (hypognathous) (fig. 10), globular; T1 enlarged and swollen dorsally (hump-like); body very elongate, with abdomen more than 5 times as long as thorax; patches of asperities on lateral portions of all thoracic segments and on apex of tergum A9, which is blunt and rounded. Tunneling in wood ..... (part) ***Lymexylidae*** p. 446

266'. Head prognathous or slightly declined (fig. 8); body not as elongate; without other characters in combination 267

267(266'). Ventral mouthparts strongly protracted (fig. 92); gular sutures long, subparallel, with heavily sclerotized internal ridges; large paired gland openings almost always present on terga A1 and A8 (fig. 138), A2 and A8, or A1–7; vestiture always including some modified setae (barbed, frayed, star-shaped). In leaf litter, on surfaces of molds and other fungi ..... (part) ***Corylophidae*** p. 495

267'. Ventral mouthparts retracted (fig. 86); gular sutures shorter and without obvious internal ridges; dorsal glands absent or inconspicuous; vestiture almost always consisting of simple setae 268

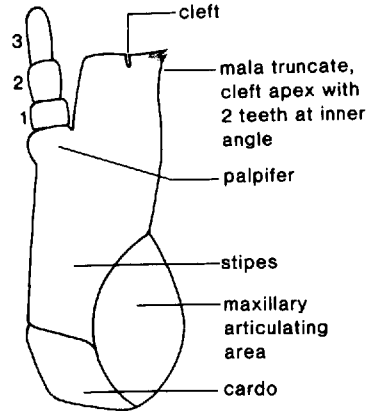


Figure 106

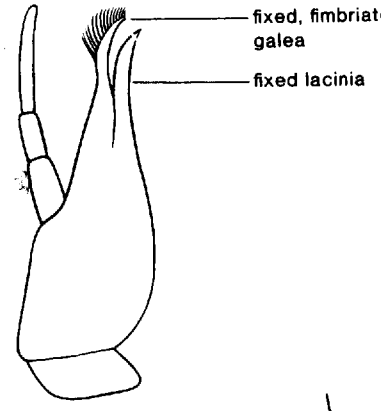


Figure 111

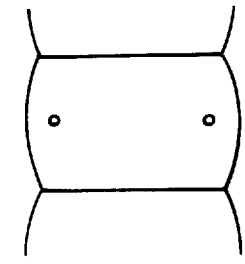


Figure 139

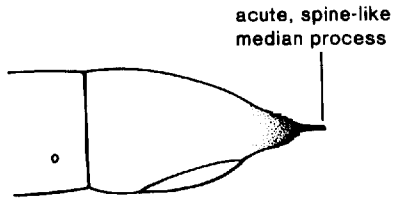


Figure 159

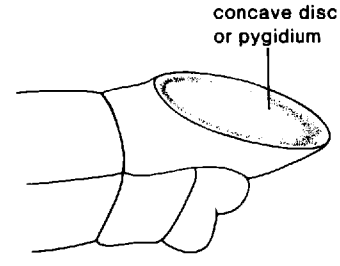


Figure 160

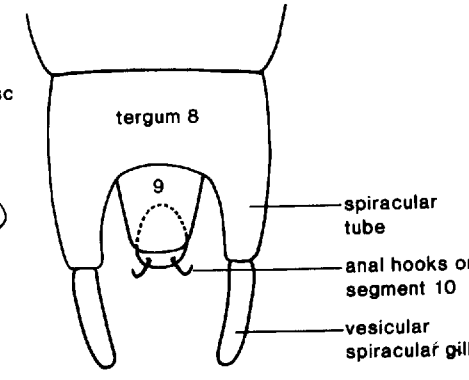


Figure 161

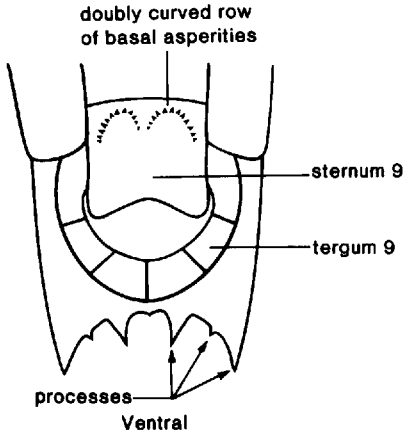


Figure 180

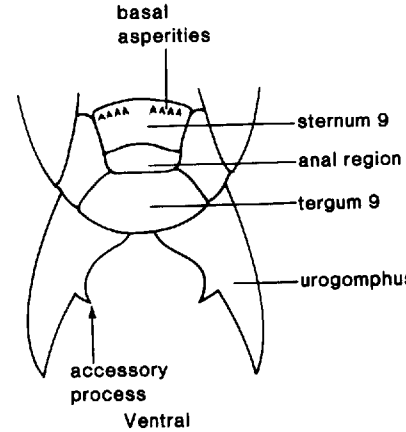


Figure 182

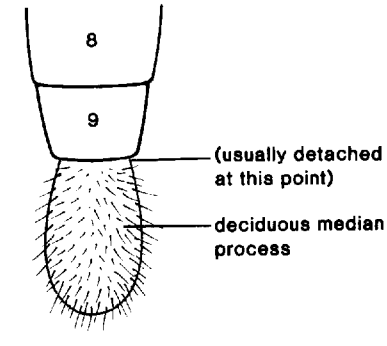


Figure 158

268(267′). Hypostomal rods absent; frontoclypeal suture present or head asymmetrical, with long epicranial stem and Y-shaped endocarina (fig. 23), and mandibular molae strongly asymmetrical with transverse ridges (fig. 74); length usually more than 10 mm 269

268′. Hypostomal rods present (figs. 86, 87); frontoclypeal suture absent; head symmetrical, without or with very short epicranial stem and lyriform frontal arms; mandibular molae occasionally asymmetrical but without transverse ridges; length usually less than 10 mm 272

269(268). Epicranial suture with a Y-shaped endocarina located beneath the stem and bases of the frontal arms (fig. 23); frontoclypeal suture absent (sometimes weakly impressed); spiracles annular-biforous (fig. 197); head usually asymmetrical (if not, paired ventral prolegs present on abdominal sterna 2–3, 3–4 or 2–4) 270

269′. Epicranial suture without Y-shaped endocarina; frontoclypeal suture distinct (fig. 13); spiracles annular (figs. 194, 195) or annular-multiforous (fig. 200); ventral prolegs never present 271

270(269). Frontoclypeal suture absent or vaguely indicated; hypopharyngeal region with a columnar prehypopharynx located just in front of sclerome; paired ventral prolegs (asperity-bearing ampullae) (fig. 149) usually present on sterna A2 and A3, A3–4 or A2–4; spiracles annular (figs. 194–195) or annular-multiforous (fig. 200). In rotten wood ..... (part) ***Oedemeridae*** p. 534

270′. Frontoclypeal suture present (fig. 13); hypopharyngeal region without prehypopharynx; paired ventral prolegs absent; spiracles annular-biforous (fig. 197). In rotten wood ..... (*Nematoplus*) (**Nematoplinae**) ***Cephaloidae*** p. 529

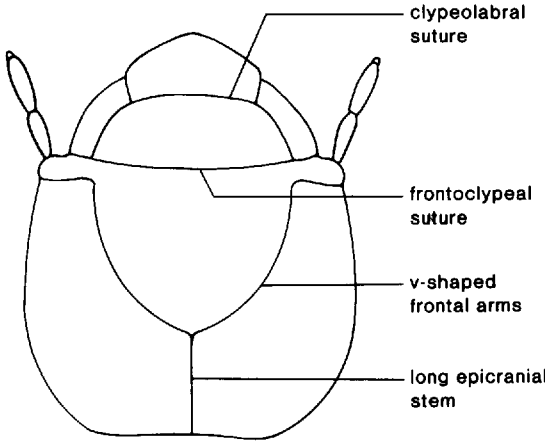


Figure 13

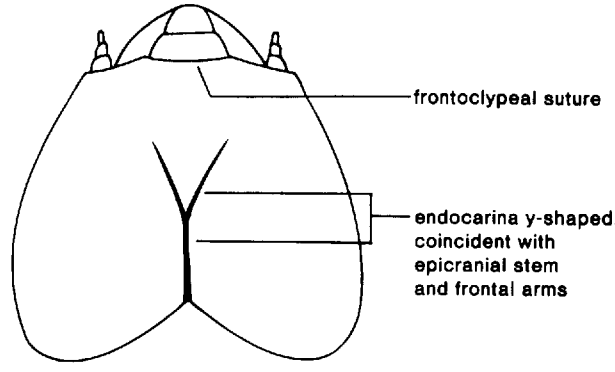


Figure 23

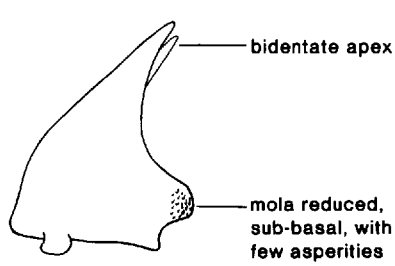


Figure 70

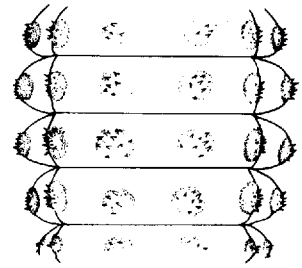


Figure 134

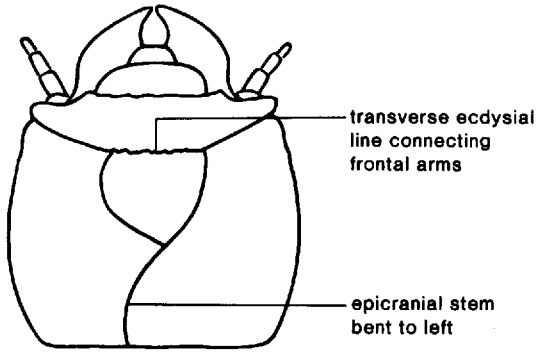


Figure 15

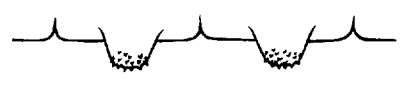


Figure 149

←— Figs. 86, 87

271(269′). Abdominal terga with rows of asperities (fig. 144); head heavily sclerotized with 5 well-developed stemmata on each side; frontoclypeal region produced on each side to form a plate; frontal arms joined anteriorly by transverse ecdysial line (fig. 15). On lichens and mosses. Exotic (New Zealand, Australia) ..... ***Chalcodryidae*** p. 520

271′. Abdominal terga without rows of asperities; without other characters in combination. Under bark, in rotten wood, soil, leaf litter ..... (part) ***Tenebrionidae*** p. 520

272(268′). Segments in labial palp 1 (fig. 91) 273

272′. Segments in labial palp 2 (figs. 88, 94, 97); spiracles annular (fig. 194) 274

273(272). Mandibles asymmetrical; mola well-developed, with tubercles or asperities extending onto ventral surface (fig. 73); setae on tarsungulus 2; spiracles annular. On fungus fruiting bodies ..... (*Thrimolus*) ***Mycetophagidae*** p. 498

273′. Mandibles symmetrical; mola reduced, bearing a few tubercles which do not extend onto ventral surface; setae on tarsungulus 1; spiracles annular-biforous (fig. 197). In flowers ..... (**Cateretinae**) ***Nitidulidae*** p. 456

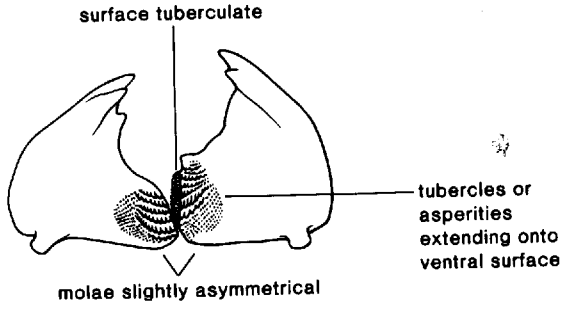


Figure 73

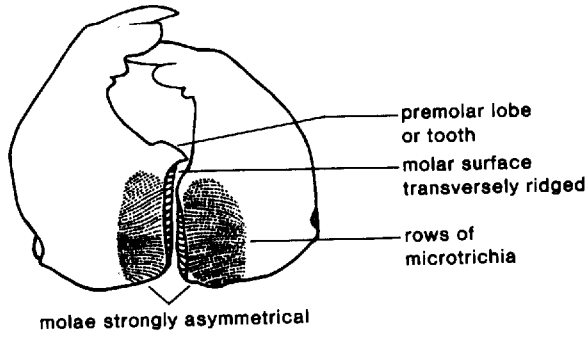


Figure 74

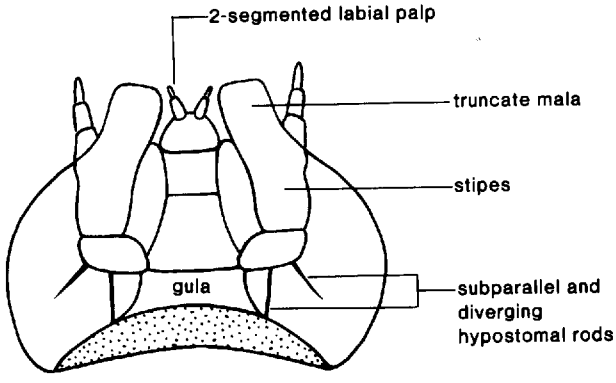


Figure 88

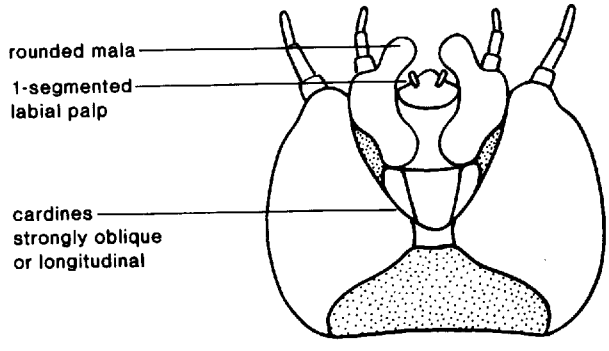


Figure 91

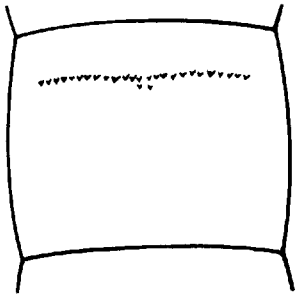
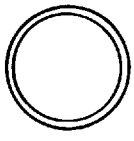
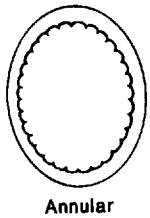
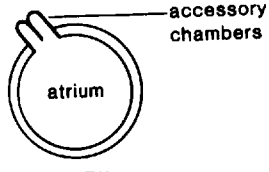


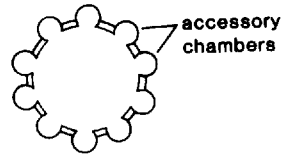
Figure 144


Annular
Figure 194


Annular
Figure 195



Annular Biforous
Figure 197



Annular Multiforous
Figure 200

Figs. 94, 97: See page 225.

274(272'). Stemmata on each side 1, each stemma with a well-developed lens; antennal segment 2 more than 2.5 times as long as segment 1; sensorium dome-like and partly surrounding segment 3; mola sub-basal, reduced, usually with a hyaline lobe or brush of hairs at base; tarsungular setae 2 (1 long and 1 very short); dorsal body surfaces smooth, with vestiture of scattered, long, simple setae ..... (part) ***Anthicidae*** p. 552

274'. Stemmata on each side 3 or 0; antennal segment 2 less than 2.5 times as long as segment 1; sensorium conical, often longer than segment 3; mola well-developed and extending to base of mandible; tarsungular setae 1; dorsal body surfaces more complex, usually with transverse rows of protuberances bearing groups of setae or simple or branched processes 275

275(274'). Cardo and stipes fused; mola reduced, sub-basal, and simple or asperate (fig. 70); dorsal surfaces of abdominal segments usually with transverse row of 6 protuberances, which may bear setose or branched processes (fig. 134); tibiae enlarged with group of spatulate setae at apex. On plant surfaces ..... (part) ***Coccinellidae*** p. 485

275'. Cardo and stipes distinct; mola well-developed, tuberculate, and extending to base of mandible; dorsal body surfaces smooth, without protuberances of any kind, clothed with scattered, simple setae; tibiae not enlarged, without spatulate setae. In soft fungi, under bark, in leaf litter .... (**Merophysiinae** and **Leiestinae**) ***Endomychidae*** p. 482

276(265'). Mandibular apex multidentate; spiracles annular; dorsal body surfaces covered with elongate, setiferous tubercles (fig. 3). Under bark of rotten logs ..... (part) ***Eucinetidae*** p. 364

276'. Mandibular apex unidentate to tridentate; spiracles cribriform (figs. 205–208), or occasionally biforous (fig. 202); dorsal body surfaces without setiferous tubercles 277

277(276'). Stemmata on each side 5; stemmata large, each with well-developed lens; segments in maxillary palp 3; head prognathous or slightly declined; ratio of antennal length to head width less than .15; body relatively straight or slightly curved ventrally, heavily pigmented dorsally; ventral epicranial ridges present (fig. 93); labium almost completely connate with maxillae (fig. 100). In sand or mud along streams ..... (part) ***Heteroceridae*** p. 402

Figure 3

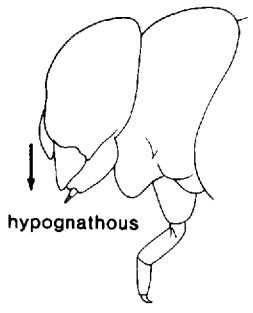


Figure 10

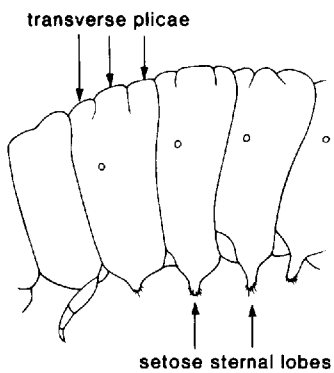


Figure 136

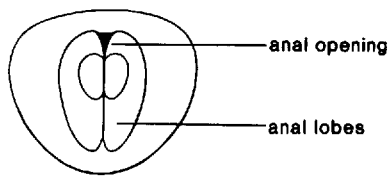
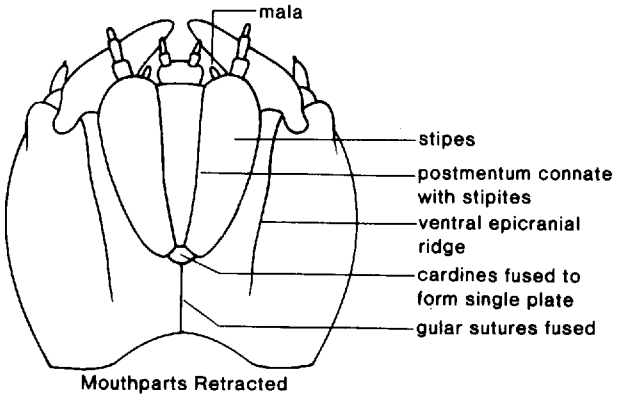


Figure 192



Mouthparts Retracted

Figure 93

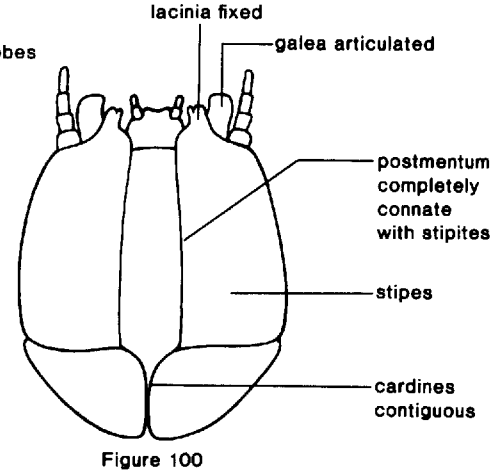


Figure 100

←— Figs. 70, 134

277'. Stemmata absent or consisting of single reduced pair; segments in maxillary palp 4; head moderately to strongly declined (hypognathous) (fig. 10); ratio of antennal length to head width greater than .15; body strongly curved ventrally (C-shaped), lightly pigmented; ventral epicranial ridges absent; labium completely free or only basally connate with maxillae (fig. 89) 278

278(277'). Tormae of epipharynx not united mesally (fig. 41); last abdominal segment without fleshy lobes around anus; tergum A3 with 4 transverse plicae bearing patches of short, stout setae. In soil (North America, West Coast) ..... (**Pleocominae**) ***Scarabaeidae*** p. 377

278'. Tormae of epipharynx united mesally (fig. 40); last abdominal segment usually with fleshy lobes around anus (fig. 192); tergum A3 with fewer than 4 transverse plicae (fig. 136), with or without patches of stout setae 279

279(278'). Anterior edge of labrum with 3 truncate lobes (fig. 35); 3rd antennal segment almost as long as 2nd, and bearing a sensorium and apical process representing fused 4th segment (fig. 34); stridulatory organs formed from pro- and mesothoracic legs. In soil, dung ..... (**Hybosorinae**) ***Scarabaeidae*** p. 377

279'. Anterior edge of labrum without 3 truncate lobes; 3rd antennal segment much shorter than 2nd, which bears 1 or more sensoria (as in fig. 29); stridulatory organs, if present, formed from T2 and T3 legs 280

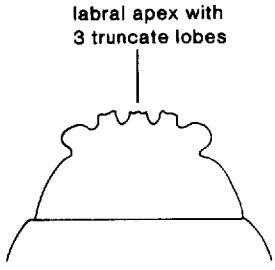


Figure 35

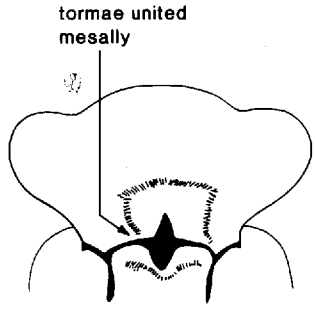


Figure 40

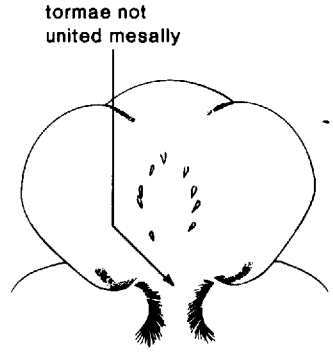


Figure 41

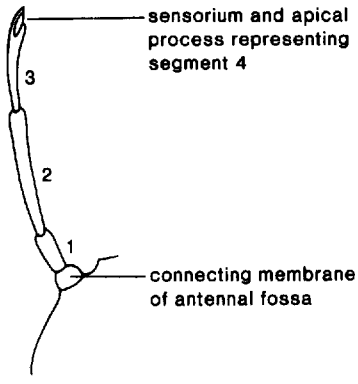
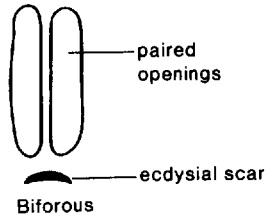
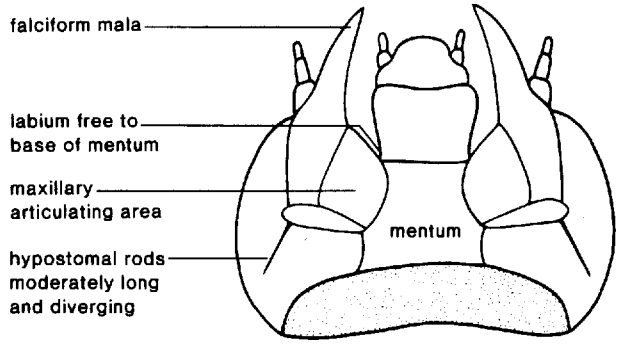


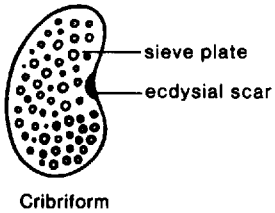
Figure 34



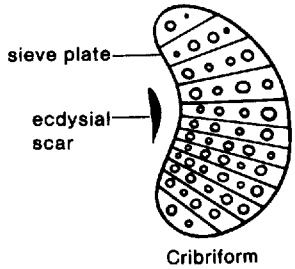
Biforous
Figure 202



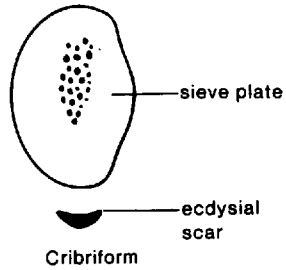
Mouthparts Retracted
Figure 89



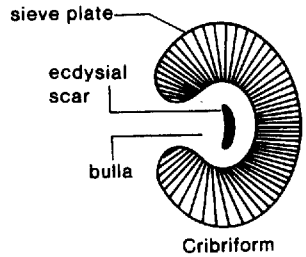
Cribriform
Figure 205



Cribriform
Figure 206



Cribriform
Figure 207



Cribriform
Figure 208

Fig. 29 ⟶

280(279′). Tergum A3 with 3 distinct transverse plicae (fig. 136), each bearing one or more rows of short, stiff setae; T2 and T3 legs not forming stridulatory organs; head much more darkly pigmented than body (except for T1 shield); spiracles cribriform (fig. 205) or biforous (fig. 202). In carcasses ..... (**Troginae**) ***Scarabaeidae*** p. 377

280′. Tergum A3 with 2 transverse plicae which do not bear rows or patches of stiff setae or asperities; head and body very lightly pigmented; legs often with fewer than 5 segments, T3 legs sometimes greatly reduced; T2 and T3 legs usually forming stridulatory organs. In burrows in ground (**see 3rd choice**) ..... (**Geotrupinae**) ***Scarabaeidae*** p. 377

280[2]. Tergum A3 without distinct transverse plicae; T2 and T3 legs always forming stridulatory organs (asperities on mesocoxa (fig. 129) and plectrum on metatrochanter (fig. 130)); head not much darker than body; spiracles always cribriform (fig. 208); abdominal terga usually with patches of asperities (fig. 141). In rotten wood ..... (part) ***Lucanidae*** p. 372

281(262′). Segments in T2 leg 5 or less including tarsungulus (fig. 126); segments in labial palp 2; frontal arms present; ligula without wedge-like sclerome; maxilla with single mala (fig. 86) 282

281′. Segments in T2 leg 6 including paired claws (fig. 124); segments in labial palp 1; frontal arms absent; ligula with wedge-like sclerome (fig. 117); maxilla with galea and lacinia (fig. 100); length less than 2mm. In rotten wood .... (caraboid larva) ***Micromalthidae*** p. 300

282(281). Abdominal terga without rows of asperities; ratio of antennal length to head width .15 to .5; head prognathous or slightly declined; ventral epicranial ridges absent; thoracic terga without patches of asperities 283

282′. Abdominal terga with rows of asperities on 1 or more segments (fig. 144); ratio of antennal length to head width less than .15; head moderately to strongly declined (hypognathous) (fig. 10); ventral epicranial ridges present (fig. 93); protergum with patch(es) of asperities. Tunneling in wood ..... (part) ***Lymexylidae*** p. 446

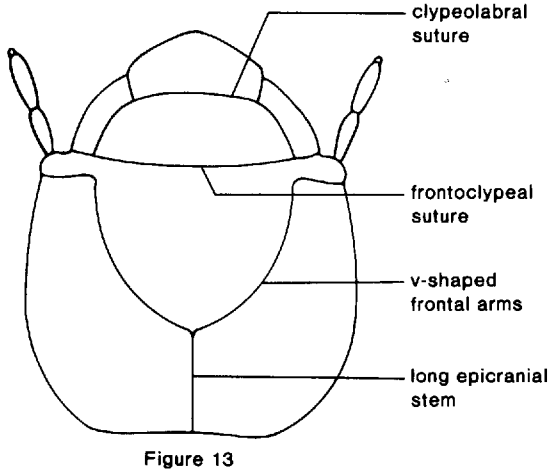


Figure 13

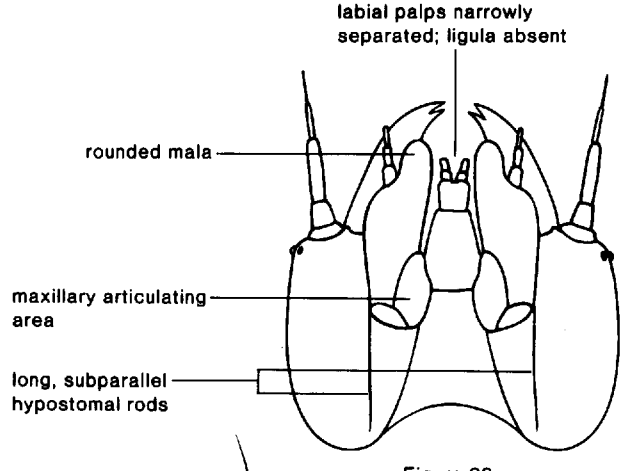


Figure 86

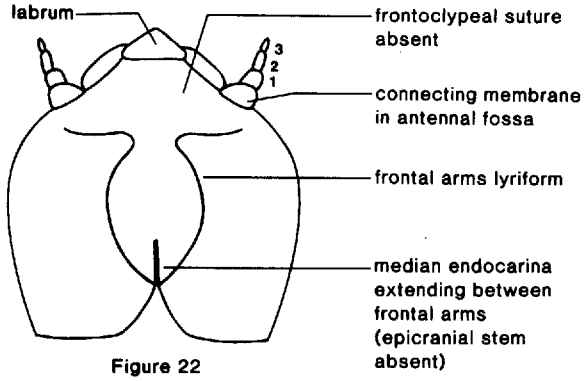


Figure 22

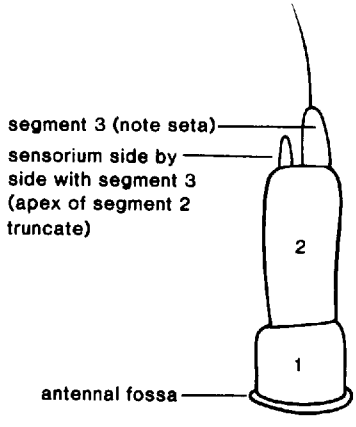


Figure 29

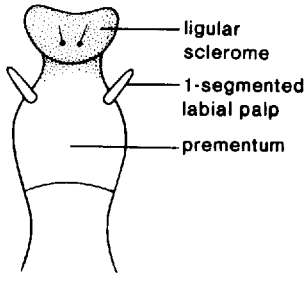


Figure 117

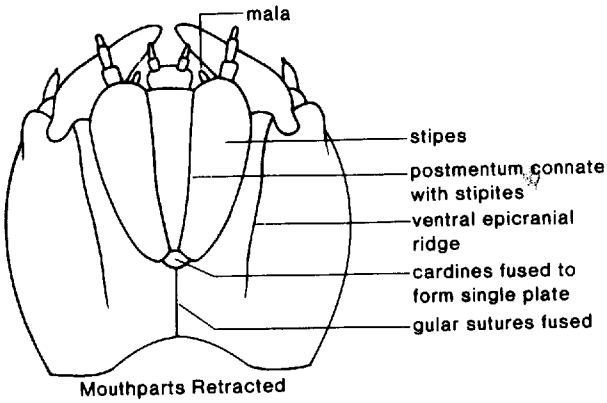
←— **Figs. 10, 89, 93, 100, 136, 202, 205, 208**

283(282). Frontal arms lyriform (fig. 22); posterior edge of head capsule distinctly emarginate dorsally; process on tergum A9 lightly pigmented, rounded, and deciduous (fig. 158) OR hypostomal rods present (fig. 89), frontoclypeal suture absent, and spiracles annular-biforous (fig. 197) 284

283'. Frontal arms V- or U-shaped (fig. 13); posterior edge of head capsule not or only slightly emarginate dorsally; process on tergum A9 not rounded or deciduous; hypostomal rods absent; frontoclypeal suture distinct (fig. 13); spiracles annular or annular-multiforous (fig. 200) ..... (part) ***Tenebrionidae*** p. 520

284(283). Paired endocarinae absent; frontoclypeal suture distinct (fig. 13); apex of mala cleft (fig. 106); hypostomal rods absent; abdominal spiracles annular. Median process on tergum A9 lightly sclerotized, rounded apically, pubescent, and deciduous (fig. 158). In leaf litter ..... (Scraptiinae) ***Scraptiidae*** p. 555

284'. Paired endocarinae present (fig. 24); frontoclypeal suture absent or vaguely indicated; apex of mala simple; hypostomal rods present (fig. 89); abdominal spiracles annular-biforous (fig. 197); median process on tergum A9 sclerotized and more or less acute (fig. 159). Under bark, in rotten wood ..... (part) ***Colydiidae*** p. 512



Mouthparts Retracted
Figure 93

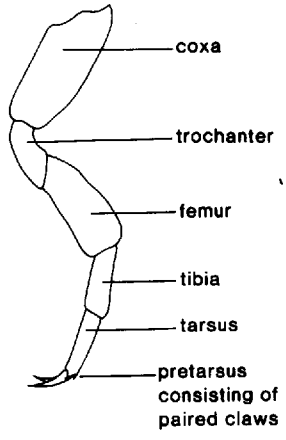


Figure 124

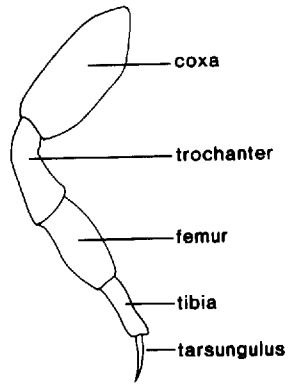


Figure 126

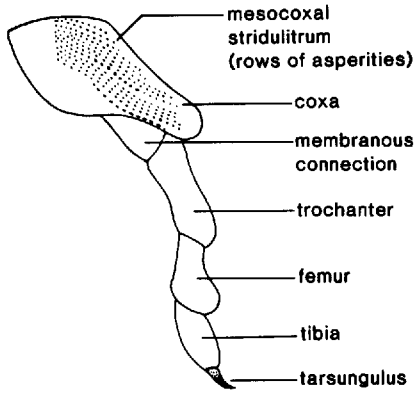


Figure 129

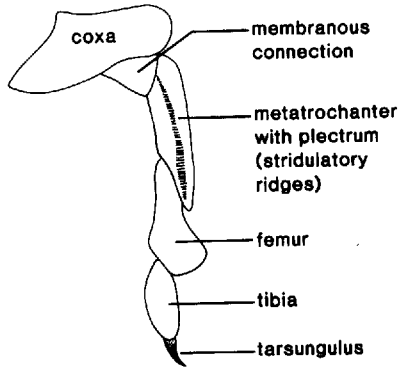


Figure 130

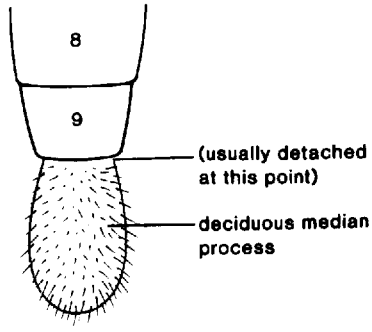


Figure 158

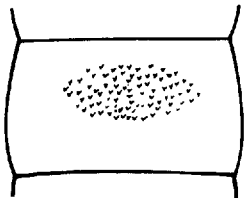
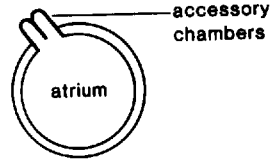
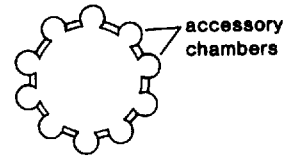


Figure 141


Figure 144



Annular Biforous
Figure 197



Annular Multiforous
Figure 200

Figs. 24, 106, 159 ——→

285(262²). Head prognathous or slightly declined (fig. 8); ratio of antennal length to head width .15 to .5; mandibles asymmetrical; thoracic terga without patches of asperities; apex of mala simple. Under bark, in rotten wood and fungus fruiting bodies ..... (part) ***Tenebrionidae*** p. 520

285′. Head moderately to strongly declined (hypognathous) (fig. 10); ratio of antennal length to head width less than .15; mandibles symmetrical; protergum with patch(es) of asperities; apex of mala cleft (fig. 106). Tunneling in wood ..... (part) ***Lymexylidae*** p. 446

286(261′). Body circular in cross-section; ventral epicranial ridges present (fig. 90); spiracles on A8 located at ends of spiracular tubes; prostheca consisting of a brush of comb-hairs (fig. 80); accessory ventral process of mandible present (fig. 80); molar surface with numerous fine ridges (fig. 80). Under bark or in rotting wood ..... (part) ***Biphyllidae*** p. 475

286′. Body slightly flattened; ventral epicranial ridges absent; abdominal spiracles not located at ends of spiracular tubes; prostheca consisting of brush of simple hairs or several hyaline processes; accessory ventral process of mandible absent; molar surface tuberculate or asperate (fig. 81). In oak catkins (western North America) ..... (*Byturellus*) ***Byturidae*** p. 476

287(261²). Tergum A9 forming articulated plate bearing median, forked process; sternum A9 almost completely concealed by sternum A8 (fig. 164); body elongate, more or less parallel-sided and strongly flattened. Under bark ..... (**Cucujinae** part) ***Cucujidae*** p. 463

287′. Tergum A9 not forming articulated plate and without forked process 288

288(287′). Maxilla with articulated galea and fixed lacinia (fig. 100); cardines approximate, not separated by labium (fig. 100); maxillary articulating area absent; labium and maxillae almost completely connate (fig. 100); mandibular mola concave, not tuberculate or asperate; spiracles cribriform (fig. 207); body clothed with dark, stiff hairs. In sand and mud along streams ..... (part) ***Heteroceridae*** p. 402

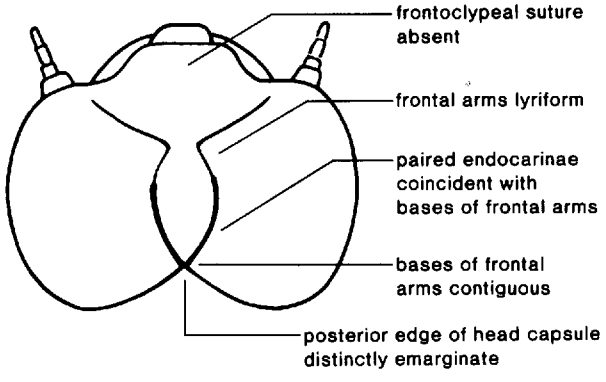
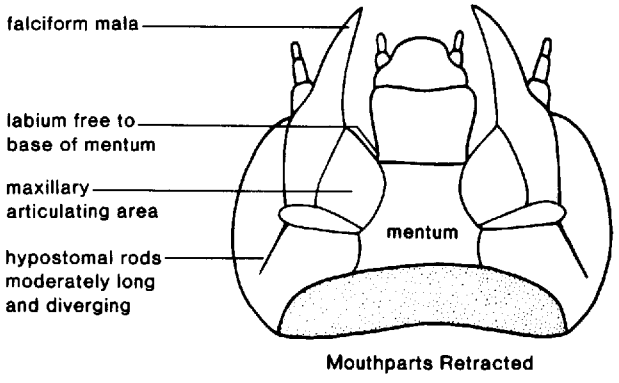


Figure 24



Mouthparts Retracted

Figure 89

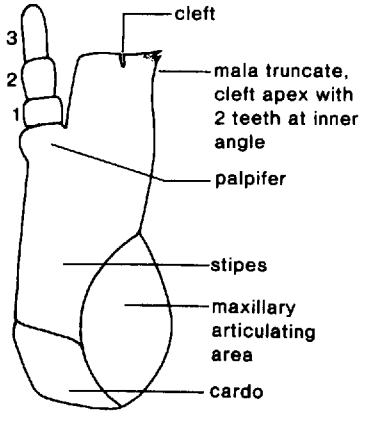


Figure 106

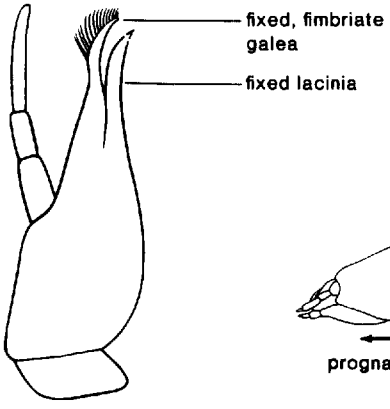


Figure 111

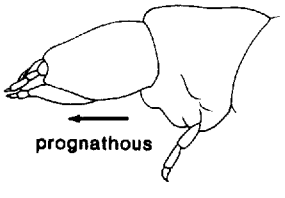


Figure 8

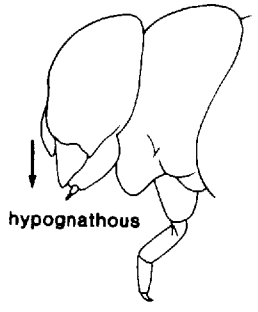


Figure 10

Figs. 86, 197

288′. Maxilla with fixed galea and lacinia (fig. 111) (**see 3rd choice**) 289

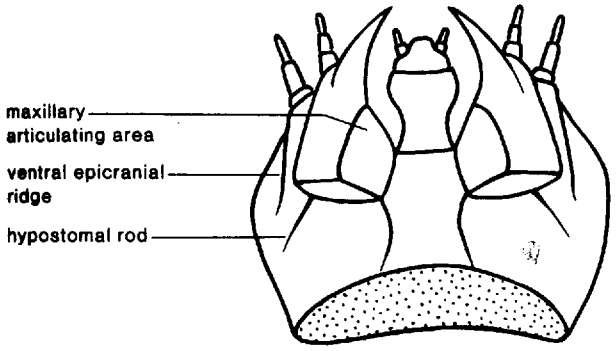
288². Maxilla with single fixed mala (fig. 86) 292

289(288′). Segments in labial palp 2; stemmata on each side 5 or 6 290

289′. Segments in labial palp 1; stemmata on each side 4 or fewer 291

290(289). Antennal segment 2 about 3 times as long as segment 3; head strongly narrowed anteriorly; spiracles annular; mandibular mola well-developed (fig. 78); stemmata on each side 5. In fruiting bodies of slime molds (Myxomycetes), in leaf litter, under bark ..... (part) ***Eucinetidae*** p. 364

290′. Antennal segment 2 less than twice as long as segment 3; head not strongly narrowed anteriorly; spiracles annular-biforous (fig. 197); mola somewhat reduced, not extending to base of mandible (fig. 70); stemmata on each side 6. On bark surfaces feeding on woolly aphids (Adelgidae) ..... (*Laricobius*) (Laricobiini) ***Derodontidae*** p. 431



Mouthparts Retracted
Figure 90

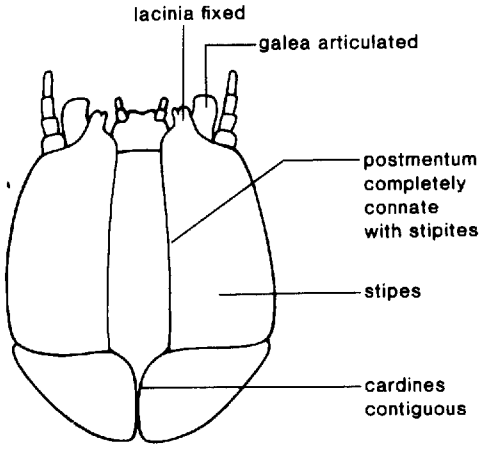


Figure 100

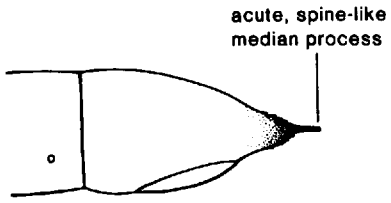


Figure 159

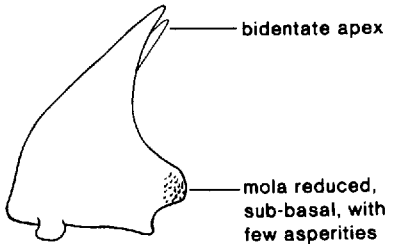


Figure 70

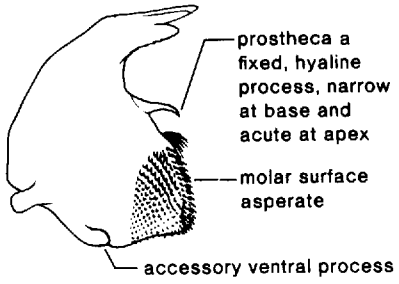


Figure 78

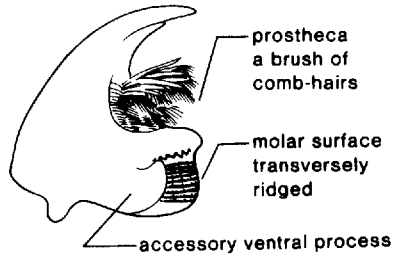


Figure 80

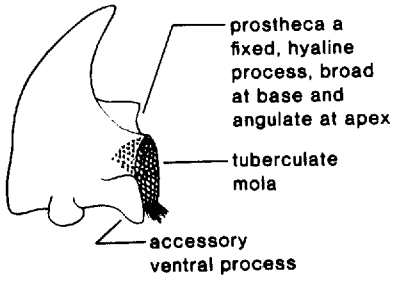
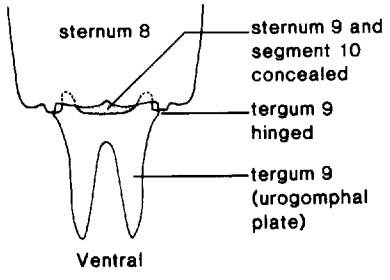
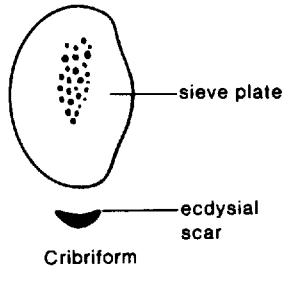


Figure 81



Ventral
Figure 164



Cribriform
Figure 207

291(289′). Ratio of antennal length to head width less than .2; antennal segment 2 only slightly longer than segment 3; segments in maxillary palp 2; thoracic and abdominal segments with lateral tergal processes; dorsal surfaces covered with setiferous tubercles (fig. 3). In leaf litter, hay stacks, fungi. Exotic (Neotropical and Old World) ..... (*Acalyptomerus*) (**Calyptomerinae**) ***Clambidae*** p. 365

291′. Ratio of antennal length to head width more than .5; antennal segment 2 much longer than segment 3; segments in maxillary palp 3; thoracic and abdominal segments without lateral tergal processes; dorsal surfaces clothed with simple setae. On molds ..... (*Eufallia*) (**Lathridiinae**) ***Lathridiidae*** p. 497

292(288²). Segment A10 with pair of hooks (fig. 163); body minute (length less than 1.2 mm), elongate and cylindrical; head moderately to strongly declined (hypognathous) (fig. 10); stemmata absent. In pore tubes of bracket fungi ..... (**Nanosellinae**) ***Ptiliidae*** p. 322

292′. Segment A10 without hooks; without other characters in combination 293

293(292′). Body broadly ovate, strongly flattened and disc-like (as in fig. 2), its edges lined with complex setae; head completely concealed from above by prothorax 294

293′. Body not broadly ovate and strongly flattened; head not concealed from above 295

294(293). Edges of body lined with barbed setae (fig. 6); head with median endocarina (fig. 19); prostheca simple and acute at apex (fig. 78); antennal segment 1 longer than segment 2. In leaf litter, rotting vegetation, stored products ..... (*Murmidius*) (**Murmidiinae**) ***Cerylonidae*** p. 480

294′. Edges of body lined with forked setae; head without median endocarina; prostheca forked at apex (fig. 83); antennal segment 1 shorter than segment 2. On fungus-covered, debarked surfaces of trees ..... (*Agaricophilus*) ***Endomychidae*** p. 482

295(293′). Prostheca broad and obtusely angulate (fig. 81) or somewhat rounded; apex of mandible often reduced and hyaline; outer edge of mandible usually with pair of long setae; ventral mouthparts often more or less protracted with hypostomal rods situated laterally. In leaf litter, stored products, associated with molds and other fungi ..... (part) ***Lathridiidae*** p. 497

295′. Prostheca narrow with apex acute (fig. 78) or bifid (fig. 83), sometimes with serrate buccal edge (fig. 82); mandibles different than above, and hypostomal rods, if present, ventrally situated 296

296(295′). Mala more or less truncate (fig. 88) 297

296′. Mala falciform (fig. 89) 299

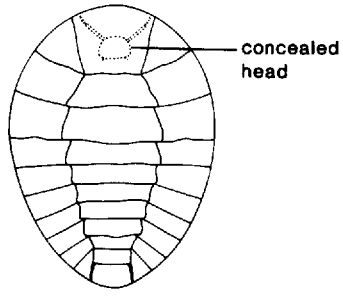


Figure 2


Figure 3

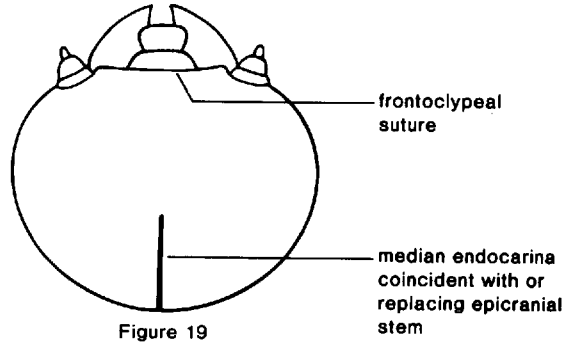


Figure 19

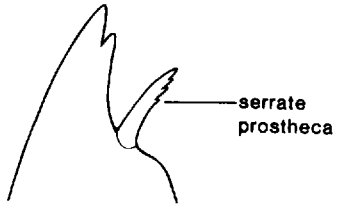


Figure 82


Figure 6

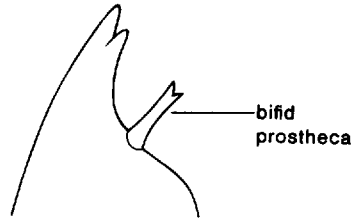


Figure 83

←— Figs. 8, 10, 78, 81

297(296). Head strongly narrowed anteriorly; stemmata on each side 4; head moderately to strongly declined (hypognathous) (fig. 10); segment A10 ventrally oriented and not visible from above. Under bark, on wood surfaces, associated with fungi ..... (**Eumorphinae**) ***Endomychidae*** p. 482

297'. Head not strongly narrowed anteriorly; stemmata on each side 6, occasionally weak or absent; head prognathous or slightly declined (fig. 8); segment A10 posteriorly or terminally oriented and more or less visible from above 298

298(297'). Antennal segment 3 much longer than 2; tarsungulus with single seta. In leaf litter, hay stacks, fruiting bodies of slime molds (Myxomycetes) ..... (**Clambinae**) ***Clambidae*** p. 365

298'. Antennal segment 2 much longer than segment 3; tarsungulus with 2 setae. In fruiting bodies of slime molds (Myxomycetes) ..... (part) ***Sphindidae*** p. 455

299(296'). Body more or less ovate; thoracic and abdominal terga produced laterally; body densely clothed with long, fine hairs; accessory ventral process of mandible absent. In leaf litter, rotten wood, fungi ..... (**Mychotheninae** part) ***Endomychidae*** p. 482

299'. Body elongate and more or less parallel-sided or somewhat narrowed posteriorly; thoracic and abdominal terga not produced laterally; accessory ventral process of mandible present (fig. 78); body not densely clothed with long hairs 300

300(299'). Segment A9 reduced, its sternum usually concealed and its tergum much shorter than that of segment A8 or A10 (fig. 167); antennal segment 3 highly reduced. Under bark, in leaf litter, stored products ..... (Silvanini part) ***Cucujidae*** p. 463

300'. Segment A9 not reduced, its sternum well-developed and exposed; antennal segment 3 not reduced 301

301(300'). Antennal segment 3 shorter than sensorium; stemmata on each side 5. In leaf litter, hay stacks ..... (*Calyptomerus*) (**Calyptomerinae**) ***Clambidae*** p. 365

301'. Antennal segment 3 much longer than sensorium; stemmata on each side 1 302

302(301'). Prostheca simple at apex; labial palps 1-segmented; spiracles annular-biforous (fig. 197). In flowers ..... (*Telmatophilus*) (**Cryptophaginae**) ***Cryptophagidae*** p. 469

302'. Prostheca bifid at apex (fig. 83); labial palps 2-segmented; spiracles annular. In leaf litter, grass piles ..... (**Atomariinae** part) ***Cryptophagidae*** p. 469

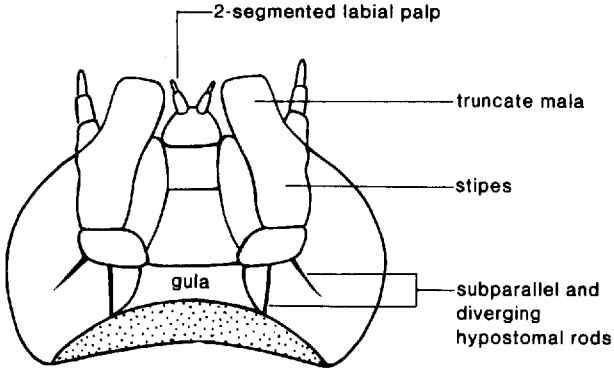
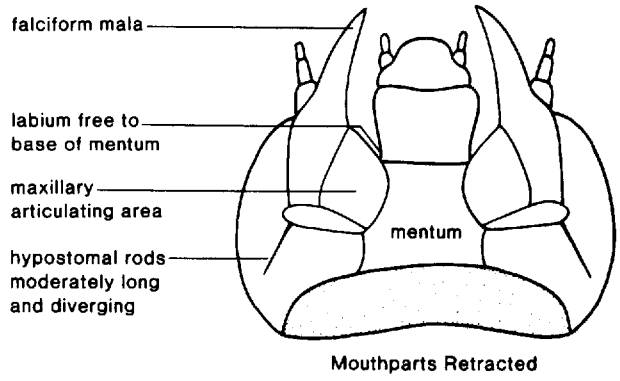


Figure 88



Mouthparts Retracted

Figure 89

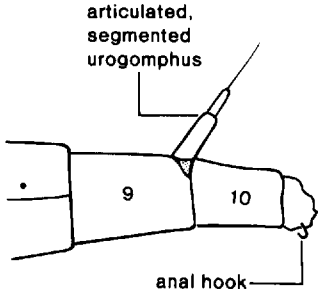


Figure 163

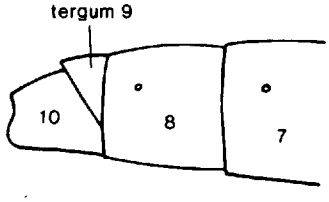
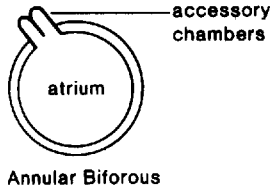


Figure 167



Annular Biforous

Figure 197

303(261⁴). Body relatively straight or only slightly curved ventrally; segment A10 without oval lobes separated by longitudinal groove; maxilla with single mala (fig. 86); head prognathous or slightly declined and protracted or slightly retracted (fig. 8). On leaf surfaces, mildew, in leaf litter, stored products ..... (part) ***Lathridiidae*** p. 497

303'. Body strongly curved ventrally (C-shaped); segment A10 with oval lobes separated by longitudinal groove (fig. 193); maxilla with galea and lacinia (fig. 215); head either hypognathous (fig. 10) or strongly retracted (fig. 9) 304

304(303'). Head moderately to strongly declined (hypognathous) (fig. 10) and protracted or slightly retracted; segments in maxillary palp 4. In fungus fruiting bodies ..... (*Endecatomus*) (**Endecatominae**) ***Bostrichidae*** p. 439

304'. Head prognathous or slightly declined and strongly retracted (fig. 9); segments in maxillary palp 3. In dead wood 305

305(304'). Spiracles on segment A8 much larger than those on A1–7 ..... (**Lyctinae** part) ***Bostrichidae*** p. 439

305'. Spiracles on segment A8 about same size as those on A1–7 ..... (**Dinoderinae, Dysidinae, Lyctinae** part) ***Bostrichidae*** p. 439

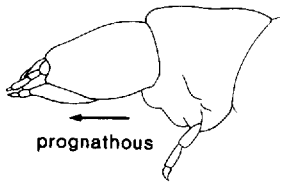


Figure 8

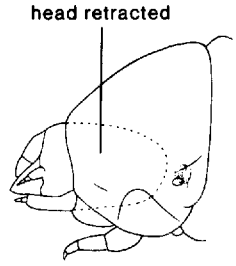


Figure 9

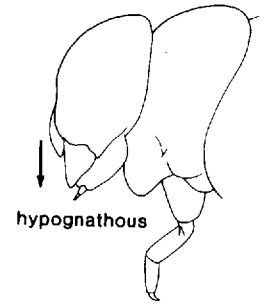


Figure 10

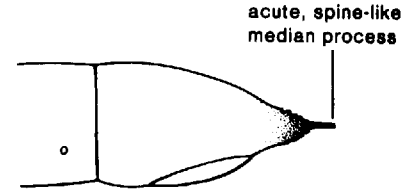


Figure 159

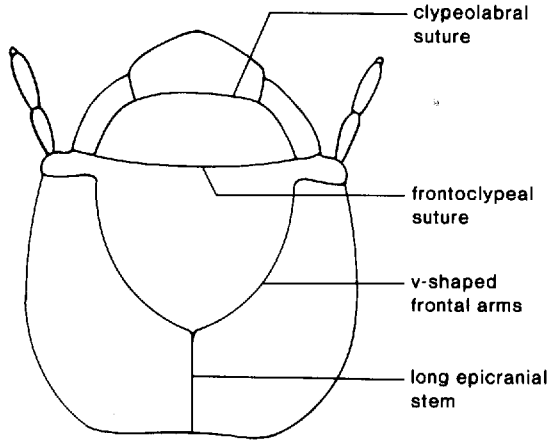


Figure 13

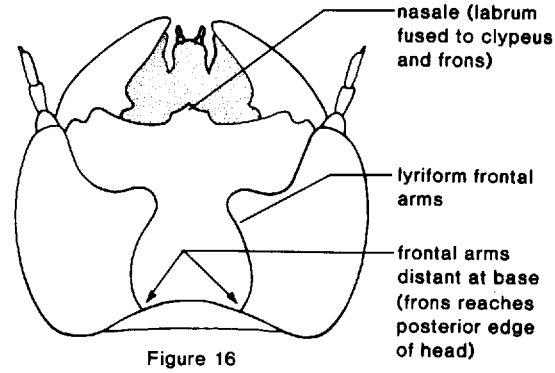


Figure 16

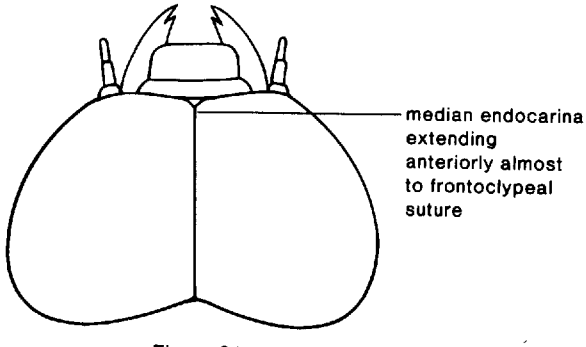


Figure 21

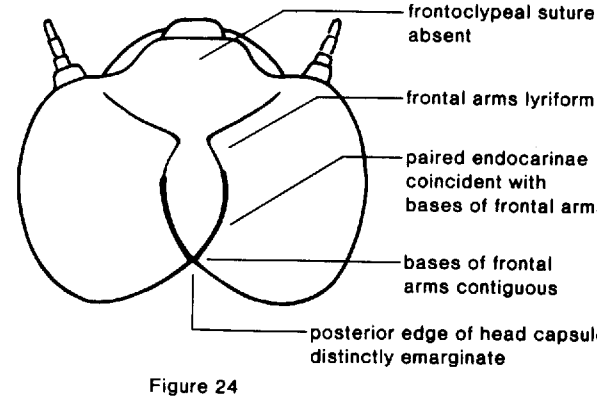


Figure 24

← Fig. 89

306(261[5]). Tergum A8 without special armature; bases of frontal arms contiguous (fig. 24); head moderately to strongly declined (hypognathous) (fig. 10); frontoclypeal suture absent or vaguely indicated; hypostomal rods present (fig. 89); stemmata on each side 4 or fewer; tergum A9 dorsal, extending onto ventral surface. Under bark, in fungus fruiting bodies, on bark surfaces ..... (part) ***Endomychidae*** p. 482

306'. Tergum A8 forming tapered process bearing spiracles at apex; bases of frontal arms distinctly separated (fig. 16); head prognathous or slightly declined (fig. 8); frontoclypeal suture distinct (fig. 13); hypostomal rods absent; stemmata on each side 5; tergum A9 completely ventral. In slime fluxes of fermenting sap ..... ***Nosodendridae*** p. 432

307(249[3]). Tergum A9 without median process; segments in T2 leg 5 or fewer including tarsungulus (fig. 126); segments in maxillary palp 4 (the last occasionally vestigal); prosternum without armature; posterior edge of head capsule not or only slightly emarginate dorsally; median endocarina, if present, not extending to frontoclypeal suture; ligula not sclerotized 308

307'. Tergum A9 with median process (fig. 159); segments in T2 leg 6 including single claw or paired claws (figs. 124, 125); segments in maxillary palp 3; prosternum with 2 patches of asperities; posterior edge of head capsule distinctly emarginate dorsally; median endocarina extending anteriorly almost to edge of clypeus (fig. 21); ligula forming sclerotized wedge (fig. 117); antennal segments 4 or 5. In rotten wood ..... (part) ***Cupedidae*** p. 298

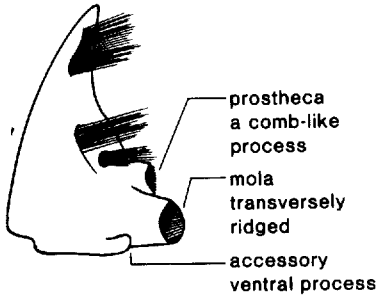


Figure 77

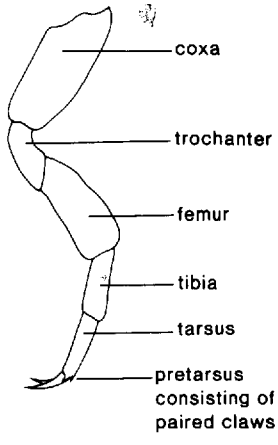


Figure 124

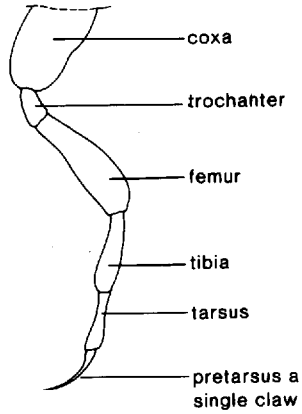


Figure 125

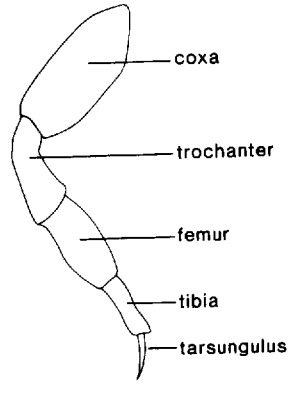


Figure 126

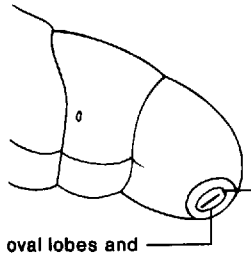


Figure 193

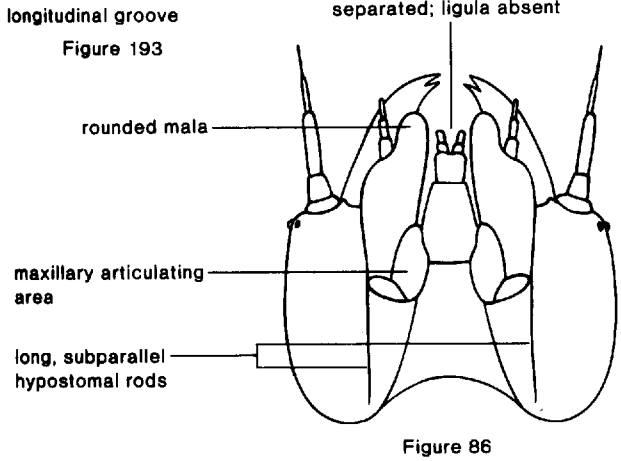


Figure 86

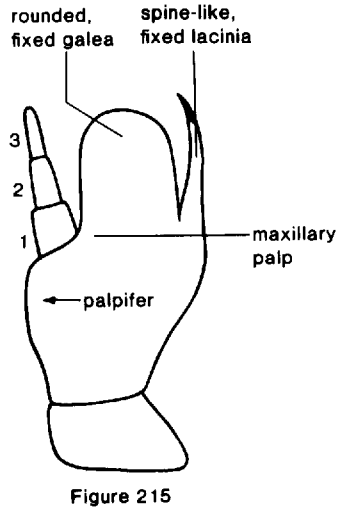


Figure 215

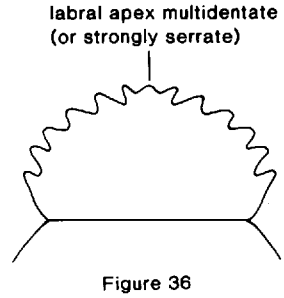


Figure 36

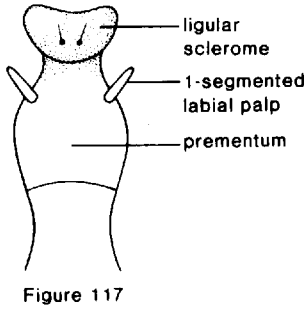


Figure 117

308(307). Antennal segments 6 or more (usually many); body relatively straight or only slightly curved ventrally; visible abdominal segments 8 or 9; abdominal apex with a respiratory chamber (pocket formed by 8th and 9th terga and enclosing enlarged A8 spiracles); prostheca complex, with sclerotized, comb-like process and brush of hairs (fig. 77). In ponds, lakes, tree holes, wet rotten wood ..... ***Helodidae*** p. 366

308′. Antennal segments 4 or 5; body strongly curved ventrally (C-shaped); visible abdominal segments 10; abdominal apex without respiratory chamber; prostheca absent 309

309(308′). Labrum with multidentate or strongly serrate apex (fig. 36); segments in labial palp 1; length usually less than 10mm. Under bark, in rotten wood, termite nests ..... (**Ceratocanthinae**) ***Scarabaeidae*** p. 377

309′. Labrum rounded, truncate, or weakly trilobed (fig. 40); segments in labial palp 2; length usually more than 10 mm. 310

310(309′). Stridulatory organs (patches or rows of asperities) present on T2 (fig. 129) and T3 (fig. 130) legs; tergum A3 without distinct transverse plicae (sometimes weakly divided into 2 parts); anterior abdominal terga with patches of asperities (fig. 142) or short, stout setae; galea and lacinia distinct (fig. 112); tormae united mesally (fig. 40); anal slit more or less vertical, bordered by 2 or 3 fleshy lobes (fig. 192). In rotten wood ..... (part) ***Lucanidae*** p. 372

310′. Stridulatory organs absent on T2 and T3 legs; tergum A3 with 3 distinct, transverse plicae (fig. 136); if anterior abdominal terga have patches of asperities, then galea and lacinia fused into single mala and tormae not united mesally; anal slit transverse or Y-shaped. In soil, roots, dung, rotten wood, animal nests ..... (part) ***Scarabaeidae*** p. 377

311(248′). Sternum A9 simple or absent 312

311′. Sternum A9 with row of apical asperities (fig. 176); body strongly flattened and lightly pigmented, with simple urogomphi; head wider than thorax; stemmata absent; mandibles asymmetrical with well-developed molae bearing numerous transverse ridges (fig. 74). In rotten wood (**see next 6 choices**) ..... ***Prostomidae*** p. 515

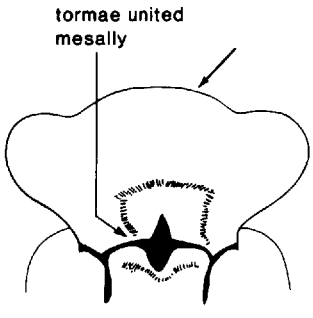


Figure 40

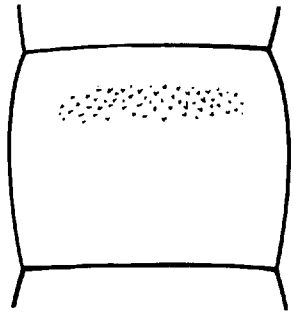


Figure 142

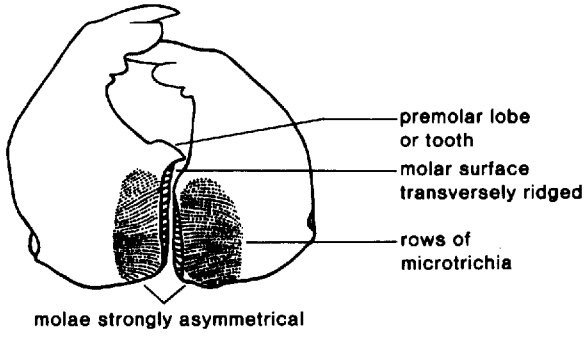


Figure 74

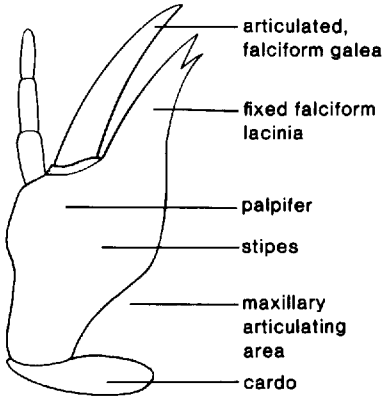


Figure 112

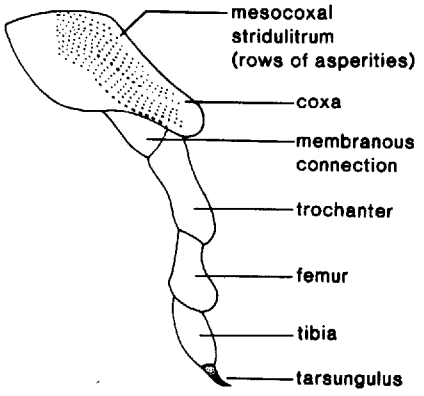


Figure 129

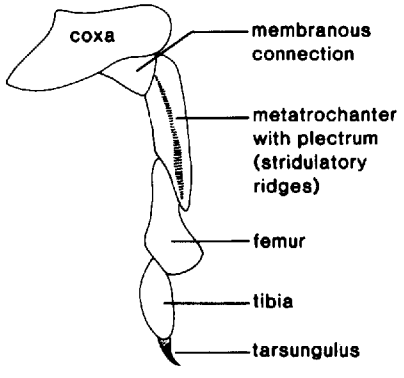


Figure 130

←— **Figs. 36, 77**

311[2]. Sternum A9 with 2 apicomesal asperities (fig. 177); body slightly flattened, lightly pigmented; urogomphi each with an accessory mesal process near base (fig. 177); stemmata absent; mandibular mola with only 2 or 3 ridges. In soil, leaf litter ..... (**Eurygeniinae**) ***Pedilidae*** p. 544

311[3]. Sternum A9 with 1 basal asperity on each side (fig. 183) 383

311[4]. Sternum A9 with 2 to 6 basal asperities on each side (fig. 182) 386

311[5]. Sternum A9 with more than 6 basal asperities on each side, forming row (figs. 178–181) 389

311[6]. Sternum A9 with 1 basal asperity on each side, 2 apicomesal asperities, and 2 more mesal asperities near the center; body strongly flattened; hypostomal rods absent; urogomphi diverging, each with several teeth at its base (**see choice 311[7]**) ..... (*Catapiestus*) ***Tenebrionidae*** p. 520

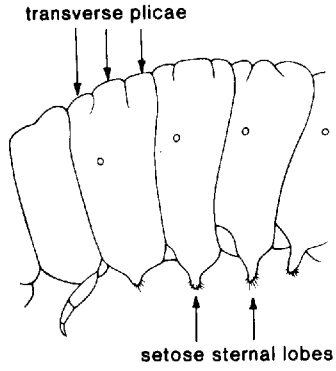


Figure 136

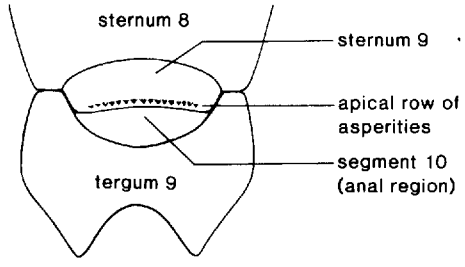


Figure 176

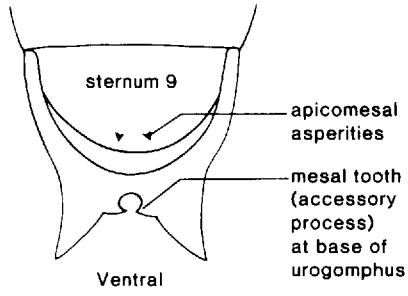


Figure 177

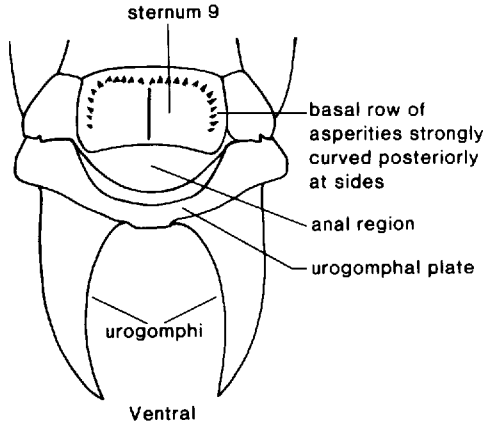


Figure 178

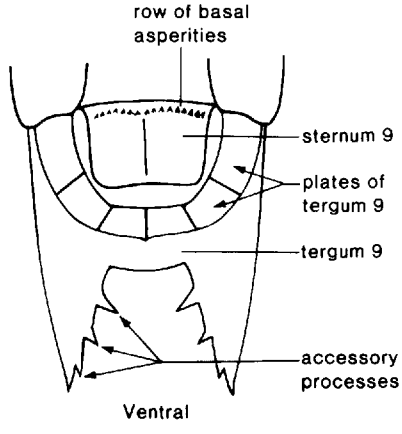


Figure 179

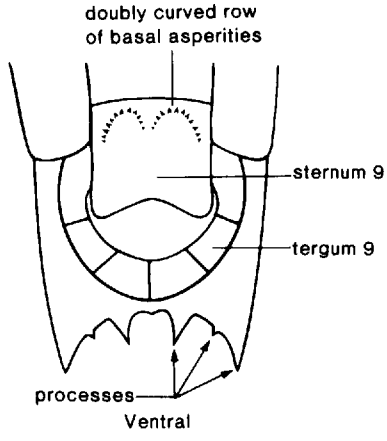


Figure 180

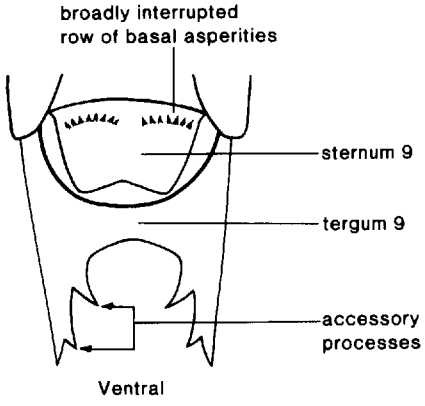


Figure 181

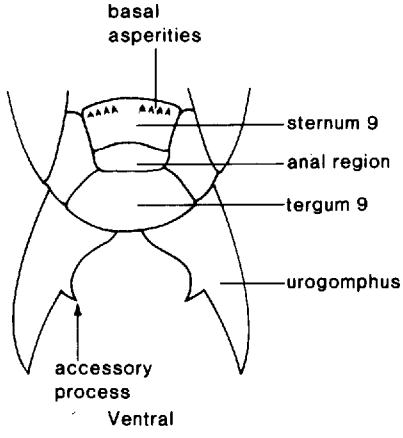


Figure 182

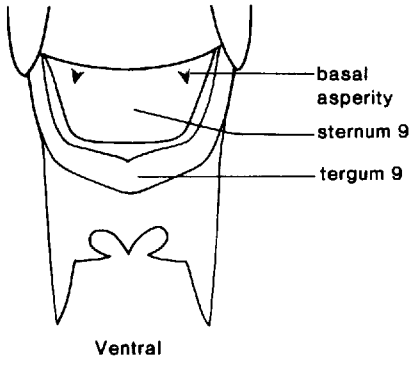


Figure 183

Fig. 192 ——→

311⁷. Sternum A9 U-shaped with apicolateral asperities (fig. 185); body strongly flattened; tergum A9 forming articulated plate 394

312(311). Segmented spiracular gills (fig. 152) present on A1–8; body broadly ovate. On rocks in streams or near waterfalls. Exotic (Brazil, South Africa, Madagascar) ..... (part) ***Torridincolidae*** p. 302

312′. Segmented spiracular gills absent 313

313(312′). Prostheca absent 314

313′. Prostheca a brush of simple or complex hairs (fig. 80) or a series of fringed membranes (fig. 79) **(see next 4 choices)** 347

313². Prostheca a fixed, rigid, hyaline process (figs. 78, 81, 82), sometimes partly sclerotized and sometimes appearing articulated 349

313³. Prostheca a simple, membranous lobe (fig. 72) 379

313⁴. Prostheca a membranous lobe fringed with hairs (fig. 84) 382

313⁵. Prostheca consisting of an acute, hyaline process and a rounded, pubescent lobe; mandibular mola reduced and simple. In bird nests. Exotic (South temperate regions) ..... (part) ***Cavognathidae*** p. 469

314(313). Paired ventral prolegs (asperity-bearing ampullae) absent 315

314′. Paired ventral prolegs (asperity-bearing ampullae) (fig. 149) on abdominal sterna 2–4 or 2–5; urogomphi very short and lightly pigmented. In rotten wood ..... (part) ***Oedemeridae*** p. 534

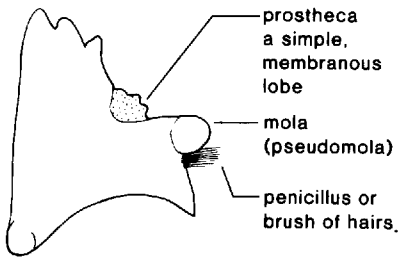


Figure 72

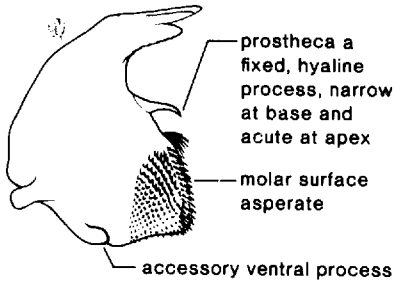


Figure 78

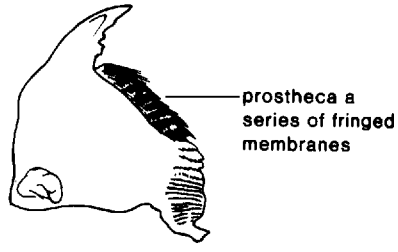


Figure 79

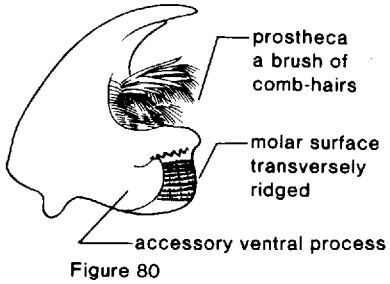


Figure 80

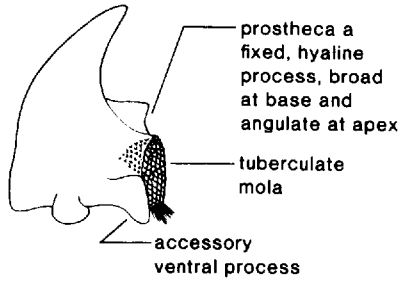


Figure 81

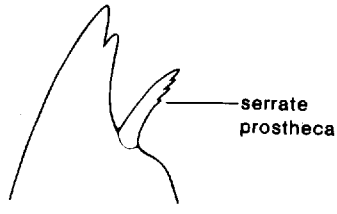


Figure 82

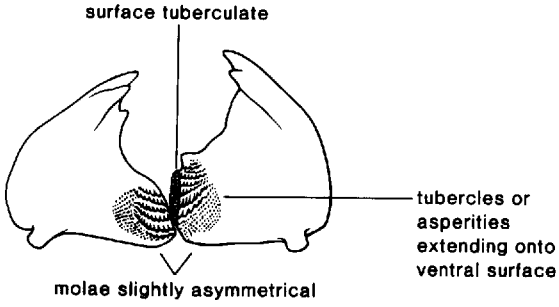


Figure 73

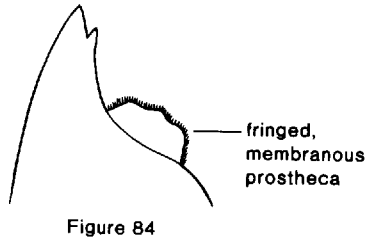


Figure 84

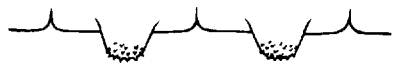


Figure 149

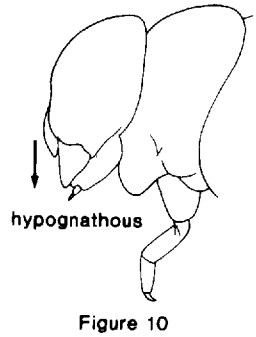


Figure 10

← Fig. 74

315(314). Antennal segments 2 316

315′. Antennal segments 3 (**see 3rd choice**) 317

315². Antennal segments 4; urogomphi articulated at base (fig. 162). In leaf litter, fungi, carrion ..... (part) ***Leiodidae*** p. 327

316(315). Head prognathous or slightly declined (fig. 8); ratio of antennal length to head width more than .15; antennae usually setose, with short dome-like sensorium; frontoclypeal suture distinct (fig. 13); single median endocarina absent; hypopharyngeal sclerome present (fig. 119). Under bark, in rotten wood, soil, leaf litter ..... (part) ***Tenebrionidae*** p. 520

316′. Head moderately to strongly declined (hypognathous) (fig. 10); ratio of antennal length to head width less than .15; antennal sensorium palpiform, longer than segment 2 (fig. 32); frontoclypeal suture absent or vaguely indicated; single median endocarina coincident with epicranial stem (fig. 19); hypopharyngeal sclerome absent. In fungus fruiting bodies ..... (**Ciinae** part) ***Ciidae*** p. 502

317(315′). Mandibles symmetrical; left and right molae more or less similar in shape 318

317′. Mandibles asymmetrical; left mola differing considerably from right one (figs. 73, 74) 336

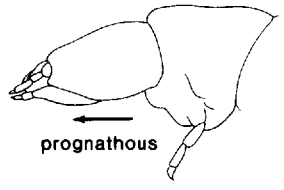
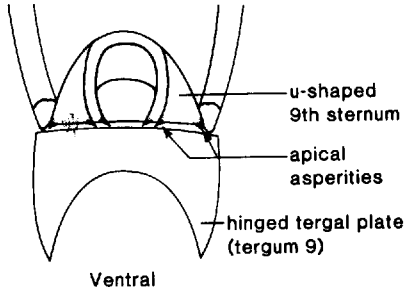


Figure 8



Ventral
Figure 185

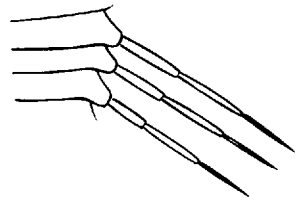


Figure 152

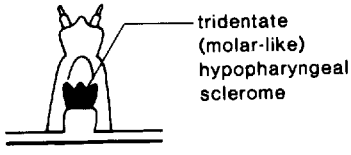


Figure 119

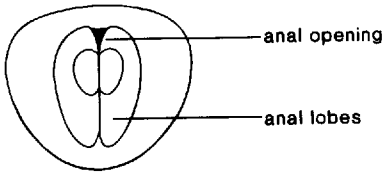


Figure 192

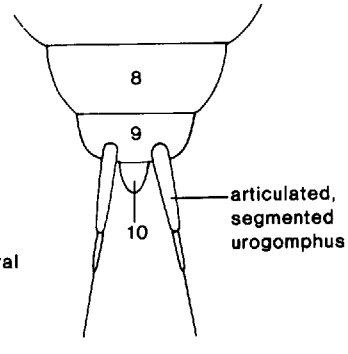


Figure 162

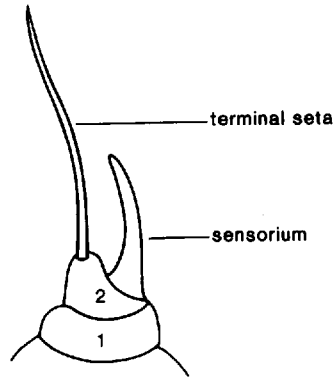


Figure 32

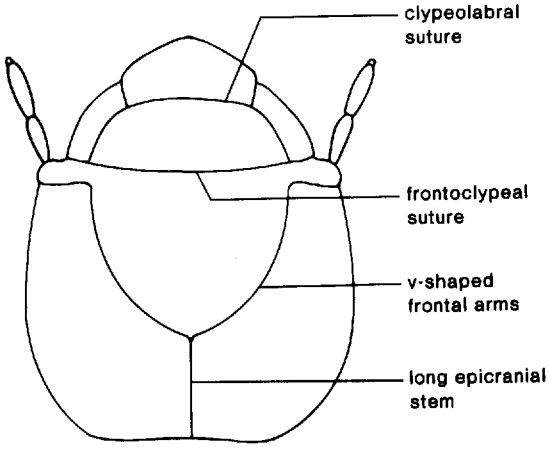


Figure 13

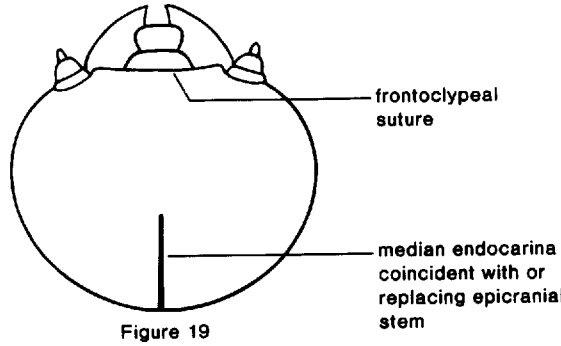


Figure 19

318(317). Segments in labial palp 1 (fig. 91) 319

318'. Segments in labial palp 2 (figs. 88, 94, 97) 320

319(318). Bases of frontal arms contiguous (fig. 24); segments in maxillary palp 3; ratio of antennal length to head width less than .15; labial palps separated by more than width of first palpal segment; hypostomal rods very short (fig. 85); body more or less cylindrical; length more than 3mm. Under bark, in rotten wood ..... (part) ***Colydiidae*** p. 512

319'. Bases of frontal arms distinctly separated (fig. 16); segments in maxillary palp 2; ratio of antennal length to head width .15 to .5; labial palps contiguous or separated by less than width of first palpal segment; hypostomal rods extending almost to posterior edge of head (fig. 86); body somewhat flattened; length less than 3mm. In leaf litter, rotting vegetation, under bark ..... (*Smicrips*) (**Smicripinae**) ***Nitidulidae*** p. 456

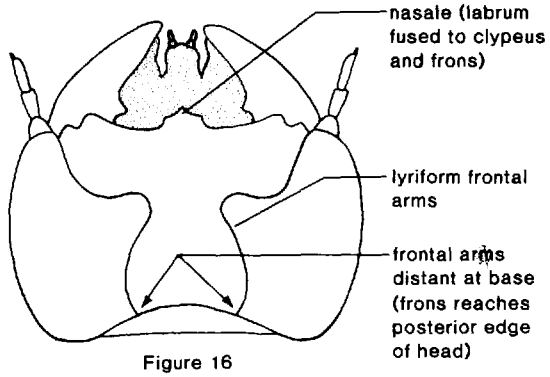


Figure 16

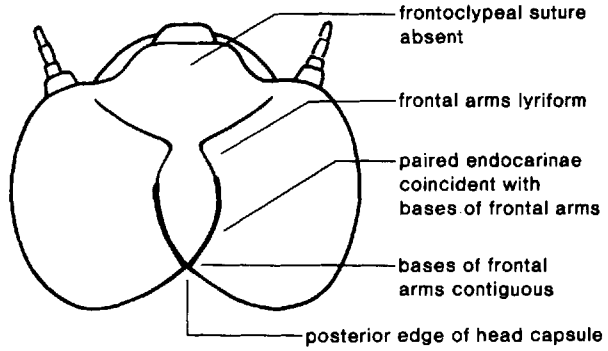


Figure 24

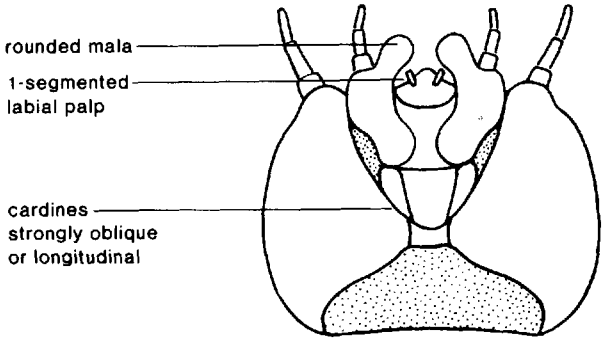
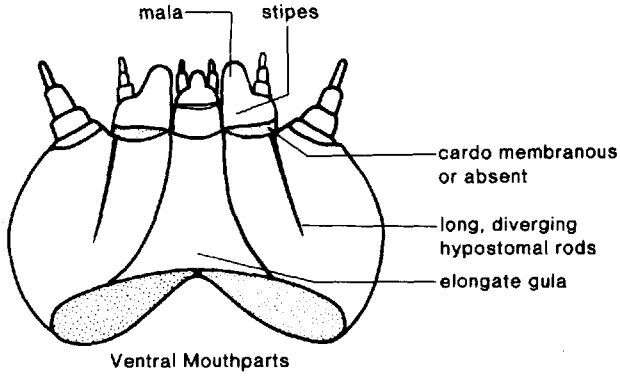


Figure 91



Ventral Mouthparts Strongly Protracted

Figure 92

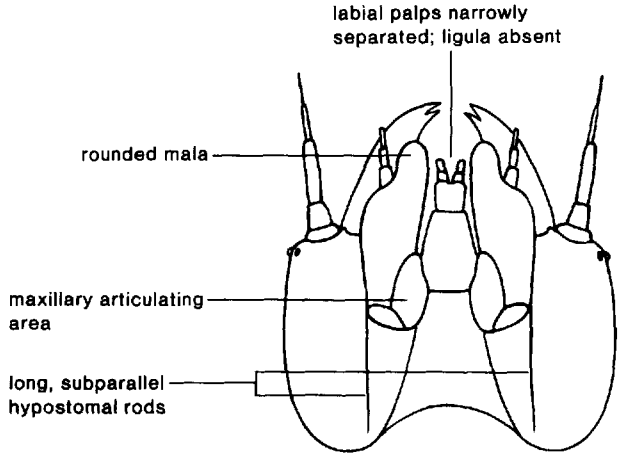


Figure 86

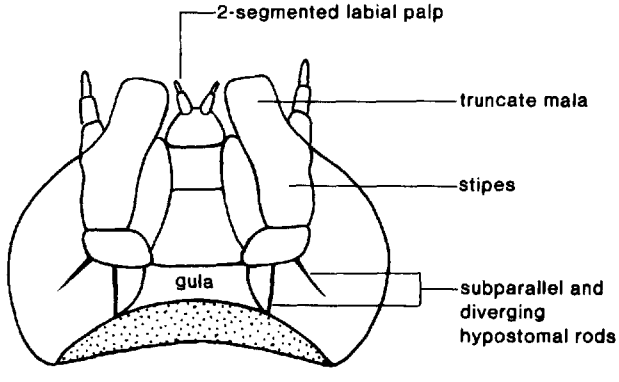


Figure 88

Figs. 94, 97: See page 225.

320(318′). Ventral mouthparts strongly protracted (fig. 92); stipes wider than long; cardo absent or membranous (fig. 92); sternum A9 completely concealed or absent (fig. 164); hypostomal rods long and diverging (fig. 92). In fungus fruiting bodies, smuts, ergots ..... (part) ***Phalacridae*** p. 466

320′. Ventral mouthparts retracted (fig. 85); stipes longer than wide; cardo distinct and sclerotized; sternum A9 exposed 321

321(320′). Segment A10 distinct and visible from above (fig. 162); urogomphi narrow, straight, and almost always articulated at base (fig. 162); dorsal body surfaces smooth; mandibular mola without pubescent lobe at base; ratio of antennal length to head width usually more than .5; apex of antennal segment 2 oblique, so that palpiform sensorium arises proximad of segment 3 (fig. 30). In leaf litter, carrion, fungi ..... (part) ***Leiodidae*** p. 327

321′. Segment A10 not visible from above, OR, if visible from above, dorsal body surfaces granulate and mandibular mola with pubescent, hyaline lobe at base (fig. 76); urogomphi usually curved and always fixed at base; ratio of antennal length to head width less than .5; apex of antennal segment 2 truncate, so that sensorium and segment 3 arise together (fig. 29), or sensorium dome-like (fig. 31) 322

322(321′). Mandibular mola with hyaline lobe at base (fig. 76) 323

322′. Mandibular mola without hyaline lobe at base 325

323(322). Stemmata on each side 6; dorsal surfaces granulate; segment A10 more or less cylindrical; setae on tarsungulus 1; spiracles annular-biforous (fig. 198). In fruits or berries ..... (*Byturus*) ***Byturidae*** p. 476

323′. Stemmata on each side 1 or 0; dorsal surfaces smooth or spiracles annular (fig. 194); segment A10 transverse; setae on tarsungulus 2 324

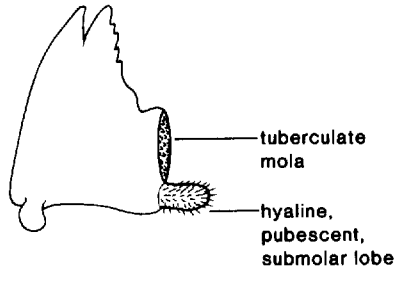


Figure 76

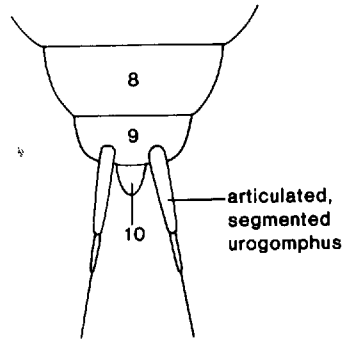


Figure 162

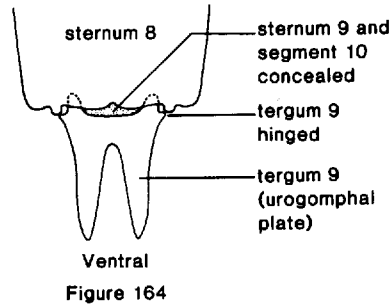


Figure 164

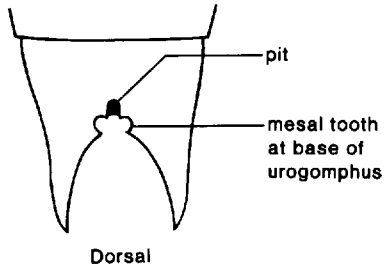
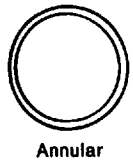
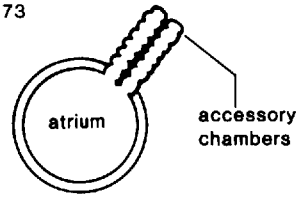


Figure 173


Annular
Figure 194



Annular Biforous
Figure 198

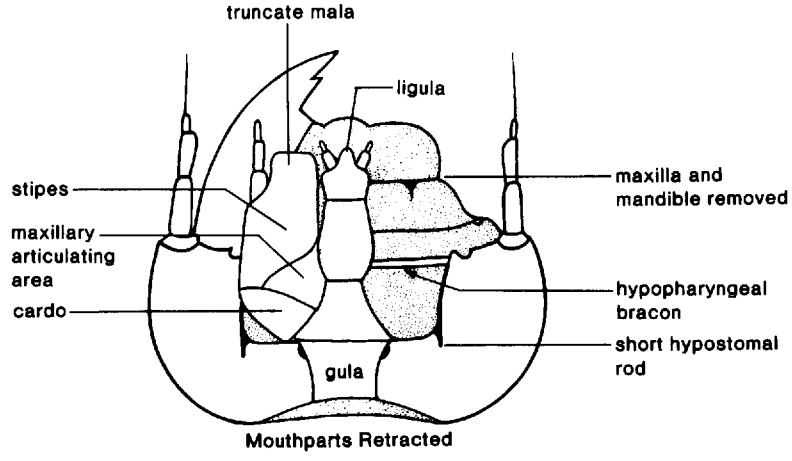


Figure 85

Figs. 29, 30, 31 ——→

324(323′). Median endocarina absent; inner apical angle of mala simple or with 1 or 2 small teeth; urogomphi well separated at base and without pit between them; hypostomal rods absent. In leaf litter, under bark ..... (part) ***Euglenidae*** p. 554

324′. Median endocarina absent; inner apical angle of mala with distinct lobe or uncus (fig. 87); urogomphi approximate at base and with pit between them (fig. 173); hypostomal rods short and converging (fig. 87). In leaf litter, under bark (**see 3rd choice**) ..... (**Anaspidinae**) ***Scraptiidae*** p. 555

324². Median endocarina extending anterad of epicranial stem (fig. 20); inner apical angle of mala simple or with 1 or 2 small teeth (fig. 106); urogomphi more or less approximate, with or without pit between them; hypostomal rods usually moderately long and converging. Under bark, stones, in leaf litter ..... (**Anthicinae**) ***Anthicidae*** p. 552

325(322′). Mandible with accessory ventral process (figs. 78, 80, 81); setae on tarsungulus 1; spiracles usually on long or short tubes (figs. 209, 210) 326

325′. Mandible without accessory ventral process; setae on tarsungulus 2; spiracles not on tubes 329

326(325). Lateral tergal processes present on segments A6–9; urogomphi short, widely separated and strongly upturned, with 2 pairs of truncate lobes between them; stemmata absent; vestiture of simple setae. In rotten wood, leaf litter ..... (**Anommatinae**) ***Cerylonidae*** p. 480

326′. Lateral tergal processes, if present, occurring on segments A1–9; urogomphi without 2 pairs of truncate lobes between them; vestiture usually including some expanded or frayed setae 327

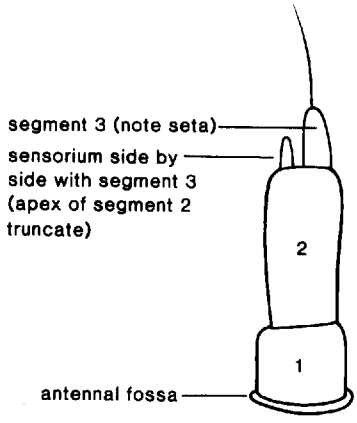


Figure 29

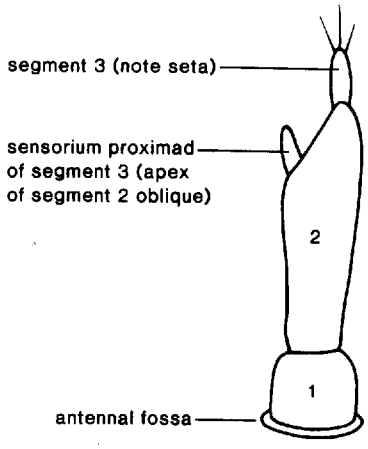


Figure 30

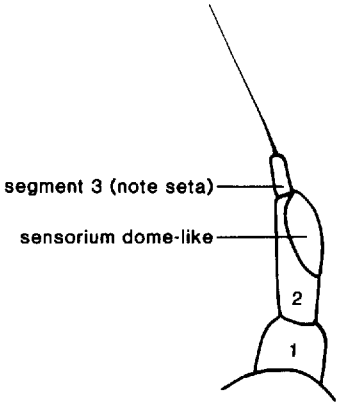
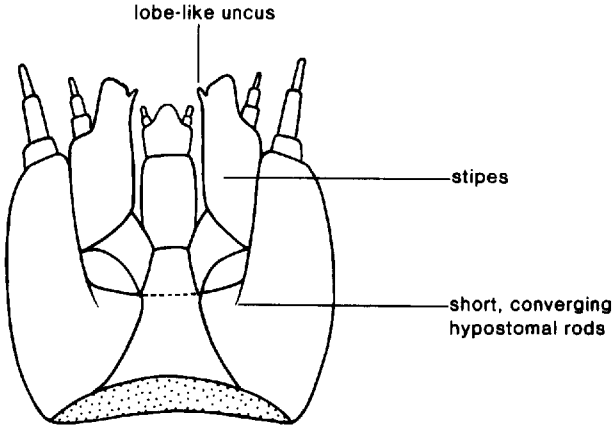
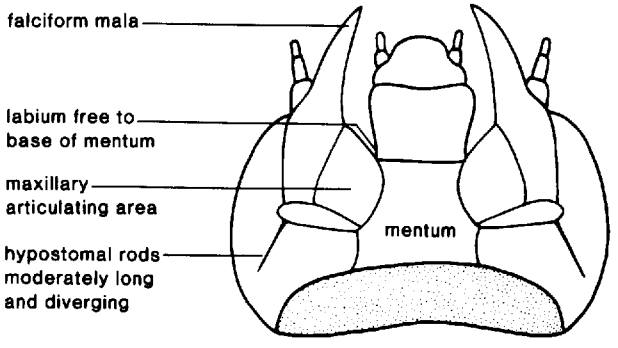


Figure 31



Mouthparts Retracted
Figure 87



Mouthparts Retracted
Figure 89

←— **Figs. 24, 85, 86, 173**

327(326′). Hypostomal rods absent; stemmata on each side 2 or fewer; urogomphi long and narrow, straight or slightly curved, usually approximate at base and diverging apically, with 2 or more accessory processes. In rotten wood, leaf litter, fungi, ant nests, guano ..... (**Euxestinae**) ***Cerylonidae*** p. 480

327′. Hypostomal rods well-developed, diverging (fig. 89); stemmata on each side 5 or 6; urogomphi widely separated at base and strongly curved at apex 328

328(327′). Mala broadly rounded at apex (fig. 86); tergum A8 with pair of conical tubercles near midline; spiracular tubes long and tooth-like, dorsally located. In fungus fruiting bodies. Exotic (Europe) ..... ***Sphaerosomatidae*** p. 479

328′. Mala narrowly rounded or subfalciform (fig. 89) at apex; tergum A8 without pair of tubercles (or paired tubercles on several abdominal terga); spiracular tubes shorter, laterally placed. In tunnels of ambrosia beetles (Platypodidae) ..... (**Teredinae**) ***Bothrideridae*** p. 477

329(325′). Abdominal terga without rows of asperities 330

329′. Abdominal terga with rows of asperities on one or more segments 334

330(329). Maxillary mala falciform (fig. 105); body elongate, cylindrical, and lightly sclerotized. In stems ..... (**Languriinae** part) ***Languriidae*** p. 471

330′. Maxillary mala rounded or truncate (fig. 85) 331

331(330′). Frontoclypeal suture present (fig. 13); hypostomal rods absent; frontal arms always V- or U-shaped (fig. 13); spiracles annular (fig. 194, 195), annular-multiforous (fig. 200), or occasionally annular-biforous with very short accessory chambers 332

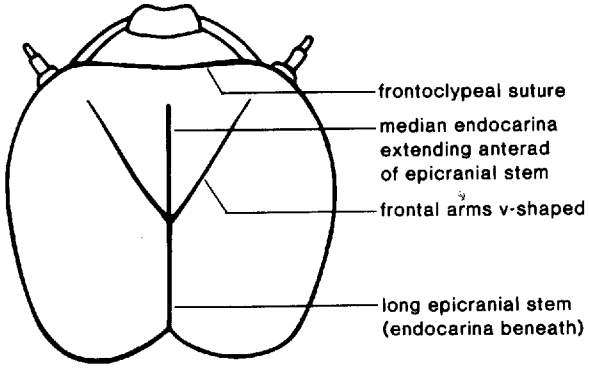


Figure 20

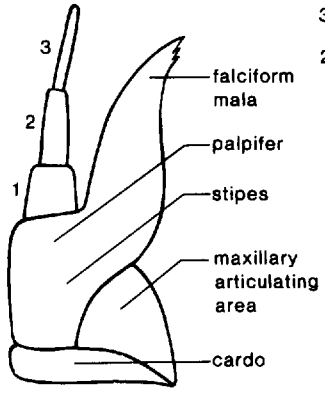


Figure 105

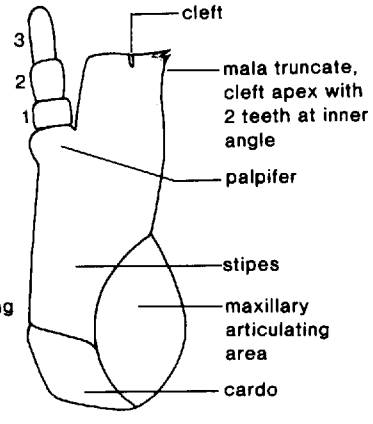


Figure 106

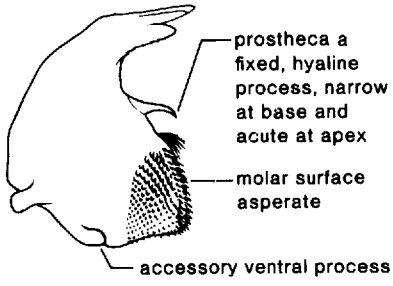


Figure 78

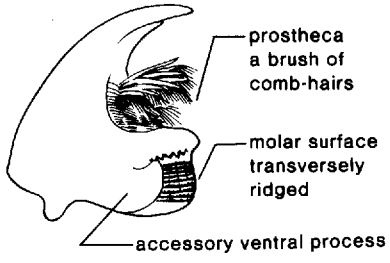


Figure 80

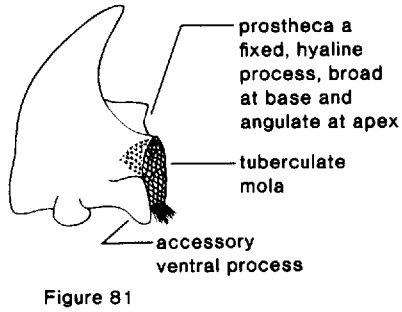
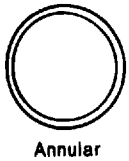
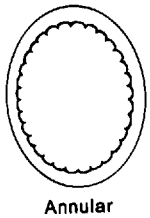


Figure 81



Annular

Figure 194



Annular

Figure 195

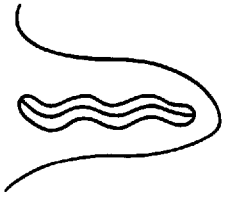


Figure 209

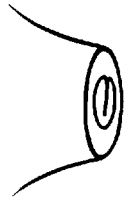
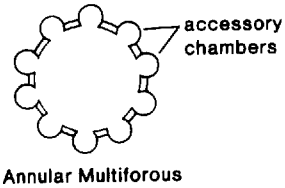


Figure 210



Annular Multiforous

Figure 200

Fig. 13 ——→

331′. Frontoclypeal suture absent (fig. 24); hypostomal rods present (figs. 85, 89); frontal arms lyriform (fig. 22); spiracles annular-biforous with well-developed accessory chambers (fig. 198) 333

332(331). Maxillary mala cleft (fig. 106); cardo distinctly divided; median endocarina Y-shaped, coincident with epicranial stem and frontal arms (fig. 23); spiracles annular-biforous with very short accessory chambers; prosternum with patch of asperities ..... (**Zopherinae**) ***Zopheridae*** p. 518

332′. Maxillary mala simple (fig. 85); cardo not divided; median endocarina absent; spiracles annular (figs. 194, 195) or annular-multiforous (fig. 200); prosternum without patch of asperities ..... (part) ***Tenebrionidae*** p. 520

333(331′). Apex of mala cleft (fig. 106); hypostomal rods (fig. 85) present; tergum A9 distinctly tuberculate; urogomphi without pit between them; ligula as long as or longer than labial palps. Under bark, in fungus fruiting bodies. Exotic (Australia) ..... (*Meryx*) (**Ulodinae**) ***Zopheridae*** p. 518

333′. Apex of mala usually simple as in fig. 85, OR, if cleft, then hypostomal rods absent; tergum A9 not tuberculate, or urogomphi with pit between them; ligula much shorter than labial palps. Under bark or in rotten wood ..... (part) ***Colydiidae*** p. 512

334(329′). Epicranial stem present (fig. 23); frontal arms V- or U-shaped (fig. 23); hypostomal rods absent; urogomphi small and approximate; transverse rows of asperities, if present, on 5 or fewer abdominal terga. In rotten wood .... (**Nosoderminae** part) ***Zopheridae*** p. 518

334′. Epicranial stem absent and frontal arms lyriform (fig. 216); hypostomal rods present (fig. 85); urogomphi large and well separated; transverse rows of asperities present on terga A1–6 335

335(334′). Length usually more than 10 mm; mala with 1 or 2 teeth at inner apical angle (fig. 106); ligula well-developed, longer than first palpal segment; labial palps separated by more than a palpal width; accessory air chambers of spiracles much shorter than atrium diameter (fig. 197); meso- and metatergum and terga A1–6 with patches of asperities (fig. 141) in addition to transverse rows. In rotten wood ..... (*Phellopsis*) (**Nosoderminae**) ***Zopheridae*** p. 518

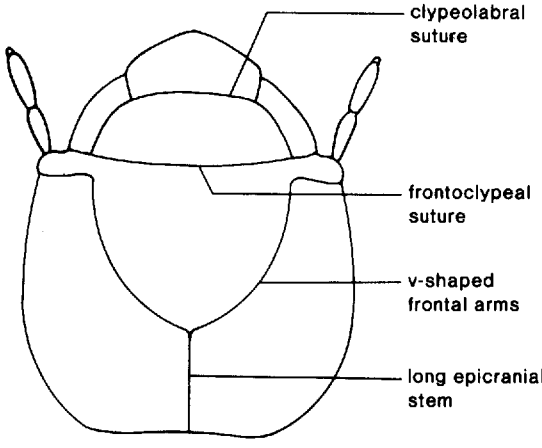


Figure 13

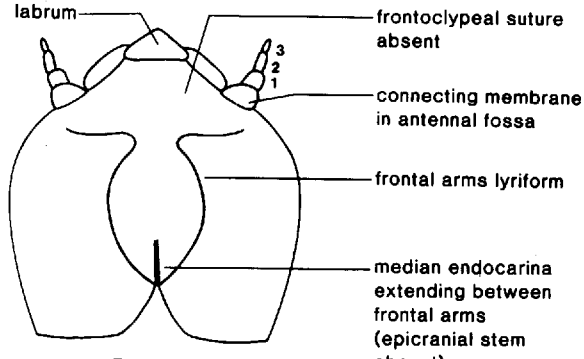


Figure 22

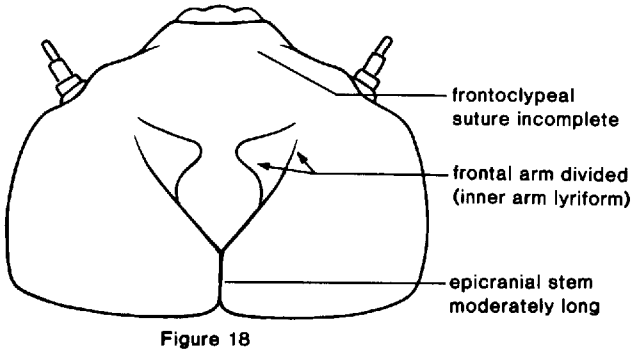


Figure 18

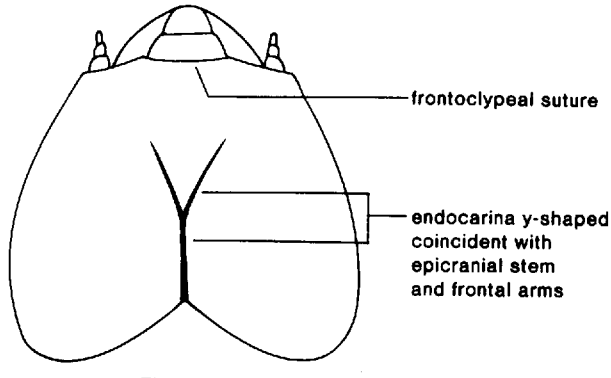


Figure 23

←— **Figs. 29, 30, 89, 105, 106, 194, 195, 200**

335′. Length usually less than 10 mm; mala with inner apical angle simple; ligula reduced; labial palps separated by less than a palpal width; accessory air chambers of spiracles at least as long as atrium diameter (fig. 198); metatergum and terga A1–6 with transverse rows of asperities only (fig. 144). In rotten wood ..... (**Usechinae**) ***Zopheridae*** p. 518

336(317′). Frontoclypeal suture absent or vaguely indicated (figs. 18, 22) 337

336′. Frontoclypeal suture distinct (fig. 13) 344

337(336). Hypostomal rods absent 338

337′. Hypostomal rods present (fig. 89) 341

338(337). Urogomphi simple and tergum A9 without additional tubercles or processes; anal region posteriorly or terminally oriented 339

338′. Urogomphi with accessory processes and tergum A9 with several additional spines or tubercles; anal region posteroventrally oriented. In rotten wood. Exotic (Southern Hemisphere) ..... (**Ulodinae** part) ***Zopheridae*** p. 518

339(338). Maxillary mala more or less falcate (fig. 105), or if maxilla with 2 apical lobes, then lacinia falcate (fig. 111); antennal segment 2 oblique at apex, so that sensorium arises proximad of segment 3 (fig. 30); urogomphi almost always articulated at base (figs. 112–113). In leaf litter, fungi, carrion ..... (part) ***Leiodidae*** p. 327

339′. Maxillary mala truncate (figs. 85, 106) or rounded (fig. 86); antennal segment 2 truncate at apex, so that sensorium and segment 3 arise together (fig. 29); urogomphi fixed at base (figs. 170–171) 340

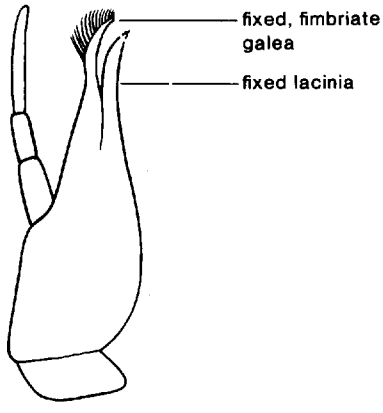


Figure 111

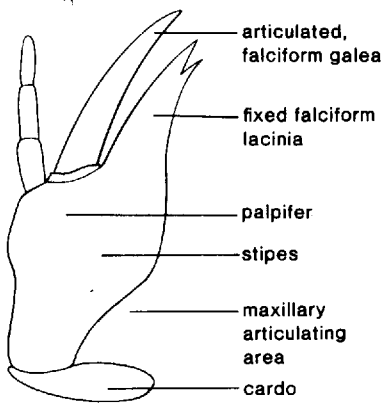


Figure 112

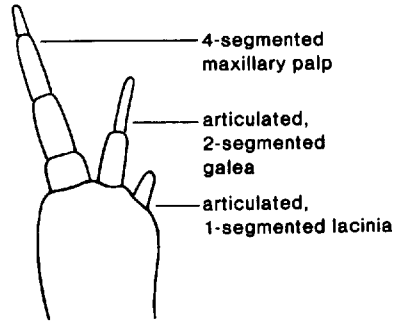


Figure 113

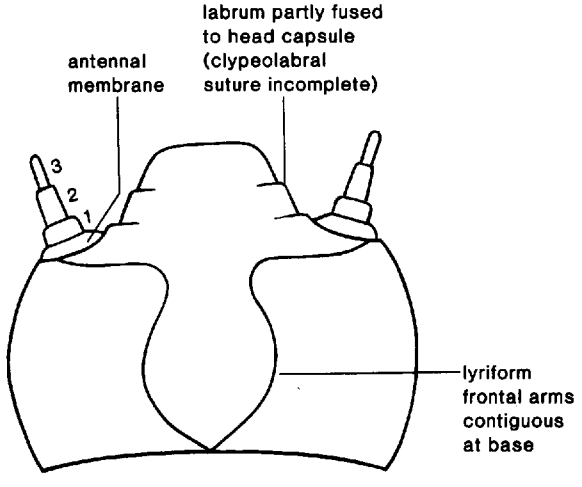


Figure 216

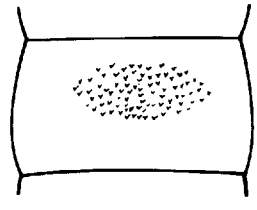


Figure 141

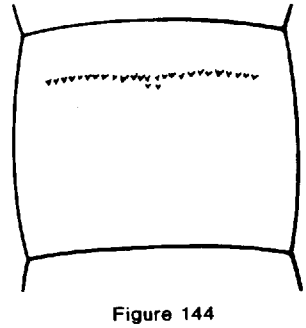
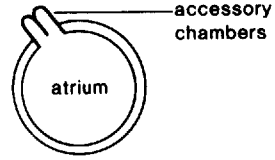
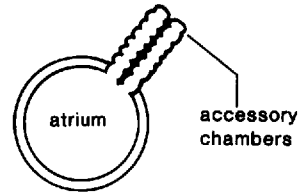


Figure 144



Annular Biforous
Figure 197



Annular Biforous
Figure 198

Figs. 24, 85, 86, 170, 171 ⟶

340(339'). Stemmata on each side 0; mandibular mola with hyaline lobe at base; body parallel-sided and somewhat flattened; length usually less than 10 mm. In leaf litter, under bark ..... (part) ***Euglenidae*** p. 554

340'. Stemmata on each side 5 or 6; mandibular mola without hyaline lobe at base; body somewhat curved ventrally and narrowing posteriorly; length usually more than 10 mm ..... (*Cephaloon*) (**Cephaloinae**) ***Cephaloidae*** p. 529

341(337'). Epicranial stem long and bent to the left (fig. 15); frontal arms joined anteriorly by transverse ecdysial line (fig. 15); spiracles on segment A8 much larger than those on A7. In fungus fruiting bodies. Exotic (Asia, East Indies, New Guinea) ..... ***Pterogeniidae*** p. 501

341'. Epicranial stem shorter and not bent to the left (fig. 18); frontal arms not joined anteriorly by transverse line; spiracles on segment A8 not larger than those on A7 342

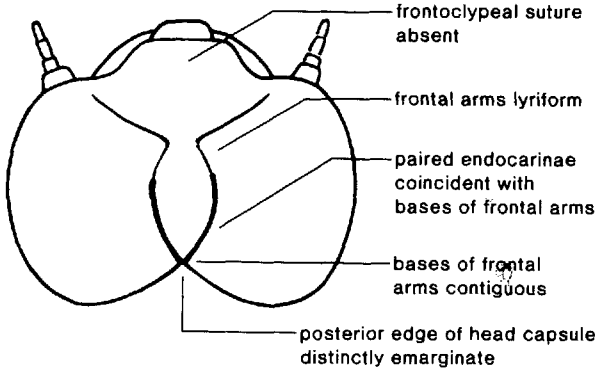


Figure 24

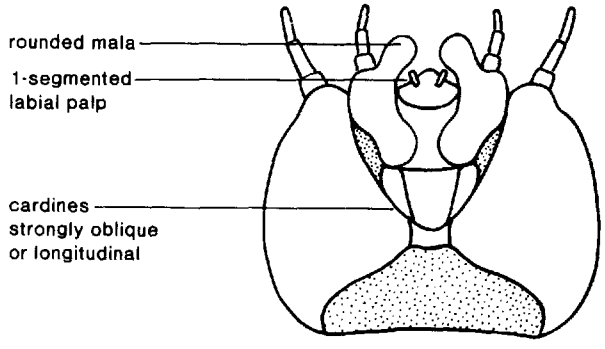


Figure 91

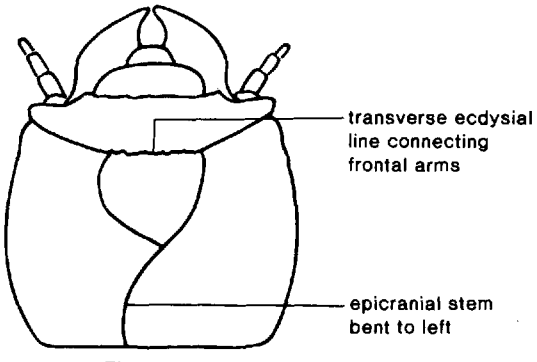


Figure 15

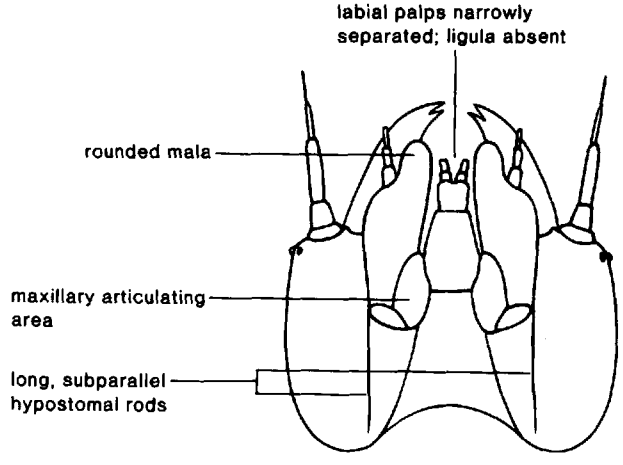
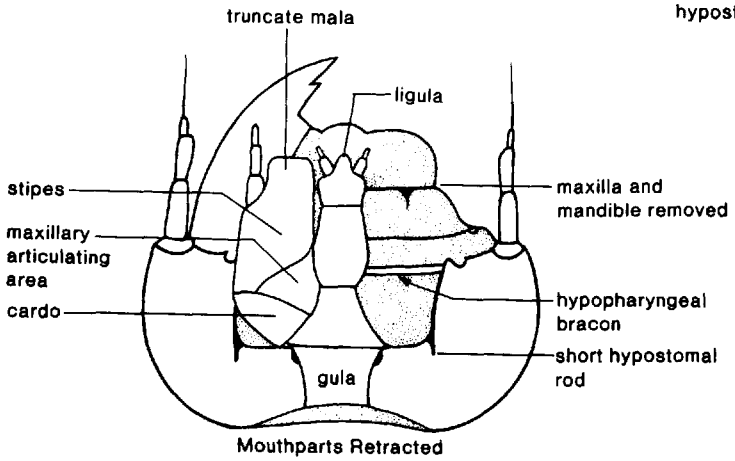


Figure 86



Mouthparts Retracted

Figure 85

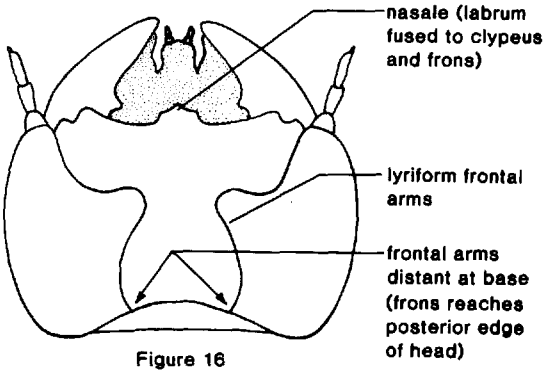


Figure 16

←— Figs. 18, 197, 198

342(341′). Anal region posteriorly or terminally oriented; spiracles annular, annular-uniforous (fig. 196), or annular-biforous with short accessory chambers (fig. 197); molae tuberculate, with tubercles extending onto ventral surface (fig. 73). In fungus fruiting bodies, leaf litter, stored products ..... (part) ***Mycetophagidae*** p. 498

342′. Anal region posteroventrally or ventrally oriented; spiracles annular-biforous with long accessory chambers (fig. 198); molae transversely ridged, without tubercles on ventral surface 343

343(342′). Urogomphi with accessory processes (fig. 196); epicranial stem moderately long (fig. 18); mala simple and rounded (fig. 86); abdominal terga without rows or patches of asperities; tergum A9 with only a few tubercles and without U-shaped groove. In fungus fruiting bodies ..... (**Piseninae** part) ***Tetratomidae*** p. 504

343′. Urogomphi simple; epicranial stem very short or absent (fig. 24); apex of mala truncate and slightly emarginate, with 3 teeth at inner apical angle; abdominal terga each with transverse row of asperities followed by a patch of irregularly distributed asperities; tergum A9 with numerous tubercles and with a U-shaped, transverse groove. In rotten wood ..... (**Stenotrachelinae**) ***Cephaloidae*** p. 529

344(336′). Hypostomal rods absent; abdominal spiracles annular (figs. 194, 195) or annular-multiforous (fig. 200). Under bark, in rotten wood, soil, leaf litter ..... (part) ***Tenebrionidae*** p. 520

344′. Hypostomal rods present (fig. 89); abdominal spiracles annular-biforous (figs. 197, 198) 345

345(344′). Epicranial stem very short; urogomphi straight, narrow, acute, lightly sclerotized and posteriorly oriented, without accessory processes (fig. 170); hypostomal rods subparallel (fig. 89); ligula absent. In fungus fruiting bodies, leaf litter ..... ***Archeocrypticidae*** p. 500

345′. Epicranial stem moderately long; urogomphi with accessory processes (fig. 169); hypostomal rods diverging posteriorly (fig. 89); ligula present 346

346(345′). Apex of mala simple; molar surface with numerous fine ridges (fig. 80); dorsal body surfaces generally smooth. In fungus fruiting bodies, under bark .... (**Piseninae** part) ***Tetratomidae*** p. 504

346′. Apex of mala cleft (fig. 106); molar surface simple (fig. 69); dorsal body surfaces generally granulate or tuberculate. Under bark, in fungus fruiting bodies. Exotic (Southern Hemisphere) ..... (**Ulodinae** part) ***Zopheridae*** p. 518

347(313′). Segments in labial palp 1; cardo strongly oblique or longitudinal (fig. 91); apex of mala rounded or truncate (fig. 91); hypostomal rods absent 348

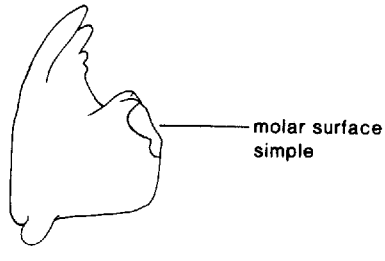


Figure 69

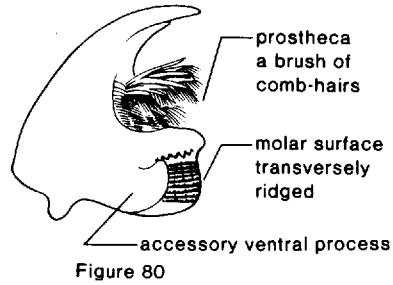


Figure 80

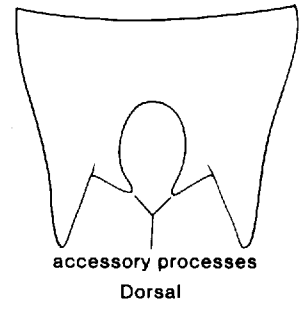
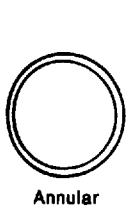
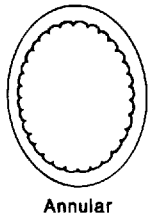
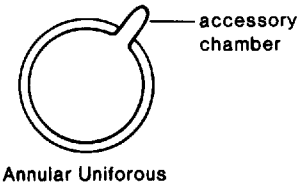


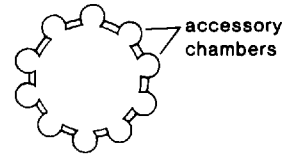
Figure 169


Annular
Figure 194

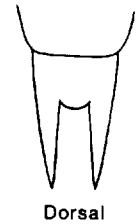

Annular
Figure 195

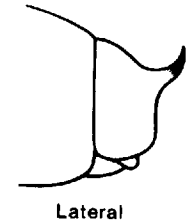


Annular Uniforous
Figure 196



Annular Multiforous
Figure 200


Dorsal
Figure 170


Lateral
Figure 171

Figs. 73, 89, 106 ——→

347′. Segments in labial palp 2; cardo transverse or slightly oblique; apex of mala falciform (fig. 89); hypostomal rods present (fig. 89). Under fermenting bark, in fungus fruiting bodies ..... (part) ***Biphyllidae*** p. 475

348(347). Bases of frontal arms contiguous (fig. 24); paired endocarinae present (fig. 24); ligula absent. In puffballs ..... (*Pocadius* part) (**Nitidulinae**) ***Nitidulidae*** p. 456

348′. Bases of frontal arms distinctly separated (fig. 16); paired endocarinae absent; ligula shorter than palp. Under bark, in leaf litter, fungus fruiting bodies, carrion, rotting fruit ..... (part) ***Nitidulidae*** p. 456

349(313²). Urogomphi articulated at base (fig. 162); maxilla with fixed galea and lacinia (fig. 111), sometimes fused or connate for part of their lengths; galea often with fringe of setae at apex (fimbriate galea) (fig. 111) 350

349′. Urogomphi fixed at base (fig. 170); maxilla usually with single, fixed mala (fig. 105) 355

350(349). Stemmata on each side 6. In decaying vegetation or carrion ..... ***Agyrtidae*** p. 324

350′. Stemmata on each side 5 or fewer 351

351(350′). Segment A10 bearing a pair of hooks (fig. 163) 352

351′. Segment A10 without a pair of hooks 353

352(351). Urogomphi 2-segmented; stemmata on each side 3 to 5; epicranial stem present (fig. 14). In sand, on rocks, or in vegetation in or near streams and ponds ..... ***Hydraenidae*** p. 320

352′. Urogomphi 1-segmented; stemmata on each side 0 or occasionally 1; epicranial stem absent. In leaf litter, decaying vegetation, rotten wood, fungi ..... (part) ***Ptiliidae*** p. 322

353(351′). Stemmata present; epicranial stem present (fig. 14); vestiture often including expanded setae (fig. 4). In leaf litter, fungi, carrion ..... (part) ***Leiodidae*** p. 327

353′. Stemmata absent; epicranial stem absent; vestiture of simple setae 354

354(353′). Urogomphi 2-segmented (fig. 162); body usually more than 1.2 mm in length; lacinia scoop-like and bidentate. In mammal nests ..... (**Leptininae**) ***Leptinidae*** p. 330

354′. Urogomphi 1-segmented; body minute, length 1.2 mm or less; lacinia not as above. In leaf litter, associated with army ants ..... ***Limulodidae*** p. 324

355(349′). Maxilla with galea and lacinia (figs. 111, 215) 356

355′. Maxilla with single mala (fig. 105) 358

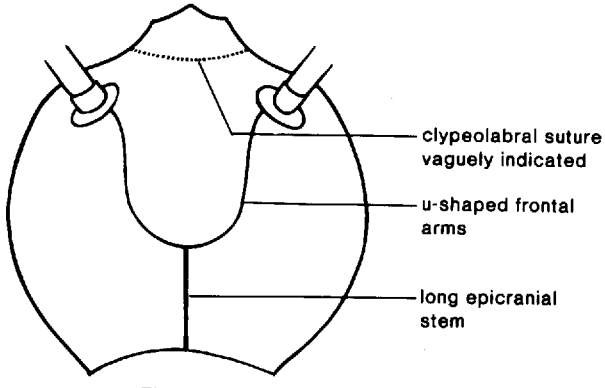
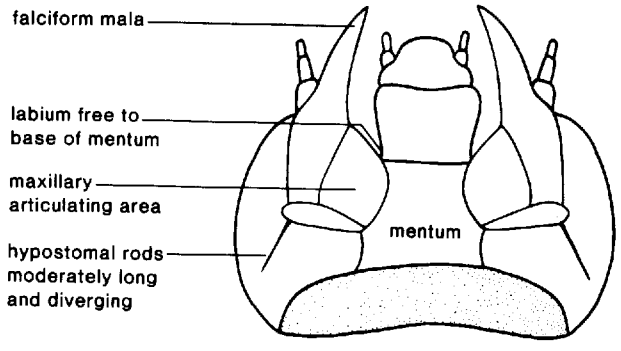


Figure 14



Mouthparts Retracted

Figure 89

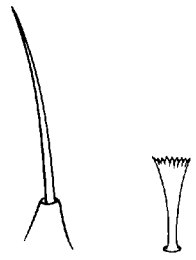


Figure 3

Figure 4

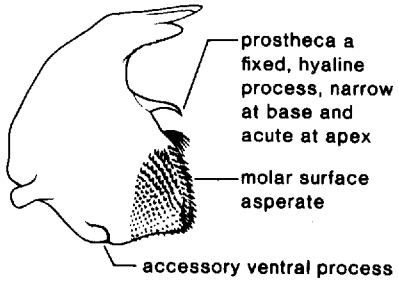


Figure 78

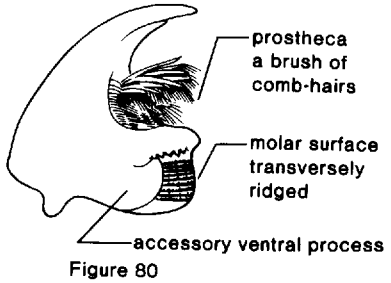


Figure 80

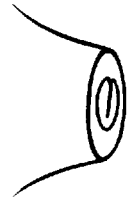


Figure 210

←— Figs. 24, 85, 170

356(355). Dorsal body surfaces coarsely granulate or tuberculate, usually with distinct setiferous processes (fig. 3); stemmata on each side 6; accessory ventral process of mandible present (figs. 78, 80); abdominal spiracles located at ends of spiracular tubes (fig. 210). Under fermenting bark, on fungi ..... (part) ***Derodontidae*** p. 431

356'. Dorsal body surfaces smooth or very finely granulate, without setiferous processes; stemmata on each side 5 or fewer; accessory ventral process of mandible absent; abdominal spiracles not located at ends of spiracular tubes 357

357(356'). Dorsal body surfaces more heavily pigmented than ventral ones; ratio of antennal length to head width less than .2; apex of antennal segment 2 truncate, so that sensorium and segment 3 arise together (fig. 29); minute (length usually less then 1.3 mm). Under bark, in rotten wood, leaf litter. Exotic (Neotropical and Old World) ..... ***Jacobsoniidae*** p. 433

357'. Dorsal and ventral body surfaces similarly pigmented; ratio of antennal length to head width more than .2; apex of antennal segment 2 oblique, so that sensorium arises proximad of segment 3 (fig. 30). In leaf litter, fungi, carrion ..... (part) ***Leiodidae*** p. 327

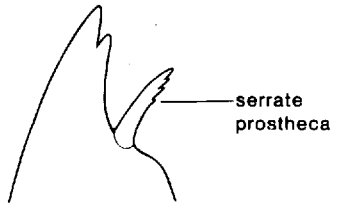


Figure 82

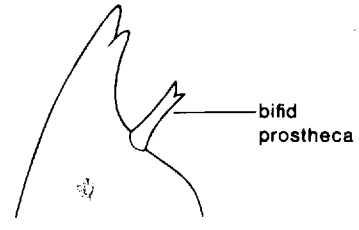


Figure 83

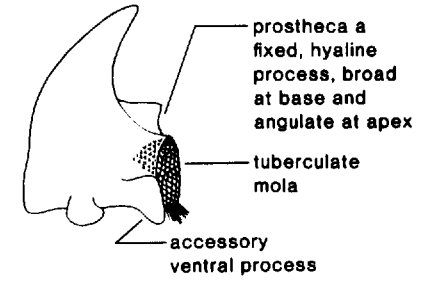


Figure 81

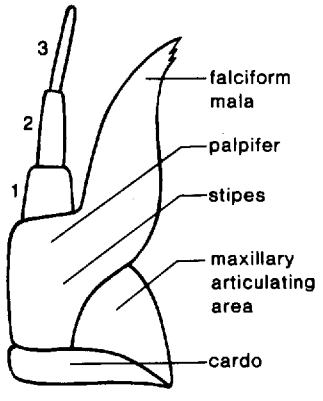


Figure 105

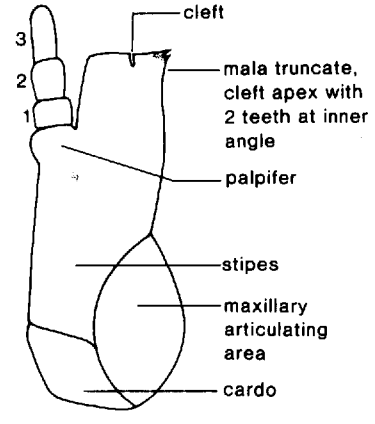


Figure 106

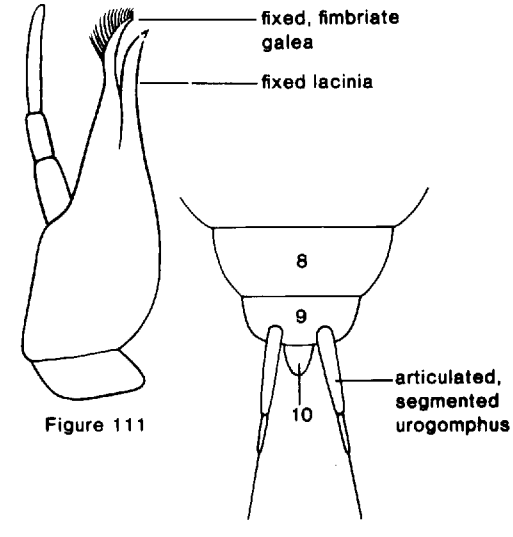


Figure 111

Figure 162

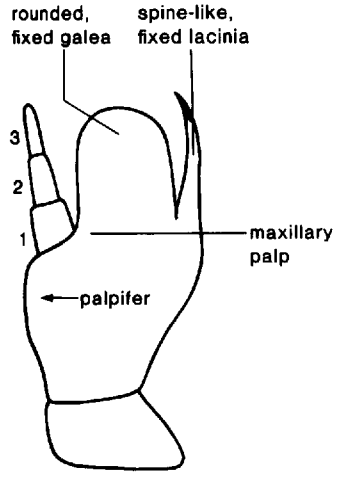


Figure 215

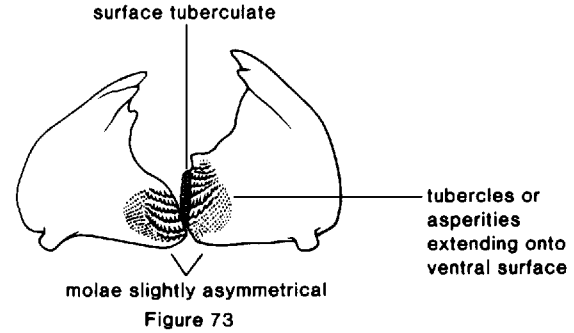


Figure 73

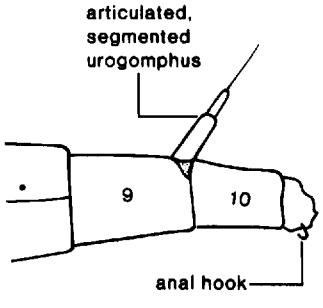


Figure 163

Figs. 16, 29, 30 ——→

358(355′). Median endocarina located between frontal arms (fig. 22). In cycad cones, stored products ..... (*Pharaxonotha*) (**Xenoscelinae**) ***Languriidae*** p. 471

358′. Median endocarina absent 359

359(358′). Prostheca broad, with apex obtusely angulate (fig. 81), or occasionally rounded 360

359′. Prostheca narrow, with apex acute (fig. 78) or occasionally bifid (fig. 83) or serrate (fig. 82) 364

360(359). Dorsal surfaces smooth; body more or less cylindrical and lightly sclerotized; epicranial stem moderately long (fig. 13); accessory ventral process of mandible absent. In stems ..... (**Languriinae** part) ***Languriidae*** p. 471

360′. Dorsal surfaces granulate or tuberculate; body usually slightly flattened; epicranial stem very short (fig. 12) or absent (fig. 24); accessory ventral process of mandible present (figs. 78, 80) 361

361(360′). Mala more or less truncate and cleft at apex (fig. 106); head moderately to strongly declined (hypognathous) (fig. 10); hypostomal rods very short (fig. 85). In fruiting bodies of higher fungi ..... (**Dacninae** part) ***Erotylidae*** p. 473

361′. Mala falciform and not cleft at apex (fig. 105); head prognathous or slightly declined (fig. 8); hypostomal rods usually long (fig. 89) 362

362(361′). Ventral epicranial ridges present (figs. 90, 93); frontal arms separated at base (fig. 16); tarsungulus with 2 subequal setae located side by side. In rotting vegetation, cycad cones, leaf axils ..... (**Xenoscelinae** part) ***Languriidae*** p. 471

362′. Ventral epicranial ridges absent; frontal arms contiguous at base (fig. 24); tarsungulus with 2 unequal setae, one located distal to the other, or occasionally with 1 seta only 363

363(362′). Thoracic and abdominal terga produced laterally to form flattened processes; urogomphi acute at apex, posteriorly oriented but upturned at apex; spiracles biforous (fig. 202). In leaf litter, stored products ..... (**Cryptophilinae**) ***Languriidae*** p. 471

363′. Thoracic and abdominal terga not or only slightly produced laterally; urogomphi straight and blunt, posterodorsally oriented; spiracles annular. In leaf litter, decaying vegetation ..... (**Toraminae**) ***Languriidae*** p. 471

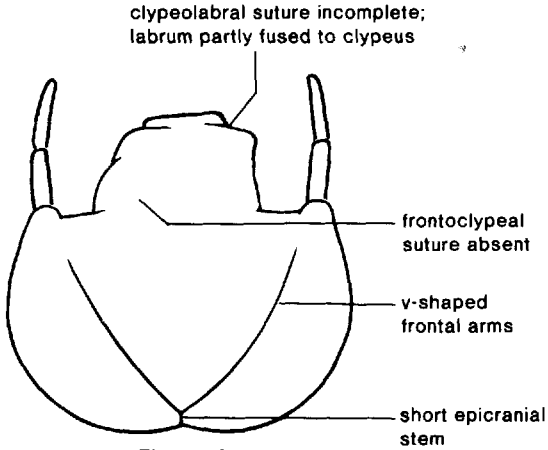


Figure 12

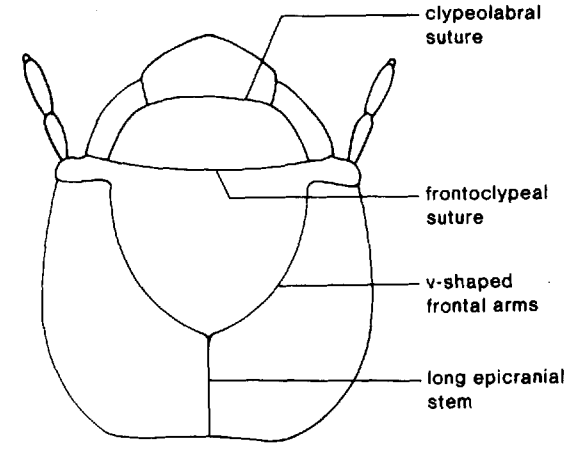


Figure 13

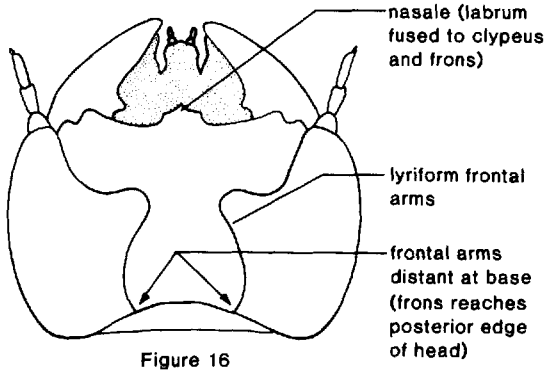


Figure 16

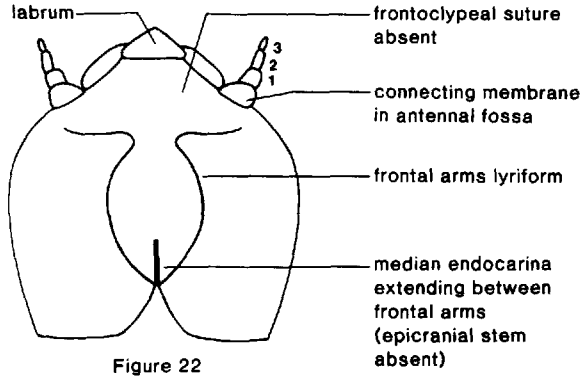


Figure 22

←— **Figs. 4, 78, 80, 81, 82, 83, 89, 105, 106**

364(359'). Mala truncate (fig. 88) or rounded (fig. 91) 365

364'. Mala falciform (fig. 105) 369

365(364). Ratio of antennal length to head width less than .15; stemmata on each side 4 or fewer 366

365'. Ratio of antennal length to head width more than .15; stemmata on each side 5 or 6 367

366(365). Abdominal segments with paired tergal processes; vestiture consisting of simple setae only; stemmata on each side 4. In puffballs ..... (*Lycoperdina*) (**Eumorphinae**) ***Endomychidae*** p. 482

366'. Abdominal segments without paired processes; vestiture including expanded setae (fig. 4); stemmata on each side 2. On molds, in stored products ..... (*Mycetaea*) (**Mycetaeinae**) ***Endomychidae*** p. 482

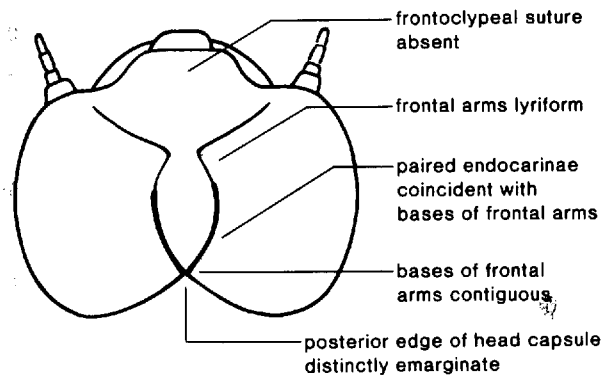


Figure 24

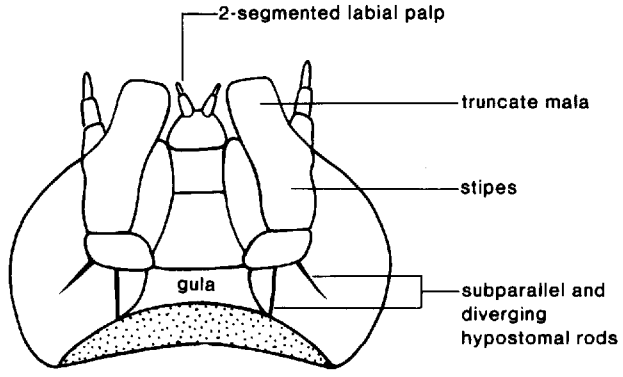
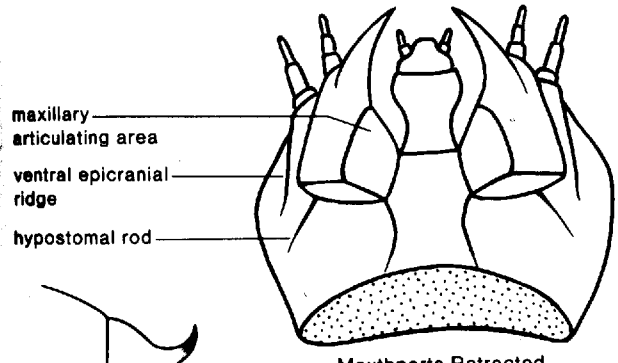
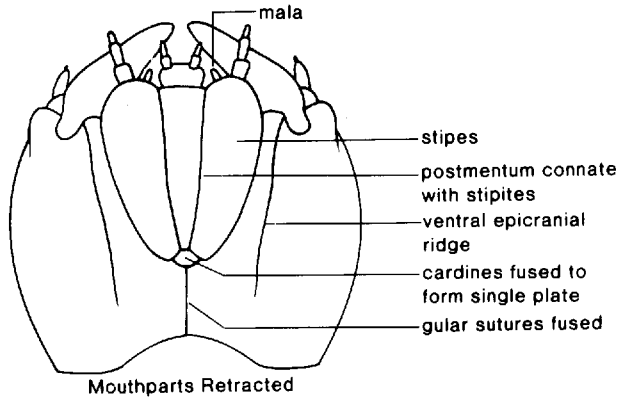


Figure 88



Mouthparts Retracted

Figure 90



Mouthparts Retracted

Figure 93

Lateral

Figure 171

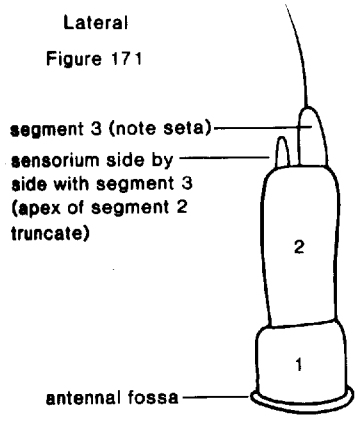


Figure 29

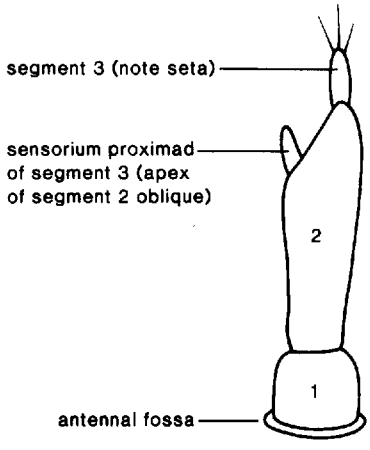


Figure 30

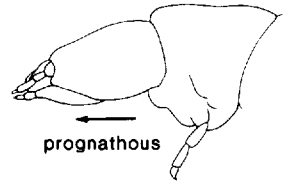


Figure 8

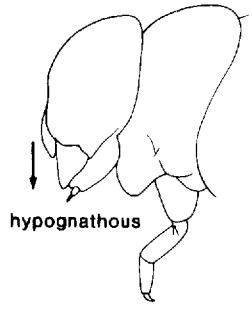


Figure 10

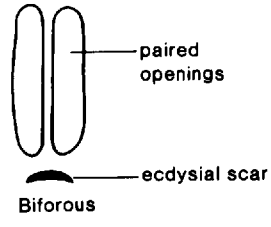


Figure 202

Figs. 85, 91 ——→

367(365′). Labial palps 1-segmented; hypostomal rods long and diverging (fig. 89); dorsal body surfaces with numerous elongate, setiferous tubercles (fig. 3). In rotting fungus fruiting bodies. Exotic (Southern Hemisphere) ..... (part) ***Hobartiidae*** p. 468

367′. Labial palps 2-segmented; hypostomal rods very short (fig. 85); dorsal body surfaces smooth or granulate-tuberculate, but without elongate, setiferous tubercles 368

368(367′). Dorsal body surfaces granulate or tuberculate; head moderately to strongly declined (hypognathous) (fig. 10); spiracles annular-biforous. In fruiting bodies of higher fungi ..... (**Dacninae** part) ***Erotylidae*** p. 473

368′. Dorsal body surfaces smooth; head prognathous or slightly declined (fig. 8); spiracles annular or occasionally annular-uniforous (fig. 196). In fruiting bodies of slime molds (Myxomycetes) ..... (*Odontosphindus*) (**Sphindinae**) ***Sphindidae*** p. 455

369(364′). Labial palps 1-segmented 370

369′. Labial palps 2-segmented 372

370(369). Hypostomal rods absent; ventral epicranial ridges present (fig. 93); dorsal body surfaces granulate or tuberculate; urogomphi not strongly upturned. In leaf litter, decaying vegetation, under bark, on spore-covered fungal surfaces ..... (**Monotominae**) ***Rhizophagidae*** p. 460

370′. Hypostomal rods long and diverging (fig. 89); ventral epicranial ridges absent; dorsal body surfaces smooth or with elongate, setiferous tubercles (fig. 3); urogomphi strongly upturned (fig. 171) 371

371(370′). Dorsal body surfaces smooth, without setiferous tubercles; spiracles not located at ends of tubes. In leaf litter, rotten wood, fungi, bee nests, stored products ..... (**Cryptophaginae** part) ***Cryptophagidae*** p. 469

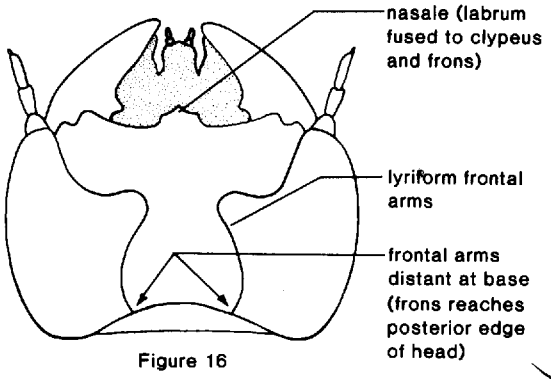


Figure 16

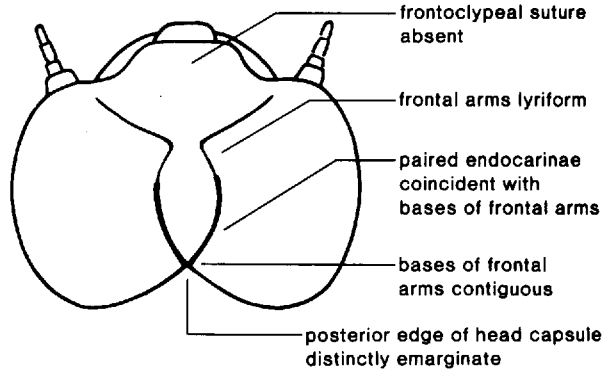


Figure 24

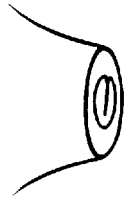
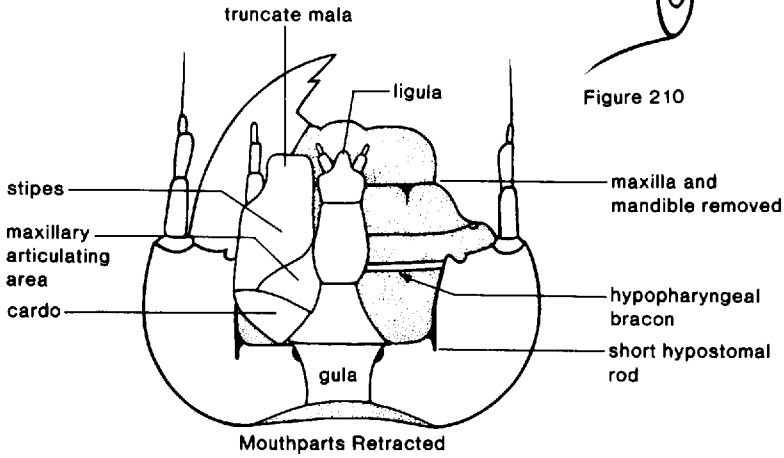


Figure 210



Mouthparts Retracted

Figure 85

Figure 3

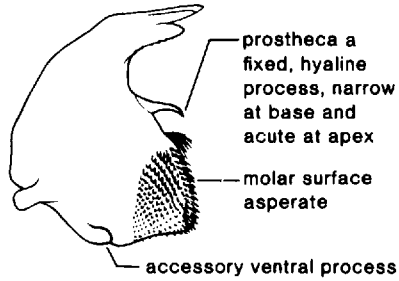
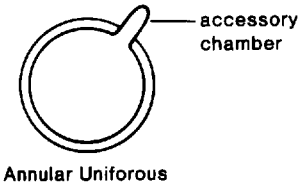


Figure 78



Annular Uniforous

Figure 196

← **Figs. 8, 10, 16, 24, 90, 93, 171**

371′. Dorsal body surfaces covered with elongate, setiferous tubercles (fig. 3); spiracles located at ends of short tubes (fig. 210). In rotting fungus fruiting bodies. Exotic (Southern Hemisphere) ..... (part) ***Hobartiidae*** p. 468

372(369′). Thoracic and abdominal segments bearing lateral tergal processes; body more or less ovate 373

372′. Thoracic and abdominal segments without lateral tergal processes; body elongate and more or less parallel-sided 374

373(372). Abdominal spiracles located at ends of tergal processes; dorsal body surfaces more or less granulate (often covered with dirt); stemmata on each side 5; accessory ventral process of mandible present (fig. 78). In leaf litter. Exotic (Australia and New Zealand) ..... (**Priasilphinae**) ***Phloeostichidae*** p. 462

373′. Abdominal spiracles not located at ends of tergal processes; dorsal body surfaces not granulate; stemmata on each side 1 or 0; accessory ventral process of mandible absent. In fungi, rotten wood, leaf litter ..... (**Mychotheninae** part) ***Endomychidae*** p. 482

374(372′). Frontal arms distant at base (fig. 16); ventral epicranial ridges present (fig. 90); stemmata on each side 4. Under bark of rotten logs ..... (*Rhizophagus*) (**Rhizophaginae**) ***Rhizophagidae*** p. 460

374′. Frontal arms approximate at base (fig. 24); ventral epicranial ridges absent; stemmata on each side 5 or 6 375

375(374′). Tergum A9 (without urogomphi) much shorter than tergum A8 (fig. 166); segment A10 posteriorly oriented; body more or less flattened 376

375′. Tergum A9 well-developed, about as long (without urogomphi) as tergum A8; segment A10 posteroventrally oriented; body usually not flattened 377

376(375). Segment A10 easily visible from above (fig. 166); body usually lightly sclerotized; urogomphi approximate and more or less parallel. In leaf litter, stored products ..... (Cryptamorphini) ***Cucujidae*** p. 463

376′. Segment A10 reduced and not visible from above; body heavily sclerotized dorsally and ventrally; urogomphi strongly diverging. Under bark ..... (*Cucujus*) (**Cucujinae**) ***Cucujidae*** p. 463

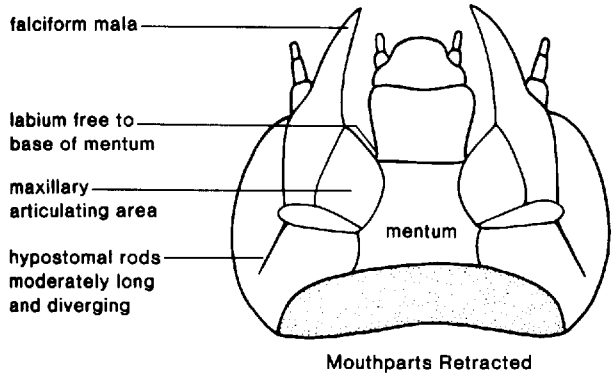
377(375′). Stemmata on each side 6; mala articulated at base; segment A10 with 2 long tubular pygopods. In male cones of cycads. Exotic (Australia) ..... (*Paracucujus*) ***Boganiidae*** p. 462

377′. Stemmata on each side 5 or fewer; mala fixed at base; segment A10 without paired pygopods 378

378(377′). Stemmata on each side 1 or 0; urogomphi simple; spiracles annular. In leaf litter, grass piles, stored products, under bark ..... (**Atomariinae** part) ***Cryptophagidae*** p. 469

378′. Stemmata on each side 5; urogomphi complex, each with 2 tubercles at base; spiracles annular-biforous (fig. 197). In sooty molds. Exotic (New Zealand) ..... (*Agapytho*) (**Agapythinae**) ***Phloeostichidae*** p. 462

379(313[3]). Head strongly retracted (fig. 9); body strongly curved ventrally (C-shaped); A8 spiracle much larger than others. In dead wood ..... (first instar) (**Lyctinae** part) ***Bostrichidae*** p. 439



Mouthparts Retracted

Figure 89

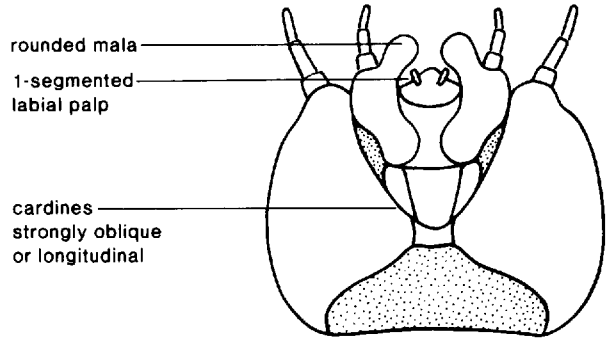


Figure 91

Figs. 9, 166, 197 ——→

379′. Head protracted or slightly retracted (figs. 8, 10); body not strongly curved ventrally; A8 spiracle about the same size as others 380

380(379′). Epicranial stem moderately long (fig. 14); maxillary palps 4-segmented; hypostomal rods absent; body densely clothed with long, fine hairs. In dead wood ..... (*Orphilus*) (**Orphilinae**) ***Dermestidae*** p. 434

380′. Epicranial stem very short (fig. 12) or absent; maxillary palps 3-segmented; hypostomal rods present; body without long, fine hairs; upper surfaces either granulate-tuberculate or with paired processes near midline on all abdominal terga 381

381(380′). Stemmata on each side 4; epicranial stem absent; frontoclypeal suture present; labial palps 1-segmented (or apparently so); spiracles annular; tarsungular setae 1; with paired processes near midline on all abdominal terga. In puffballs ..... (*Lycoperdina* part) ***Endomychidae*** p. 482

381′. Stemmata on each side 5 or 6; epicranial stem present; frontoclypeal suture absent; labial palps 2-segmented; spiracles annular-biforous (fig. 197); tarsungular setae 2; without paired tergal processes; upper surface usually granulate or tuberculate. In fungus fruiting bodies (usually Basidiomycetes) ..... (part) ***Erotylidae*** p. 473

382(313[4]). Bases of frontal arms contiguous (fig. 24). In puffballs ..... (*Pocadius* part) (**Nitidulinae**) ***Nitidulidae*** p. 456

382′. Bases of frontal arms distinctly separated (fig. 16). Under bark, in leaf litter, fungus fruiting bodies, carrion, rotting fruit ..... (part) ***Nitidulidae*** p. 456

383(311[3]). Abdominal terga with patches of asperities (fig. 141) on most segments; prothoracic sternum with median tooth (fig. 123); tergum A9 with indistinct pit between urogomphi. Under bark ..... ***Synchroidae*** p. 516

383′. Abdominal terga without patches of asperities; prothoracic sternum without median tooth; tergum A9 without pit or with 2 distinct pits between urogomphi 384

384(383′). Tergum A9 with 2 distinct pits between urogomphi (fig. 175). Under bark or in rotting vegetation ..... (**Pedilinae**) ***Pedilidae*** p. 544

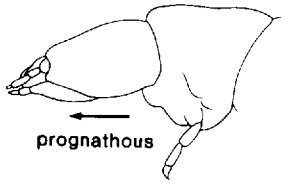


Figure 8

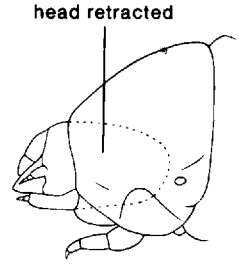


Figure 9

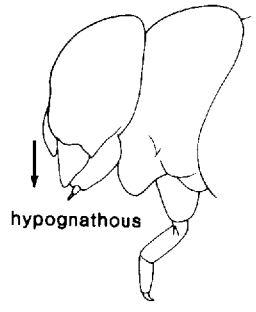
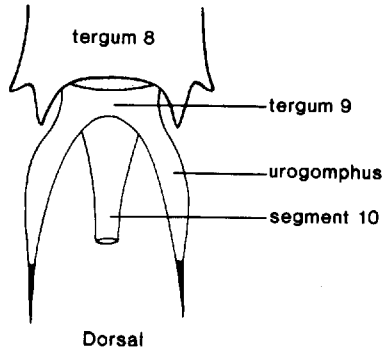


Figure 10



Dorsal
Figure 166

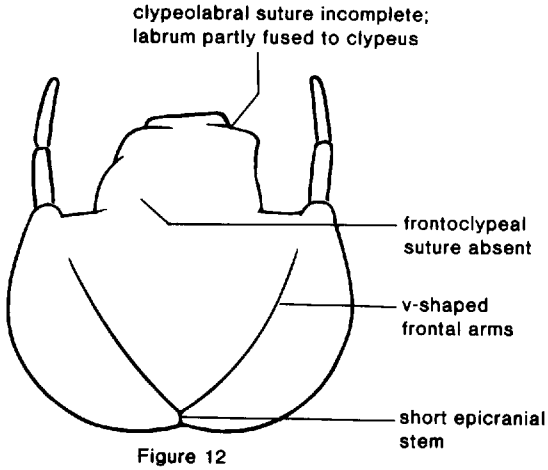


Figure 12

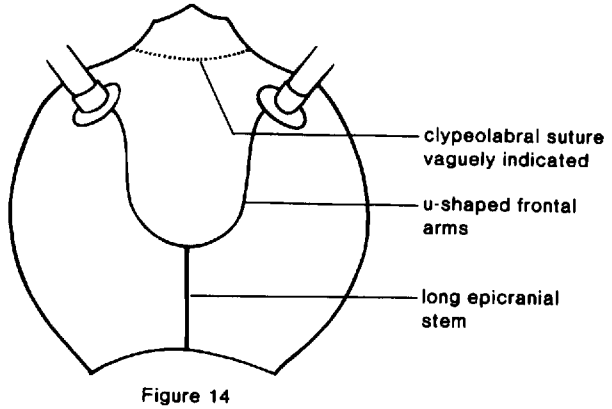


Figure 14

←— **Figs. 16, 24, 85, 89**

384′. Tergum A9 without pit between urogomphi (sometimes the appearance of a pit is caused by the proximity of the 2 small, mesal teeth at the urogomphal bases, as in fig. 177) 385

385(384′). Each urogomphus with small, mesal tooth near base; hypostomal rods very short (fig. 85); epicranial stem absent; paired endocarinae absent; mola well-developed and tuberculate or asperate (fig. 73). In leaf litter, stored products, guano ..... (*Aglenus*) (**Agleninae**) ***Othniidae*** p. 547

385′. Urogomphi simple; hypostomal rods moderately long but not extending to posterior edge of head (fig. 89); epicranial stem moderately long (fig. 18); paired endocarinae absent; mola well-developed and tuberculate or asperate (fig. 73). In fungus fruiting bodies (**see 3rd choice**) ..... (**Hallomeninae**) ***Melandryidae*** p. 505

385[2]. Urogomphi bifurcate (fig. 184); hypostomal rods extending almost to posterior edge of head (fig. 86); epicranial stem absent; paired endocarinae coincident with frontal arms (fig. 24); mola consisting of a few teeth only (fig. 71). Under bark, in rotten wood, stems, leaf litter ..... (**Salpinginae** part) ***Salpingidae*** p. 549

386(311[4]). Paired ventral prolegs (asperity-bearing ampullae) absent; frontoclypeal suture absent or vaguely indicated; abdominal terga without patches of asperities 387

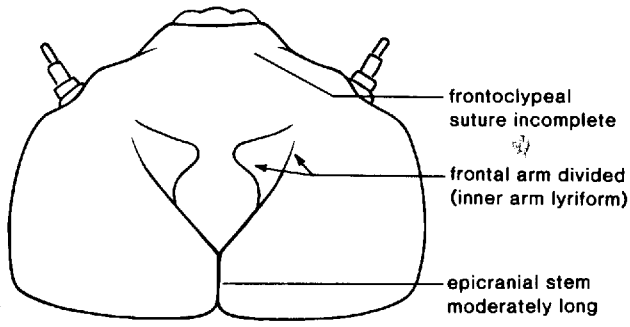


Figure 18

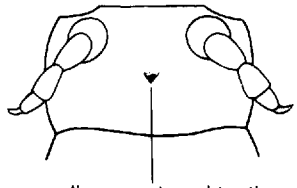


Figure 123

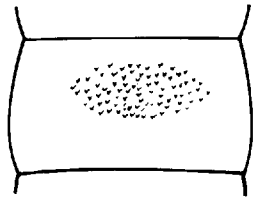
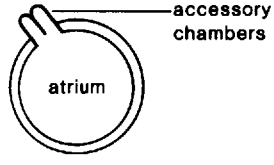
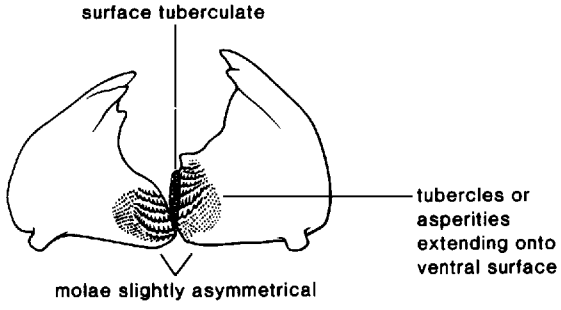


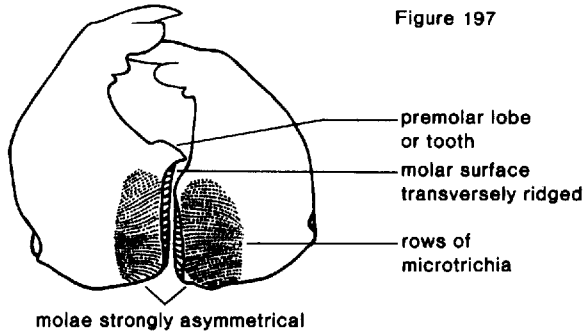
Figure 141



Annular Biforous
Figure 197



molae slightly asymmetrical
Figure 73



molae strongly asymmetrical
Figure 74

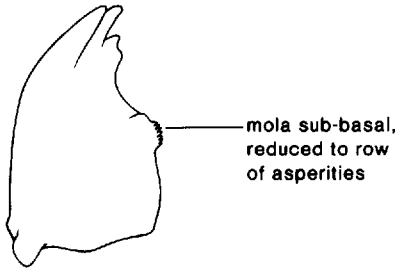
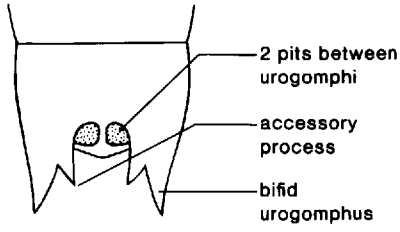
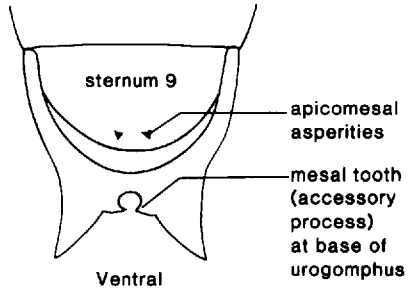


Figure 71



Dorsal
Figure 175



Ventral
Figure 177

Fig. 86: See p. 296. Fig. 184 ——→

386′. Paired ventral prolegs (asperity-bearing ampullae) (fig. 149) on sterna A2–4 or A2–5; frontoclypeal suture distinct (fig. 13); abdominal terga with patches of asperities (fig. 143) on 1 or more segments. In rotten wood ..... (*Calopus*) (**Calopodinae**) ***Oedemeridae*** p. 534

387(386). Urogomphi simple, somewhat converging, with 2 distinct pits between them (fig. 175); stemmata absent; apex of mala cleft (fig. 106); mandibles more or less symmetrical. In decaying vegetation in dry, sandy areas ..... (**Cononotinae**) ***Pedilidae*** p. 544

387′. Urogomphi bifid or with accessory processes (fig. 182), without or with a single weakly defined pit between them; stemmata present; apex of mala simple and rounded; mandibles asymmetrical (figs. 73, 74) 388

388(387′). Stemmata on each side 1; ligula well-developed and labial palps distinctly separated (fig. 85) ..... (**Trogocryptinae** part) ***Othniidae*** p. 547

388′. Stemmata on each side 2 or 5; ligula absent and labial palps subcontiguous (fig. 86) ..... ***Inopeplidae*** p. 551

389(311[5]). Row of basal asperities on sternum A9 straight or slightly sinuate and only slightly curved posteriorly at sides (figs. 179, 181) 390

389′. Row of basal asperities on sternum A9 strongly curved posteriorly at sides (fig. 178); body strongly flattened; segment A8 much longer than A7; tergum A9 forming articulated plate bearing simple, posteriorly oriented urogomphi with 2 pits between them (fig. 175). Under bark (**see 3rd choice**) ..... ***Pyrochroidae*** p. 541

389[2]. Row of basal asperities on sternum A9 strongly, doubly curved (fig. 180); body cylindrical or slightly flattened; segment A8 not much longer than A7; tergum A9 bearing complex urogomphi with single pit between them and 6–8 tubercles forming row in front of them (fig. 174). Under bark, in rotten wood ..... (**Pythinae** part) ***Pythidae*** p. 539

390(389). Row of basal asperities on sternum A9 broadly interrupted at middle (fig. 181); hypostomal rods very short (fig. 85) or long and diverging (fig. 89); urogomphi without or with single pit between them 391

390′. Row of basal asperities on sternum A9 more or less continuous (fig. 179); hypostomal rods absent or urogomphi with 2 pits between them (fig. 175) 392

391(390). Hypostomal rods very short (fig. 85); urogomphi with no pit between them and with row of 6 asperities in front of them ..... (*Sphalma*) (**Pythinae**) ***Pythidae*** p. 539

391′. Hypostomal rods moderately long (fig. 89); urogomphi with single pit between them and 4 asperities in front of them ..... (*Elacatis*) (**Othniinae**) ***Othniidae*** p. 547

392(390′). Urogomphi with 2 pits between them (fig. 175); tergum A9 forming sclerotized, articulated plate; hypostomal rods moderately long (fig. 89); body strongly flattened. Under bark. Exotic (Southern Hemisphere) ..... (**Pilipalpinae** = **Techmessinae**) ***Pythidae*** p. 539

392′. Urogomphi complex with single pit between them and 8 or more tubercles in front of them (fig. 174); hypostomal rods absent; body only slightly flattened. Under bark (**see 3rd choice**) ..... (*Pytho*) (**Pythinae**) ***Pythidae*** p. 539

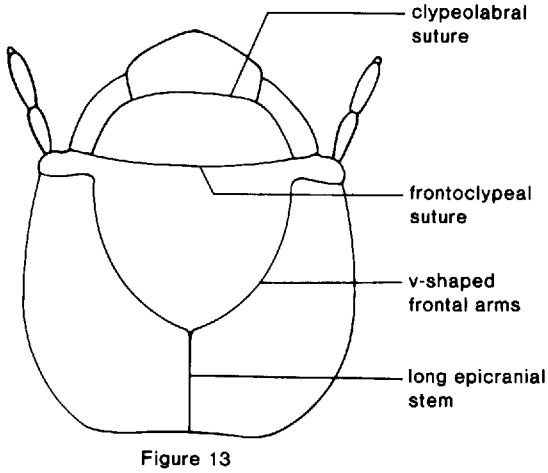
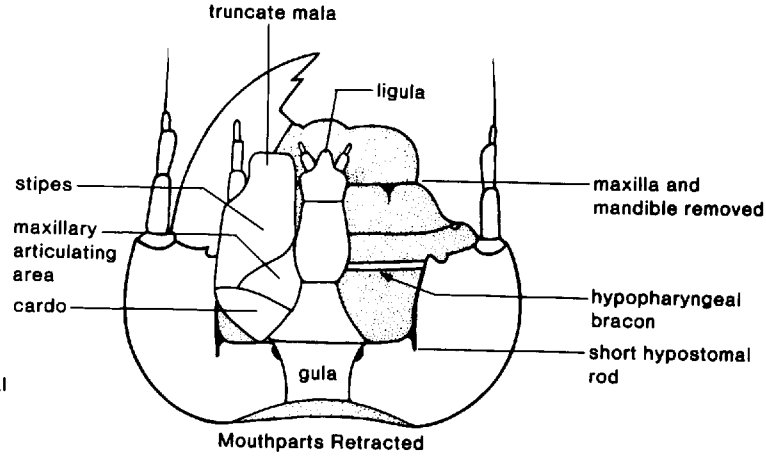


Figure 13



Mouthparts Retracted

Figure 85

←— Figs. 73, 74

392². Urogomphi without pit between them; hypostomal rods absent. Exotic ..... p. 393

393(392²). Urogomphi simple, more or less parallel, upturned at apex; meso- and metaterga, terga A1–7 and sterna A2–8 with series of longitudinal ridges. Length of mature larva greater than 100 mm. Exotic (Southeast Asia and East Indies) ..... ***Trictenotomidae*** p. 539

393'. Urogomphi diverging, each bearing 5 or more long spines; without longitudinal ridges on thorax and abdomen. Exotic (Japan) ..... (*Istrisia*) ***?Salpingidae*** p. 549

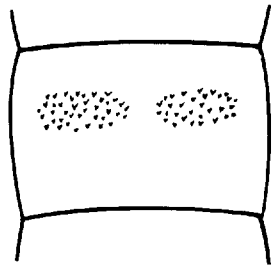


Figure 143

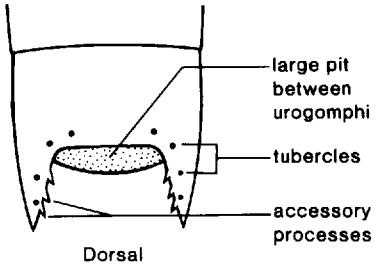


Figure 174

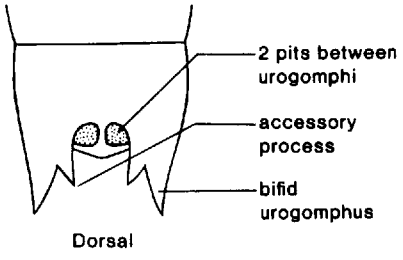


Figure 175

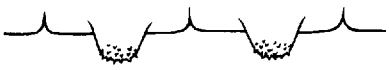


Figure 149

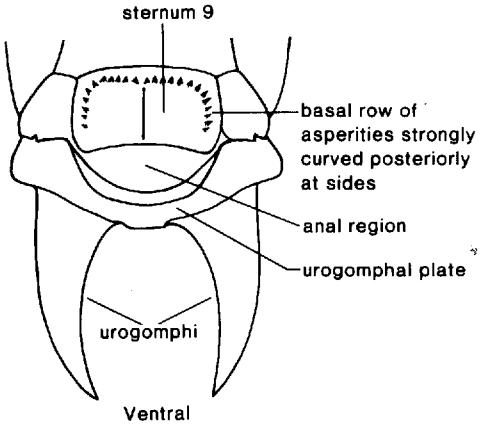


Figure 178

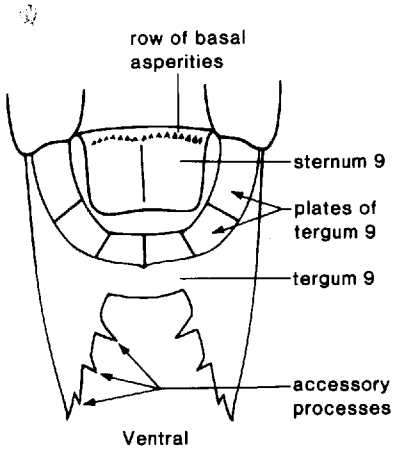


Figure 179

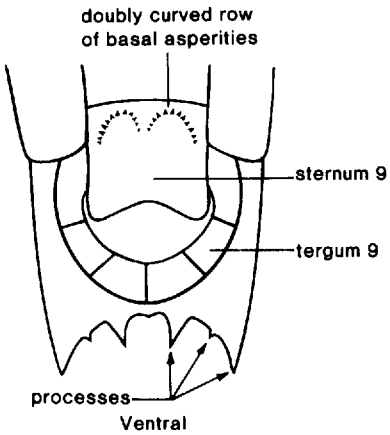


Figure 180

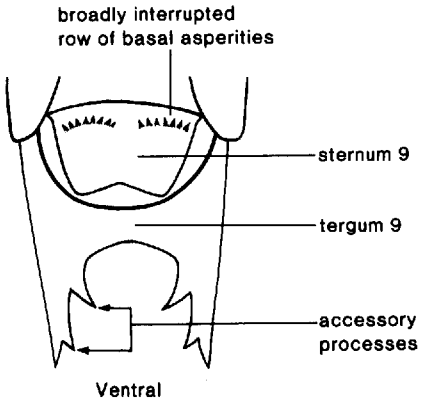


Figure 181

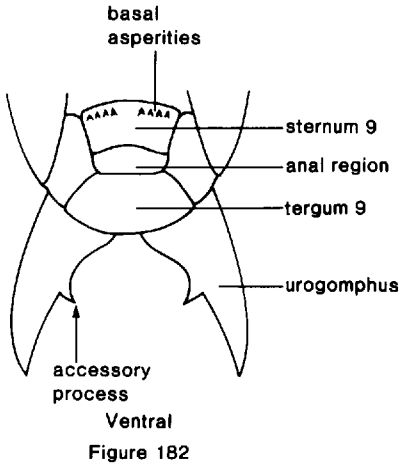


Figure 182

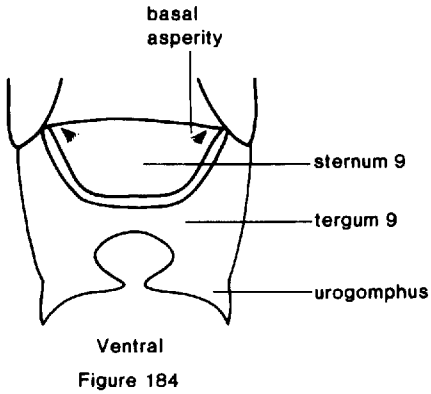


Figure 184

Figs, 86, 89, 106 ——→

394(311[7]). Ratio of antennal length to head width .15 to .5; cardo strongly oblique (fig. 91); abdominal terga with paired rows of asperities forming incomplete rings (fig. 147); posterior edge of head capsule distinctly emarginate dorsally. Under bark, in leaf axils ..... **(Mycterinae** and **Lacconotinae)** ***Mycteridae*** p. 535

394'. Ratio of antennal length to head width more than .5; cardo transverse or slightly oblique; abdominal terga without rows of asperities; posterior edge of head capsule not or only slightly emarginate dorsally 395

395(394'). Segments in labial palp 1; mandibles symmetrical; apex of mala simple (as in fig. 86); tergum A9 without pit between urogomphi; median endocarina present (fig. 22). At bases of cycad fronds ..... **(Hemipeplinae)** ***Mycteridae*** p. 535

395'. Segments in labial palp 2; mandibles asymmetrical; apex of mala cleft (fig. 106); tergum A9 with 2 pits between urogomphi (fig. 175); median endocarina absent. Under bark ..... ***Boridae*** p. 537

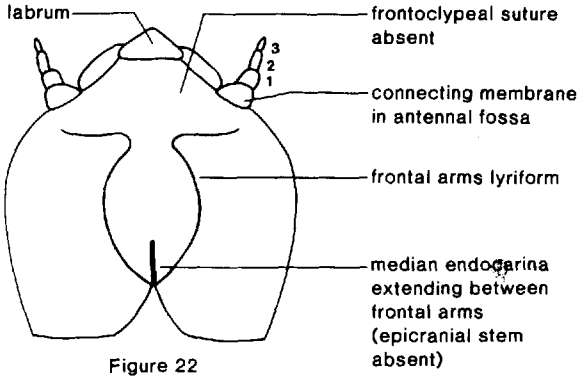


Figure 22

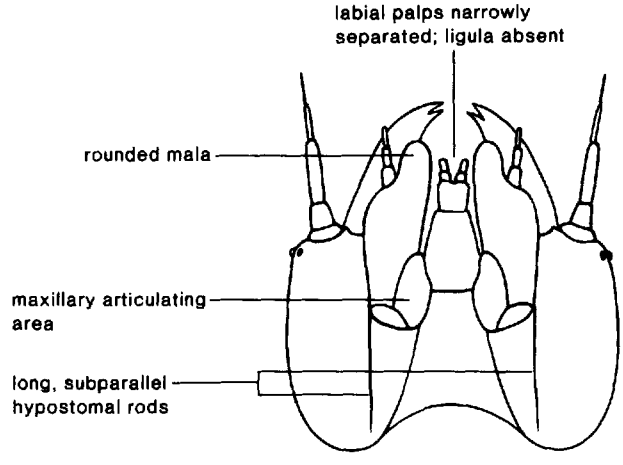
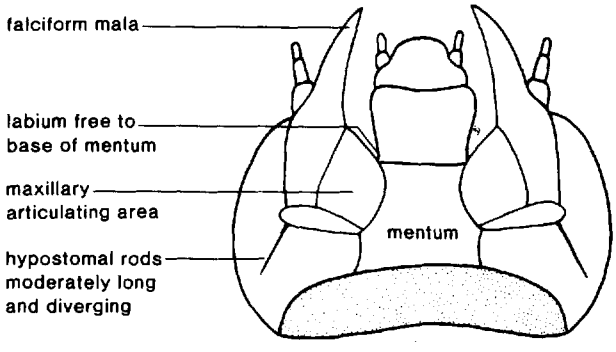


Figure 86



Mouthparts Retracted

Figure 89

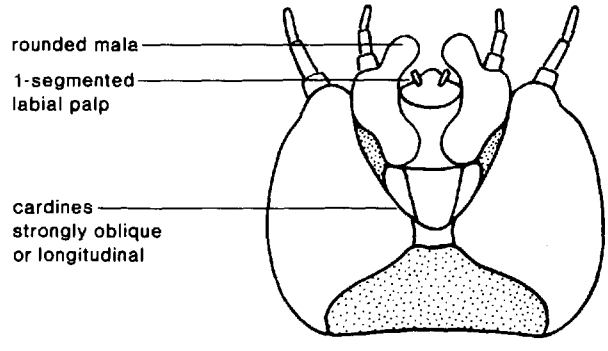


Figure 91

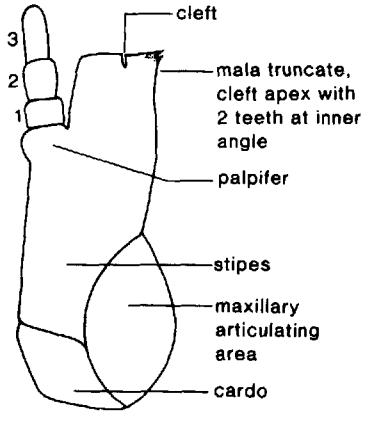


Figure 106

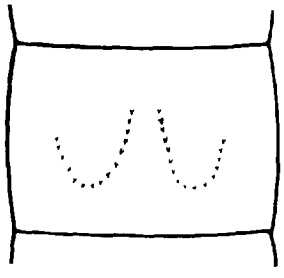


Figure 147

← Fig. 175

Selected Bibliography for Introduction

Anderson 1936 (labium).
Anderson 1974b (larval characters in Curculionoidea).
Ashlock and Lattin 1963 (stridulation).
Beier 1949 (morphology of *Helodes* larva).
Beier 1952 (feeding mechanism in larval Helodidae).
Benick 1952 (fungus beetles).
Bitsch 1966 (head capsule).
Böving 1914b (abdominal structure in campodeiform larvae).
Böving 1929b (larval descriptions and illustrations).
Böving 1936 (epipharynx and raster in scarab larvae).
Böving 1954 (morphology of anobiid larvae).
Böving and Craighead 1931 (larval keys and illustrations).
Borror, DeLong and Triplehorn 1981.
Brass 1914 (locomotory function of 10th abdominal segment).
Britton 1974 (larval key).
Burke 1919 (cocoon making in Bothrideridae).
Butcher 1930 (cocoon making in Gyrinidae).
Butt 1951 (feeding mechanism in epilachnine Coccinellidae).
Candeze 1861.
Carpenter and MacDowell 1912 (mouthparts in dascillid and scarabaeid larvae).
Chapuis and Candeze 1853.
Chu 1949 (larval key).
Cogan and Smith 1974 (collection and preservation).
Corbière-Tichané 1973 (sensory structure in larval Leiodidae).
Cornell 1972a (larval bibliography).
Costa et al. 1985.
Crowson 1955 (larval characters in keys).
Crowson 1962 (Cupedidae).
Crowson 1964d (larval characters in Cleroidea; tarsungulus problem).
Crowson 1981 (larval morphology).
Daggy 1947 (pupae of Tenebrionidae).
Dallwitz 1974, 1978, 1980, 1984 (computer keys and descriptions).
Danilevskii 1976 (digestive system in larval Cerambycidae).
Das 1937 (musculature of mouthparts).
Dorsey 1943 (musculature of labrum, labium and pharynx).
Doyen and Lawrence 1979 (larval Tenebrionidae and Zopheridae).
Duffy 1953 (morphology of larval Cerambycidae).
Eidt 1958 (anatomy and histology of an elaterid larva).
Eidt 1959 (feeding mechanism of an elaterid larva).
Emden 1934 (tarsus in Polyphaga).
Emden 1942a (techniques for study and collection).
Emden 1942c (larval key).
Emden 1946 (egg bursters).
Ford and Spilman 1979 (feeding mechanism in Eucnemidae).
Frank and Thomas 1984 (glands in aleocharine Staphylinidae).
Freeman 1980 (stored products pests).
Fuchs 1974 (pollen feeding in beetles).
Gage 1920 (larvae of Coccinellidae; terminology for cuticular armature).
Gardiner 1966 (egg bursters in Cerambycidae).
Gardner 1935b (larval Eucnemidae).
Gardner 1947 (larval bibliography).
Gilyarov 1964b (larval morphology and key).
Glen 1950 (morphology of larval Elateridae).
Goulet 1977 (technique for larval study).
Grandi 1959 (morphological adaptations in various beetle larvae).
Hackman 1984 (cuticle chemistry).
Hayashi 1981, 1986 (larval illustrations).
Hayes 1928 (epipharynx in Scarabaeoidea).
Hickman 1931 (feeding mechanism in Heliplidae).
Hicks 1959, 1962, 1971 (fauna of bird nests).
Hinton 1945b (stored products beetles).
Hinton 1946a (gin traps in beetle pupae), 1946b (pupae).
Hinton 1947 (spiracles and molting in aquatic larvae).
Hinton 1948a (dorsal cranial areas in caterpillars).
Hinton 1949 (pupae).
Hinton 1955 (respiratory adaptations in Psephenidae).
Hinton 1958 (panorpoid orders).
Hinton 1963 (ventral ecdysial lines).
Hinton 1966 (respiratory adaptations in psephenid pupae).
Hinton 1967a (spiracles in Myxophaga).
Hinton 1967c (ecdysial process in Scarabaeoidea).
Hinton 1981 (eggs of Coleoptera).
Hiznay and Krause 1956 (larval head and mouthparts in Passalidae).
Honomichl 1980 (digitiform sensilla in adult beetles).
Hyslop and Böving 1935 (morphology of larval Elateridae).
Kasule 1966 (larval Staphylinoidea).
Kemner 1918 (abdominal apex).
Kingsbury and Beveridge 1977 (elutriator).
Kinzelbach 1971 (Strepsiptera).
Klausnitzer 1978 (larval keys).
Kristensen 1981 (phylogeny of insect orders).
Kristensen 1984 (Lepidoptera: Agathiphagidae).
Kristensen and Nielsen 1983 (Lepidoptera: Heterobathmiidae).
Larsson 1942 (larval key).
Lawrence 1977b (larval mouthparts and feeding mechanisms).
Lawrence 1981 (larval Lucanidae).
Lawrence 1982c (larval descriptions).
Lawrence and Hlavac 1979 (feeding mechanisms in larval Derodontidae).
Leiler 1976 (eucnemid larvae).
Lengerken 1924 (extraoral digestion).
Lepesme 1944 (stored products beetles).
Martin 1977 (collection and preservation).
May 1967 (terminology for weevil larvae).
McAlpine *et al.*, 1981 (Diptera).
Meixner 1935 (larval morphology).
Merritt and Cummins 1984 (aquatic collecting techniques).
Nakamura 1981 (cerambycid pupae).
Nikitsky 1976c, 1980.
Oldroyd 1958 (collection and preservation).
Parkin 1933 (anobiid larvae terminology).
Paulian 1943 (general).
Paulian 1949a (general).
Paulus 1979 (larval eyes).
Perris 1855, 1862, 1876–1877 (larval descriptions).
Peterson 1951 (larval descriptions, illustrations, keys).
Peterson 1959 (collection, preservation, rearing techniques).
Phuoc and Stehr 1974 (pupae of Coccinellidae).
Pilgrim 1972 (Mecoptera: Nannochoristidae).
Riek 1970a (Megaloptera).
Riek 1970b (Neuroptera).
Riek 1970c (Strepsiptera).
Riek 1970d (Mecoptera).
Ritcher 1966 (larvae of Scarabaeoidea).
Roberts 1930 (larval key terminology).
Roberts 1936 (spiracles of first instar weevil larvae).
Ross and Pothecary 1970 (first instar *Priacma*).
Rozen 1963a (pupae of Nitidulidae).
Rozen 1963b (pupae of Archostemata).
St. George 1924 (morphology of tenebrionid larvae).
St. George 1939 (morphology of perimylopid larvae).
Schicha 1967 (functional morphology of mouthparts in adult pollen-feeders).
Schiödte 1864–1883 (larval descriptions).
Schmidt 1971 (mandibles in wood-boring insects).
Scott 1936, 1938 (paedogenesis in Micromalthidae).
Seeger 1971 (morphology and habits of Haliplidae).
Seevers 1957 (termitophilous Staphylinidae).
Sivinski 1981 (bioluminescence).
Smith and Sears 1982 (mandibular morphology and feeding habits).
Snodgrass 1935 (insect morphology).
Snodgrass 1947 (insect cranium).
Srivastava 1959 (maxillary glands in larval beetles).
Steinke 1919 (larval spiracles).
Stickney 1923 (adult head capsule and tentorium).
Striganova 1961a (feeding mechanism and morphology of Helodidae).
Striganova 1964c (mouthparts in phytophagous larvae).

Striganova 1967 (morphology of head and mandibles in burrowing larvae).
Striganova 1971 (morphology of mouthparts of predacious larvae).
Thomas 1957 (morphology of larval Scolytidae).
Thorpe and Crisp 1949 (plastron respiration).
Tillyard 1923 (Lepidoptera: Micropterygidae).
Torre-Bueno 1937 (glossary).
Treherne 1952 (respiration in helodid larvae).
Treherne 1954 (osmotic regulation in helodid larvae).
Upton and Norris 1980 (collection and preservation).
Verhoeff 1923 (larval morphology).
Viedma 1964 (larval key).
Wade 1935 (larval bibliography).
Wade and St. George 1923 (morphology of larval Tenebrionidae).
Walsh and Dibb 1975 (techniques of collecting and study).
Watt 1970 (larvae of Perimylopidae, terminology).
Watt 1974b (larvae of Tenebrionidae).
Wheeler and Blackwell 1984 (mycophagy).
Yasuda 1962 (Lepidoptera: Micropterygidae).
Yuasa 1922 (Hymenoptera: Symphyta).
Zacharuk 1962a (sense organs on head of elaterid larva).
Zacharuk 1962b (larval characters in Elateridae).

OMMATIDAE (ARCHOSTEMATA)

(= OMMADIDAE, INCLUDING TETRAPHALERIDAE)

John F. Lawrence,
Division of Entomology, CSIRO

The family Ommatidae, as delimited by Lawrence and Newton (1982), includes 3 genera: *Omma,* with 2 species in eastern Australia; *Tetraphalerus,* with 2 species in southern Brazil, Argentina, and Bolivia; and *Crowsoniella,* with a single species, *C. relicta* Pace, from central Italy. The group belongs in the Archostemata, along with the Cupedidae and Micromalthidae, and fossils attributable to the family are known from the Lower Jurassic.

Little is known about the biology of ommatids, and no immature forms have been described. Adults of *Omma* are rarely collected from central Queensland to South Australia, not only in the heavily forested areas adjacent to the coast, but also in the more open and arid *Eucalyptus* woodland west of the Great Divide. *Tetraphalerus* species often occur in open, dry areas with little or no tree cover, and adults may be attracted to lights. *Crowsoniella relicta* was found in rather dry and granular, calcareous soil at the bases of old chestnut trees, along with other interstitial beetles, like species of *Leptotyphlus* and *Scotonomus* (Staphylinidae), and *Anommatus* (Cerylonidae). Larval ommatids may be found eventually among the root systems of large shrubs or trees, or possibly in the rotting central cores of old standing trees or stumps.

Selected Bibliography

Crowson 1962 (review of Cupedidae and Ommatidae), 1975 (fossil record), 1976 (*Crowsoniella*).
Lawrence and Newton 1982.
Monros and Monros 1952 (South American Archostemata).
Neboiss 1960 (*Omma* distribution).
Pace 1976 (*Crowsoniella*).
Ponomarenko 1969 (fossil Archostemata).
Vulcano and Pereira 1975 (South American Archostemata).

CUPEDIDAE (ARCHOSTEMATA)

(= CUPESIDAE)

John F. Lawrence,
Division of Entomology, CSIRO

Reticulated Beetles

Figures 34.67a-e

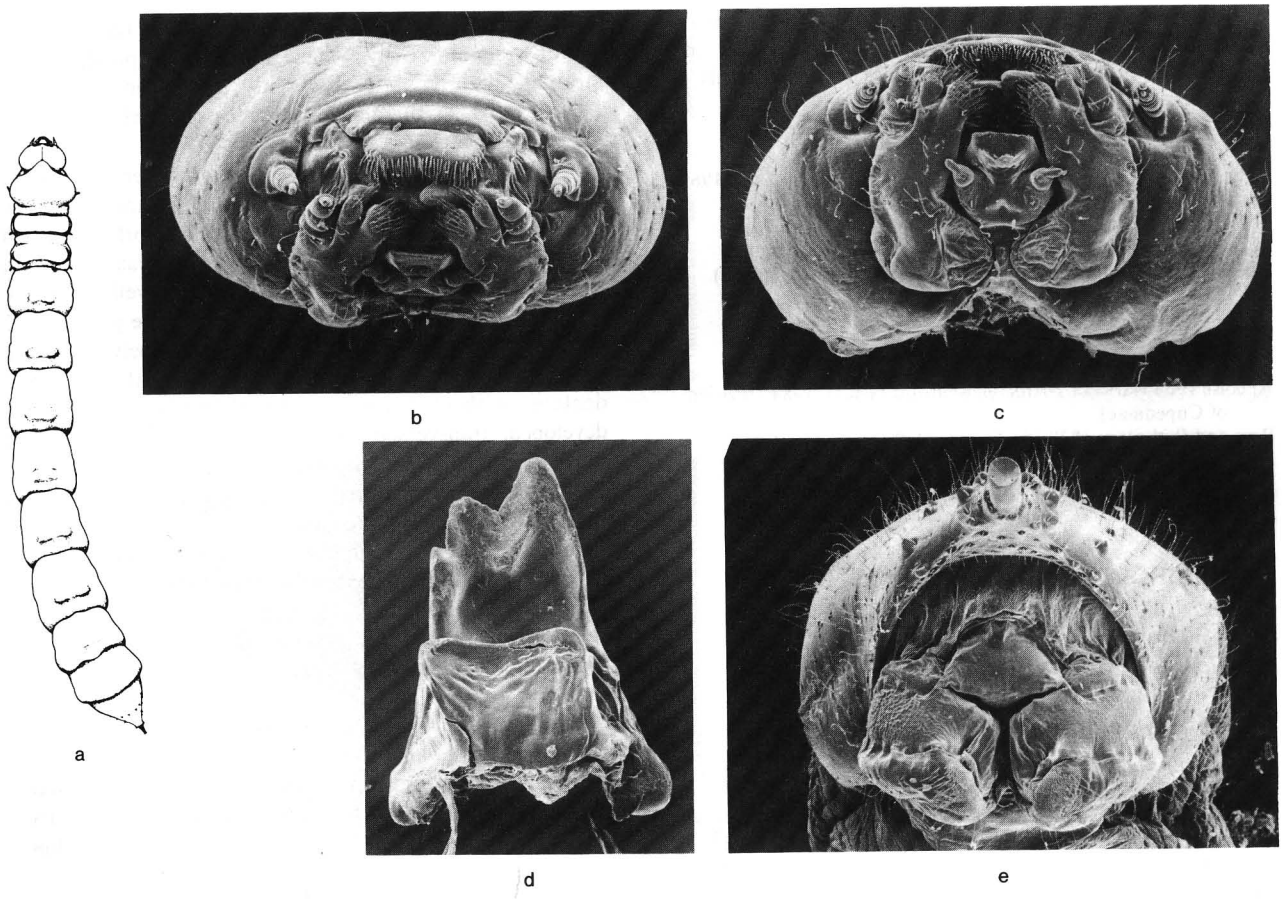
Relationships and Diagnosis: Cupedidae is one of three families comprising the oldest and most primitive suborder of beetles, the Archostemata. The formerly included genera *Omma* and *Tetraphalerus* have been placed in a separate family, Ommatidae, along with the minute, soil-dwelling *Crowsoniella relicta* Pace (Crowson, 1976; Lawrence, 1982c; Lawrence and Newton, 1982).

Cupedid larvae resemble other wood-boring types, like those of some Cephaloidae, Cerambycidae, Lymexylidae, Melandryidae, Oedemeridae, and Tenebrionidae, in that they are lightly sclerotized and more or less cylindrical, with relatively short legs and thoracic and abdominal ampullae. They differ from all of these, however, in having 6-segmented legs, a heavily-sclerotized, wedge-like ligula, and usually 4-segmented antennae. A combination of mandibular mola and separate galea and lacinia separates cupedids from all but Lymexylidae, which lack an anteriorly projecting median endocarina and have a hypognathous head without a gular region. A wedge-like ligula also occurs in Micromalthidae and Callirhipidae, but larvae of the latter are quite unlike cupedids in most respects. *Micromalthus* is the only other archostematan for which the larva is known. It resembles the cupedid larva in many ways, but is much smaller and may be distinguished by a sternal process on segment A9, the lack of legs in the cerambycoid stage, and the long, narrow tarsus with two moveable claws in the caraboid or triungulin stage.

Biology and Ecology: All known larvae bore through firm but fungus-infested wood, with the aid of their thoracic and abdominal ampullae, and apparently feed on wood fibers, fungal hyphae, and fungal biproducts. Larvae of the Japanese *Tenomerga mucida* (Chevrolat) are reported to feed in wood infected with the fungus *Stromatoscypha* (as *Porothelium*) (Basidiomycetes: Schizophyllaceae) (Fukuda, 1941). Some have been found in seasoned timber, but only in those portions attacked by a dry rot. Pupation occurs within the wood. *Priacma* larvae are known only as first instars, which hatched from eggs laid by a female beaten from a hemlock tree (*Tsuga*); it is probable that these larvae also feed on decayed wood (Ross and Pothecary, 1970). Adults are known to feed on pollen and may fly to lights (Crowson, 1962), while males of *Priacma serrata* (LeConte) are known to be attracted to bleach solution (Atkins, 1957); females are rare.

Description: Mature larvae 15 to 35 mm. Body elongate, parallel-sided, straight, subcylindrical, and lightly sclerotized, whitish, except for anterior part of head and tip of terminal process. Surfaces smooth; vestiture of scattered, simple, fine hairs, moderately dense in places.

Head: Protracted and prognathous, broad, transverse, slightly flattened, and deeply emarginate posteriorly. Epicranial stem absent; frontal arms usually indistinct or absent,



Figures 34.67a-e. Cupedidae. *Tenomerga concolor* (Westwood). East Lansing, Michigan. Length = 34 mm. **a.** Larva, dorsal; **b.** Head, anterior; **c.** Head, anteroventral; **d.** Left mandible, mesal; **e.** Abdominal apex, posteroventral.

sometimes V-shaped (lyriform in first instar of *Priacma*). Median endocarina extending anteriorly almost to edge of clypeus. Stemmata usually absent; occasionally 1 or more small eye spots on each side. Antennae usually well-developed and 4-segmented; rarely with 5 or 6 segments; 3-segmented in early instar *Cupes;* 2-segmented in first instar *Priacma.* Frontoclypeal suture present, sometimes indistinct; labrum free. Mandibles (fig. 34.67d) symmetrical or slightly asymmetrical, robust, tridentate or bidentate with large, subapical tooth, and without accessory ventral process; mola well-developed, simple or with a few tubercles or transverse ridges; prostheca absent. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp with large palpifer, articulated, rounded galea, and fixed, rounded lacinia. Labium with mentum and submentum fused; ligula forming a wedge-like sclerome, extending well beyond labial palps, which are usually 2-segmented (1-segmented in first instar *Priacma*). Hypopharyngeal sclerome well-developed, forming a single unit with ligular sclerome. Hypostomal rods long and slightly diverging at base and converging at apex. Ventral epicranial ridges absent. Gula transverse.

Thorax and Abdomen: Thorax relatively small, less than a fourth the length of the abdomen in later instars. Prothorax slightly larger than meso- or metathorax, with large, paired patches of asperities on sternum. Legs short, widely separated, 6-segmented, including simple or bifurcate claw. Meso- and metaterga, abdominal terga and sterna 1–7 each with transverse ampulla. Tergum A9 with median, sclerotized process, blunt at apex and with asperities around base, or in *Priacma* with median process bearing 2 dorsal and 2 ventral tubercles. Sternum A9 well-developed, simple. Anal region bordered laterally by 2 large, rounded lobes.

Spiracles: Annular, longitudinally oval, with more or less crenulate peritreme.

Comments: The Cupedidae is a small family containing 9 genera and 26 species worldwide, with 4 genera and 4 species in N. America. There are two subfamilies: Priacminae with the monotypic genus *Priacma* from northwestern N. America, and Cupedinae containing the rest of the genera. The Cupedinae have been revised recently (Neboiss, 1984) and now include: *Cupes* (1 species; N. America); *Tenomerga* (10 species; Holarctic, southeast Asia, New Guinea, South Africa); *Distocupes* (1 species; Australia); *Adinolepis* (4 species; Australia); *Ascioplaga* (2 species; New Caledonia);

Rhipsideigma (4 species; East Africa and Madagascar); *Prolixocupes* (2 species; southwestern N. America and southern S. America); and *Paracupes* (1 species; Brazil).

Selected Bibliography

Atkins 1957 (attraction of male *Priacma serrata* to bleach), 1963 (review of family).
Böving 1929b (larva of *Tenomerga concolor* (Westwood)).
Böving and Craighead 1931 (larva of *Tenomerga concolor*).
Crowson 1962 (review of family), 1976 (*Crowsoniella relicta*).
Fukuda 1938 (larva of *Tenomerga mucida*), 1941 (biology of *Tenomerga mucida*).
Lawrence 1982c.
Lawrence and Newton 1982.
Neboiss 1968 (larva of *Distocupes varians* (Lea)), 1984 (revision of Cupedinae).
Ross and Pothecary 1970 (first instar of *Priacma serrata*).
Rozen 1963b (pupa of *Tenomerga concolor*).
Vulcano and Pereira 1975 (S. American Archostemata).

MICROMALTHIDAE (ARCHOSTEMATA)

John F. Lawrence,
Division of Entomology, CSIRO

Telephone-pole Beetles

Figures 34.68a–i

Relationships and Diagnosis: Although tentatively placed in the Cantharoidea by Arnett (1968), the Micromalthidae have been shown to be members of the Archostemata on the basis of both adult and larval characters (Lawrence and Newton, 1982). The larvae are very similar to those of Cupedidae, and the leg-bearing triungulins (caraboid larvae) might be mistaken for first instar cupedids, from which they differ in having a long, narrow tarsus bearing two moveable claws, an apical process on abdominal sternum 9, and a differently formed hypopharyngeal sclerome.

Biology and Ecology: Micromalthid larvae are usually found in localized colonies in red rotten wood of *Quercus* and *Castanea,* but they are capable of infesting rotten building materials of various woods, including *Pinus, Pseudotsuga, Acacia,* and *Eucalyptus,* when used in flooring, furniture, telephone poles, railroad ties, bridge abutments, and mine timbers. The life cycle is more complex than that found in any other insect group. The first instar (caraboid larva) is an active triungulin, which develops into a legless, feeding form (cerambycoid larva), which may undergo three molts. The cerambycoid larva may pupate to become an adult diploid female or may develop into one of three types of larviform reproductives: (1) a thelytokous paedogenetic female, which, in turn, produces viviparously a number of triungulins; (2) an arrhenotokous paedogenetic female, which lays a single egg destined to be a stump-legged curculionoid larva, which, in turn, devours the mother and pupates to form an adult haploid male; and (3) an amphitokous paedogenetic female, which may produce either form. The production of various larval types is apparently affected by environmental conditions. (Barber, 1913a, 1913b; Pringle, 1938a; Scott, 1936, 1938, 1941).

Description: Length of mature larva (cerambycoid stage) 4 to 6 mm. Body elongate, more or less parallel-sided, straight, slightly flattened, lightly pigmented, except for buccal region and tips of terminal processes. Surfaces smooth; vestiture of scattered, simple hairs.

Head: Protracted and prognathous, broader than thorax, transverse, slightly flattened. Epicranial suture apparently absent. Median endocarina extending anteriorly almost to edge of clypeus. Stemmata usually absent; occasionally with a single stemma on each side. Antennae well-developed, 3-segmented, with segment 3 more than twice as long as 2 and narrower than antennal sensorium. Frontoclypeal suture present; labrum free. Mandibles asymmetrical, robust, tridentate, without accessory ventral process; mola well-developed, transversely ridged; prostheca absent. Ventral mouthparts retracted. Maxilla with transverse cardo, elongate stipes, well-developed articulating area, 3-segmented palp, articulated, truncate galea, and fixed, rounded lacinia. Labium with mentum and submentum fused; ligula forming a wedge-like sclerome, extending well beyond labial palps, which are 1-segmented. Hypopharyngeal sclerome well-developed, subtriangular, transversely ridged. Hypostomal rods long and subparallel. Ventral epicranial ridges absent. Gula transverse.

Thorax and Abdomen: Thorax reduced, less than a fifth the length of the abdomen. Legs absent. Meso- and metaterga, abdominal terga and sterna 1–7 each with transverse ampulla. Tergum A9 with median appendage, which curves ventrally and has several teeth at apex, and which almost meets a similar appendage extending from the apex of sternum A9. Anal region with a large, rounded lobe on each side.

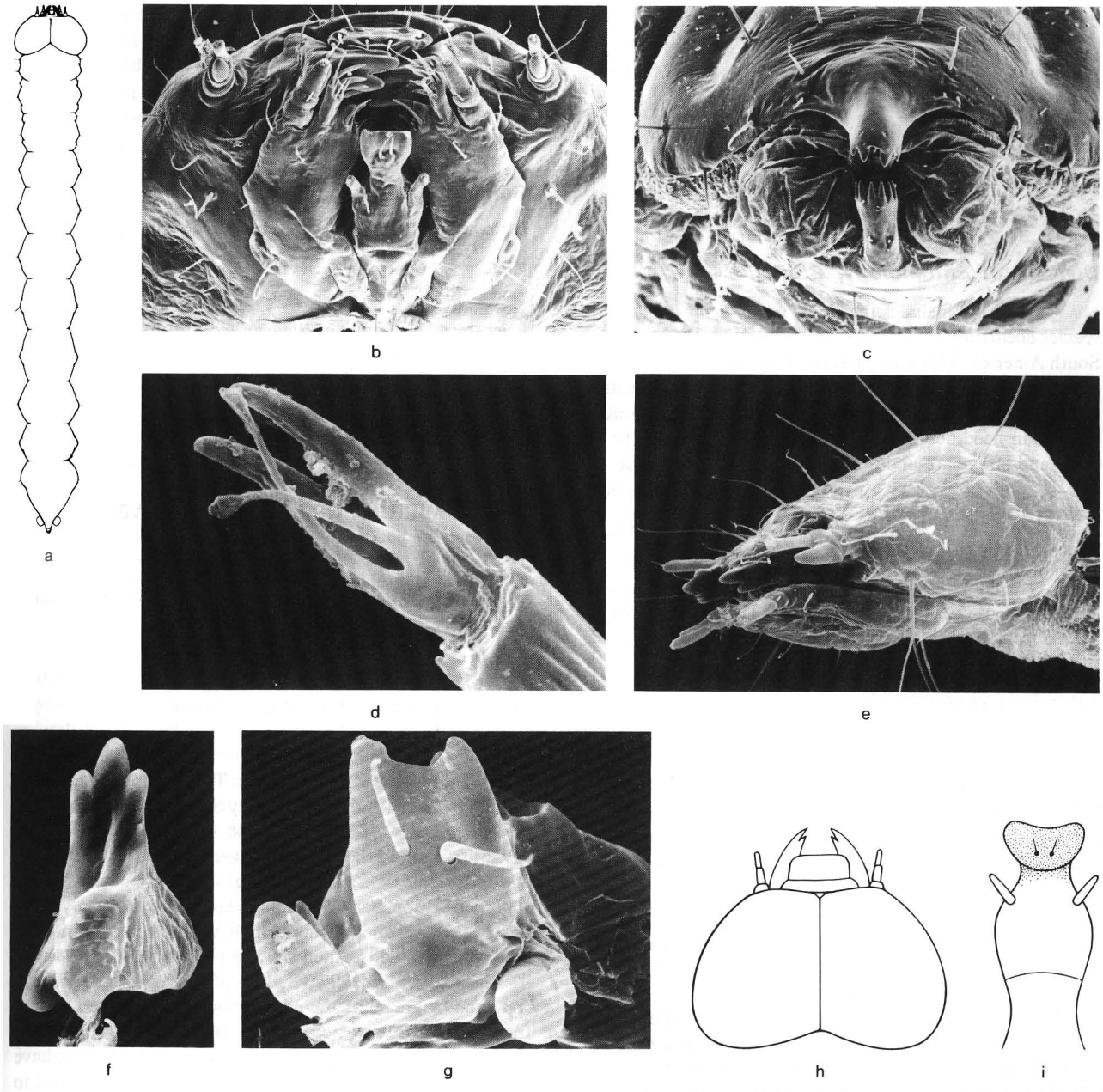
Spiracles: Annular, very small.

Triungulin (caraboid Larva): Length 1.3 to 2 mm. Similar to cerambycoid larva, but with well-developed, 6-segmented legs, each with a very long and narrow tarsus and with 2 moveable claws with pair of spatulate appendages beneath them.

Curculionoid Larva: More or less grub-like, with narrower head, short, stump-like legs, and no terminal abdominal processes.

Reproductive Forms: More or less similar to legless cerambycoid larva, but with narrower head and no terminal abdominal processes. Developing eggs or viviparous larvae usually can be seen within abdomen.

Comments: This family includes the single species *Micromalthus debilis* LeConte, whose natural range includes the northeastern part of the United States, from Kentucky to Michigan and east to the Atlantic. The total range of the species is far greater, with records from British Columbia; New Mexico; Florida; Oahu, Hawaii; Cuba; the states of Bahia, Minas Gerais, and São Paulo in Brazil; Gibraltar; Victoria and Kowloon, Hong Kong; and Witwatersrand and Johannesburg in South Africa. All peripheral records, however, as well as those from other parts of the world, are based on infestations of human artifacts, usually made from wood imported from North America. The South African specimens, for instance, were found in mines, where the original timbers were made from pitch pine imported from the United States.



Figures 34.68a-i. Micromalthidae. *Micromalthus debilis* LeConte. **a.** Clinton Co., Ohio. Cerambycoid larva, dorsal, length = 3.7 mm; **b.** Rose Lake, Clinton Co., Michigan. Cerambycoid larva. Head, anteroventral; **c.** Abdominal apex, posterior; **d.** Clinton Co., Ohio. Caraboid larva. Tarsal claws and attached appendages; **e.** Hong Kong. Caraboid larva. Head, anterolateral; **f.** Right mandible, mesal; **g.** Labium, anteroventral; **h.** Head, dorsal; **i** Labium, showing sclerotized ligula.

Although South African specimens are thought to be conspecific with American forms, those from Hong Kong (triungulins without associated adults) could represent a distinct species, since they possess a single pair of stemmata, absent in triungulins of *M. debilis*. (Marshall and Thornton, 1963; Pringle, 1938a; Silvestri, 1941; Swezey, 1940). Fossil triungulins are known from the Miocene of Mexico (Rozen, 1971) and the Oligocene of Europe (Lawrence, unpublished), while a related form is known from the Cretaceous of Lebanon (Crowson, 1981).

Selected Bibliography

Barber 1913a (life cycle), 1913b (life cycle).
Böving 1929b (larva and triungulin).
Böving and Craighead 1931 (larva and triungulin).
Crowson 1981.
Lawrence and Newton 1982.
Marshall and Thornton 1963 (triungulin from Hong Kong).
Peterson 1951 (larva).
Pringle 1938a (occurrence in South Africa; larva; life cycle).
Rozen 1963b (pupa), 1971 (fossil triungulin).

Scott 1936 (haploidy), 1938 (life cycle; paedogenesis), 1941 (production of males and females).
Silvestri 1941 (distribution).
Swezey 1940 (occurrence in Hawaii).

CYATHOCERIDAE (MYXOPHAGA)

(= LEPICERIDAE)

John F. Lawrence,
Division of Entomology, CSIRO

This family includes the single genus *Lepicerus*, with 2 species occurring in Mexico, Central America, and northern South America. This group has the diagnostic features of the suborder Myxophaga, but is somewhat isolated from the other myxophagan families. Adults have been collected along streams in flood debris, but nothing else is known of the biology and larvae are undescribed.

Selected Bibliography

Hinton 1934 (habitat of *Lepicerus*).
Reichardt 1976c (review of family).

TORRIDINCOLIDAE (MYXOPHAGA)

John F. Lawrence,
Division of Entomology, CSIRO

H. Reichardt,*
Universidade de São Paulo, Brazil

This family includes 27 species comprising 6 genera: *Hintonia, Ytu,* and *Claudiella* from southeastern Brazil; *Incoltorrida* from Madagascar; *Torridincola* from central and southern Africa; and *Delevea* from southern Africa and Japan. The group is placed in the suborder Myxophaga, and adults resemble Triassic fossils in the archostematan families Schizophoridae and Catiniidae.

Larvae are minute (less than 2.5 mm), broad and flattened, with a large prognathous head, free labrum, elongate 2- or 3-segmented antennae, and 3 to 5 stemmata on each side. The epicranial stem is short and the frontal arms lyriform. The mandibles have a large, tuberculate mola and a prostheca. The galea and lacinia are more or less fused, and the maxillary palps are 1- or 3-segmented. The labium is broad, with 2-segmented palps. The legs have 5 segments, including the tarsungulus. Abdominal segments 1 to 8 each has a pair of 2- or 3-segmented, lateral, spiracular gills, most of the surfaces of which are covered with plastron mesh. Tergite A9 usually bears a pair of fixed urogomphi. Pupae are obtect and have 2 pairs of long, spiracular gills.

Larvae and adults occur on rock surfaces which are covered with a thin film of moving water (hygropetric habitat) or which are located in the spray zone beneath waterfalls; they feed on algae growing on the rocks. Adults usually possess a plastron on the abdomen, while larvae have a plastron on the gills. According to Spangler (1980b), *Ytu brutus* Spangler and an associated hydrophilid (*Oocyclus* sp.) were literally swimming in the water film running over a wet guard rail across from a waterfall.

Selected Bibliography

Bertrand 1962 (larva of *Delevea*, as an undescribed genus of Hydraenidae).
Hinton 1967a (larval spiracles in Myxophaga), 1969 (adult plastron).
Lawrence and Newton 1982.
Reichardt 1973a (larvae of *Hintonia* and *Ytu*), 1976b.
Reichardt and Costa 1967.
Reichardt and Vanin 1976.
Sato 1982 (Japanese *Delevea*).
Spangler 1980b (larva of *Ytu*).
Steffan 1964 (larva of *Torridincola*).

MICROSPORIDAE (MYXOPHAGA)

(= SPHAERIIDAE)

John F. Lawrence,
Division of Entomology, CSIRO

H. Reichardt,*
Universidade de São Paulo, Brazil

Figures 34.69a, b

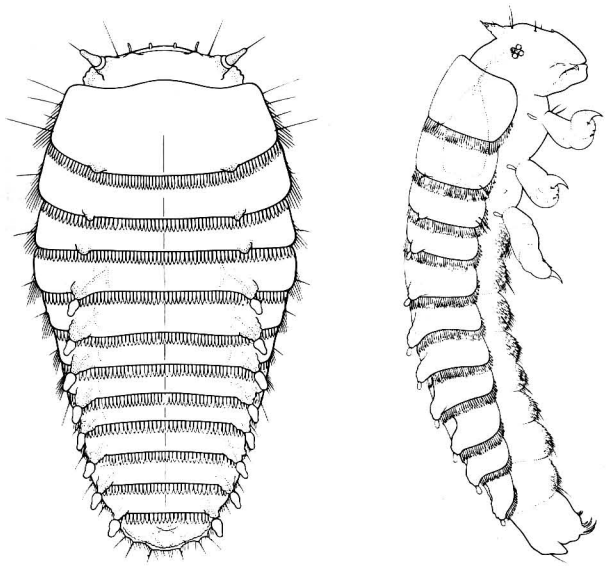
Relationships and Diagnosis: The Microsporidae were originally placed in the superfamily Staphylinoidea and some workers (Barlet, 1972) still retain them there, but Forbes (1926) recognized the hydradephagan features of their wings, and Crowson (1955) placed the group in his newly formed suborder Myxophaga. Microsporid larvae are extremely small (0.8 to 1.2 mm) and are unique in having vesicular spiracular gills on abdominal segments 1 to 8 (Hinton, 1967a).

Biology and Ecology: Species of Microsporidae occur in wet sand or gravel at the edges of streams or rivers, where they may occur with Georyssidae, Hydraenidae, Hydrophilidae, or Elmidae (Lesne, 1936; Britton, 1966). Larvae have been collected by allowing a sample of wet sand or gravel to drain through metal gauze into a jar or placing such a sample in an elutriator. Because of their small size, microsporids form part of the interstitial fauna, and their food almost certainly consists of algae occurring among the sand grains. Females were observed to lay large, single eggs (Britton, 1966).

Description: Mature larvae about 1.2 mm. Body elongate, fusiform, narrowed posteriorly, slightly flattened, lightly sclerotized, yellowish. Dorsal surfaces smooth; vestiture of longer and shorter, simple setae, with bands of densely packed, stout, highly refractive setae at posterior ends of trunk segments.

Head: Protracted and hypognathous, broad, narrowed anteriorly. Epicranial stem and frontal arms indistinct. Median

*Deceased



Figures 34.69a,b. Microsporidae. *Microsporus ovensensis* (Oke). **a.** Larva, dorsal; **b.** lateral. Length = 1.2 mm. (from Britton, 1966 and 1974, Supplement to The Insects of Australia, Melbourne University Press).

endocarina absent. Stemmata 4 on each side; lenses well-developed. Antennae short, 3-segmented, with segments 2 and 3 indistinctly separated, giving the appearance of a 2-segmented antenna with a long sensorium arising from middle of apical segment; antennal insertions dorsally placed and well separated from mandibular articulations. Frontoclypeal suture present; clypeal area enlarged; labrum apparently fused to head capsule. Mandibles symmetrical, short and broad, bidentate, without accessory ventral process; mola large and tuberculate; prostheca apparently absent. Ventral mouthparts retracted. Maxilla with oblique cardo, elongate stipes, well-developed articulating area, and falciform mala with 2 or 3 stout setae at inner edge; palp 3-segmented. Labium not distinctly subdivided; ligula broad, bilobed; labial palps 2-segmented, widely separated. Hypostomal rods and ventral epicranial ridges absent. Gula transverse.

Thorax and Abdomen: Thoracic and abdominal segments strongly transverse. Legs moderately large, stout, close together; tarsungulus short, with 1 seta. Abdominal segments 1–8 each with posteriorly directed spiracular tube on each side near posterior edge. Tergum A9 simple, truncate at apex. Segment A10 ventrally oriented, with 3 pairs of hooks.

Spiracles: Present on abdominal segments 1–8; forming vesicular gills, which are more or less ovate.

Comments: The family contains the single genus *Microsporus* with 18 species occurring throughout the Northern Hemisphere and in Australia and Madagascar (Britton, 1966; Lesne, 1936; Paulian, 1949b); two or three species are known from N. America.

Selected Bibliography

Barlet 1972.
Bertrand 1972.
Britton 1966 (larva of *Microsporus ovensensis* (Oke)).
Crowson 1955.
Forbes 1926.
Hinton 1967a (spiracular gills).
I.C.Z.N., 1985 (*Microsporus*).
Lawrence and Newton 1982.
Lesne 1936 (distribution).
Paulian 1949b (occurrence in Madagascar).
Reichardt 1973a.

HYDROSCAPHIDAE (MYXOPHAGA)

John F. Lawrence,
Division of Entomology, CSIRO

H. Reichardt,*
Universidade de São Paulo, Brazil

Figures 34.70 a, b

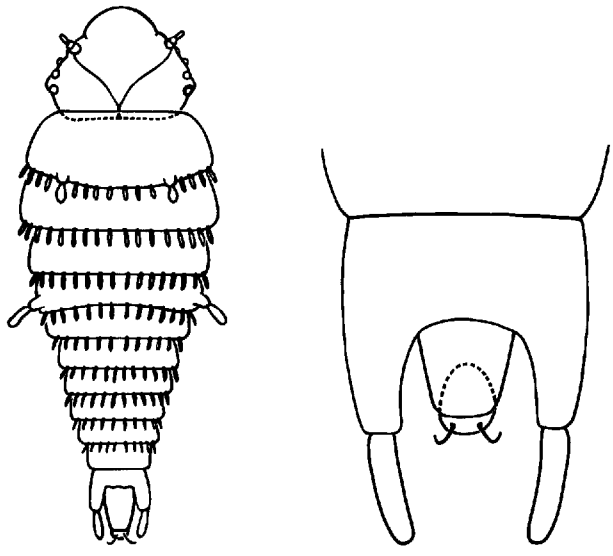
Relationships and Diagnosis: The Hydroscaphidae are placed by most workers in the primitive suborder Myxophaga (Crowson, 1955, 1960b; Lawrence and Newton, 1982), but they have been included at various times in Hydrophiloidea (Böving, 1914a), Staphylinoidea (Paulian, 1941), or Adephaga (Barlet, 1972; Forbes, 1926). The larvae are easily distinguished by their small size and the presence of spiracular gills on the prothorax and abdominal segments 1 and 8. The gills are almost always vesicular like those of Microsporidae, but they are more elongate and occupy different positions on the body (Hinton, 1967a). The gills of Torridincolidae occur on abdominal segments 1 to 8, but they are segmented. Some hydraenid larvae (*Tympanogaster*) have snorkel-like spiracular tubes on the prothorax, but these do not bear vesicles.

Biology and Ecology: Adults and larvae of Hydroscaphidae are usually found feeding on algae over which a thin film of water is flowing, usually into a stream or river, but some species have been found in hot springs, at the edges of swimming pools, under rocks in fast-flowing streams, or in flood debris. Adults of *Hydroscapha natans* LeConte have been collected in large numbers flying at dusk, along with a species of *Microsporus*. Hydroscaphids pupate among the algae, usually beneath the water, and the pupae have various aquatic adaptations, such as long spiracular processes or plastron-bearing spiracular gills (Böving, 1914a; Reichardt and Hinton, 1976).

Description: Mature larvae about 1.5 mm. Body elongate, fusiform, narrowing posteriorly, slightly flattened, lightly sclerotized or moderately sclerotized dorsally. Dorsal surfaces smooth or somewhat tuberculate; vestiture of longer and shorter, simple setae, sometimes broad and flattened.

Head: Protracted and prognathous, transverse, moderately broad and slightly flattened. Epicranial stem very short; frontal arms V-shaped. Median endocarina absent. Stemmata 5 on each side, each with well-developed lens. Antennae

*Deceased



Figures 34.70a,b. Hydroscaphidae. *Hydroscapha natans* LeConte. **a.** larva, dorsal, length = 1.5 mm; **b.** abdominal apex, dorsal. (redrawn from Böving 1914a)

very short, 2-segmented; segment 2 more than 3 times as long as 1; sensorium slightly longer than segment 2. Frontoclypeal suture absent; clypeal area enlarged; labrum indistinct, highly reduced or fused to clypeus. Mandibles more or less symmetrical, with very broad base and reduced apex, which is tridentate; accessory ventral process absent; mola well-developed, tuberculate; prostheca consisting of a fixed, hyaline lobe, bifid or trifid at apex and attached to a membranous lobe. Ventral mouthparts retracted. Maxilla with strongly oblique cardo, slightly elongate stipes, well-developed articulating area, and falciform mala with 2 or 3 teeth at apex; palp 2-segmented with well-developed sensilla on segment 1. Labium with mentum and submentum fused; ligula short and broad; labial palps 2-segmented and widely separated. Hypopharyngeal sclerome present. Hypostomal rods absent; ventral epicranial ridges absent. Gula transverse.

Thorax and Abdomen: Thorax enlarged, more than half as long as abdomen. Posterior edges of thoracic terga and abdominal terga 1–7 in *Hydroscapha* fringed with short, stout setae (becoming finer posteriorly); lateral edges of thoracic and abdominal terga in *Scaphydra* lined with setiferous tubercles. Protergum with short, dorsally-projecting spiracular tube on each side toward the lateral margin near posterior edge (*Hydroscapha*) or laterally-projecting tube near each posterior angle (*Scaphydra*). Legs well-developed, 5-segmented, separated by about 1 coxal diameter; tarsungulus long, with 1 seta. Abdominal segments gradually decreasing in width posteriorly. Tergum A1 with short, laterally-projecting spiracular tube on each side near posterior angle. Tergum A8 with pair of long, posteriorly-projecting, spiracular tubes. Segment A9 with simple tergum and sternum. A10 forming ventrally-hinged operculum, with pair of long hooks at apex (not described for *Scaphydra*).

Spiracles: Present on prothorax and abdominal segments 1 and 8; anterior two pairs forming oblong, vesicular gills in *Hydroscapha* or tuft-like gills in *Scaphydra;* posterior pair forming elongate vesicular gills.

Comments: The family contains 3 genera: *Hydroscapha,* with about 9 species occurring in western North America, Mexico, Eurasia, North Africa, Madagascar, and southeast Asia; *Yara* with 2 species in Panama and Brazil; and *Scaphydra,* with 3 species in Brazil.

Selected Bibliography

Barlet 1972.
Bertrand 1972.
Böving 1914a (larva of *Hydroscapha natans* LeConte).
Böving and Craighead 1931 (larva of *Hydroscapha natans* LeConte).
Forbes 1926.
Hinton 1967a (spiracular gills).
Lawrence and Newton 1982.
Paulian 1941.
Reichardt 1971, 1973a, 1973b, 1974 (larva of *Scaphydra angra* Reichardt).
Reichardt and Hinton 1976.

RHYSODIDAE (ADEPHAGA)

Ross T. Bell, *University of Vermont*

Wrinkled Bark Beetles

Figures 34.71, 72

Relationships and Diagnosis: There are 2 conflicting ideas about the relationships of Rhysodidae. Some regard them as an independent family of possibly primitive Adephaga, while Bell and Bell (1962) consider them to be highly specialized Carabidae. The larvae are recognized as Adephaga by the combination of 6-segmented legs with the absence of a mola on the mandible. They are soft-bodied, slow-moving, and grub-like. They differ from most Carabidae in the complete absence of urogomphi. They can be distinguished from those parasitic or myrmecophilous Carabidae which also lack urogomphi by lacking distinct segmented labial palpi, and by having, at least in the final instar, a transverse row of spinulae on at least some of the thoracic and abdominal tergites.

Biology and Ecology: The larvae are found in short galleries in rotten wood. The gallery behind the larva is tightly packed with wood shavings. They probably feed on slime molds and fungi in the wood, and not on the wood itself. Larvae are usually associated with adults, but the latter can also live in harder wood than the larvae can. In most species at least, the adults do not excavate distinct galleries, but push their way among the rotting wood fibers. Pupation is in the larval gallery.

Description: Small, pale larvae, 9 mm or less in length; body feebly sclerotized, short, depressed, tapered at both ends.

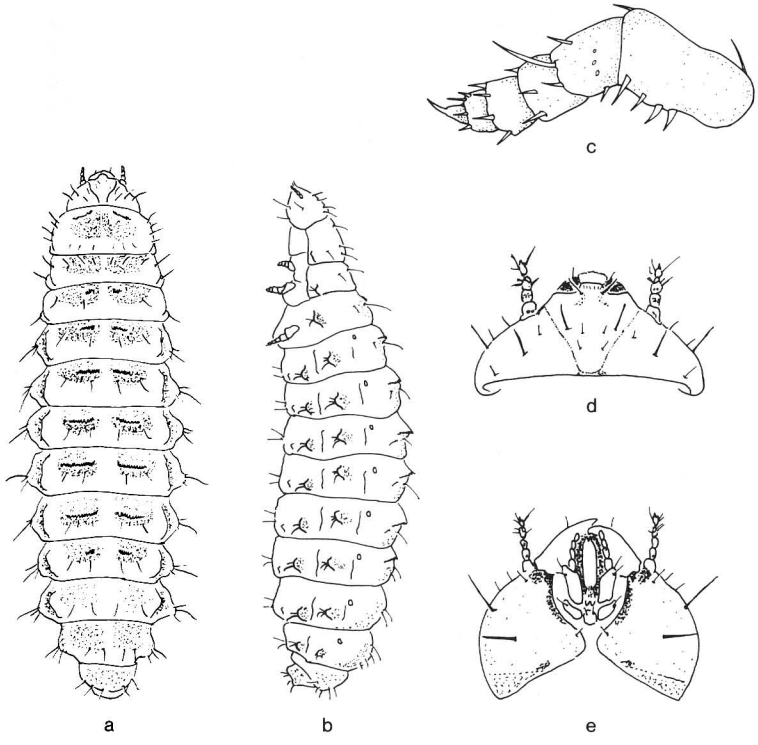


Figure 34.71

Figures 34.71a-e. Rhysodidae. *Omoglymmius americanus* (Laporte). **a.** larva, dorsal; **b.** lateral; **c.** leg, showing coxa, trochanter, femur, tibia, tarsus, and pretarsus; **d.** head, dorsal; **e.** head. ventral.

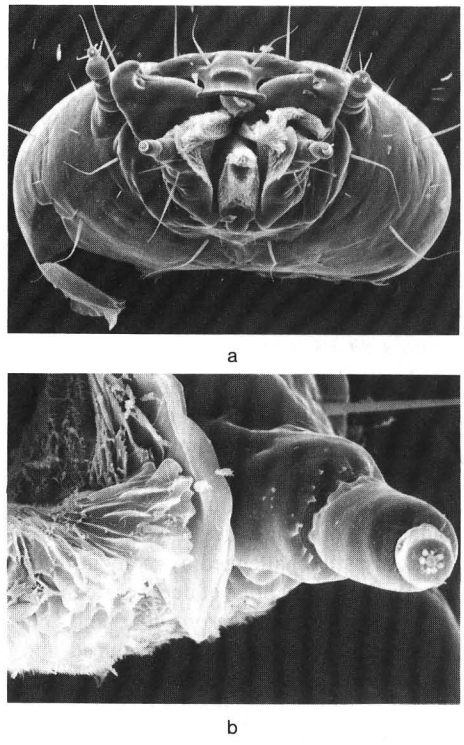


Figure 34.72

Figures 34.72a,b. Rhysodidae. *Omoglymmius hamatus* (LeConte). 1.9 mi. E Crane Flat, Tuolumne Co., Calif. **a.** Head, anteroventral; **b.** detail of maxillary apex.

Head: Prognathous; eyes absent; antennae short, 4-segmented; anterior margin of head with simple median lobe forming nasale; mandibles short, curved; mola absent; maxilla with well developed, 4-segmented palp; maxillary apex reduced, lightly sclerotized, sometimes bearing a series of fringed membranes; labial palps inconspicuous, 1-segmented, located at apex of elongate prementum, which may be clothed with microtrichia or fringed membranes.

Thorax and Abdomen: Prosternum and pronotum more sclerotized than remaining body segments; each leg with six segments, including a simple pointed pretarsus forming a claw; most body segments each with a pair of lightly sclerotized tergal humps, each with a transverse row of spinulae; rows of spinulae always interrupted at midline (in *Clinidium* also interrupted near lateral margin). Spinulae always present on metanotum and on abdominal tergites 1–6 (in *Clinidium,* also present on mesonotum and on tergite 7); ninth abdominal tergite narrow, in dorsal view appearing to form posterior end of body; tenth segment a narrow ring around anus, forming pygopod. Abdominal segments each with a pair of prominent ventrolateral tubercles in *Omoglymmius.* (These very poorly developed in *Clinidium.*)

Spiracles: Annular, on mesothorax and abdominal segments 1–8.

Comments: A poorly known group both taxonomically and ecologically. There are about 130 described species, but Bell and Bell are currently working on a world revision, and have found nearly 200 undescribed species. Eight species are known from North America, two from the western half of the continent and six from the eastern region. They are of no known economic importance, but are of great interest in zoogeography. Rhysodidae are especially prominent in insular faunas. Böving and Craighead (1931) illustrated a larva as *Clinidium sculptile* Newman. It has since been discovered that five species have been confused under this name, so it is uncertain which species they studied. Grandi (1955) and Burakowski (1975a) have illustrated and described the larvae of two European species. No keys are available to North American larvae.

Selected Bibliography

Bell 1970.
Bell and Bell 1962, 1978, 1979, 1982.
Böving and Craighead 1931.
Burakowski 1975a.
Grandi 1955.
Vanin and Costa 1978.

CARABIDAE (ADEPHAGA)

(INCLUDING BRACHINIDAE, CICINDELIDAE, OMOPHRONIDAE, PAUSSIDAE, PSEUDOMORPHIDAE, TRACHYPACHIDAE, ETC.)

Yves Bousquet, *Biosystematics Research Centre, Agriculture Canada*

Ground Beetles, Tiger Beetles

Figures 34.73-104

Relationships and Diagnosis: Carabidae, commonly known as ground beetles, belong to the suborder Adephaga. They form a large and cosmopolitan family with about 1500 genera and 30,000 species (Lawrence 1982c) of which some 2,500 occur in North America. The relationships of the Carabidae with other families of Adephaga, as well as its natural limits, are still challenged by many authors.

With the exception of degenerate instars of ectoparasitic larvae of *Brachinus, Pheropsophus* and *Lebia,* carabid larvae are recognized by the well developed and 2- (usually) or 4-segmented labial palpi, the 6-segmented (including single or paired claws) legs, the 10 well differentiated abdominal segments (except in Metriini, Paussini and Ozaenini which have the last 3 segments markedly modified or reduced), and the sublateral position (between the tergum and the epipleurite) of all spiracles on the abdominal segments.

Carabid larvae are likely to be confused with larvae of Staphylinidae, Silphidae and Histeridae. The 6-segmented legs in carabid larvae instead of 5-segmented legs in the other families will distinguish them.

Biology and Ecology: Only some aspects of the biology of carabids will be considered here. The reader is referred to the publication of Thiele (1977) for more information.

In temperate and boreal regions, the majority of carabid species are terrestrial. Adults and larvae are commonly found under rocks and debris in fields, forests and on shores, in leaf litter and under bark of logs in forest areas, or among gravel along river banks. Some species are hygrophilous, living in bogs, swamps, or marshes where they are collected by treading the vegetation under water. Many species, particularly within the Trechini, are cave inhabiting. Although some species regularly climb trees, bushes or plants, very few, such as species of *Dromius,* are truly arboreal; however, the number of species living on trees increases in the tropics.

At least in the temperate and boreal regions, carabids appear to be univoltine (Thiele 1977). Hibernation occurs in adult and/or larval stages. In the cases of *Amara infima* Duftschmid (Schjøtz-Christensen 1965) and *Sphaeroderus nitidicollis brevoorti* LeConte (Bousquet and Pilon 1980), indirect evidence suggests that winter is spent in the adult and egg stages.

Many species lay their eggs individually in small hollows dug out in the substrate. Others encase their eggs individually in mud cells which are dropped on the substrate or attached to stems or leaves. Some species of Pterostichini have developed parental care; the female lays her eggs in a cell made in the soil or in rotten logs and stays on or near them until the larvae hatch and become pigmented. The presence of the female apparently protects the eggs from fungal attack rather than predators (Löser 1970).

Most Carabidae have 3 larval instars; a few species have 2 (some species of *Amara* (Bílý 1975b), some species of *Harpalus* (Kirk 1974), *Thermophilum sexmaculatum* Fabricius (Paarmann 1979)), 4 (*Eurycoleus macularis* Chevrolat (Erwin 1975)) or 5 instars (*Brachinus* (Erwin 1967)). One larval instar has been recorded for species of *Aphaenops* (Deleurence, cited by Dajoz 1961), but this requires confirmation. Though in many species development of immature stages is fast, in some groups of Carabidae, such as *Scaphinotus, Nebria, Patrobus, Calathus, Synuchus,* and some Pterostichini, larvae have a thermic diapause. Pupation usually occurs in a cell a few centimeters below the substrate.

Adults of most species are polyphagous (Hengeveld 1980) and ingest both animal and plant matter. However, some groups are exclusively carnivorous and often somewhat specialized: adults of *Carabus* feed on worms and snails, those of *Calosoma* on caterpillars, those of Cychrini on snails and slugs, those of *Notiophilus* and *Loricera* on Collembola. Adults of other species are phytophagous and variably specialized: *Zabrus tenebroides* Goeze consumes ripe grains of rye, wheat, barley and corn (Thiele 1977), *Ditomus clypeatus* Rossi feeds on seeds of plantain (Schremmer 1960), and *Carterus calydonius* Rossi those of carrot (Brandmayr and Brandmayr Zetto 1974).

Information on the nutrition of carabid larvae is scarce. However, most species are probably carnivorous in their larval stages and mainly feed on soft bodied insects, snails, and worms. A few species are even very specialized in their feeding habits: larvae of *Orthogonius* live on termites, and those of the South African species, *Arsinoe grandis* Péringuay cling to and suck on the larvae of the tenebrionid *Catamerus revoili* Fairmaire. Ectoparasitic larvae are also known amongst Carabidae: larvae of *Lebia* are parasitic on larvae and pupae of Chrysomelidae, those of *Brachinus* on pupae of aquatic beetles, those of *Pheropsophus* on mole cricket eggs, and those of *Pelecium* on beetle pupae and millipedes. Larvae of some species have been reported to be phytophagous such as those of *Harpalus puncticeps* Stephens and *Carterus calydonius* which feed on carrot seeds (Brandmayr Zetto and Brandmayr 1975, Brandmayr and Brandmayr Zetto 1974). While larvae of most species actively search for their prey, those of others, such as species of Cicindelinae and *Sphallomorpha,* passively wait at the top of their burrow. Under laboratory conditions, cannibalism has been commonly observed.

The economic importance of carabid beetles is moderate. They feed on many injurious insects but are unable to control effectively any pest. Consequently, they should best be considered as valuable natural "auxiliaries" (Thiele 1977). Damage by carabids to crops and stored products is minimal.

Insectivores, bats, rodents, birds, frogs and toads, ants, robber flies and spiders are the most important predators of Carabidae. A number of Nemathelminthes, Acari (especially Podapolipidae), Hymenoptera (Proctotrupoidea, Braconidae, Mutillidae) and Diptera (Tachinidae) are known to be parasitic on adults and/or larvae.

Description: Body length of mature larvae, 2 to 50 mm. General shape campodeiform (figs. 34.73, 74, 76) for most species, rarely onisciform (e.g., Cychrini; fig. 34.75) or physogastric (e.g. some instars of *Brachinus* and *Pheropsophus*, some Pseudomorphini).

Head: Prognathous. Frons, clypeus and labrum fused to form frontale (= frontal piece), its anterior portion (nasale) usually prominent and variable in form. Epicranial suture present, of various shapes (figs. 34.77–84); epicranial stem present (figs. 34.77, 81, 82) or absent (figs. 34.78–80, 83, 84). Parietale in general with 6 stemmata on each side in 2 vertical rows of 3 per row, sometimes with fewer than 6 or without stemmata. Cervical groove present in many groups (e.g., figs. 34.81, 82). Antenna in general nearly as long as or longer than mandible, and 4-segmented, rarely 3-segmented (Anthiini, with second and third segments fused). First antennal segment in some Pterostichini (e.g., *Cyclotrachelus, Molops, Abax*) with circular membranous area near base and therefore seemingly 5-segmented. Third antennal segment usually with 3 small sensilla and 1 large, generally bulbous sensorium anterolaterally (= sensorial appendage of van Emden 1942b).

Mouthparts protracted from anterior part of cephalic capsule. Mandible more or less falcate or subtriangular, symmetrical, without mesal hyaline process (present in Paussini according to van Emden 1942b) or molar region; retinaculum present in nearly all species, consisting of single tooth of various shapes (figs. 34.85–87, 89), occasionally bidentate (*Omophron;* fig. 34.88); penicillus consisting of one to many closely associated setae (figs. 34.85–87, 89), or absent (fig. 34.88). Maxilla with cardo proportionally small; stipes elongate and in general membranous or thinly sclerotized dorsally; lacinia absent (figs. 34.90–92) or developed as a small, rounded or acuminate tubercule (fig. 34.93), or as a protuberance sometimes nearly as long as galea (e.g. *Metrius, Omophron;* fig. 34.94); galea palpiform, 2-segmented (figs. 34.91–95), rarely 1-segmented (e.g., *Metrius, Brachinus;* fig. 34.90); maxillary palp 4-segmented (figs. 34.90–94), rarely 5-segmented (Trechini, with last segment subdivided; fig. 34.95). Labium with prementum in general short, arising from membranous mentum; labial palp 2-segmented (figs. 34.96, 97), or rarely 4-segmented (Trechini, with double subdivision of last segment; fig. 34.98); ligula (usually bearing apical pair of setae) present in many groups as a short (fig. 34.98) or long (e.g., *Metrius, Omophron;* fig. 34.97) protuberance.

Thorax and Abdomen: Thoracic dorsum formed by single sclerite divided medially by narrow membranous area (ecdysial line). Pleural region usually with epimeron and episternum on all 3 segments and also with trochantin and pleurite on meso- and metathorax. Ventral side of thorax in general mostly membranous, except for anterior part of prothorax with large and often more or less triangular, rarely divided (Cicindelinae), prosternite. Legs in general long, 6-segmented (fig. 34.99) including one or two, unequal or subequal, movable claws, rarely 5-segmented (Collyrini, with tarsus and claws fused, according to van Emden 1935b), or 3-segmented (some degenerate instars of Brachinini, according to Erwin 1967).

Abdomen 10-segmented. Segment 9, with rare exceptions (e.g., Cicindelinae, some Cychrini, some Harpalini), with pair of dorso-apical urogomphi; urogomphus articulated (fig. 34.101) or fixed (figs. 34.100, 102–104), segmented or entire, with (fig. 34.104) or without membranous areas (figs. 34.100–103), short (figs. 34.100, 102) or long (figs. 34.101, 103, 104). In Metriini, Ozaenini and Paussini, eighth and ninth segments highly modified (*see* Bousquet 1986). Tenth segment usually tubular, acting as proleg, often with paired eversible vesicles bearing coarse pointed microsculpture. Terga 1–8 usually formed by single sclerite divided by narrow, median membranous area (ecdysial line). In Cicindelinae, fifth tergite modified, bearing 2 or 3 pairs of hooks. Pleural region of segments 1–8 with epipleurite (subdivided in some groups) and hypopleurite (not apparent in first instar of some groups, e.g., *Omophron*). Ventral side of segments 1–7 usually with 7 sclerites: small paired anterior sternites, median sternite (anterior ventrite of van Emden 1942b), and paired inner and outer sternites (postventrites of van Emden 1942b). These sclerites fused or partly fused, often also with hypopleurites on eighth and ninth segments.

Spiracles: Annular, on mesothorax and between tergum and epipleurite of abdominal segments 1–8.

Comments: The first larval instar of most species differs from subsequent instars by having paired egg-bursters located posteriorly on the frontale or rarely basally on the dorsal side of the parietale (some *Bembidion,* D. R. Maddison, pers. comm.). In some Bembidiini, the egg-bursters consist of coarse pointed microsculpture; however, they are usually formed by one or two raised microspines (derived from pointed microsculpture) or a longitudinal series of microspines often fused or partly fused into a carina. Larval instars of most species can also be distinguished by the chaetotaxy. The first instar has primary setae, while the second and third instars often bear, in addition, secondary setae which are in general more numerous in the third instar. The width of the cephalic capsule is often also used to distinguish the larval instars.

The keys of van Emden (1942b) and Thompson (1979a) are useful for the identification of the Nearctic and Palaearctic carabid larvae at tribal level. Larval characteristics of Nearctic species are poorly known, as many taxa are undescribed (larvae of only about 7% of the Nearctic species have been described, according to Thompson 1977) and most descriptions are incomplete or superficial. It is hoped, however, that the rearing and preparation techniques improved by Goulet (1976, 1977) will stimulate research in this field. His study of Elaphrini larvae (Goulet 1983) should stand as a guide.

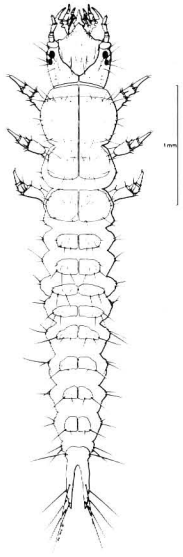


Figure 34.73

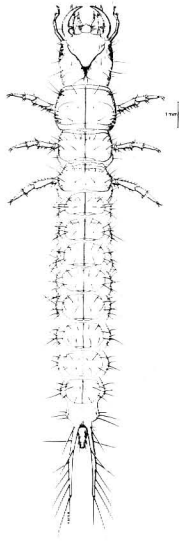


Figure 34.74

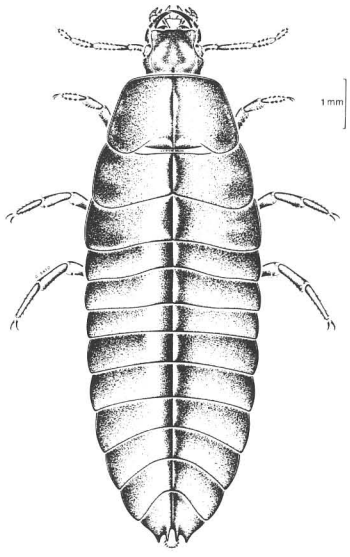


Figure 34.75

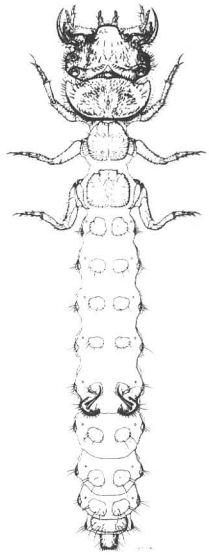


Figure 34.76

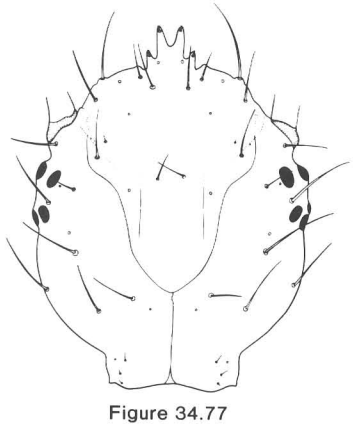


Figure 34.77

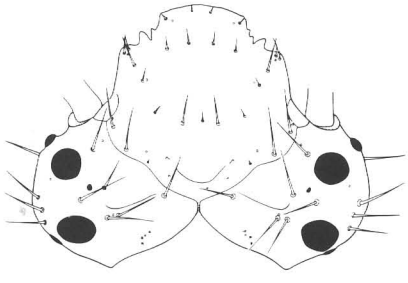


Figure 34.78

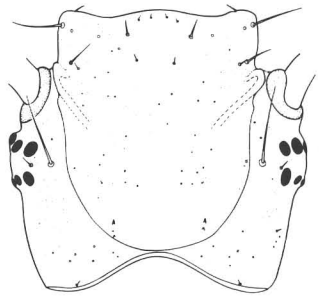


Figure 34.79

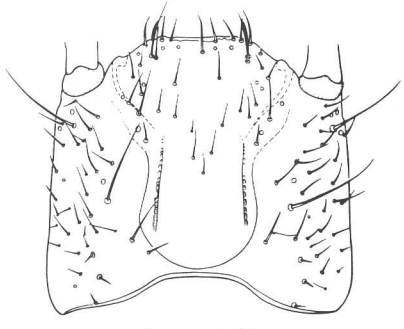


Figure 34.80

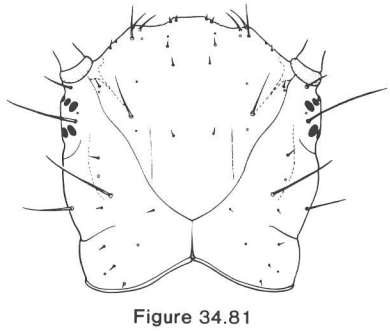


Figure 34.81

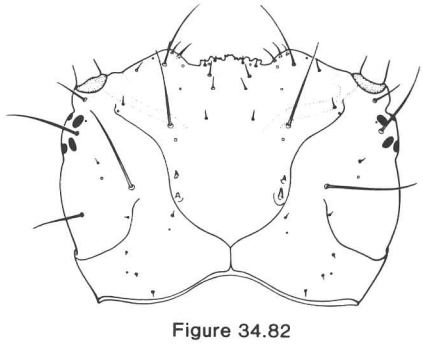


Figure 34.82

Figure 34.73. Carabidae. *Omophron tesselatus* Say, first instar.

Figure 34.74. Carabidae. *Pterostichus diligendus* Chaudoir, third instar.

Figure 34.75. Carabidae. *Sphaeroderus lecontei* Dejean, third instar.

Figure 34.76. Carabidae. *Cicindela* sp., second instar. Cape Breton, Nova Scotia, Canada.

Figures 34.77–34.82. Carabidae. HEAD CAPSULES, dorsal, all first instars.

Figure 34.77. *Nebria* sp.

Figure 34.78. *Cicindela* sp.

Figure 34.79. *Sphaeroderus lecontei* Dejean.

Figure 34.80. *Promecognathus laevissimus* Dejean.

Figure 34.81. *Pterostichus diligendus* Chaudoir.

Figure 34.82. *Anisodactylus nigrita* Dejean.

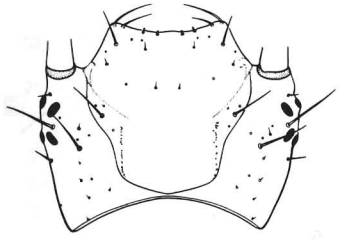


Figure 34.83

Figure 34.84

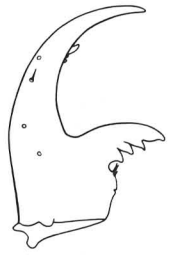


Figure 34.85

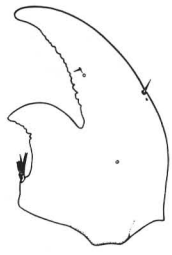


Figure 34.86

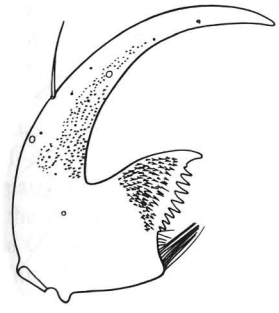


Figure 34.87

Figure 34.88

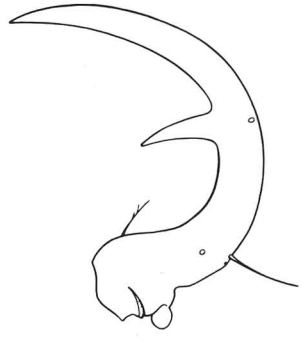


Figure 34.89

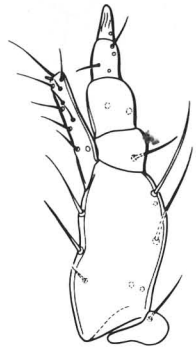


Figure 34.90

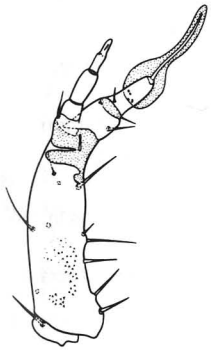


Figure 34.91

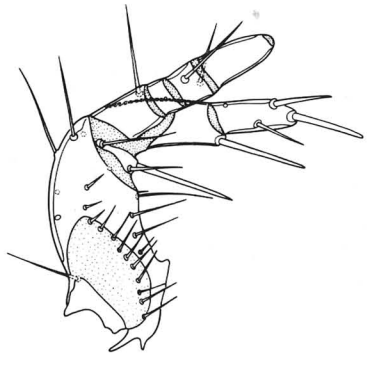


Figure 34.92

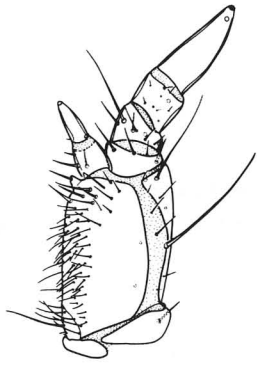


Figure 34.93

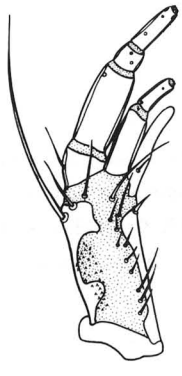


Figure 34.94

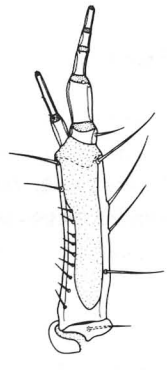


Figure 34.95

Figures 34.83–34.84. Carabidae. HEAD CAPSULES, dorsal, all first instars.

Figure 34.83. *Diplocheila striatopunctata* LeConte.

Figure 34.84. *Calleida punctata* LeConte.

Figures 34.85–34.95. Carabidae. MOUTHPARTS, dorsal, all first instars except where noted.

Figure 34.85. *Loricera pilicornis* Fabricius, left mandible.

Figure 34.86. *Calosoma frigidum* Kirby, right mandible.

Figure 34.87. *Sphaeroderus lecontei* Dejean, left mandible.

Figure 34.88. *Omophron tesselatus* Say, left mandible.

Figure 34.89. *Abax parallelepipedus* Piller and Mitterpacher, right mandible.

Figure 34.90. *Brachinus* sp., right maxilla.

Figure 34.91. *Loricera pilicornis* Fabricius, left maxilla.

Figure 34.92. *Cicindela* sp., left maxilla.

Figure 34.93. *Sphaeroderus lecontei* Dejean, right maxilla.

Figure 34.94. *Omophron tesselatus* Say, left maxilla.

Figure 34.95. *Trechus rubens* Fabricius, right maxilla, 3rd instar.

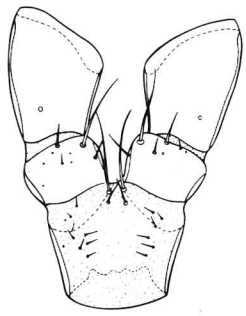


Figure 34.96

Figure 34.97

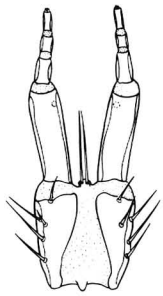


Figure 34.98

Figure 34.99

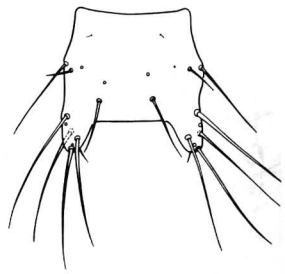


Figure 34.100

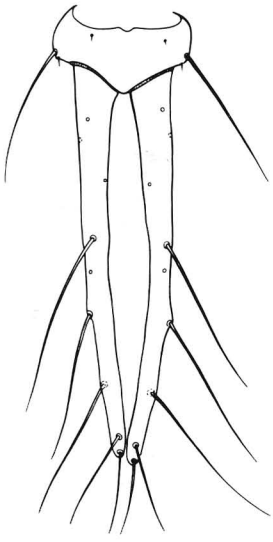


Figure 34.101

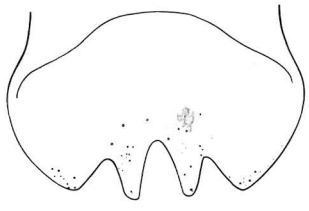


Figure 34.102

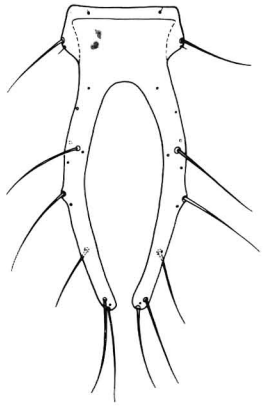


Figure 34.103

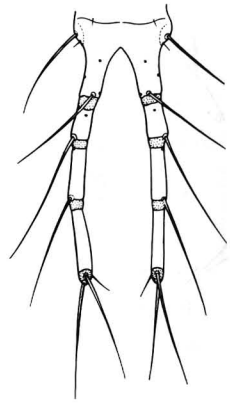


Figure 34.104

Figures 34.96–34.98. Carabidae. MOUTHPARTS, dorsal, all first instars except where noted.

Figure 34.96. *Sphaeroderus lecontei* Dejean, labium.

Figure 34.97. *Omophron tesselatus* Say, labium.

Figure 34.98. *Trechus rubens* Fabricius, labium, 3rd instar.

Figures 34.99–34.104. Carabidae. All first instars.

Figure 34.99. *Sphaeroderus lecontei* Dejean, median leg (anterolateral).

Figure 34.100. *Brachinus* sp., ninth tergite and urogomphi (dorsal).

Figure 34.101. *Nebria* sp., ninth tergite and urogomphi (dorsal).

Figure 34.102. *Sphaeroderus lecontei* Dejean, ninth tergite and urogomphi (dorsal).

Figure 34.103. *Pterostichus adstrictus* Eschscholtz, ninth tergite and urogomphi (dorsal).

Figure 34.104. *Cymindis* sp., ninth tergite and urogomphi (dorsal).

Selected Bibliography (for Carabidae).

Bily 1975b
Bousquet 1985, 1986, 1987.
Bousquet and Goulet 1984.
Bousquet and Pilon 1980.
Böving and Craighead 1931.
Brandmayr and Brandmayr Zetto 1974, 1982.
Brandmayr Zetto and Brandmayr 1975.
Dajoz 1961.
Emden 1935b, 1936, 1942b.
Erwin 1967, 1975, 1981.
Erwin et al. 1979.
Gardner 1929, 1930b, 1931b, 1933a, 1936b, 1938a.
Goulet 1976, 1977, 1983.
Habu and Sadanaga 1961, 1963, 1965, 1969, 1970.
Hamilton 1925.
Hengeveld 1980.
Houston and Luff 1975.
Hurka and Ducháč 1980a, 1980b.
Hurka and Smrz 1981.
Kirk 1974.
Landry and Bousquet 1984.
Lawrence 1982c.
Lindroth 1960.
Löser 1970.
Luff 1969, 1972, 1976, 1978, 1980, 1985.
Moore 1964, 1965, 1966, 1974.
Paarmann 1979.
Pearson 1988.
Peyrieras 1976.
Schjøtz-Christensen 1965.
Schremmer 1960.
Sharova 1976.
Sharova and Makarov 1984.
Silvestri 1905.
Smrz 1979.
Thiele 1977.
Thompson 1977, 1979a, 1979b.
Vanek 1984.

HALIPLIDAE (ADEPHAGA)

Paul J. Spangler, *Smithsonian Institution*

Crawling Water Beetles

Figures 34.105, 106

Relationships and Diagnosis: The family Haliplidae belongs to the suborder Adephaga; however, unlike all other known adephagan larvae, haliplid larvae have only 1 instead of 2 claws.

Haliplid larvae may be distinguished immediately from other adephagous aquatic beetle larvae by the 9 or 10 abdominal segments and the 6-segmented leg including a single claw. Larvae are of 2 types. Larvae of *Apteraliplus, Brychius,* and *Haliplus* (fig. 34.106) are elongate and taper from head to apex of the last abdominal segment that ends in a subspiniform process that may be bifurcate; they have rough and rigid cuticle, therefore, the body is stiff and can bend very little; gills are absent. Larvae of *Peltodytes* (fig. 34.105) have slender, rather stiff, hairlike gills (prothorax with 3 pairs, meso- and metathorax each with 2 pairs, abdominal segments 1–8 each with 2 pairs, and segments 9 and 10 each with 1 pair); these gills are about as long as or slightly longer than the length of the body which is moderately stiff but can assume a C-shape. Mature larvae range in length from 5.0 to 12.0 mm.

Biology and Ecology: Known haliplid larvae feed on algae. Adults and larvae of various species of *Haliplus* are commonly found on *Chara, Nitella,* and *Ceratophyllum;* species of *Peltodytes* occur more often on *Spirogyra.* Adults and larvae of *Apteraliplus, Haliplus,* and *Peltodytes* normally occur in weedy ditches, ponds, lakes and similar lentic habitats. Species of *Brychius* favor lotic habitats although some have been collected in lakes. Most haliplids occur in shallow water but Hickman (1931) found some species of *Haliplus* 6 feet below the surface. When haliplid larvae are collected they at first feign death and, when they move, they crawl very slowly; therefore, they may be easily overlooked among the vegetation and associated debris in an aquatic net.

The life cycles of some species of *Haliplus* and *Peltodytes* are reasonably well known as a result of Hickman's studies (1930, 1931); however, those of *Apteraliplus* and *Brychius* have not been described. In the United States and Canada, egg laying by *Haliplus* and *Peltodytes* begins in spring and continues through the summer. Adults of *Peltodytes* attach their eggs to the host plants, and females of *Haliplus* insert their eggs inside plant cells. Larvae of both genera molt 3 times before the last instar leaves the water, digs into suitably moist soil, and forms a pupal cell. Adults normally pass the winter underwater. Larvae that attain maturity late in the summer occasionally overwinter in moist soil above the waterline.

Description: Body elongate, cylindrical or subcylindrical, and tapering or not posteriorly. Gills elongate and hairlike (*Peltodytes*) or gills absent (*Apteraliplus, Brychius, Haliplus*). The cuticle of *Apteraliplus, Brychius,* and *Haliplus* is rough because of numerous tuberculate and spinous processes. Integument and sclerites whitish in freshly hatched and freshly molted larvae; sclerotized areas becoming light yellowish brown to reddish brown with aging.

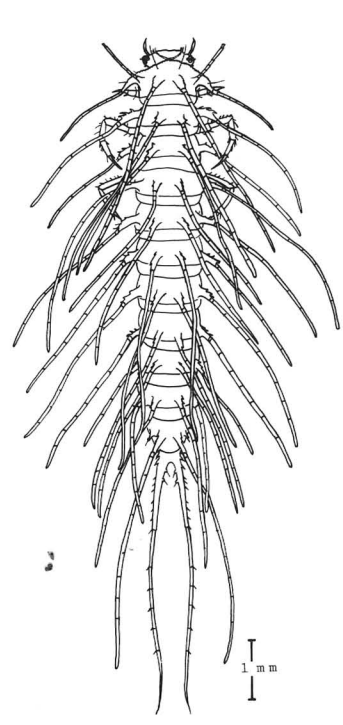


Figure 34.105

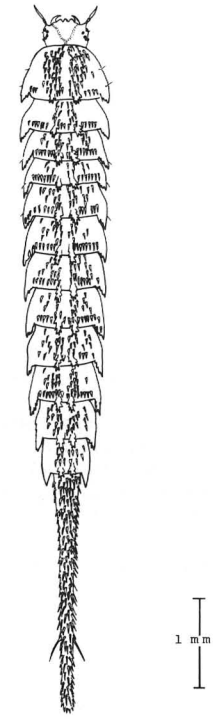


Figure 34.106

Figure 34.105. Haliplidae. *Peltodytes* sp., dorsal.

Figure 34.106. Haliplidae. *Haliplus* sp., dorsal.

Head: Semiprognathous to hypognathus. Antenna, 4-segmented. Stemmata, 6 pairs. Ecdysial cleavage line and labrum absent. Mandible as wide as long, hook-shaped, hollow; with sharp apical tooth. Maxilla short and broad; cardo small; stipes large and broad; mala with setae; palp, 3-segmented. Labium small; labial palp small, 2-segmented.

Thorax and Abdomen: Prothoracic, meso- and metathoracic terga well sclerotized. Prothorax with 3 pairs of gills; meso- and metathorax each with 2 pairs of gills. Legs, 6 segmented, including single claw; because the fourth segment is produced they are weakly to moderately chelate and serve to grasp algae.

Abdomen of 10 segments. In *Peltodytes,* segments 1–8 each bear 2 pairs of threadlike gills; segments 9 and 10 each bear 1 pair of gills; segment 10 ends bluntly. *Apteraliplus, Brychius,* and *Haliplus* lack gills and segment 10 tapers to a subspiniform process that may be bifurcate or not. Microtracheal "gills" have been reported in *Haliplus* (Seeger, 1971).

Spiracles: Absent, except in last instar, which has annular spiracles on mesothorax and abdominal segments 1–7.

Comments: Haliplids are found throughout the world with most species occurring in the temperate regions. The number of taxa is small with about 200 species in 5 genera

in the world. At present 4 of the 5 genera and 67 of the approximately 200 species described are known from the United States and Canada. Haliplids and their larvae are not known to be economically important but they assist in recycling nutrients and are a food item in the aquatic ecosystem.

Keys to larval stages of the four North American genera have been provided by Chandler (1956), Leech and Sanderson (1959), Pennak (1978), Brigham (1982b), and White, Brigham and Doyen (1984).

Selected Bibliography

Bertrand 1972.
Böving and Craighead 1931.
Brigham 1982b.
Chandler *in* Leech and Chandler 1956 (key to larvae of *Haliplus* and *Peltodytes*).
Hickman 1930, 1931.
Leech and Sanderson 1959.
Matheson 1912.
Pennak 1978.
Seeger 1971.
White et al. 1984.
Wilson 1923.

HYGROBIIDAE (ADEPHAGA)

(= PELOBIIDAE)

John F. Lawrence,
Division of Entomology, CSIRO

This family includes the genus *Hygrobia,* with 5 species occurring in western China, western and central Europe, North Africa, and Australia (southeastern part, Northern Territory, and Cape York). The group is generally considered to belong to the complex of aquatic families including Amphizoidae, Noteridae, and Dytiscidae.

Larvae are about 10 mm in length and fusiform, with a large, prognathous head and enlarged thorax. The head has a long epicranial stem, 4-segmented antennae, a labrum fused to the head capsule, and 6 stemmata on each side. Mandibles are falcate, but not perforate, and the protracted ventral mouthparts include maxillae without apical lobes, 4-segmented maxillary palps and 2-segmented labial palps. Gular sutures are completely separated. The legs are relatively long and slender, 6-segmented, including paired, movable claws, and have fringes of swimming hairs on the tibiae and tarsi. Segments A8 and A9 are reduced; segment A8 bears a long, narrow, median process, without spiracles at the apex, and segment A9 bears a pair of long, narrow urogomphi. Segment A10 is reduced and membranous. Paired gill tufts arise from the coxal bases and from abdominal sternites 1–3. Reduced spiracles are present on the mesothorax and abdominal segments 1–7 in the last instar only.

Hygrobiids are bottom-feeding predators in ponds, and adults may be attracted to lights. They occur only in ponds in which the bottom is covered with fine ooze, in which they feed on insect larvae and *Tubifex* worms. The adult maintains an air bubble beneath the elytra and may remain submerged for up to 30 minutes. Fully grown larvae leave the water to pupate within a closed cell in sand or mud.

Selected Bibliography

Balfour-Browne 1922 (biology).
Bertrand 1928 (larva), 1972 (larva).
Böving and Craighead 1931 (larva).
Britton 1981 (Australian *Hygrobia*).
Hammond 1979 (relationships).

AMPHIZOIDAE (ADEPHAGA)

David H. Kavanaugh,
California Academy of Sciences

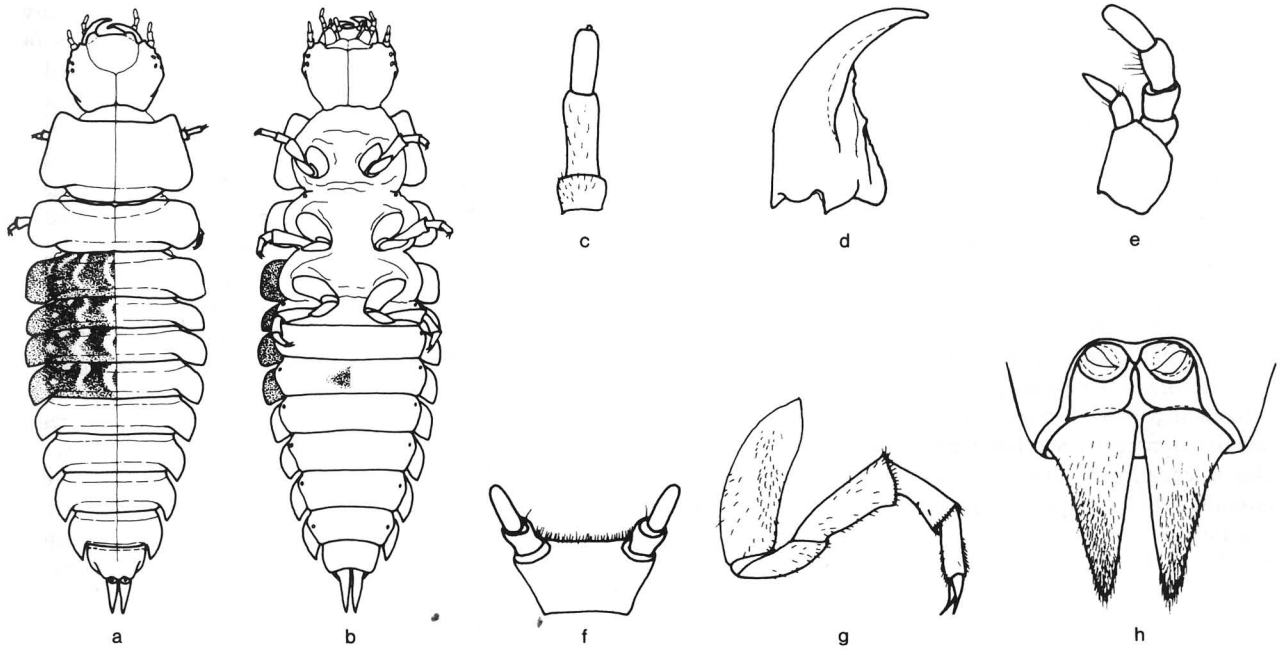
Trout-Stream Beetles

Figures 34.107a-h

Relationships and Diagnosis: Members of the genus *Amphizoa* LeConte represent a family distinct from but clearly related to the other Caraboidea. They share many characteristics with Carabidae on one hand and Dytiscidae on the other (Edwards, 1951; Horn, 1883; Hubbard, 1892a, 1892b; Leech and Chandler, 1956; Roughley, 1981). Based on a cladistic analysis of both extinct and extant "families" of Adephaga, Kavanaugh (1986) concluded that amphizoids represent the earliest divergent lineage from the common ancestor of all Hydradephaga, excluding Haliplidae, and that this divergence probably occurred in the Triassic.

Larval amphizoids are most similar in size and form to carabid larvae of the tribe Cychrini or to silphid larvae (e.g. genus *Silpha* or *Nicrophorus*); however, their aquatic habits readily distinguish them from members of these other groups. Further, amphizoid larvae are distinguished from larvae of all other North American beetles in having their mandibles sulcate medially, without an internal duct, thoracic legs ambulatory, each 6-segmented, including pretarsus with two movable, terminal claws, the abdomen 8-segmented, without hooks at apex, urogomphi present, short, 1-segmented, and with the spiracles of the eighth abdominal segment located paramedially on the dorsum (basal to urogomphi).

Biology and Ecology: Amphizoids are primarily aquatic, although both adults and larvae are sometimes found out of water; eggs deposited in moist places on land will develop and hatch, and mature larvae leave the water to pupate on land. They inhabit cool or cold fresh water streams (from small rills to large rivers) and (less frequently) lakes, where they are confined to the shallow shorelines. Neither adults nor larvae swim. They crawl over submerged rocks, logs, and vegetation in search of food and shelter, and are often found clinging to floating debris, especially in eddies and backwashes. If dislodged from their substrate, they make feeble walking movements and drift with the current. They are much more agile out of water. Adults have fully formed wings and are no doubt capable of dispersal by flight (Darlington, 1930). Both adults and larvae must come to the surface for air. Larvae assume a posture such that the apex of the abdomen breaks the water surface and the spiracles of the eighth segment are in contact with air.



Figures 34.107a-h. Amphizoidae. *Amphizoa insolens* LeConte. **a.** dorsal (pigmentation pattern for left half of metathoracic and abdominal terga 1-3); **b.** ventral (pigmentation pattern for right half of metathorax and abdominal segments 1-3); **c.** left antenna, dorsal; **d.** left mandible, dorsal; **e.** left maxilla, ventral; **f.** labium, ventral; **g.** left metathoracic leg, anterior; **h.** apex of abdomen, posterodorsal oblique aspect, showing spiracles of abdominal segment 8 and urogomphi.

Although previously assumed to feed as scavengers on sluggish or dead and drifting insects. Edwards (1954) found that all stages of larvae and adults studied fed exclusively on living stonefly (Plecoptera) larvae. However, if kept out of water, amphizoids will accept a variety of freshly macerated insects presented as food.

Eggs, which are very large (over 2 mm in length), may be deposited in protected spots under water, such as in cracks on the undersurfaces of floating logs (Edwards, 1954; Leech and Chandler, 1956), or in moist places on land adjacent to water bodies. Oviposition is usually in late August or early September. First instar larvae, also exceptionally large, are found in September through November and again in early spring. This is probably the normal overwintering stage. Mature larvae appear in May through August and leave the water to pupate under stones on adjacent shores in July and August. Adults may be found throughout the year, but teneral (newly-emerged) adults are common only in August.

Description: Mature (i.e. third instar) larvae with total length 12.0 to 17.0 mm, maximum width 3.5 to 4.7 mm. Body form (figs. 34.107a, b), elongate, spindle-shaped, depressed, broadest at mid-length and tapered toward both ends, moderately convex and markedly sclerotized dorsally, flat and only faintly sclerotized ventrally; combined lengths of head and thorax almost equal to length of abdomen; thoracic and abdominal terga broadly explanate laterally as thin, laterally projected lobes; dorsal midline, from vertex of head to apex of abdomen, with a deeply incised longitudinal furrow (actually the ecdysial line of weakness). Dorsum brown (teneral individuals may be testaceous) to piceous, with maculation pattern as in fig. 34.107a but less evident in darkest individuals; venter pale, yellowish white, except undersurface of head and eighth abdominal sternum brown; darkest individuals also with darkened areas along midline on 1 or more abdominal sterna. Surface of dorsal sclerites finely punctulate and/or transversely rugulose, sparsely covered with short, fine, apically hooked, prostrate setae; ventral sclerites smooth and glabrous, except ventrolateral surfaces of head with fine punctures and setae as on dorsum.

Head: Large, protruded, circular in silhouette, narrowed posteriorly, flattened dorsally, moderately convex ventrally, with lateral margins (of genae) carinate. Antennae (fig. 34.107c) short, apparently 3-segmented, but with reduced 4th segment at apex. Three pairs of lateral stemmata present on each side, 1 pair each above, on, and below the lateral margin. Labrum trapezoidal, vertical, glabrous dorsally (anteriorly), except for a fringe of short setae at clypeolabral suture. Mandibles (fig. 34.107d) sickle-shaped, each with a deep, longitudinal groove medially (but without an internal duct), retinaculum minutely dentiform, ventral cutting edge minutely denticulate, without prostheca or penicillus, molar region simple, narrow, unmodified, without denticles. Maxillae (fig. 34.107e) stout, with cardo and stipes fused, lacinia and galea fused as a 2-segmented mala, palpifer present, palp 3-segmented. Labium (fig. 34.107f) broad, transverse, with a fringe of short setae across apical margin, without distinct ligula, palps 2-segmented. Gula absent, gular suture simple, linear in midline.

Thorax and Abdomen: Broad, with prothorax relatively long and narrow; lateral lobes of prothoracic tergum short, subrectangular, narrowed anteriorly, those of pterothoracic terga longer, more broadly rounded in outline. Legs (fig. 34.107g) moderate in length, 6-segmented, the pretarsus bearing 2 movable claws.

Abdomen eight-segmented, explanate lateral lobes of terga 1–7 thin, successively more acutely pointed, slightly overlapped; eighth segment trapezoidal in outline, tergum with lateral explanations present only as lateral carinae. Urogomphi (fig. 34.107h) present, 1-segmented, short but prominent, conical and apically pointed, articulated (not fused) with eighth tergum posterolaterally.

Spiracles: Thoracic spiracles restricted to a single mesothoracic pair located anterolateral to bases of mesocoxae, annular, apparently non-functional. Paired abdominal spiracles of segments 1–7 (fig. 34.107b) located ventrally, anterolaterally near base of each explanate lateral lobe, apparently non-functional; spiracular pair of eighth segment (fig. 34.107h) valvular, functional, located dorsomedially between bases of urogomphi and posteromedial margin of eighth tergum on short, sclerotized turrets.

Comments: The family is very small, with only three species known from North America (Kavanaugh, 1986) and one species from western China. In North America, the family is restricted to the western half of the continent, from the Rocky Mountains west to the Pacific Coast, and from southern Alaska and Yukon Territory to southern California and northern Arizona and New Mexico. The larvae of *Amphizoa insolens* LeConte and *A. lecontei* Matthews have been described and illustrated (Böving and Craighead, 1931; Hubbard, 1892a, 1892b; Peterson, 1951) and their habits discussed (Darlington, 1930; Edwards, 1951, 1953, 1954; Leech and Chandler, 1956). Neither immatures nor adults of this family have apparent economic importance.

Selected Bibliography

Böving and Craighead 1931.
Darlington 1930.
Edwards 1951, 1953, 1954.
Horn 1883.
Hubbard 1892a, 1892b.
Kavanaugh 1986.
Leech and Chandler 1956.
Peterson 1951.
Roughley 1981.

NOTERIDAE (ADEPHAGA)

Paul J. Spangler, *Smithsonian Institution*

The Noterids

Figures 34.108a–e, 34.109

Relationships and Diagnosis: The noterids were formerly considered a subfamily of the Dytiscidae. However, morphological and biological differences readily distinguish them from the dytiscids.

Noterid larvae may be distinguished from dytiscid larvae by the following combination of characters: compact fusiform body shape; short legs; very short urogomphi; mandibles with retinaculum, but not sulcate nor tubular as they are in dytiscid larvae. Also, all noterid pupae presently known were found pupating underwater in watertight cocoons made by the larvae; these cocoons were attached to aerenchymatous cells of aquatic plant stems, leaves, or roots. Mature noterid larvae range in length from 2.0 to 4.5 mm.

Biology and Ecology: Adults and larvae of *Hydrocanthus, Suphis,* and *Suphisellus* are commonly found among roots of floating aquatic plants, especially *Eichhornia* and *Pistia;* they also occur, but in lesser numbers, among emergent plants where floating plants are absent. The habitat of the larvae of *Pronoterus* is not definitely known but presumably they occur in floating mats of aquatic plants where their adults have been found. Larvae of *Notomicrus* also are unknown but the adults have been collected from freshwater in weedy margins of shallow ponds, in *Sphagnum* swamps, in woodlands where there were small temporary puddles containing culicid larvae, in water-filled tire ruts, and brackish water in crabholes excavated by land crabs; presumably, their tiny larvae will be found in the same habitats where the adults live.

The life cycles of most noterids are unknown. However, F. Balfour-Browne and J. Balfour-Browne (1940) described the interesting larval and pupal stage of the European species *Noterus capricornis* Herbst and showed that pupation took place underwater in cocoons attached to aerenchymatous cells of roots of aquatic plants. Spangler (1981, 1982) reported the same pupal habits for the genera *Hydrocanthus, Suphis,* and *Suphisellus.*

Because noterid larvae are present in the United States in the months of June through August, it is presumed that noterids oviposit in late spring or early summer. Because the ovipositor is long and soft, it is assumed that the eggs are laid on aquatic plants or in the mud near the plants. The complete life cycle has not been established for any noterid but the available evidence suggests that it is similar to that of dytiscid beetles except noterid pupation occurs underwater instead of on land.

The food habits of the noterids are poorly known. Wesenberg-Lund (1912) assumed from the shape of the mandibles of a European larva of *Noterus* that it was entirely vegetarian. However, F. Balfour-Browne and J. Balfour-Browne (1940) observed that larvae of *Noterus* feed readily on dead *Chironomus* larvae and dead individuals of their own kind; they also saw the larvae work their mandibles on the surface of roots but seemed not to get anything off. They suggested that the larval mandibles may be a modification of the phytophagous type of mandible and stated, "possibly, therefore, the larva flourishes on a mixed diet." Young (1967) reported that noterid larvae and adults are vegetation-detritus feeders.

Description: Body cylindrical, spindle shaped, or teardrop shaped (*Suphis*); usually tapering strongly posteriorly; subcylindrical in cross section. Cuticle relatively smooth. Integument and sclerotized parts white when freshly hatched but yellow to reddish-brown upon aging. Larvae of some species of *Hydrocanthus* may have dark bands in early instars.

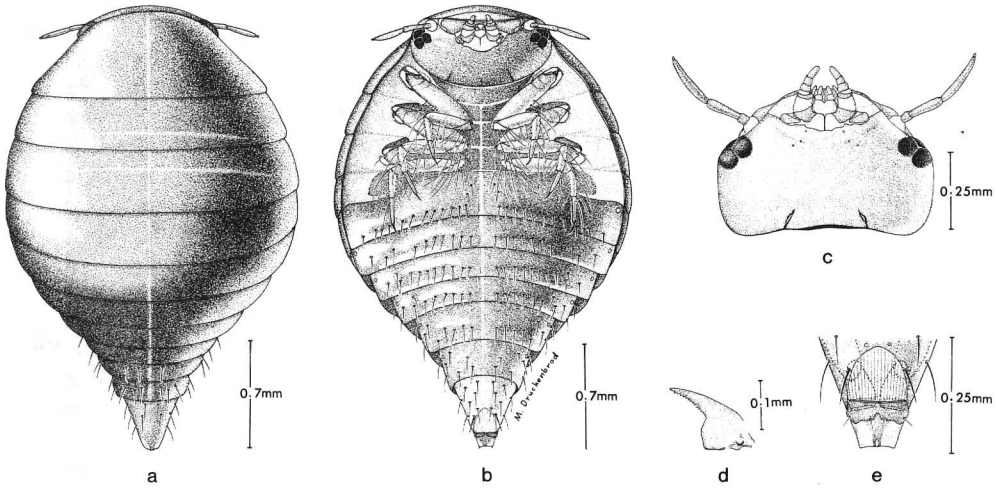


Figure 34.108

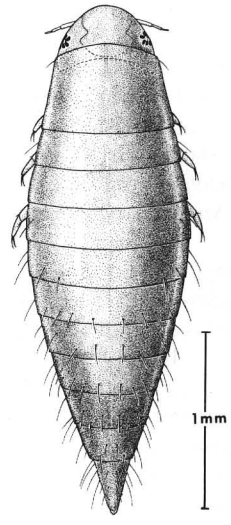


Figure 34.109

Figures 34.108a-e. Noteridae. *Suphis inflatus* (LeConte). **a.** dorsal; **b.** ventral; **c** head, ventral; **d.** mandible; **e.** last abdominal segment, ventral.

Figure 34.109. Noteridae. *Hydrocanthus* sp., dorsal.

Head: Partially retracted into pronotum, prognathous, globose (fig. 34.108c); without temporal spines; anterior margin arcuate; ecdysial cleavage lines present. Antenna 4-segmented, elongate, slender. Clypeus and labrum fused. Mandible curved, moderately slender; inner margin smooth, serrate, or dentate; neither sulcate nor tubular (fig. 34.108d). Maxillary palp short, 3-segmented; cardo small, stipes long and broad. Labial palp short, stout, 2-segmented. Six pairs of stemmata.

Thorax and Abdomen: Prothoracic, meso-, and metathoracic terga well sclerotized. Prothorax about as long as meso- and metathorax combined. Legs short, 6-segmented, including 2 slender claws. Abdomen of 8 visible segments, urogomphi extremely short (fig. 34.108e).

Spiracles: Annular, present on abdominal segments 1–8, the eighth pair lying together at end of eighth segment and beneath small extension of that tergum. Functional spiracles present on segment 8 only in first and second instars.

Comments: Noterids are cosmopolitan but occur primarily in tropical regions. A few taxa occur widely in temperate regions of the Eastern and Western Hemispheres. The family is small in number of taxa, with 12 described genera and 230 species in the world fauna. Five genera and 13 species have been reported from the United States. Adults and larvae are not known to have any economic importance but Young (1967) pointed out that they are important in recycling nutrients. They also serve as a food item in the diet of various predators in the aquatic ecosystem.

Leech (1956) discussed the biology and immature stages, and Chandler (1956) provided a key to larvae of 2 of the 5 genera known from North America. Spangler and Folkerts (1973b) described the larva of *Suphis inflatus* (LeConte) and included a key to larvae of 3 of the 5 genera found in North America. Bertrand (1972) reviewed and summarized the literature available on noterid biology and immature stages and included a key to larvae of 6 of the 12 genera in the world fauna.

Selected Bibliography

Balfour-Browne and Balfour-Browne 1940.
Bertrand 1972.
Brigham 1982e (biology; key to larvae of *Hydrocanthus, Suphis,* and *Suphisellus*).
Chandler *in* Leech and Chandler 1956.
Crowson 1955.
Leech *in* Leech and Chandler 1956.
Peterson 1951 (description and figure of *Hydrocanthus* larva).
Spangler 1981, 1982, 1986.
Spangler and Folkerts 1973b.
Wesenberg-Lund 1912.
White et al. 1984.
Young 1954, 1967.

DYTISCIDAE (ADEPHAGA)

Paul J. Spangler, *Smithsonian Institution*

Predacious Diving Beetles

Figures 34.110–126

Relationships and Diagnosis: Dytiscid larvae may be distinguished by the following combination of characters. Head prominent, prognathous, exserted; form may be subquadrate, rounded, pyriform, flattened, or subcylindrical; anterior margin moderately to strongly produced; ecdysial cleavage lines present. Antenna, 4-segmented (sometimes with as many as 5 additional small accessory segments), elongate,

slender. Clypeus and labrum fused. Mandible curved, usually long, slender, and grooved or hollow for sucking. Maxillary palp slender, elongate, 4- to 10-segmented. Labial palp, 2- to 4-segmented. Stemmata, 6 pairs; absent in subterranean forms. Legs 6-segmented, including pretarsus with 2 claws. Abdomen of 8 visible segments; eighth segment may be very elongate; ninth segment reduced; lateral gills rarely present. Mature larvae range in length from 1.5 to 70.0 mm.

Dytiscid larvae may be immediately distinguished from hydrophilid larvae by their 6-segmented legs, including 2 claws on each leg, and lack of a breathing atrium on the apex of the eighth abdominal segment.

Biology and Ecology: Dytiscid beetles are cosmopolitan, and adults and larvae are normally found in the same aquatic situations. They are found in diverse habitats ranging from microhabitats such as potholes in rock outcroppings, water-filled holes of land crabs, hygropetric niches, springs, and artesian wells to sheltered coves along the margins of large lakes. However, the majority of dytiscid taxa are found in the smaller, shallow, weedy habitats such as the margins of ponds, drainage ditches, gravel pits and stock ponds. In more arid regions, dytiscids may be found in virtually any aquatic habitat available such as pools in intermittent streams, stock tanks, irrigation ditches and overflow areas, and saline and mineral springs or pools. Oftentimes in one of these habitats, large numbers of adults and larvae of a single species will be found and the larvae may be recognized easily by association although it is preferable to rear the larva to the adult to confirm the relationship.

The type of ovipositor generally indicates where the female will lay her eggs. Dytiscid ovipositors are of three major types: (1) Those in which the genital valves are short, blunt, weak, dorsoventrally flattened, obviously not adapted for piercing plant tissues, but setose and apparently tactile—dytiscids with this type of ovipositor, such as *Desmopachria,* generally glue their eggs to surfaces of aquatic plants, drop their eggs at random, or insert them in a muddy substrate (done by many of the Hydroporinae); (2) Those in which the ovipositor is similar to the type described above but is very elongate—undoubtedly the elongate ovipositors allow females to insert their eggs wherever a small, deep, crevice or space narrow enough to conceal the eggs from predators or parasites can be found, such as between or under leaves, sticks, bark, stones, etc.; (3) Those with the genital valves well sclerotized and usually serrate or with toothlike margins—dytiscids with this type of ovipositor, such as *Laccophilus* and *Ilybius,* use it to make incisions in plant tissues in each of which they deposit an egg. Others with piercing valves, such as *Graphoderus* and *Hydaticus,* reportedly place a number of eggs in each hole (Wesenberg-Lund, 1912).

Dytiscids have 3 larval instars. As far as is known, all dytiscid larvae, unlike the Noteridae, leave their aquatic habitat and pupate on land in earthern cells in friable soil where the larvae can burrow beneath the surface a short distance. The pupal chamber is shaped by wriggling movements of the larva which compress the soil so the wall of the chamber will not collapse easily. Some larvae pupate among matted roots of mosses or other plants or under rocks, boards, leaves, logs, etc. Freshly eclosed dytiscid beetles usually remain in their pupal chambers for 3 to 7 days (sometimes much longer) before they leave and enter the aquatic habitat.

Description: Body variously shaped—usually elongate, fusiform, cylindrical, subcylindrical, moderately flattened, usually widest at metathorax or middle of abdomen. Integument white, yellow, greenish, or brown; sclerotized areas becoming yellowish, brown, or reddish brown with aging; may be spotted, striped, or unicolored.

Head: Prognathous; usually exserted; subquadrate, rounded, pyriform, flattened, or subcylindrical; ecdysial cleavage lines usually present and obvious. Clypeus and labrum fused; anterior margin moderately arcuate or moderately to strongly dentiform or prolonged as a nasale. Stemmata 6 pairs or absent (in stygobiontic taxa). Antenna of 4 principal segments, slender, elongate, sometimes with accessory segments. Maxilla slender; cardo small; stipes short and broad or narrow and elongate; palp slender, elongate, 3 or 4 principal segments, sometimes with accessory segments. Labial palp usually 2-segmented; sometimes 3- or 4-segmented. Mandible distinct, curved, usually slender and usually grooved or hollow for sucking blood of hosts.

Thorax and Abdomen: Prothorax usually longer than meso- and metathorax combined. Thoracic terga usually well developed. Legs usually long and slender; some genera with fringes of swimming hairs on femur, tibia, and tarsus; legs 6-segmented including pretarsus consisting of 2 claws.

Abdomen of 8 visible segments; eighth segment may be very elongate; ninth segment reduced; lateral gills rarely present; 8 or 9 pairs of spiracles. Urogomphi usually long and slender but sometimes short and stubby.

Spiracles: Annular, on abdominal segments 1–8 and usually mesothorax in last instar. Early instars with functional spiracles present only on segment 8.

Comments: This family is cosmopolitan, but a greater number of genera and species occur in the tropical regions. There are about 145 genera and 3,000 species of dytiscids known in the world fauna, with 42 genera and about 446 species of Dytiscidae described from America north of Mexico. Larvae of representatives of 28 of these genera have been described.

Most dytiscid larvae are not known to be economically important, but when larvae of the larger dytiscids, such as *Cybister,* become numerous in fish hatcheries, they are destructive to fingerlings (Wilson, 1923). However, most dytiscid larvae probably are beneficial because they feed on larvae of mosquitoes, ceratopogonids, and other noxious insects, as well as other aquatic organisms. Dytiscid larvae are also preyed upon by other insects, birds, and various mammals, and, in this manner, they play an important part in the aquatic food web.

Because of the large number of species, their cosmopolitan distribution, attractive size, color, form, and the accessibility to living specimens, the bionomics of the adult and immature stages of the Dytiscidae are reasonably well known. The most comprehensive studies of dytiscid larvae are those by Bertrand (1928, 1972, 1977). The publications on larval Coleoptera by Böving and Craighead (1931) and Peterson (1951), on dytiscid biologies by Wesenberg-Lund (1912),

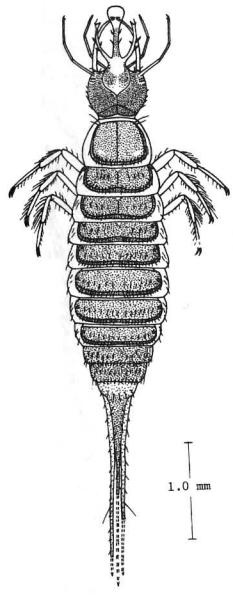


Figure 34.110

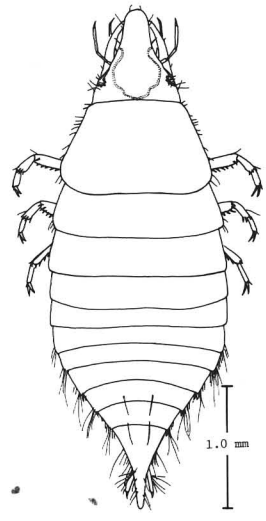


Figure 34.111

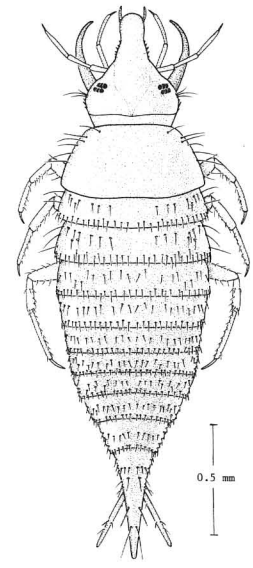


Figure 34.112

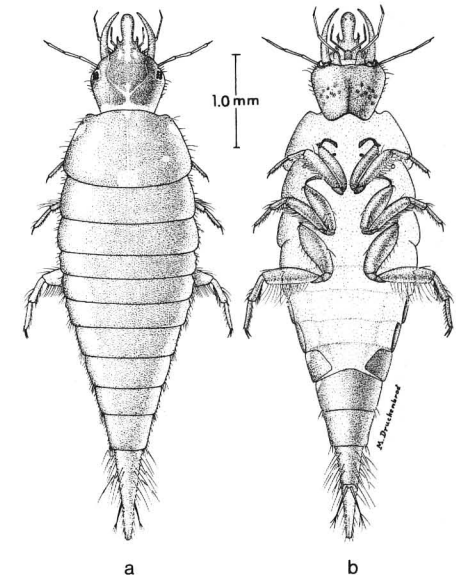


Figure 34.113

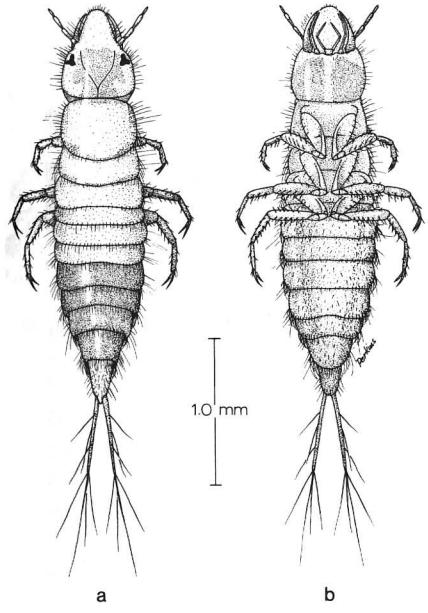


Figure 34.114

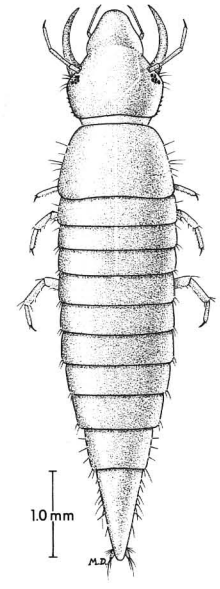


Figure 34.115

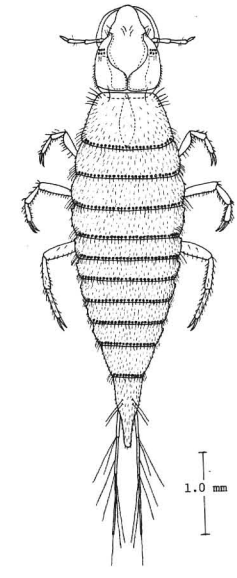


Figure 34.116

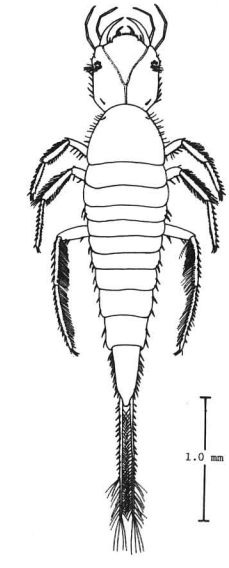


Figure 34.117

Figure 34.110. Dytiscidae. *Derovatellus ibarrai* Spangler.

Figure 34.111. Dytiscidae. *Hydrovatus* sp.

Figure 34.112. Dytiscidae. *Desmopachria* sp.

Figures 34.113a,b. Dytiscidae. *Pachydrus princeps* (Blatchley). **a.** dorsal; **b.** ventral.

Figures 34.114a,b. Dytiscidae. *Neoclypeodytes cinctellus* (LeConte). **a.** dorsal; **b.** ventral. [Figures 34.114 a, b. after Perkins, 1981.]

Figure 34.115. Dytiscidae. *Laccornis difformis* (LeConte).

Figure 34.116. Dytiscidae. *Hygrotus sayi* (J. Balfour-Browne).

Figure 34.117. Dytiscidae. *Laccophilus* sp.

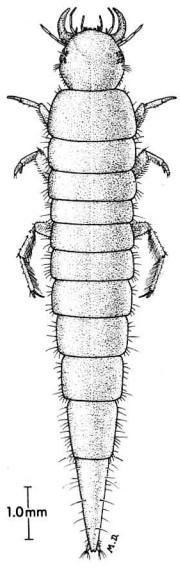


Figure 34.118

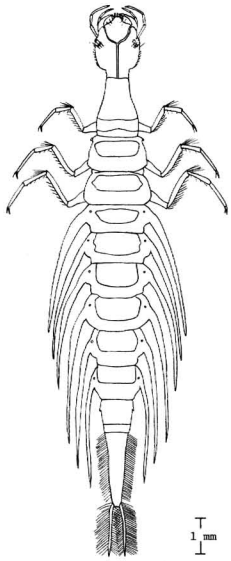


Figure 34.119

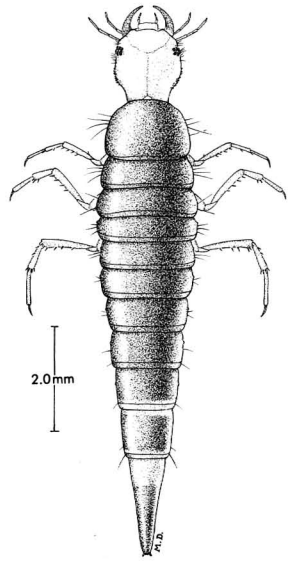


Figure 34.120

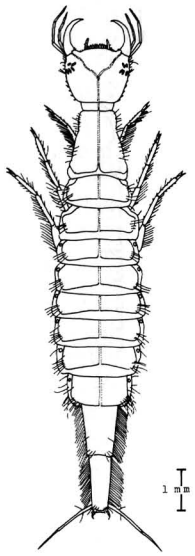


Figure 34.121

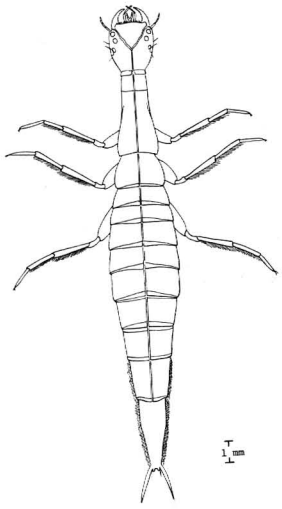


Figure 34.122

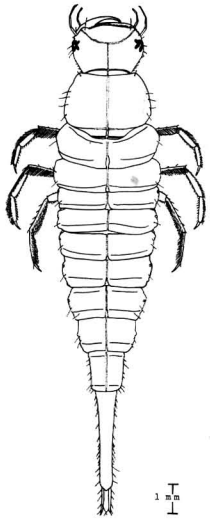


Figure 34.123

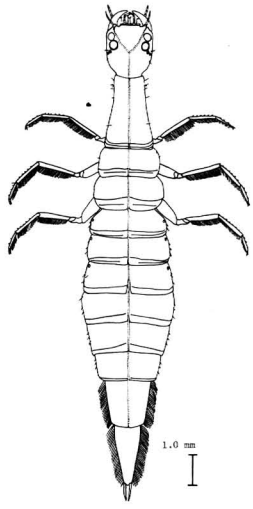


Figure 34.124

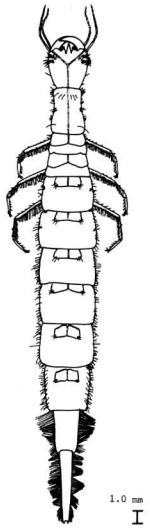


Figure 34.125

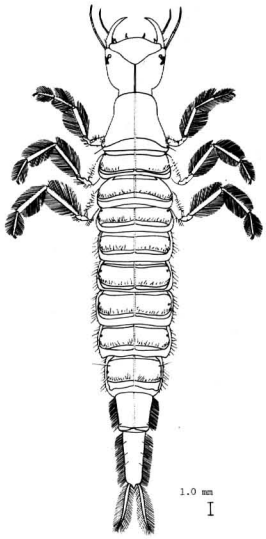


Figure 34.126

Figure 34.118. Dytiscidae. *Matus bicarinatus* (Say).
Figure 34.119. Dytiscidae. *Coptotomus* sp.
Figure 34.120. Dytiscidae. *Agabetes acuductus* (Harris).
Figure 34.121. Dytiscidae. *Hydaticus bimarginatus* (Say).
Figure 34.122. Dytiscidae. *Acilius* sp.
Figure 34.123. Dytiscidae. *Rhantus calidus* (Fabricius).
Figure 34.124. Dytiscidae. *Thermonectus basillaris* (Harris).
Figure 34.125. Dytiscidae. *Cybister fimbriolatus* (Say).
Figure 34.126. Dytiscidae. *Dytiscus fasciventris* (Say).

Balduf (1935), and Leech (1956), and the keys to genera by Chandler (1956), Leech and Sanderson (1959), Pennak (1978), Brigham (1982a), and White, Brigham, and Doyen (1984) will be helpful in identifying larvae.

Selected Bibliography

Balduf 1935.
Barman 1973.
Bertrand 1928, 1972, 1977.
Böving and Craighead 1931.
Brigham 1982a.
Chandler *in* Leech and Chandler 1956.
DeMarzo 1979.
Galewski 1971.
Hilsenhoff 1974.
James 1969.
Leech *in* Leech and Chandler 1956.
Leech and Sanderson 1959.
Longley and Spangler 1977.
Matta 1983, 1986.
Matta and Peterson 1985, 1987.
Pennak 1978.
Perkins 1981b.
Peterson 1951.
Spangler 1962a, 1962b, 1966b, 1973, 1974a, 1981, 1982, 1986.
Spangler and Folkerts 1973a.
Spangler and Gillespie 1973.
Spangler and Gordon 1973.
Watts 1970.
Wesenberg-Lund 1912.
White et al. 1984.
Wilson 1923.
Wolfe 1980.
Wolfe and Roughley 1985.
Young 1954.

GYRINIDAE (ADEPHAGA)

Paul J. Spangler, *Smithsonian Institution*

Whirligig Beetles

Figures 34.127–132

Relationships and Diagnosis: Gyrinids are highly adapted to their aquatic habitats. They appear to have been derived from caraboid stock because their larvae have 2 movable claws on each leg, a character unknown outside of the Adephaga.

Gyrinid larvae may be distinguished easily from other aquatic beetle larvae by the following combination of characters: lateral gills on abdominal segments 1–9; 2 claws on each leg; 10 abdominal segments; 4 decurved hooks on tenth abdominal segment (fig. 34.132).

Because of their elongate form, lateral gills, hooked anal feet, and creamy white color, gyrinid larvae resemble freshly molted larvae of some megalopteran genera and the dytiscid genus *Coptotomus*. However, gyrinid larvae may be easily distinguished from the megalopteran and dytiscid genera by their 4 hooked anal feet arising from the tenth abdominal segment. In contrast, megalopteran larvae have 2 hooked anal prolegs or a single long median process arising from the ninth abdominal segment. In addition, gyrinid larvae have lateral gills on abdominal segments 1–9 and larvae of *Coptotomus* have lateral gills only on segments 1–6.

Biology and Ecology: Gyrinid adults are highly adapted for life in the aquatic environment and are the only family of beetles that normally use the surface film for support. They are the fastest and most efficient swimmers of all the aquatic beetles and are equally at home underwater. They are found on the surface of clean lotic and lentic habitats where they may occur singly or in large aggregations composed of 1 to 8 species. Larvae occur in the same habitats as the adults but they live submerged until they leave the water to pupate. Both adults and larvae normally occur in shallow weedy margins of their lentic or lotic habitats.

Gyrinid females in temperate areas begin laying eggs in spring. Eggs are laid in rows or masses on floating or submerged plant stems and leaves. Larvae undergo 3 molts and last-instar larvae leave the water to pupate. Larvae of *Gyrinus* climb emergent vegetation or crawl onto shore to pupate; at this time they gather debris (from the emergent plant stems or the shore), mix the debris with an adhesive substance, crawl to a suitable place, attach the debris to plant stems or other surfaces, dig into the mass, and form a closed chamber by wriggling movements of the body. Larvae that crawl onto shore may make their cocoons from sand or mud and attach them to standing objects or beneath rocks, boards, etc. Pupal cocoons of *Gyrinus* often are common near the top or on top of plants such as *Eleocharis, Typha, Scirpus,* and other emergent plants. Cocoons of *Dineutus* usually are found on shore, near the water, and under objects such as boards or rocks. There are several genera of Hymenoptera that parasitize gyrinid pupae and parasitized pupae may be found quite frequently.

Larval gyrinids, like the adults, are voracious predators; however, adults feed primarily on the surface of their habitats and larvae feed underwater where they seek out soft-bodied larvae of chironomids, tubificids, odonate larvae, etc.; when confined they also feed on their siblings.

Description: Mature larvae, 6.0 to 25.0 mm in length. Body form elongate, narrow, depressed, with lateral gills. Integument white with sclerotized parts yellow to yellow brown and sometimes with dark brown, grey, or black spots on the head capsule.

Head: Prognathous, exserted; subquadrate, depressed; ecdysial cleavage lines present. Anterior margin of nasale truncate or lobed (figs. 34.129–131). Stemmata, 6 pairs. Antenna 4-segmented, slender, elongate. Maxillae slender, elongate; cardo and stipes large; stipes quadrangular, with a galea and lacinia; maxillary palp slender, elongate, 4-segmented. Labial palp elongate, slender, 3-segmented.

Thorax and Abdomen: Prothoracic terga with 2 moderately large sclerites; meso- and metathoracic terga membranous, without sclerites. Legs 6-segmented, including pretarsus with 2 claws.

Abdomen of 10 segments; with a pair of lateral gills on segments 1–8; ninth with 2 pairs of gills; tenth without gills, with 4 stout decurved hooks; some gills may be naked but most have hairlike fringes.

Spiracles: Absent in first and second instars, present on abdominal segments 1–3 in last instar.

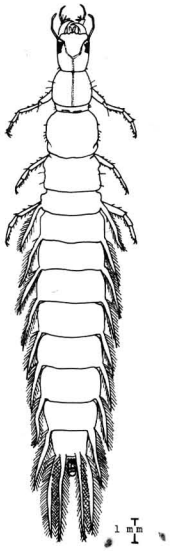


Figure 34.127

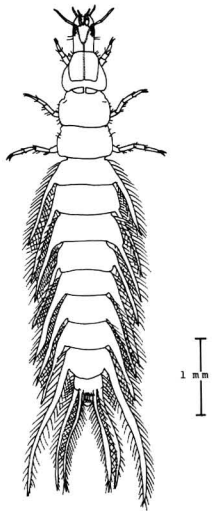


Figure 34.128

Figure 34.129

Figure 34.130

Figure 34.131

Figure 34.132

Figure 34.127. Gyrinidae. *Dineutus* sp.

Figure 34.128. Gyrinidae. *Gyrinus* sp.

Figures 34.129–34.131. Gyrinidae. Nasales, dorsal. **(34.129.)** *Dineutus* sp.; **(34.130.)** *Gyrinus* sp.; **(34.131.)** *Gyretes* sp.

Figure 34.132. Gyrinidae. Caudal hooks, *Dineutes* sp. (from Peterson, 1951).

Comments: The family Gyrinidae is cosmopolitan; however, it is richest in taxa pantropically although numerous taxa occur in the temperate regions of the world. The family includes 11 genera and about 1,100 species in the world fauna and is represented in America north of Mexico by 52 species in 4 genera. In North America, the larvae of *Gyretes* and *Spanglerogyrus* remain undescribed; however, *Gyretes* is included in keys to larvae by Chandler (1956), Sanderson (1982), and White, Brigham, and Doyen (1984). Gyrinid beetles are not known to be economically important, but they serve as food for other organisms, and their predatory habits assist in recycling nutrients in aquatic ecosystems.

Very few studies have been published on the biology and immature stages of North American Gyrinidae. However, those that are available are thorough and informative. The most useful of these publications is Wilson's (1923) descriptions of the life cycles and immature stages of *Dineutus* and *Gyrinus*. The publications by Butcher (1930) on the construction of the pupal cocoon and parasitoids of pupae (1933) are also very interesting. In addition, the review of the family by Leech (1956) nicely summarizes the information available for the family. Sanderson (1982) provides a discussion of gyrinid bionomics and includes a key to the larvae of the genera *Dineutus, Gyretes,* and *Gyrinus*. White, Brigham, and Doyen (1984) also include a key to three of the four gyrinid genera of North America. For a summary of information on immature stages of gyrinids of the world *see* Bertrand (1972).

Selected Bibliography

Bertrand 1972.
Böving and Craighead 1931 (key to genera, including *Dineutus, Gyretes,* and *Gyrinus*).
Butcher 1930, 1933.
Carthy and Goodman 1964.
Chandler *in* Leech and Chandler 1956 (key to *Dineutus, Gyretes* and *Gyrinus*).
Folkerts 1979 (new subfamily; adult key to subfamilies, tribes and genera of U.S.).
Hatch 1927.
Leech *in* Leech and Chandler 1956.
Leech and Sanderson 1959.
Sanderson 1982.
Steiner and Anderson 1981.
White et al. 1984.
Wickham 1893, 1894.
Wilson 1923 (larva, pupa and life cycle of *Dineutus* and *Gyrinus*).

SUBORDER POLYPHAGA

HYDRAENIDAE (STAPHYLINOIDEA)

(= LIMNEBIIDAE)

Paul J. Spangler, *Smithsonian Institution*

Hydraenid Beetles

Figures 34.133a,b–135a,b

Relationships and Diagnosis: The hydraenid beetles were originally placed in the family Hydrophilidae and the superfamily Hydrophiloidea. However, as a result of a study of the comparative morphology of Coleoptera larvae, Böving and Craighead (1931) placed the family in the superfamily Staphylinoidea. Coleopterists have different opinions on the proper assignment of the Hydraenidae. Crowson (1955) states that the hydraenid "relationship to the hydrophiloids is indicated by the palpicorn type of antennae and general aquatic adaptations of the adults while the mouthparts are quite primitive and without any indication of the predacious specialisations." Dybas (1976) disagrees with this placement and comments as follows: "Though there has been lack of agreement as to the systematic position of the family Hydraenidae, I regard it as clearly belonging in the Staphylinoidea because of the characters of the larva (particularly the maxilla of *Hydraena*) and because of the close resemblance in numerous features of the dorsum of the abdomen of the adult to that of the generalized ptiliid *Nossidium* (unpublished data)." In the latest discussion of the family assignment, Perkins (1981a) reports the following: "Based on adult antennal form, aquatic habits, and metendosternite, relationships appear to be with

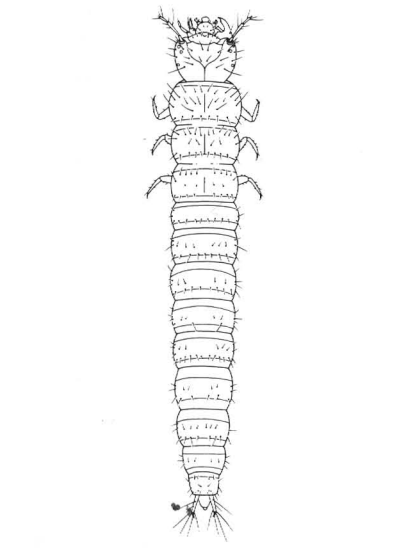


Figure 34.133

Figures 34.133a,b. Hydraenidae. *Ochthebius impressus* Marsham. **a.** larva; **b.** head.

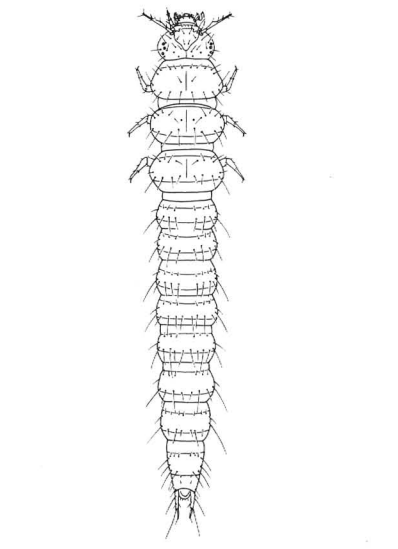


Figure 34.134

Figures 34.134a,b. Hydraenidae. *Limnebius* (?)*papposus* Mulsant. **a.** larva; **b.** head.

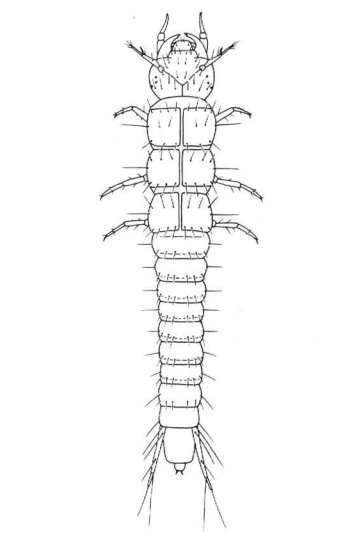


Figure 34.135

Figures 34.135a,b. Hydraenidae. *Hydraena pennsylvanica* Kiesenwetter. **a.** larva; **b.** head.

(Figures 34.133a, b and 34.134a, b redrawn from Böving and Craighead, 1931. Figures 135a, b redrawn from Richmond, 1920.)

the Hydrophiloidea. The wings, however, are similar to Staphylinoidea, and larvae markedly resemble those of the Ptiliidae." Perkins concludes that "It is evident that phylogenetic relationships of the Hydraenidae remain equivocal, a fertile area for further research."

The tiny larvae (1.3 to 3.0 mm) superficially resemble those of various smaller Staphylinoidea, such as Ptiliidae, Leiodidae, and Staphylinidae. Hydraenid larvae are distinguished from those of any staphylinid by the presence of a distinct roughened or tuberculate mandibular mola and a pair of recurved hooks on the last abdominal segment. The lack of hooks on segment 10 also distinguishes larvae of Leiodidae, Leptinidae, and Limulodidae from those of hydraenids. Ptiliid larvae have a mandibular mola and recurved hooks at the abdominal apex, but they differ from larvae of Hydraenidae in having urogomphi with only 1 segment (or occasionally no urogomphi) and in lacking stemmata (rarely with 1 pair).

Biology and Ecology: Most hydraenid adults are aquatic and inhabit the margins of cascades, rills, and hygropetric habitats where they occur in leaf packs or matted roots; others occur in splash zones of cascades and waterfalls on moss-covered rocks or other damp or wet plant materials. Adults are also found in sandy margins of streams, potholes, rock outcrops beside streams, in marshy margins of ponds, holes and woodland ponds; others occur on rocky coastlines that are periodically submerged by rising tides. Although most hydraenids are found in fresh water habitats, a few may occur abundantly in brackish to very saline coastal or inland waters. The exotic genus *Meropathus,* lives on moss-covered rocks alongside streams and in grasses and offal around nests of seabirds in their rookeries. All of the larvae known from N. America are terrestrial, but they are usually found along the damp margins of the aquatic habitats of the adults.

Those hydraenids whose egg-laying habits are known deposit their eggs in moist sites out of water, often on leaves, rocks, or algae adjacent to the adult habitat. Eggs are deposited singly and usually secured with a sparse covering or

blanket of silklike strands secreted from caudal spinnerets; occasional eggs are deposited without being secured with silklike strands. Larval life was reported by d'Orchymont (1913) to last 2 or 3 months. Beier and Pomeisl (1959) reported that the European *Ochthebius exsculptus* Germar pupates in cocoons constructed a few centimeters above the waterline and on rocks and boulders in torrents.

Reports on the food habits are conflicting. Some authors say that larvae and adults are phytophagous and feed primarily on algae (Bertrand, 1972); others say the larvae are predators (Leech, 1958); still others (Böving and Hendriksen, 1938) say that larvae of "*Ochthebius, Hydraena,* and *Limnebius* feed on infusoria, spores and decaying particles in water." The larval mandibles suggest that the larvae are predators but a study of the food habits is needed.

Description: Mature larvae (figs. 34.133a–135a), 1.3 to 3.0 mm in length. Body form elongate, subcylindrical, slightly flattened in cross section; thoracic and abdominal terga with large sclerites; cuticle with numerous setae; annuliform spiracles present. Color: integument white, becoming light yellowish with age.

Head: Prognathous to semihypognathous; rounded or ovoid, globular; ecdysial cleavage lines present and distinct (figs. 34.133b–135b). Clypeus distinct, arcuate, wider than labrum. Labrum somewhat semicircular. Stemmata, 5 pairs. Antenna 3-segmented. Mandibles essentially symmetrical with large roughened or tuberculate molar area. Maxillae with cardo short and broad; stipes wider than and twice as long as segment-like palpifer; palp closely united with stipes. Ligula short, rounded, bearing papillae.

Thorax and Abdomen: Prothoracic, meso- and metathoracic terga each with a large, well-developed sclerite. Legs about as long as prothorax is wide, 5-segmented; tarsus and pretarsus fused, forming a single claw-like tarsungulus.

Abdomen of 10 segments; 1–8 covered with broad sclerite; 9 bearing a pair of movable, 2-segmented urogomphi; 10 bearing a pair of stout, recurved hooks.

Spiracles: Annular, on mesothorax and abdominal segments 1–8.

Comments: Hydraenids are cosmopolitan with about 900 species known from the world. At present there are 90 species in 5 genera known from America north of Mexico. They are not reported to be economically important, but they often are very abundant in microhabitats where they must be efficient in recycling food items upon which they feed.

Although all hydraenid larvae known from the United States and Canada are terrestrial, some Australian larvae apparently are aquatic. These larvae have a pair of large well-developed prothoracic spiracles borne on dorsal tubercles that appear to function as a snorkel; this suggests that these larvae may live under a thin film of water such as is found in hygropetric habitats. Some of the exotic hydraenid larvae reportedly lack the pair of hooks found on the tenth abdominal segment of the described N. American larvae.

References to the immature stages of hydraenids are few. The most thorough descriptions of North American hydraenid larvae are found in Richmond's (1920) treatise. All subsequent keys to genera of larvae (Bertrand, 1972; Böving and Hendriksen, 1938; Chandler, 1956; Leech and Sanderson, 1959; Brigham, 1982c; White, Brigham, and Doyen, 1984) are based entirely or in part on Richmond's descriptions and key. Perkins' (1981a) revision of the Hydraenidae of the Western Hemisphere has changed the status of some taxa. Because of this, all larvae keying to *Ochthebius* in present keys to larvae of North American genera should be considered *Ochthebius* or *Gymnochthebius.*

Selected Bibliography

Arnett 1968.
Beier and Pomeisl 1959.
Bertrand 1972.
Böving and Craighead 1931.
Böving and Hendriksen 1938.
Brigham 1982c.
Chandler *in* Leech and Chandler 1956.
Dybas 1976.
Hrbácek 1950.
Leech *in* Leech and Chandler 1956.
Leech and Sanderson 1959.
d'Orchymont 1913.
Ordish 1971.
Perkins 1981a.
Richmond 1920.
Samuelson 1964.
White et al. 1984.

FAMILY PTILIIDAE (STAPHYLINOIDEA)

Henry S. Dybas,*
Field Museum of Natural History

Featherwing Beetles

Figures 34.136–139

Relationships and Diagnosis: The family Ptiliidae, which contains the smallest known beetles, is distributed worldwide in both temperate and tropical regions. Larvae are most similar to those of the Limulodidae, but the only known species of the latter lacks anal hooks. The families also show numerous similarities to the Hydraenidae, Leptinidae, and Leiodidae, particularly in the possession (in some members of each family, at least) of a unique and presumably derived structure—the fringed galea of the maxilla (fig. 34.136b). The Hydraenidae, like the Ptiliidae, possess 1 pair of anal hooks. This grouping of the 5 families within the Staphylinoidea essentially corresponds to the "leptinid association" of families recognized by Böving and Craighead (1931) on the basis of other larval characters.

Ptiliidae larvae can be distinguished from larvae of related families of Staphylinoidea by the following characters: unusually small size (ca. 1.0–2.0 mm long), linear form, unpigmented body, lack of eyespots, usually 1-segmented urogomphi, and a pair of anal hooks. Exceptions and additional characters are detailed below.

Biology and Ecology: Adults and larvae occur chiefly in moist, decaying, organic matter in habitats such as the forest floor, tree holes, decaying logs, compost heaps, animal dung, under bark of dead trees, rubbish heaps of ants (e.g., *Atta*

*Deceased

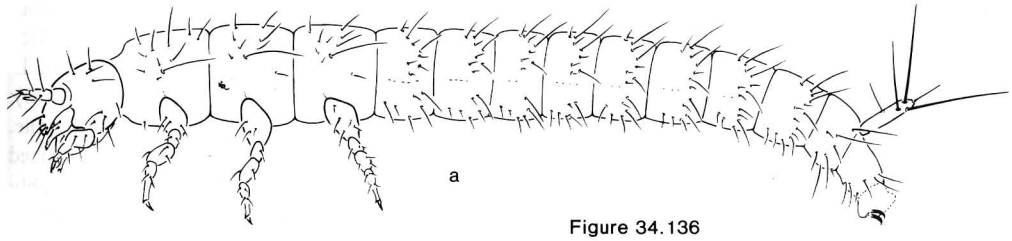


Figure 34.136

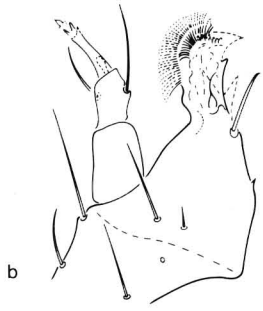
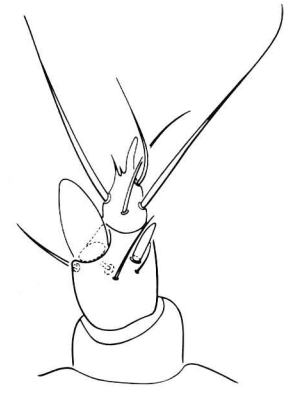


Figure 34.137



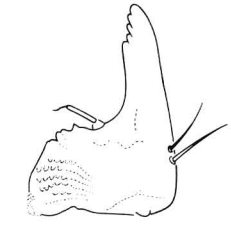


Figure 34.138

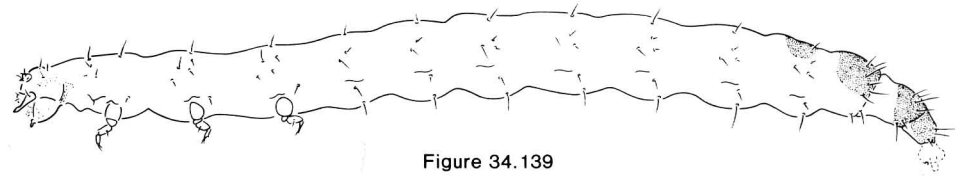


Figure 34.139

Figures 34.136a,b. Ptiliidae. *Pteryx* sp. **a.** late instar larva, lateral, setal pattern approximate; **b.** maxilla, ventral, showing lacinia and fringed galea united on mala.

Figures 34.137a,b. Ptiliidae. *Nossidium americanum* Motschulsky. **a.** head capsule, dorsal, maxillae not shown; **b.** left antenna, ventral.

Figure 34.138. Ptiliidae. *Nossidium,* left mandible, ventral.

Figure 34.139. Ptiliidae. *Throscoptilium duryi* Barber, lateral, showing yellowish pigmented areas at apex of abdomen (note absence of urogomphi on segment 9).

spp., leaf-cutting ants), decaying piles of seaweed, and similar moist decaying organic materials suitable for the growth of molds and other fungi, where they are frequently the most abundant beetles. These habitats are best sampled by means of the Berlese or Tullgren funnel. Some species of *Actidium,* and a related undescribed genus in the United States, occur on bare sand and gravel bars and flats along water-courses, and can be collected by flotation techniques. One group of ptiliids, *Nanosella* and allies, is found on the underside of shelf fungi (Polyporaceae) where larvae and adults live in the spore tubes and feed on growing spores. This group includes the smallest of all beetles (as small as 0.30 mm long). When the fungus is disturbed, adults and larvae leave the spore tubes and cross the under surface for a short distance before entering other tubes. They can be picked off the under surface with a wetted forceps point.

The main food of both adult and larval Ptiliidae appears to be spores and hyphae of fungi and, probably, soft organic materials containing microorganisms. Under favorable conditions, ptiliids appear to reproduce continuously, as evidenced by finding larvae and teneral and fully hardened adults together at different times of the year. Only a single egg, usually about 1/3–1/2 the length of the female, is matured at a time. Development seems to be fast, 32–45 days from egg to adult at 20° C in 3 species of *Ptinella* (Taylor, 1975). The number of instars in *Ptinella* is 3 (Taylor, 1975). The pupal stage has been adequately described only for *Acrotrichis fascicularis* (Hinton, 1941a).

Description: Ptiliidae larvae are linear, about 1.0–2.0 mm. long (figs. 34.136a, 34.139). Body usually entirely white (unpigmented) or with a yellowish tinge on the more sclerotized regions (mandibles, head capsule), but species of *Actidium* from the exposed riparian habitats are dark. Pigmented eyespots lacking, except in a new species of the generalized genus *Nossidium* (*s.l.*) from Panama. The 10-segmented abdomen possesses a membranous anal vesicle which is furnished with a pair of anal claws or hooks (fig. 34.136a); the ninth abdominal segment has a pair of articulated, 1-segmented urogomphi (fig. 34.136a) that are lacking in species (*Nanosella* and allies) that live in spore tubes of shelf fungi (fig. 34.139). Except in the darkly pigmented species of *Actidium,* the epicranial lines of the head capsule are not (or

only rarely) detectable, and the tergal sclerites are not or only feebly evident. Other important characters are the fringed galea of the maxilla (fig. 34.136b) which, however, is not detectable in the spore-tube genera; the form of the mandible, which has a greatly enlarged molar region and a slender, articulated prostheca (fig. 34.138); and the labrum which is free and not united to the clypeal region (fig. 34.137a). For a more detailed family description of Ptiliidae larvae, as well as descriptions and illustrations of 9 North American genera, see Dybas (1976).

Spiracles: Annular, on mesothorax and abdominal segments 1–8.

Comments: About 62 genera and 400 species have been described, of which 23 genera and about 115 species have been recorded from the United States. Judging by existing collections, the majority of the species are still undescribed. The family is notable, not only because it contains the smallest beetles, but because of the high incidence of parthenogenesis (Dybas, 1966, 1978) and of a striking form of polymorphism (e.g. species of *Ptinella, Pteryx,* and *Ptinellodes*). In these genera there are 2 strongly differentiated morphs in each species, generally represented in both sexes: 1) a *normal morph* with normal compound eyes, featherwings, and body pigmentation, and 2) a *vestigial morph* in which eyes, wings, and other structures are reduced or completely absent (Dybas, 1978).

Larvae should be killed and preserved in 70% ethanol. For study they are mounted directly into Hoyer's medium on microscope slides, or first treated with cold KOH and then mounted in Hoyer's medium or in glycerine gel. Hoyer's medium (not a good permanent mount) is soluble in water, and larvae can be soaked off and remounted in different positions. Larvae in glycerine gel can be repositioned by placing the slide on a slide-warming table for a few moments to soften the gel, and then manipulating the specimens with a fine needle. Ptiliidae larvae are best studied with a compound microscope at magnifications of 400× or more, using phase contrast optics (which eliminates the need for staining).

Selected Bibliography

Böving and Craighead 1931.
Dybas 1966, 1976, 1978.
Hinton 1941a.
Taylor 1975.

FAMILY LIMULODIDAE (STAPHYLINOIDEA)

(= CEPHALOPLECTIDAE)

Henry S. Dybas,*
Field Museum of Natural History

Limulodids

Figures 34.140a-d

Relationships and Diagnosis: The Limulodidae are closely related to the Ptiliidae. At present the larvae are characterized on the basis of 3 larvae of 1 species, *Limulodes parki* Seevers and Dybas, from Illinois (fig. 34.140). The previous assignment (Paulian, 1941) of a larva found in Costa Rica with *Cephaloplectus mus* Mann, (a highly specialized limulodid beetle) has been shown to be in error (Dybas, 1976); the larva probably belongs to some genus of Staphylinidae. When other larvae are studied, particularly of specialized genera like *Cephaloplectus,* the diagnosis will very probably have to be revised. The larvae of *L. parki* closely resemble typical larvae of the Ptiliidae (cf. *Pteryx* sp., fig. 34.136a) except for the apparent loss of the 2 anal hooks in the anal membrane of abdominal segment 10, the absence of the terminal tuft of the third segment of the maxillary palp (fig. 34.140b), and the presence of 4 obtusely-pointed denticles under the anterior margin of the labrum (fig. 34.140c).

Biology and Ecology: Adults and presumed larvae of *Limulodes parki* were collected in March–May, Cook County, Illinois, under a flat rock covering a colony of *Aphaenogaster rudis s.l.* ants. It could not be determined whether the larvae were in the galleries or in the surrounding soil. The digestive tract of 1 larva was packed with indeterminate matter among which were small soil particles. The adults were reported by Park (1933, under the name *Limulodes paradoxus* Matth.) to feed by scraping oils and other materials from the integument of the ant larvae, pupae and workers.

Description: Similar to Ptiliidae except as noted above.

Spiracles: Annular, on mesothorax and abdominal segments 1–8.

Comments: There are 5 genera and 28 described species, the majority of which (including the most specialized forms) are associated with army ants (Dorylinae) in the American tropics. Four species in 2 genera are known to occur in the United States. All species are found only in association with ants and occur only in the New World and the Australian region. Adults are blind, flightless, compactly built, with a smoothly contoured tear-drop shape reminiscent of *Limulus* (horseshoe crab) from which the family name is derived. A general account of the classification and biology is given in Seevers and Dybas (1943); see also Wilson *et al.,* (1954), Park (1933), and Dybas (1976).

Selected Bibliography

Dybas 1976.
Park 1933.
Paulian 1941.
Seevers and Dybas 1943.
Wilson, Eisner and Valentine 1954.

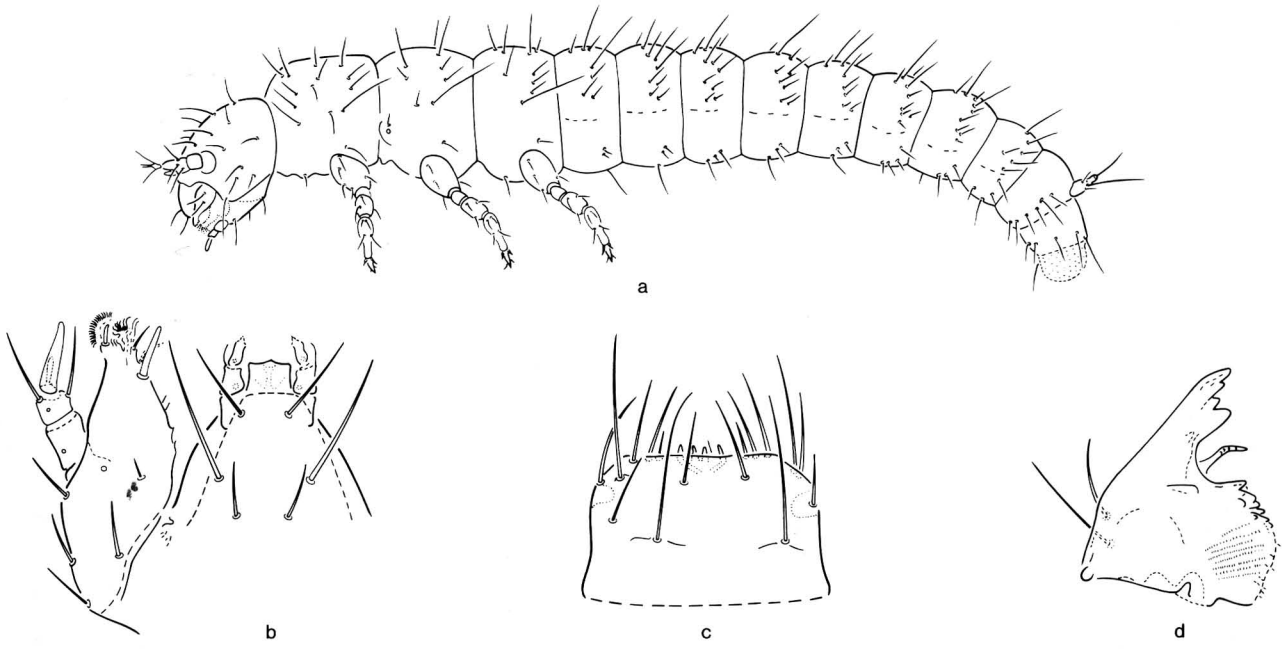
AGYRTIDAE (STAPHYLINOIDEA)

Alfred F. Newton, Jr.,
Field Museum of Natural History

Figures 34.141-145

Relationships and Diagnosis: The family Agyrtidae has usually been considered a subfamily of Silphidae. Based on studies soon to be published (Newton, in preparation), agyrtids are placed as a distinct family most closely related to Leiodidae rather than to Silphidae and allied families (Lawrence and Newton 1982, Anderson and Peck 1985).

*Deceased



Figures 34.140a-d. Limulodidae. *Limulodes parki* S. & D. **a.** late instar larva, lateral; **b.** right maxilla and labium, ventral; **c.** labrum, dorsal; **d.** right mandible, ventral.

Agyrtid larvae may be distinguished from all other Coleoptera larvae by their possession of a combination of: mandibles with large contiguous molar lobes; 6 stemmata on each side of the head; and articulated, 2-segmented urogomphi. Larvae of Leiodidae, Ptiliidae and Hydraenidae are very similar but have at most 5 stemmata, while larvae of Silphidae and all remaining Staphylinoidea lack molar lobes on the mandibles. In addition, mature larvae of agyrtids are large, about 8 mm or longer, while larvae of related families such as Leiodidae are usually much smaller.

Biology and Ecology: Relatively little is known about the natural history of most agyrtids. *Necrophilus* species are found at small decaying animal carcasses and feces; *N. pettiti* Horn has been reared on mouse feces and decayed squirrel meat (J. A. Payne, unpublished observations) and the European *N. subterraneus* (Dahl) has been reared on decaying snails (Will 1886, Zwick 1981). *Ipelates* species have been found around decaying trees and in forest litter, while *Lyrosoma* species are confined to marine beaches fringing the northern Pacific Ocean. *Pteroloma* and *Apteroloma* species occur under stones and debris in mountainous areas, often above timberline (e.g., Bolívar y Pieltain 1940), and are probably predators as adults (personal observations).

Egg nearly round, yellowish white.

Pupa exarate, with functional abdominal spiracles on segments 1–2.

Description: Mature larvae about 8–20 mm long, elongate and more or less parallel-sided, slightly flattened, straight or slightly curved ventrally. Body surfaces heavily to lightly pigmented and sclerotized, smooth or finely microspinose or granulate, with sparse vestiture of simple setae only or including frayed or bifid setae.

Head: Prognathous or slightly declined, protracted, without differentiated neck. Epicranial stem short, frontal arms V-shaped to lyriform, each arm anteriorly bifurcate; endocarinae absent. Stemmata 6, well separated, on each side of head. Antenna 3-segmented, about 0.6–1.4 times as long as head width, sensorium of preapical segment anterad of apical segment and conical or awl-shaped. Frontoclypeal suture absent. Labrum free, tormae present. Mandibles symmetrical, apex with single tooth, incisor edge with 1 large and several fine subapical teeth; mesal surface of mandibular base with mola bearing numerous fine transverse ridges, distal portion of molar lobe with rounded or tooth-like prostheca and large ventral setose area which extends to mesal edge. Cardines transverse, externally divided, widely separated from each other by submentum. Stipes elongate. Mala long, fixed, divided at apical third to half into fixed galea and lacinia; galea with 2 long setiform sensilla and with apical fringe of 2–5 rows of setae, fringe rarely absent; lacinia falcate, spinose along mesal edge. Maxillary palp 3-segmented. Labium consisting of prementum, mentum and submentum. Ligula shorter or longer than first palpal segment but shorter than palp, apex bilobed. Labial palps 2-segmented, separated by more than width of first palpal segment. Gula transverse. Occipital foramen divided into 2 parts by tentorial bridge.

Thorax and Abdomen: Thoracic terga and abdominal terga and sterna with 1 or more sclerotized plates, without patches or rows of asperities, without lateral tergal processes. Legs long, 5-segmented including bisetose tarsungulus. Abdomen 10-segmented, about 1.5–2 times as long as thorax. Tergum A9 with pair of long 2-segmented urogomphi which may be multiannulate. Segment A10 visible from above, anal region terminally oriented, with membranous anal lobes bearing numerous fine teeth.

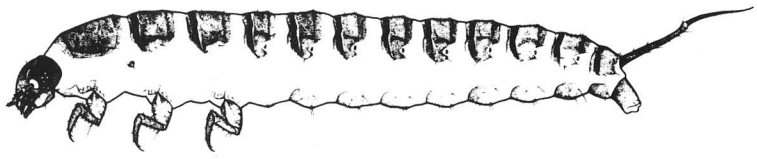
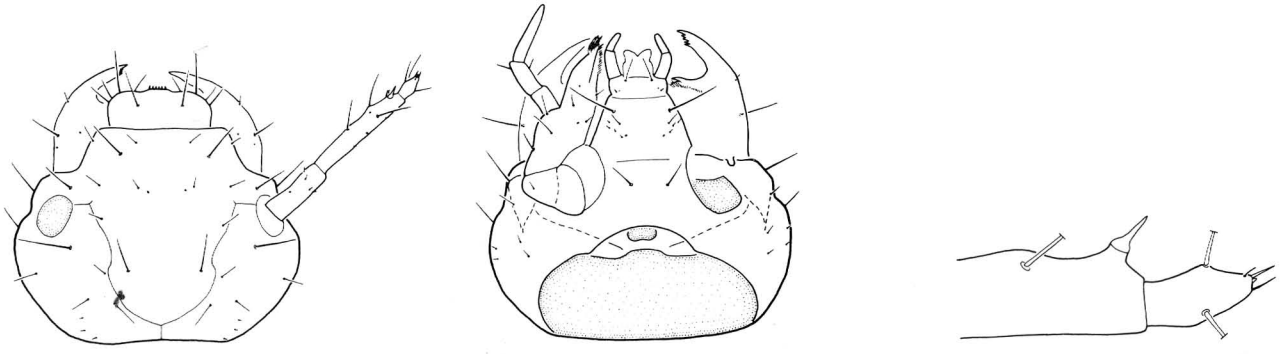


Figure 34.141

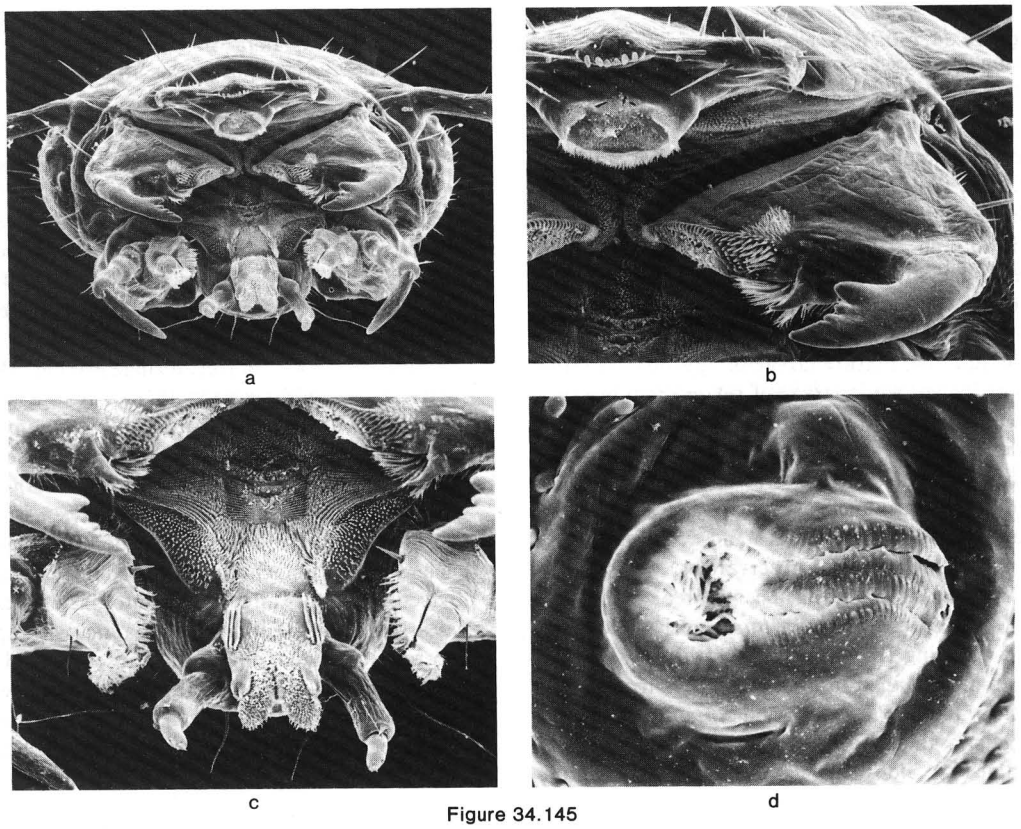
Figure 34.143

Figure 34.144



a b c

Figure 34.142



a b c d

Figure 34.145

Figure 34.141. Agyrtidae. *Necrophilus hydrophiloides* Mannerheim. Inverness (1 mile southeast), California; February; on rotten potatoes. Mature larva, lateral. Length = 18 mm.

Figures 34.142a-c. Agyrtidae. *Necrophilus pettiti* Horn. Perry, Georgia; January; reared on feces and carrion. **a.** second instar larva, head, dorsal, left antenna not shown; **b.** head, ventral, left maxilla not shown; **c.** right antenna, dorsal view of apex.

Figure 34.143. Agyrtidae. *?Pteroloma nebrioides* Brown. Cameron Lake, Waterton Park, Alberta; August; moss etc. Right maxilla, ventral view of apex.

Figure 34.144. Agyrtidae. *?Apteroloma tenuicorne* (LeConte). Sagehen Creek, Nevada County, California; October. Right antenna, dorsal view of apex.

Figures 34.145a-d. Agyrtidae. *Necrophilus pettitii.* **a.** head, anterior, mouthparts spread apart; **b.** detail of labrum, left mandible; **c.** detail of labium, maxilla; **d.** abdominal spiracle, dorsal.

Spiracles: Annular, annular-biforous or modified annular with several peripheral chambers to one side; dorsolateral; closing apparatus present.

Comments: The family is a small one of about 8 genera and 60 species. It is nearly confined to the Holarctic region, with the notable exception of *Necrophilus prolongatus* Sharp, found only in New Zealand. Six genera and about 14 species are known from N. America (Anderson and Peck, 1985). The species are seldom encountered without special effort, and none are known to be of any economic importance.

Larvae have not been adequately described. Only 3 species are treated at all in the literature: *Necrophilus subterraneus* (Will 1886, Zwick 1981); *N. prolongatus* (Hudson 1934); and *Apteroloma* sp. (Bolívar y Pieltain 1940). The present treatment is based on larvae of 4 *Necrophilus* species, and on 3 kinds of unreared larvae from western N. America tentatively attributed (based on distribution, habitat and association with adults) to the genera *Ipelates, Pteroloma* and *Apteroloma.*

Selected Bibliography

Anderson and Peck 1985 (classification, adult ecology).
Blaisdell 1901.
Bolívar y Pieltain 1940.
Hudson 1934.
Lawrence and Newton 1982.
Will 1886.
Zwick 1981.

LEIODIDAE (STAPHYLINOIDEA)

(= ANISOTOMIDAE, LIODIDAE, INCLUDING CAMIARIDAE, CATOPIDAE, CHOLEVIDAE, COLONIDAE, LEPTODIRIDAE)

Alfred F. Newton, Jr.,
Field Museum of Natural History

Round Fungus Beetles, Small Carrion Beetles and Allies

Figures 34.146-155

Relationships and Diagnosis: The family is used here in the broad sense to include what are sometimes (e.g., Jeannel 1957) considered to be as many as 4 families: Leiodidae (= Anisotomidae), Camiaridae, Colonidae and Cholevidae (= Catopidae, = Leptodiridae). Leptinidae are very closely related and are included in Leiodidae in some recent concepts of the family (Crowson 1981, Lawrence and Newton 1982). All of these taxa were at one time included in Silphidae and are occasionally still cited under that family, but the only closely related family of Staphylinoidea is Agyrtidae, a recent removal from Silphidae (Lawrence and Newton 1982).

Most leiodid larvae are distinguishable from other beetle larvae by possession of a combination of: 2- or 1-segmented urogomphi; mandibles with molar lobes; 5 or fewer stemmata (in North America 3 or fewer) on each side of the head, rather than 6 stemmata as in otherwise very similar agyrtids; and anal lobes with numerous fine hooks or without hooks rather than with a pair of large hooks as in hydraenids and ptiliids. Those few species that lack well developed molar lobes have the other characters and have the occipital foramen divided into 2 parts by the tentorial bridge, in contrast to Staphylinidae, Silphidae and other families lacking a mola which have an undivided foramen. A few Leiodinae with short fixed urogomphi have the other characters listed above, a dorsally curved abdomen and subterranean feeding habits. Leptinid larvae will fall out with leiodids according to the above diagnosis but differ from leiodids in having either a scoop-like lacinia or mandibles without molar lobes and with ventrally curved apices.

Biology and Ecology: Leiodids are generally, and perhaps primitively, saprophages and scavengers in a variety of habitats including forest litter, dung, carrion, rotting fungi and other decomposing organic matter, and in nests of mammals, birds, ants, termites and stingless bees. Many species, including a majority of the many Palearctic Bathysciini and the isolated North American genus *Glacicavicola,* are obligate cave dwellers. Molds and other fungi may form a part of the diet of larvae and adults of many species, and a number of taxa are obligate mycophages of specific groups of fungi, including Agathidiini and *Neopelatops* on slime molds (Myxomycetes); *Creagrophorus* and *Nargomorphus* on puffballs (Gasteromycetes); Hydnobiini, Leiodini, and possibly Catopocerinae and Coloninae on diverse hypogean fungi; and a few miscellaneous species on Polyporaceae and allied epigean fungi. Larval development is generally rapid, taking as little as 2 days in some *Anisotoma* species feeding on short-lived slime mold fruiting bodies. See Arzone (1970, 1971), Casale (1975), Crowson (1984a), Deleurance-Glaçon (1963), Newton (1984), Wheeler (1979, 1984, 1985) and Zwick (1979).

Egg ovoid, white, smooth.

Pupa exarate, with functional abdominal spiracles on segments 1–2.

Description: Mature larvae about 2–8 mm long, elongate and more or less parallel-sided or (*Neocamiarus*) broadly ovate, slightly to strongly flattened, straight to slightly curved ventrally or (Hydnobiini, Leiodini) curved dorsally. Body surfaces heavily to very lightly pigmented and sclerotized, smooth to microspinose, with vestiture consisting of fine setae only or including expanded or complex setae.

Head: Prognathous, protracted, without differentiated neck. Epicranial stem very short to moderately long, rarely absent; frontal arms V- or U-shaped to lyriform or with bases separate, each arm sometimes anteriorly bifurcate; endocarinae absent. Stemmata 5, 3, 2 or 1 on each side, or absent. Antenna 3- or 4-segmented (*Prionochaeta*), about 0.2–1.2 times as long as head width, sensorium on preapical segment anterad of apical segment and conical or palpiform. Frontoclypeal suture absent. Labrum free, tormae present. Mouthparts forming piercing-sucking tube in *Myrmicholeva* (Australia). Mandibles symmetrical to moderately asymmetrical, broad at base and narrow at apex, or triangular, or (*Myrmicholeva*) stylet-like; apex with single tooth or bifid, incisor edge with 1 or 2 subapical teeth or serrate or simple; mesal surface of mandibular base with mola bearing ridged or asperate surface, or (Camiarini and *Agathidium* (*s. str.*))

with membranous setose lobe, or (*Myrmicholeva*) simple; prostheca consisting of membranous or partly sclerotized lobe or absent. Cardines transverse, divided by internal ridge, widely separated from each other by submentum. Stipes elongate. Mala large, fixed, often divided apically into galea and lacinia; galea falcate or rounded, apex glabrous, setose or bearing up to 3 setal combs; lacinia or mala falcate, spinose. Maxillary palp 3-segmented. Labium consisting of prementum, mentum and submentum. Ligula longer than first palpal segment to as long as palp, apex bilobed, quadrilobed, truncate or complex. Labial palps 2-segmented, separated by more than width of first palpal segment (except *Myrmicholeva*). Gula variable. Occipital foramen divided into 2 parts by tentorial bridge.

Thorax and Abdomen: Thoracic terga and abdominal terga and sterna consisting of 1 or more sclerotized plates, without patches or rows of asperities, without lateral tergal processes. Legs 5-segmented including bisetose tarsungulus. Abdomen 10-segmented, about twice or more as long as thorax. Tergum A9 with pair of urogomphi which may be 2-segmented with very long multiannulate apical segment to short and (some Hydnobiini and Leiodini) 1-segmented or fixed. Segment A10 visible from above, anal region terminally oriented, membranous anal lobes with or without numerous fine teeth.

Spiracles: Annular, annular-biforous or modified annular with several peripheral chambers; lateral or dorsolateral; closing apparatus present.

Comments: The family includes about 300 genera and 2300 species worldwide, especially from northern and southern temperate regions, with about 30 genera and 200 species in America north of Mexico. Most of the genera and species are placed in the 2 large subfamilies Leiodinae and Cholevinae, but the monogeneric subfamilies Coloninae, Catopocerinae and Glacicavicolinae also occur in North America, and the latter 2 subfamilies are confined to this continent. With the exception of some Cholevinae attracted to carrion and dung, the species are not commonly encountered and are of no known economic importance.

Immature stages of Leiodidae are poorly known and no comprehensive treatment exists. Best known are larvae of European genera of Cholevinae, with recent keys provided by Zwick *in* Klausnitzer (1978) for non-Bathysciini and Deleurance-Glaçon (1963) for Bathysciini. The few described leiodine genera are treated by Schiödte (1862, 1864), Saalas (1917), Paulian (1941), Klausnitzer (1978), Wheeler (1979, 1985), Hayashi (1986) and Angelini and DeMarzo (1984). Larvae of the primitive south temperate subfamily Camiarinae have only recently been described (Jeannel 1957, Zwick 1979), and larvae of Coloninae and Glacicavicolinae are unknown. The present treatment is based on previously undescribed larvae of about two dozen genera including *Catopocerus* (Catopocerinae), as well as previously known genera.

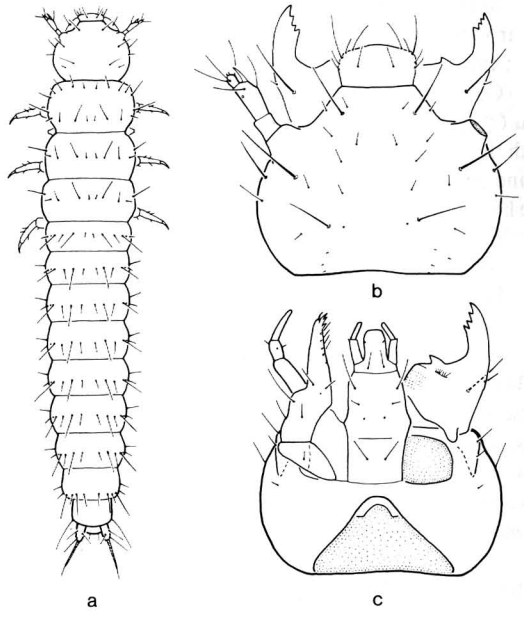


Figure 34.146

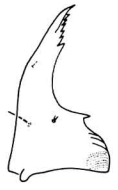


Figure 34.147

Figure 34.148

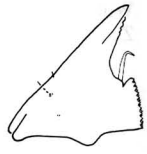


Figure 34.149

Figure 34.150

Figure 34.151

Figures 34.146a-c. Leiodidae. *Catopocerus appalachianus* Peck (Catopocerinae). Ellis Cave, Madison County, Alabama; reared. Length = 3.5 mm. **a.** mature larva, dorsal; **b.** head, dorsal, right antenna not shown; **c.** head, ventral, left maxilla not shown.

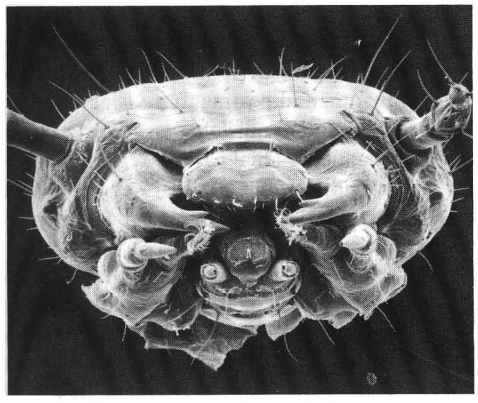
Figure 34.147. Leiodidae. *Hydnobius crestonensis* Hatch (Leiodinae). McKenzie Pass vicinity, 5147 feet, Oregon; October; on hypogeous *Gautieria* sp. fungus. Right mandible, ventral.

Figure 34.148. Leiodidae. *Agathidium* (s. str.) *oniscoides* Beauvois (Leiodinae). Bedford, Massachusetts; July; on yellow slime mold plasmodium. Right mandible, ventral.

Figure 34.149. Leiodidae. *Zearagytodes maculifer* (Broun) (Camiarinae). Waipoua State Forest, New Zealand; March; on *Ganoderma* sp. fungus. Right mandible, ventral.

Figure 34.150. Leiodidae. *Myrmicholeva acutifrons* Lea (Camiarinae). Alfred National Park, Victoria, Australia; May; ex rotting logs. Right mandible, ventral.

Figure 34.151. Leiodidae. *Nemadus ?horni* Hatch (Cholevinae). Pine Mountain, New Hampshire; July; in forest floor litter. Right mandible, ventral.



a

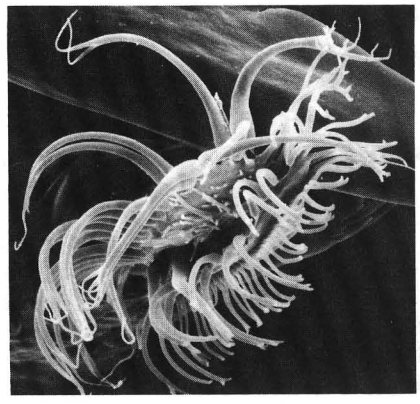


Figure 34.152 b

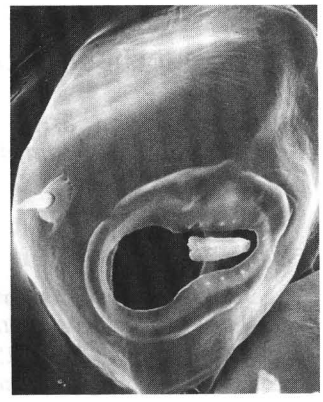


Figure 34.153

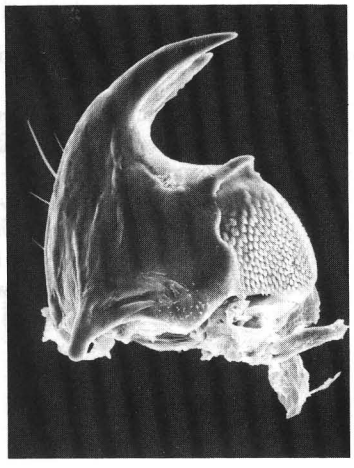
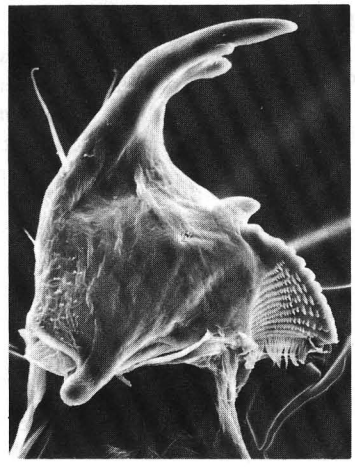


Figure 34.154



a

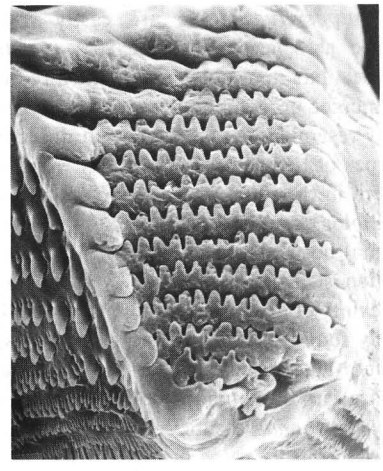


Figure 34.155 b

Figures 34.152a,b. Leiodidae. *Anisotoma errans* Brown (Leiodinae). Longmire (4.7 miles west), Washington; July; on *Stemonitis* sp. fruiting bodies. **a.** head, anterior; **b.** galeal fringe, anterior.

Figure 34.153. Leiodidae. *Zearagytodes maculifer.* Left mesothoracic spiracle, lateral.

Figure 34.154. Leiodidae. *Anisotoma errans.* Right mandible, ventral.

Figures 34.155a,b. Leiodidae. *Colenis impunctata* LeConte (Leiodinae). Rancocas State Park, New Jersey; June; litter under fermenting sap. **a.** right mandible, ventral; **b.** right mandible, mesal view of molar lobe.

Selected Bibliography

Angelini and DeMarzo 1984.
Arzone 1970, 1971.
Benick 1952.
Blas and Vives 1978.
Böving and Craighead 1931.
Casale 1975.
Corbière-Tichané 1973.
Crowson 1981, 1984a.
Deleurance-Glaçon 1963.
Fogel and Peck 1975.
Hayashi 1986 (*Catops, Sphaeroliodes* larvae).
Hayashi et al. 1959 (*Catops* larva).
Jeannel 1957 (*Neocamiarus* larva).
Kistner 1982.
Klausnitzer 1978.
Lawrence and Newton 1980, 1982.
Newton 1984.
Paulian 1941.
Peck 1973 (biology, ecology).
Peyerimhoff 1907.
Rehfous 1955.
Russel 1979.
Saalas 1917 (*Agathidium* larva).
Samuelson 1964 (*Paracatops* larva).
Scheerpeltz and Höfler 1948.
Schiödte 1862, 1864.
Westcott 1968.
Wheeler 1979 (*Creagrophorus* larva), 1984, 1985.
Zwick 1978.
Zwick 1979 (larvae of several Australian genera).

LEPTINIDAE (STAPHYLINOIDEA)
(INCLUDING PLATYPSYLLIDAE)

Alfred F. Newton, Jr.,
Field Museum of Natural History

Mammal Nest Beetles

Figures 34.156–158

Relationships and Diagnosis: A close relationship of the louse-like *Platypsyllus* to *Leptinus* and allied genera has long been established (*see* Wood 1965). It is also clear that leptinids are very closely allied to leiodids, and the family is included as a subfamily in some recent, expanded concepts of Leiodidae (Crowson 1981, Lawrence and Newton 1982).

Platypsyllus larvae are easily recognized by their obligate association with beavers (*Castor* spp.) and by their peculiar mandibles with ventrally-directed apices and 1-segmented urogomphi. Larvae of the other 3 leptinid genera closely resemble leiodid larvae but differ in having a scooplike apex of the lacinia. They differ from larvae of other Coleoptera in the same way as Leiodidae (q.v.).

Biology and Ecology: All leptinids are associated with mammal hosts as far as known. In *Leptinus* species the association is a loose one; the life cycle is completed in the nests of a variety of ground-dwelling mammals, but adults are frequently found in other habitats and the species are apparently not host-specific. The other 3 genera are host-specific ectoparasites of semiaquatic mammals, as follows: *Silphopsyllus desmanae* Olsufiev on *Desmana moschata*, a Russian mole; *Leptinillus aplodontiae* Ferris on *Aplodontia rufa*, the mountain beaver; and *L. validus* (Horn) and *Platypsyllus castoris* Ritsema on beavers, *Castor* spp. Adults and larvae are apparently scavengers on the host or in the host nest (Wood 1965, Ising 1969).

Egg ovoid, white, smooth.

Pupa exarate, with functional abdominal spiracles on segments 1–2.

Description: Mature larvae about 2–6 mm long, elongate and more or less parallel-sided, slightly to strongly flattened, relatively straight. Body surfaces very lightly pigmented and sclerotized, smooth, with vestiture consisting of fine setae.

Head: Prognathous, protracted, without differentiated neck. Epicranial stem short, frontal arms lyriform (stem and arms not visible in *Platypsyllus*); endocarinae absent. Stemmata absent. Antenna 3-segmented, about 0.75 or (*Platypsyllus*) 0.25 times as long as head width, sensorium of preapical segment anterad or (*Platypsyllus*) dorsad of apical segment and conical or palpiform. Frontoclypeal suture absent. Labrum free, tormae present. Mandibles symmetrical, apex bilobed, incisor edge simple, mesal surface of base with mola bearing asperate surface, prostheca consisting of partly sclerotized lobe; or (*Platypsyllus*) mandibles with single tooth at ventrally directed apex, incisor edge simple, mesal surface of base with setose lobe, prostheca absent. Cardines transverse, divided by internal ridge, widely separated from each other by submentum. Stipes elongate. Mala large, fixed, divided apically into galea and lacinia, galea bearing pair of setal combs, lacinia with scooplike apex, or (*Platypsyllus*) mala undivided, rounded and setose at apex. Maxillary palp 3-segmented. Labium consisting of prementum, mentum and submentum, or prementum and postmentum. Ligula shorter than first palpal segment and quadrilobed or (*Platypsyllus*) longer than palp and rounded. Labial palps 2-segmented, separated by more than width of first palpal segment. Gula transverse or (*Platypsyllus*) absent. Occipital foramen divided into 2 parts by tentorial bridge.

Thorax and Abdomen: Thoracic terga and abdominal terga and sterna consisting of 1 or more sclerotized plates, without patches or rows of asperities, without lateral tergal processes. Legs 5-segmented including bisetose tarsungulus. Abdomen 10-segmented, more than twice as long as thorax. Tergum A9 with pair of 1- or 2-segmented urogomphi. Segment A10 visible from above, anal region terminally oriented, membranous anal lobes without teeth.

Spiracles: Annular, lateral or dorsolateral, closing apparatus present.

Comments: This small family includes 4 genera: the Holarctic *Platypsyllus* (1 species, *castoris* Ritsema) and *Leptinus* (9 species, 3 in North America); the North American *Leptinillus* (2 species); and *Silphopsyllus desmanae* Olsufiev from the USSR. Larvae of all 4 genera have been described; see Böving and Craighead (1931) and Wood (1965) for North American species. The family is of no known economic importance.

Selected Bibliography

Arnett 1968 (adult classification).
Böving and Craighead 1931.
Casale 1975.
Crowson 1981.
Ising 1969.
Lawrence and Newton 1982.
Neumann and Piechocki 1984, 1985.
Parks and Barnes 1955.
Peck 1982 (*Leptinus* adult classification).
Peterson 1951.
Reid 1942a.
Semenov-Tian-Shansky and Dobzhansky 1927.
Wood 1965.

SCYDMAENIDAE (STAPHYLINOIDEA)

Alfred F. Newton, Jr.,
Field Museum of Natural History

Figures 34.159–167

Relationships and Diagnosis: Scydmaenids have long been recognized as a distinctive family of Staphylinoidea, although their precise relationships remain controversial. They have been considered related to leiodids (e.g., Brown and Crowson 1980), to pselaphids (e.g., Böving and Craighead 1931), and to certain groups of "higher" Staphylinidae (Lawrence and Newton 1982).

The diversity of body forms and absence of any distinctive common characteristics can make scydmaenid larvae difficult to recognize. Most larvae can be recognized by common possession of the following characteristics: size small (under

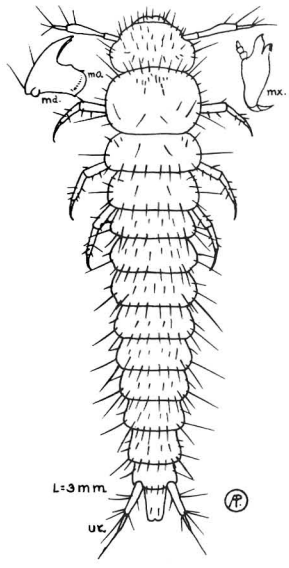


Figure 34.156

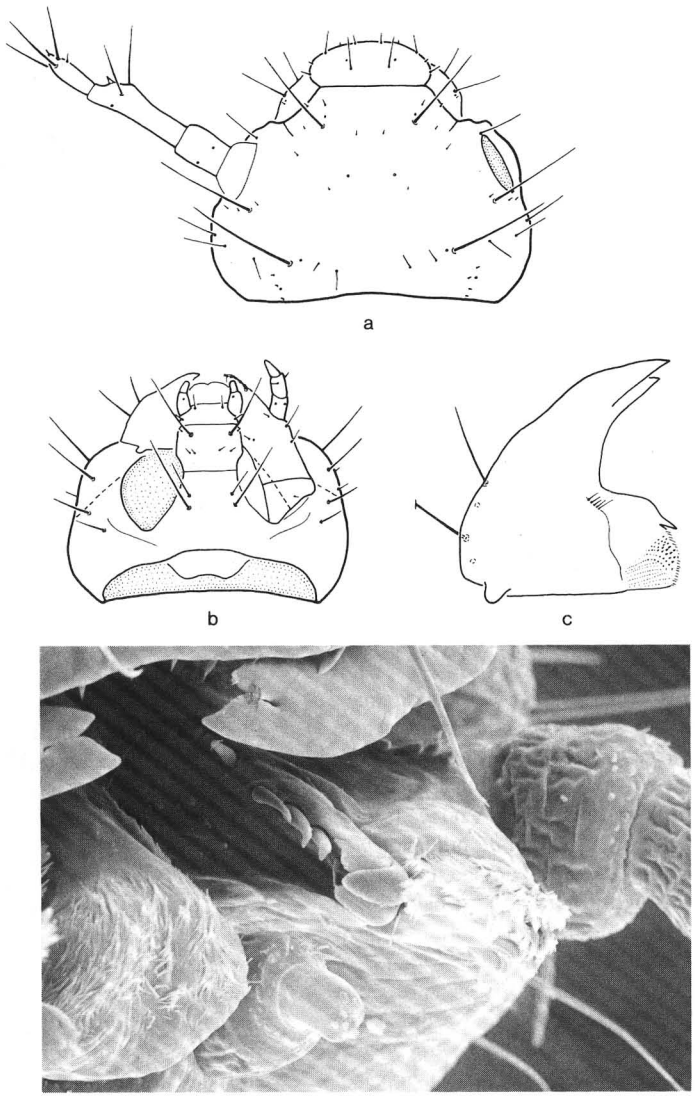


Figure 34.157

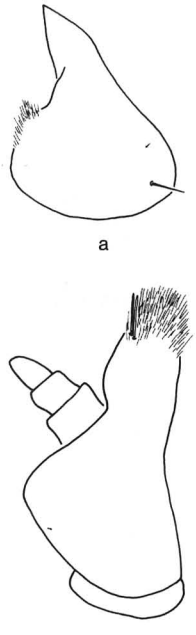


Figure 34.158

Figure 34.156. Leptinidae. *Leptinus* sp. Larva, dorsal. Length = 3 mm. (From Peterson 1951).

Figures 34.157a-d. Leptinidae. *Leptinillus validus* (Horn). Gatineau Park, Quebec; November; on beaver. **a.** mature larva, head, dorsal, right antenna not shown; **b.** head, ventral, right maxilla not shown; **c.** right mandible, ventral; **d.** left maxilla, anteromesal view of apex of lacinia and galea.

Figures 34.158a,b. Leptinidae. *Platypsyllus castoris* Ritsema. Alameda, California; November; on beaver. **a.** mature (?) larva, left mandible, ventral; **b.** right maxilla, ventral.

5 mm long); head lacking differentiated neck; stemmata 3 or fewer on each side, in close cluster; antenna large, often club-shaped; labrum fused to head capsule; mandible falcate, usually with single mesal edge bearing several, 1, or no teeth; mala large, fixed, rounded or blunt at apex and sometimes bilobed; ligula absent; and urogomphi fixed and very short (except Eutheiini) or absent. They are most easily confused with pselaphid larvae, but lack eversible glandular structures between the antennae, have the principal antennal sensorium conical to domelike and more or less anterior in position rather than palpiform or complex and differently situated, and have tibiae gradually tapered rather than abruptly narrowed apically. Faronine pselaphid larvae, which resemble scydmaenids in these respects, have large fixed urogomphi and a palpiform antennal sensorium while the only scydmaenids with large urogomphi (Eutheiini) have a domelike sensorium.

Biology and Ecology: Scydmaenids are fairly common inhabitants of forest floor litter, mosses, rotting logs, tree holes, sawdust piles and similar habitats, and a few species occur in mammal or ant nests and caves. Adults and larvae are believed to be predatory on mites and other small organisms in

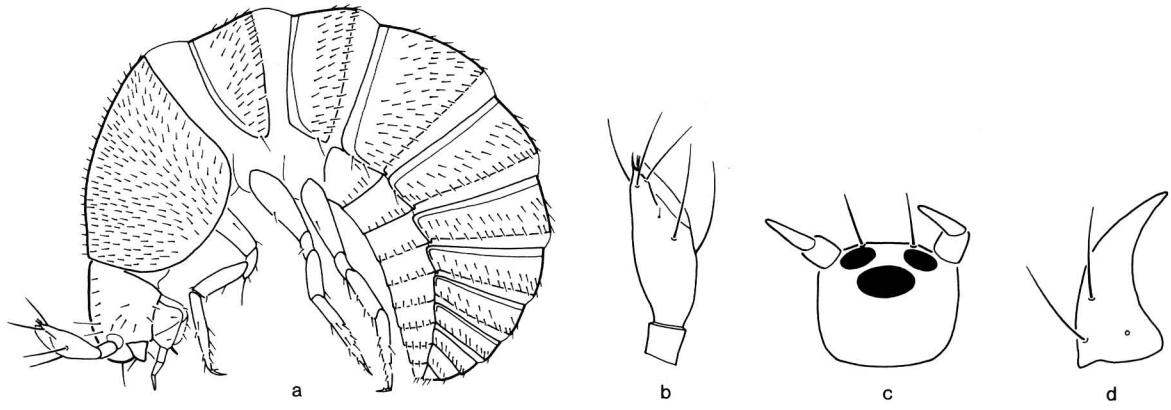


Figure 34.159

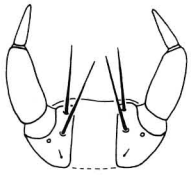


Figure 34.160

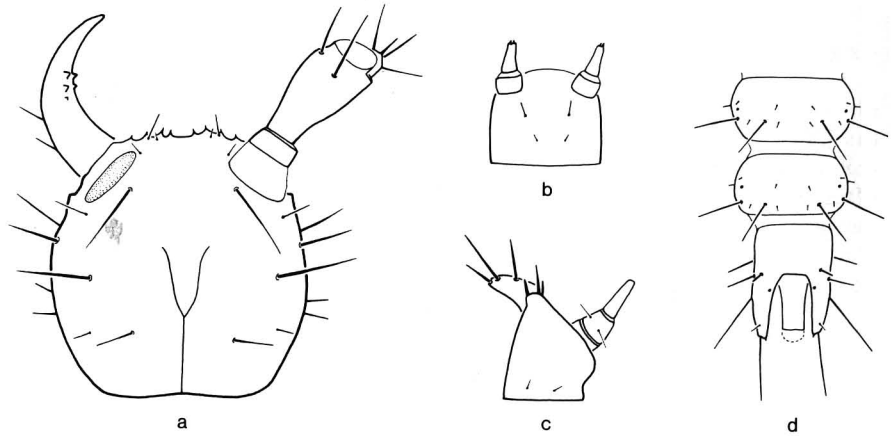


Figure 34.161

Figure 34.162

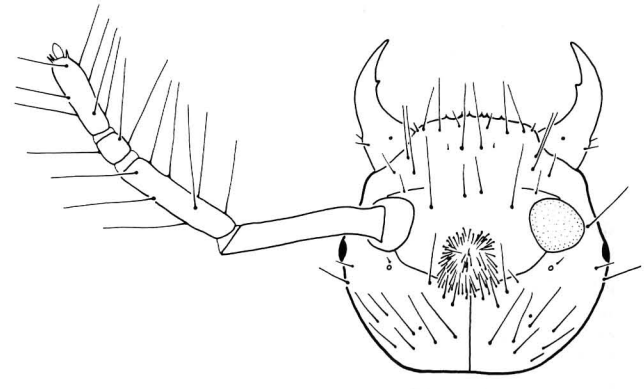


Figure 34.163

Figures 34.159a-d. Scydmaenidae. *Coatesia* sp. (Cephenniini). Lord Howe Island, Australia; May; in forest litter. Length = 1.0 mm. **a.** mature larva, lateral; **b.** right antenna, ventral; **c.** prementum, anterodorsal, showing apparent adhesive discs in black; **d.** left mandible, dorsal.

Figure 34.160. Scydmaenidae. *Mastigus ruficornis schimitscheki* Mach. (Mastigini). Bolu (25km east), 1000m, Turkey; May. Prementum, ventral.

Figures 34.161a-d. Scydmaenidae. *Veraphis* sp. (Euthiini). Crane Flat (1.9 miles east), 6600 feet, Mariposa County, California; May; in forest litter. **a.** head, dorsal, left antenna not shown; **b.** prementum, ventral; **c.** left maxilla, ventral; **d.** abdominal apex, dorsal.

Figures 34.162a,b. Scydmaenidae. *Scydmaenus* sp. (Scydmaenini). Madden Preserve, Panama; June; in refuse deposit of *Atta* sp. **a.** abdominal apex, dorsal; **b.** head, ventral, right maxilla not shown.

Figure 34.163. Scydmaenidae. *Mastigus ruficornis schimitscheki.* Head, dorsal, right antenna not shown.

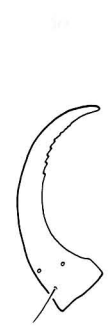


Figure 34.164

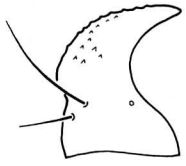


Figure 34.165

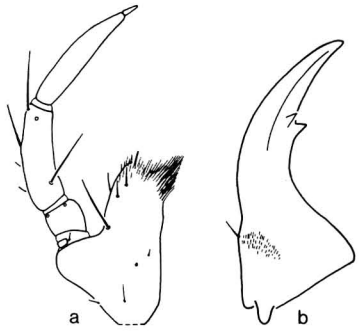


Figure 34.166

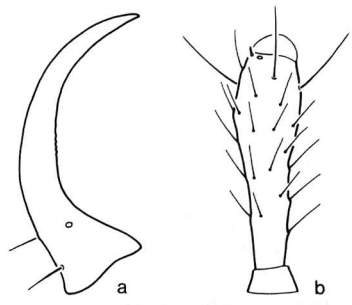


Figure 34.167

Figure 34.164. Scydmaenidae. *Stenichnus collaris* Müller and Kunze (Stenichnini). Praz-de-Fort, 1200m, Switzerland; June; in mosses. Left mandible, dorsal.

Figure 34.165. Scydmaenidae. *Cephennium thoracicum* Müller (Cephenniini). Veytaux, Switzerland; October; at base of chestnut tree stump. Left mandible, dorsal.

Figures 34.166a,b. Scydmaenidae. *Mastigus ruficornis schimitscheki.* **a.** right maxilla, ventral; **b.** right mandible, ventral.

Figures 34.167a,b. Scydmaenidae. *?Euconnus* sp. (Euconnini). Tallahassee, Florida; March; in forest litter. **a.** left mandible, dorsal; **b.** left antenna, dorsal.

these habitats, but published observations are few. Adults and larvae of at least some species of *Cephennium* are known to specialize on oribatid mites; larvae "stick" the mite to their mouths (possibly with apparently adhesive labial discs described below) and rasp a hole in the mite with the rough outer edges of the mandibles (Schuster 1966a, b). Early instar larvae of *Mastigus pilifer* Kraatz feed only on a secretion left by the female, but final instar larvae leave the oviposition site to feed (DeMarzo, 1983). Egg ovoid, orange, smooth (DeMarzo, 1983). Pupa exarate (DeMarzo, 1984).

Description: Mature larvae about 2–5 mm long. Form very variable, from elongate, parallel-sided, straight and slightly flattened to ovate, ventrally curved and capable of rolling into a ball, to broadly ovate and strongly flattened, disclike. Body surfaces moderately to lightly pigmented and sclerotized, rarely darkly pigmented dorsally; smooth or microspinose; vestiture of fine setae only or including long bristles or complex setae.

Head: Prognathous, protracted and visible from above or (Cepheniini and a few other species) retracted and concealed from above by prothorax; without differentiated neck. Epicranial stem moderately long, frontal arms V- or U-shaped; endocarinae absent or median endocarina present at base of stem. Stemmata on each side 3 (in close triangle or nearly fused) or 1 or absent. Antenna of 2, 3 or (*Mastigus*) 4 segments, about half or more as long as head width, often apically thickened and club-shaped; sensorium of second segment anterad or anterodorsad of apical segment or its unarticulated remnant (in *Mastigus* at apex of fourth segment), conical or domelike. Frontoclypeal suture absent. Labrum fused to head capsule, forming nasale which may bear numerous small teeth. Mandibles symmetrical, narrow and falcate, apex with single tooth; incisor edge simple, serrate, with 1 or 2 small teeth, or with 1 to several teeth on each edge of double mesal edges; mesal surface of base simple, mola and prostheca absent (outer edge of apical half of mandible tuberculate in *Cephennium*). Cardines transverse to strongly oblique, undivided, separated from each other by submentum, or cardines mesally fused to submentum. Stipes elongate to transverse. Mala large, fixed, apically rounded or truncate, setose, sometimes with fixed dorsomesal lobe. Maxillary palp usually 3-segmented but 2- and 4-segmented in *Eutheia* and *Mastigus,* respectively. Labium consisting of prementum, mentum and submentum. Ligula absent. Labial palps 2-segmented, separated by much more than width of first palpal segment. Adoral surface of prementum with 2 or 3 adhesive (?) discs in Cepheniini and some other species. Gular sutures absent or partly or completely fused, gula absent. Occipital foramen not divided by tentorial bridge which, if evident, originates from posterior arms of tentorium.

Thorax and Abdomen: Thoracic and abdominal terga and sterna consisting of 1 or more sclerotized plates, without patches or rows of asperities; with or without lateral tergal processes; sterna rarely membranous. Legs long, 5-segmented including bisetose tarsungulus which in Stenichnini also bears fine subapical spines; tibiae evenly tapered to apex. Abdomen 10-segmented or apparently 9-segmented, slightly longer to more than twice as long as thorax. Tergum A9 variable in shape, sometimes pear-shaped, usually without urogomphi but sometimes with fixed pair of minute and spiniform or (Eutheiini) long and thick urogomphi. Segment A10 distinct and visible from above, anal lobes with or without several hooks (segment 10 invaginated or apparently absent in Cephenniini).

Spiracles: Annular, lateral or dorsolateral, elevated or not, closing apparatus present; spiracles of 1–4 apical abdominal segments atrophied in some species.

Comments: The family is large and widely distributed, with over 3600 known species worldwide, mostly from warm temperate and tropical regions; nearly half of these species are placed in the single broadly defined genus *Euconnus.* About 13 genera and 180 species are found in the United States and Canada. The species are relatively common but of no economic importance.

Scydmaenid larvae are poorly known. The most recent and complete key to genera (8) is that of Brown and Crowson (1980) as modified by DeMarzo (1984); a few North American species of the same genera are described by Böving and Craighead (1931) and Wheeler and Pakaluk (1983). A detailed description of all three larval instars and the pupa of *Mastigus* is given by DeMarzo (1984). The present treatment is based on the known genera plus *Veraphis, Coatesia* and several unidentified larval types probably belonging to *Euconnus* (*sensu lato*).

Selected Bibliography

Arnett 1968 (adult classification).
Böving and Craighead 1931.
Brown and Crowson 1980.
DeMarzo 1983, 1984.
Hayashi 1986 (unidentified larva).
Jeannel and Paulian 1945 (*Scydmaenus* larva).
Kasule 1966 (family characterization).
Kistner 1982.
Klausnitzer 1978.
Lawrence and Newton 1982.
Paulian 1941.
Schuster 1966a, b.
Wheeler and Pakaluk 1983.

MICROPEPLIDAE (STAPHYLINOIDEA)

Alfred F. Newton, Jr.,
Field Museum of Natural History

Figures 34.168-169

Relationships and Diagnosis: Micropeplids have always been closely associated with staphylinids and are often treated as a subfamily of Staphylinidae, placed in the vicinity of Proteininae. Separation of the 2 families is based largely on the unusual (for Staphylinidae) habitus and mouthpart structure of *Micropeplus* larvae.

Known micropeplid larvae have a very distinctive habitus which, in combination with the small size (under 3 mm long) and mouthpart structure (including characteristic mandibles and maxillae) will separate them from other beetle larvae (*see* figures).

Biology and Ecology: Most species of *Micropeplus* and *Pelomicrus* are found in forest floor litter, but a few species of the former genus are apparently restricted to nests of certain mammals such as wood rats and beavers. *Kalissus nitidus* LeConte has been found on the pebbly or muddy margins of lakes, and at least 1 species of *Micropeplus* (*sculptus* LeConte) inhabits swamps and bogs (Campbell 1968). The biology of the family is poorly known, although Hinton and Stephens (1941b) found that larvae and adults of some *Micropeplus* species fed primarily on mold spores and hyphae. These feeding habits may be normal for the family; records from fruiting bodies of higher fungi are probably accidental (Newton 1984).

Egg unknown.

Pupa exarate, with functional abdominal spiracles on segments 1–2.

Description: Mature larvae about 2–3 mm long, oblong to ovate, relatively straight, moderately flattened. Body surfaces moderately to very lightly pigmented and sclerotized, generally spinose, with sparse vestiture including expanded setae or very long tapered setae.

Head: Hypognathous, protracted, without differentiated neck. Epicranial sutures indistinct, stem absent, frontal arms V-shaped, their bases separated or contiguous; endocarinae absent. Stemmata absent. Antenna 3-segmented, about a third to half as long as head width, sensorium of preapical segment longer than and anteroventrad of apical segment, palpiform. Frontoclypeal suture absent. Labrum free, tormae absent. Mandibles symmetrical, short and stout, each with single apical tooth and large subapical pseudomola bearing 2 or more coarse teeth; mesal surface of base simple, mola and prostheca absent. Cardines transverse, divided by internal ridge, widely separated by submentum. Stipes elongate. Mala large, fixed, divided at apex into articulated galea and fixed lacinia; galea with 2 membranous fringed lobes; lacinia falcate, with single apical spur and spinose mesal edge. Maxillary palp 3-segmented. Labium consisting of prementum, mentum and submentum. Ligula longer than first palpal segment, broadly rounded. Labial palps short, 2-segmented, separated by much more than width of first palpal segment. Gular sutures absent. Occipital foramen not divided by tentorial bridge, which arises from posterior margin of head.

Thorax and Abdomen: Thoracic and abdominal terga and sterna consisting of 1 or more sclerotized plates; terga microspinose on disc to coarsely spinose along posterior margins, laterally bearing tergal processes consisting of a single lobe (abdominal segments 1–9) or bifid or trifid lobes (thorax). Legs short, 4-segmented including bisetose tarsungulus, femur and trochanter fused, tibiae with bifid setae. Abdomen 10-segmented, more than twice as long as thorax. Tergum A9 with fixed tergal lobe as in preceding segments, without articlated urogomphi. Segment A10 short, scarcely visible from above, anal region terminally oriented, membranous anal lobes with very fine teeth or spines.

Spiracles: Annular, lateral, at ends of short tubes below tergal lobes, closing apparatus present.

Comments: The family is small, with 4 genera and fewer than 60 species known worldwide: the Holarctic genus *Micropeplus*, including 15 species in North America; *Kalissus*, with a single species *nitidus* LeConte in British Columbia and Washington State; *Peplomicrus* with 7 species in tropical Central and South America and Africa, and *Cerapeplus* with one Oriental species (Campbell 1968, Löbl and Burckhardt 1988). The species are quite rare, and of no economic importance.

The larva of only 1 species, *Micropeplus staphylinoides* (Marsham), has been described (Lubbock 1868; Kasule 1966). Hinton and Stephens (1941b) have described the only known pupa, that of *M. fulvus* Erichson. Larvae of *M. fulvus* and *M. neotomae* Campbell have been examined for this treatment.

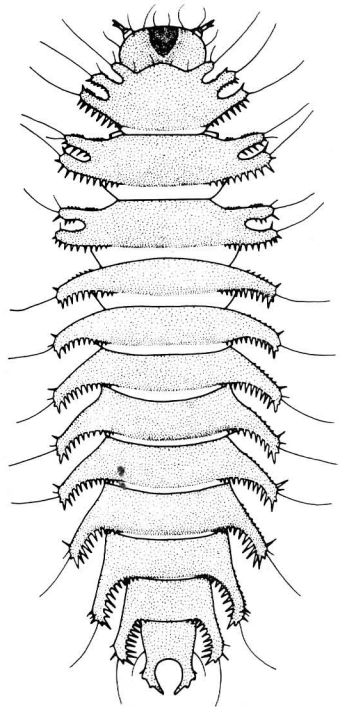


Figure 34.168

Figure 34.168. Micropeplidae. *Micropeplus neotomae* Campbell. Los Gatos (7.5 miles south), Santa Clara County, California; February; *Neotoma* house. Mature (?) larva, dorsal. Length = 3.0 mm.

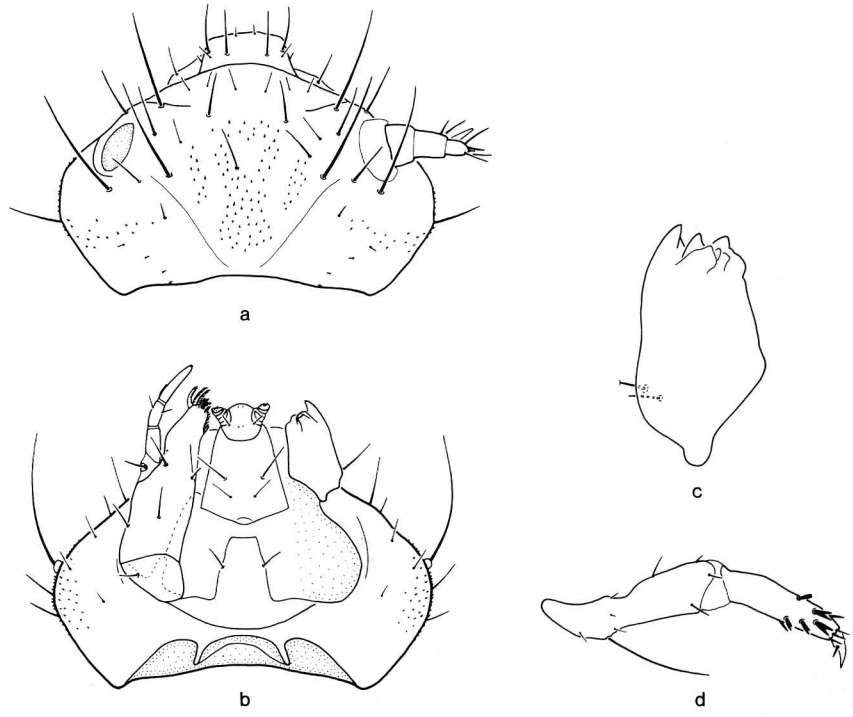


Figure 34.169

Figures 34.169a-d. Micropeplidae. Same species as figure 34.168. Suver Junction (1 mile north), Polk County, Oregon; March; ex fecal material, *Neotoma* nest. **a.** head, dorsal, left antenna not shown; **b.** head, ventral, left maxilla not shown; **c.** right mandible, ventral; **d.** left proleg, anterior.

Selected Bibliography

Campbell 1968 (adult classification, ecology).
Hinton and Stephens 1941b.
Kasule 1966.
Löbl and Burckhardt 1988 (adult classification).
Lubbock 1868.
Newton 1984.
Thayer 1987 (family relationships).
Topp *in* Klausnitzer 1978.

DASYCERIDAE (STAPHYLINOIDEA)

Alfred F. Newton, Jr.,
Field Museum of Natural History

Figures 34.170a-h

Relationships and Diagnosis: The genus *Dasycerus* was included in Lathridiidae until Crowson (1955) placed it tentatively as a family of Staphylinoidea. More recently it has been considered related to certain subfamilies of Staphylinidae (Lawrence and Newton 1982, Thayer 1987).

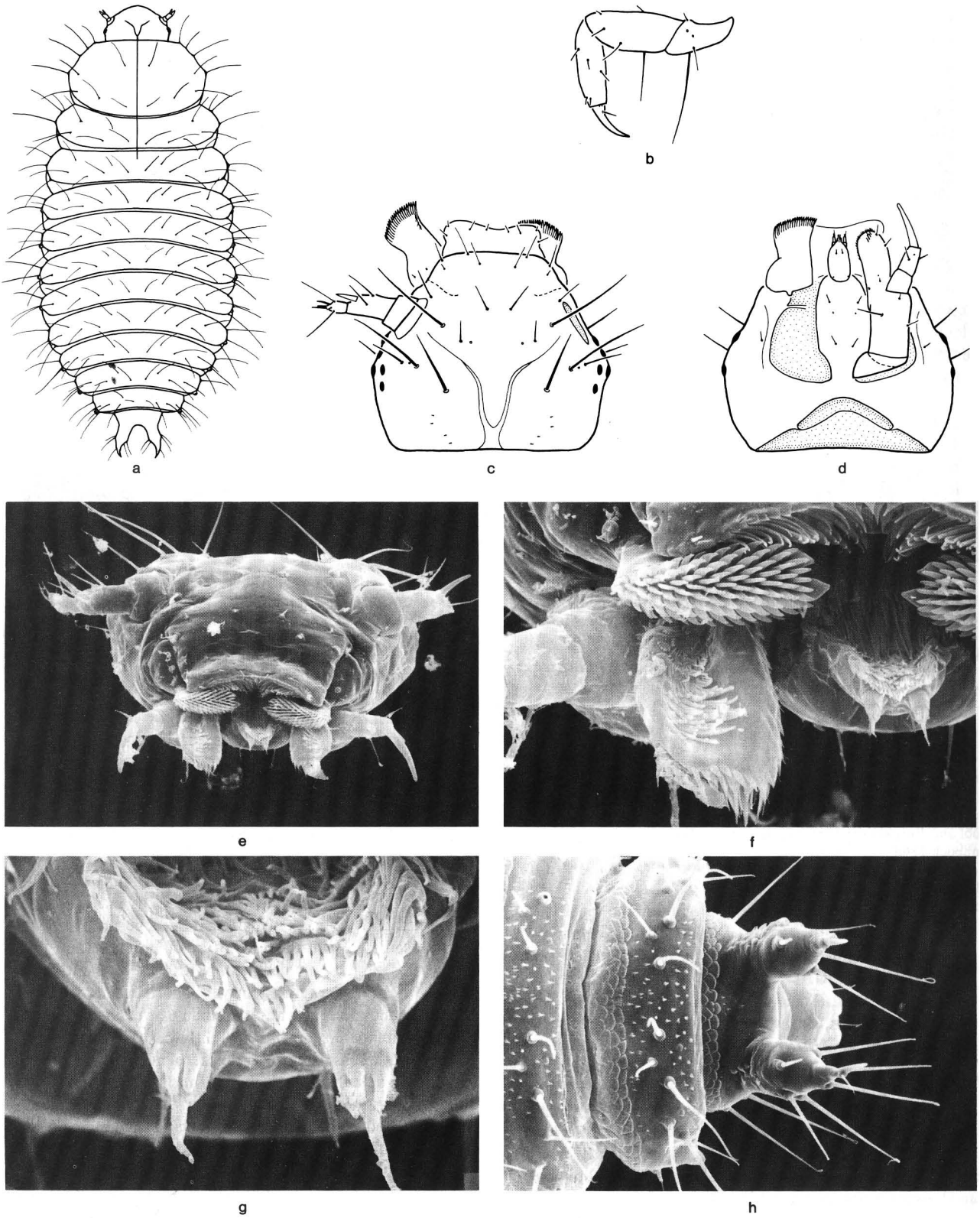
Larvae are easily recognized by the unique structure of their mandibles.

Biology and Ecology: The species, most of which are flightless, apparently inhabit forest floor litter or decaying trees. The only known large series of adults and larvae, of an undescribed North American species, was from the bark surface of a decaying log (*Aesculus* sp.) covered with *Stereum* sp., an undetermined ascomycete, lichens and moss. Food of adults and larvae remains uncertain but may include molds (Newton 1984, Wheeler 1984b).

Egg and pupa unknown.

Description: Mature larvae about 2–3 mm long, ovate, slightly or not at all flattened, straight. Body surfaces moderately to lightly pigmented and sclerotized, generally smooth or microspinose, with sparse vestiture of simple setae.

Head: Moderately declined, protracted, without differentiated neck. Epicranial stem very short, frontal arms V-shaped; endocarinae absent. Stemmata 6 on each side, widely spaced. Antenna 3-segmented, slightly less than half as long as head width, sensorium of preapical segment anterad of and longer than apical segment, palpiform. Frontoclypeal suture absent. Labrum free, tormae absent. Mandibles symmetrical, short and stout, apex of each truncate and bearing dense array of slender teeth, incisor edge and base simple, mola and prostheca absent. Cardines transverse, divided by internal ridge, widely separated by submentum. Stipes elongate. Mala large, fixed, with rounded setose apex. Maxillary palp 3-segmented. Labium consisting of prementum, mentum and submentum. Ligula nearly as long as palp, with long setae. Labial palps short, 2-segmented, separated by much more than



Figures 34.170a-h. Dasyceridae. *Dasycerus* n. sp. Ramsey Cascade Trail, 3900 feet, Great Smoky Mountains National Park, Tennessee; May; on bark of log of *Aesculus* sp. covered with *Stereum* sp., an undetermined ascomycete, lichens and moss. Length = 2.0 mm. **a.** penultimate instar (?) larva, dorsal; **b.** right proleg, anterior; **c.** head, dorsal, right antenna not shown; **d.** head, ventral, right maxilla not shown; **e.** head, anterior; **f.** head, anterior, detail of maxilla, mandible; **g.** head, anterior, detail of labium; **h.** abdominal apex, dorsal.

width of first palpal segment. Gula transverse. Occipital foramen not divided by tentorial bridge, which arises from posterior edge of head.

Thorax and Abdomen: Thoracic and abdominal terga and sterna consisting of 1 or more sclerotized plates; terga microspinose. Legs short, 5-segmented including bisetose tarsungulus. Abdomen 10-segmented, less than twice as long as thorax. Tergum A9 with pair of large fixed urogomphi with spine at apex. Segment A10 scarcely visible from above, anal region terminally oriented, membranous anal lobes without hooks or teeth.

Spiracles: Annular, lateral, slightly elevated, closing apparatus present.

Comments: The family includes the single genus *Dasycerus,* with 10 species in Eurasia and 3 from the United States: 1 from California and 2 (1 undescribed) from the southern Appalachian Mountains. The species are rare and of no economic importance.

Larvae have not been previously described. The present treatment is based on larvae associated with the undescribed Appalachian species and with *D. japonicus* Nakane.

Selected Bibliography

Crowson 1955.
Lawrence and Newton 1982.
Löbl 1977 (revision, adult ecology).
Newton 1984.
Thayer 1987 (family relationships).
Wheeler 1984b.

SCAPHIDIIDAE (STAPHYLINOIDEA)

Alfred F. Newton, Jr.,
Field Museum of Natural History

Shining Fungus Beetles

Figures 34.171-176

Relationships and Diagnosis: Scaphidiids have generally been considered closely related to staphylinids, and have recently been placed in the vicinity of a group of staphylinid subfamilies including Piestinae, Osoriinae and Oxytelinae (Kasule 1966, Lawrence and Newton 1982); Kasule (1966) and Lawrence (1982c), in fact, reduced them to a subfamily of Staphylinidae.

Scaphidiid larvae can usually be recognized by a combination of a toothed or crenulate emargination of the anterior margin of the labrum, mandibles without basal molar lobes, but often with subapical dentate or spinose lobes, and articulated urogomphi which may be minute or (some *Baeocera* species) absent. The crenulate labral emargination is absent from the otherwise similar larvae of certain Staphylinidae. The association with fungi of various kinds and the usual presence of 5 well separated stemmata on each side of the head are also useful recognition traits.

Biology and Ecology: Adults and larvae are associated with and feed on fungi of various kinds, as follows: *Scaphidium, Toxidium,* most *Scaphisoma* and some *Baeocera* species on hyphae of tree fungi (Polyporales); *Cyparium, Scaphium* and some *Scaphisoma* species on hyphae of mushrooms and coral fungi (Agaricales and Clavariaceae); and *Scaphobaeocera* and most *Baeocera* species on fruiting bodies of slime molds (Myxomycetes) (Lawrence and Newton 1980, Newton 1984; Ashe, 1984a). Larval development in *Baeocera* is very rapid, taking only a few days of feeding on the spores of the short-lived host, but life histories have not been worked out in detail for any scaphidiid species.

Egg oval, white, smooth.

Pupa exarate, with functional abdominal spiracles on segments 1–3.

Description: Mature larvae about 2–12 mm long, elongate and more or less parallel-sided to ovate, slightly or not at all flattened, straight or slightly curved ventrally. Body surfaces moderately or lightly pigmented and sclerotized, smooth, with sparse vestiture of simple setae.

Head: Prognathous or slightly declined, protracted or slightly retracted, without differentiated neck. Epicranial stem moderately long, frontal arms V-shaped or lyriform, sometimes joined anteriorly by transverse line; endocarinae absent. Usually 5 well separated stemmata on each side, sometimes 6 or (*Cyparium*) 3. Antenna 3-segmented, about half or more as long as head width, sensorium of preapical segment anterad of apical segment and conical or palpiform. Labrum free, anterior edge with crenulate emargination; tormae absent. Mandibles symmetrical, broad and stout, apex of each bilobed or with a single lobe, incisor edge serrate and sometimes with a subapical pseudomola bearing teeth or spines, mesal surface of base simple, mola and prostheca absent. Cardines transverse, internally divided, separated from each other by submentum or postmentum. Stipes elongate. Mala large, fixed, falcate, apex glabrous and with single large tooth, mesal edge spinose. Maxillary palp 3-segmented. Labium consisting of prementum, mentum and submentum, or prementum and postmentum only. Ligula shorter or slightly longer than first palpal segment, transverse, and rounded, truncate, or obtusely pointed at apex. Labial palps 2-segmented, separated by width of first palpal segment or more. Gular sutures absent. Occipital foramen not divided by tentorial bridge, which arises from posterior arms of tentorium.

Thorax and Abdomen: Thoracic and abdominal terga and sterna consisting of 1 or more sclerotized plates, without patches or rows of asperities. Legs long, 5-segmented including bisetose tarsungulus. Abdomen 10-segmented, about twice or more as long as thorax. Tergum A9 with pair of 1- or 2-segmented urogomphi which may be minute or (some *Baeocera* species) absent. Segment A10 visible from above, anal region terminally oriented, membranous anal lobes bearing numerous fine teeth.

Spiracles: Annular, lateral or dorsolateral, closing apparatus present.

Comments: The family is moderately large, with 50 genera and over a thousand species known from throughout the world, especially from warm temperate and tropical areas. About 60 species, placed in 7 genera, occur in North America. Many species are commonly encountered on fungi; none are of any known economic importance.

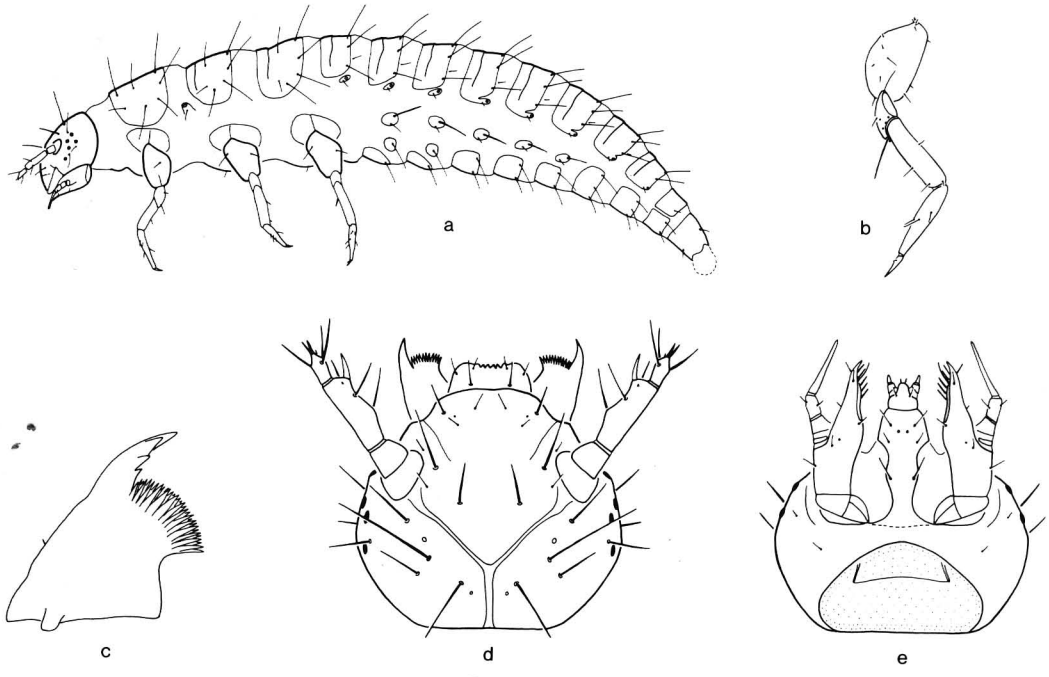


Figure 34.171

Figure 34.172

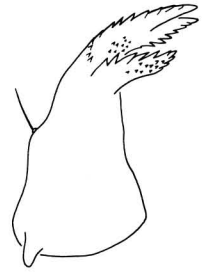


Figure 34.173

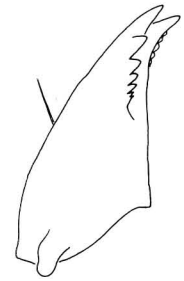


Figure 34.174

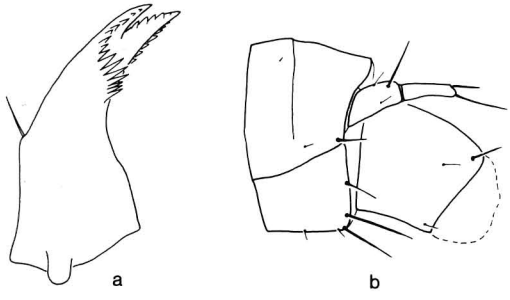
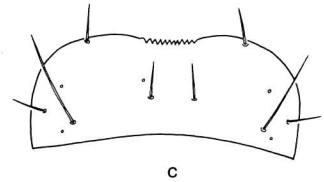


Figure 34.175



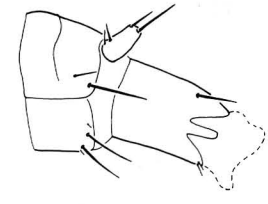


Figure 34.176

Figures 34.171a-e. Scaphidiidae. *Baeocera picea* Casey. Bedford, Massachusetts; August; on slime mold, *Ceratiomyxa fruticulosa*. Length = 2.6 mm. **a.** mature larva, lateral; **b.** right proleg, posterolateral; **c.** right mandible, ventral; **d.** head, dorsal; **e.** head, ventral.

Figure 34.172. Scaphidiidae. *Scaphisoma* sp. Manchester, Vermont; September; on coral fungus, *Clavaria coronata*. Right mandible, ventral.

Figure 34.173. Scaphidiidae. *Cyparium terminale* Matthews. Tenancingo, Mexico; September; on coral fungus, *?Clavaria* sp. Right mandible, ventral.

Figure 34.174. Scaphidiidae. *Scaphidium* sp. Cerro Azul, Panama; June; on fungusy log. Right mandible, ventral.

Figures 34.175a-c. Scaphidiidae. *Scaphium castanipes* Kirby. George Lake, Alberta; August; on mushroom, *Cortinarius* sp. **a.** right mandible, ventral; **b.** abdominal apex, lateral; **c.** labrum, dorsal.

Figure 34.176. Scaphidiidae. *Cyparium terminale*. Abdominal apex, lateral.