

Fig. 7.7.4. Larval head structures. A, nasale and adnasalia, *Systolosoma lateritium*, *S. breve*, *Trachypachus holmbergi*; B, antennae, *S. lateritium*, *T. holmbergi*; C–E, *S. lateritium*. C, mandible; D, maxilla. E, labium; F–H, tergite IX. F, *S. lateritium*; G, *T. holmbergi*; H, *S. breve*. From Beutel & Arndt (1995), redrawn.

morphies (Arndt & Beutel 1995): sensorial appendage on lateral side of antennomere III absent, replaced by ventral sensorial field, apical part of maxillary palpomere 3 with additional setae, number of nasal teeth increased (6–8), urogomphi fixed, horn-shaped (groundplan), eight long setae on tergite IX (including those on urogomphi). The specific shape of the parameres (Lindroth 1961–69; Beutel 1994) is an autapomorphy of adults. The absence of the katasigma, the specific sculpture of the elytra, the kidney-shaped sensorial field of the larval antennomere 3 and the large, ventral sensorial field of antennomere 4 are larval autapomorphies of *Systolosoma*. The dilated larval distal maxillary palpomere with two separated sensorial fields is an autapomorphy of *Trachypachus*.

Acknowledgements

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7.8. Carabidae Latreille, 1802

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In most recent classifications Rhysodidae (-ni), Cicindelinae and Paussinae are included. However, Rhysodidae were excluded by Kryzhanovskij *et al.* (1995) and Lawrence & Newton (1995). They are tentatively treated as a separate family here (s. 1–7.9).

Distribution. World-wide (except Antarctica), more than 40000 spp. and 1500 genera. Distribution of subgroups see below.

Biology and Ecology. Carabidae live in all terrestrial habitat types from the subarctic to the wet tropical regions. The majority of species except those of tropical rain forests and subtropical montane forests (e. g., Mexico, Hawaii) is ground

dwelling. Adults and larvae live in soil, in leaf litter or are active on the ground surface, sometimes climbing bushes or plants. Many species, mainly in Trechini, Anillini and Platynini, inhabit caves or deep soil microcaves (mss). Even though many species occur in moist habitats, an amphibious way of life is reported in only very few cases (e.g., *Carabu variolosus* at small streams in *Fagus* forests, *C. clathratus* and some other *Carabus* species in swamps; Sturani 1962; Cicindelinae in inundation forests; Adis & Messner 1997; *Rawlinsius* in shallow regions of rapid mountain streams; Davidson & Ball 1998). A large percentage of species in tropical rain forests and subtropical montane forests, and few species in temperate regions are arboreal and resting under leaves or bark. The majority of carabid species is able to fly and has a great dispersal power. Some species are dimorphic regarding their wing and muscle development; usually the minority of individuals is wingless (e.g., most *Carabus*, Anthiini). Even species exclusively moving on the ground have an enormous dispersal power; migrations of 77 m per night and running speeds of 0.16 m/s were estimated in *Carabus* species (Thiele 1977). Carabid beetles show a circadian rhythm and outside the tropical regions also an annual rhythm. The majority of species is nocturnal; some species change their activity dependent from climate or season but some taxa are active during day light (e.g., Cicindelini). The annual rhythm controls the reproductive period; different mechanisms of diapause are described for species of the temperate and subtropical regions (Paarmann 1979). During inactive periods in winter quarters or hiding places during day time, aggregations of several hundred specimens are possible.

Carabidae are bisexual. Females lay eggs (as far as known) separately or in small groups in small hollows in substrate or under bark or in cases made of mud (King 1919; Thiele 1977) or algae and bark (Will 1998). The number of eggs per female varies between four and several hundreds depending on the species (the highest numbers recorded are 653 for *Calosoma sycophanta*; Thiele 1977 and 660 for *Colpodes buchani*; Paarmann & Bolte 1990). The egg development lasts few days to several weeks. Most of the species have three larval instars. Exceptions are two larval instars in some representatives of Zabrinini, Harpalini, Lebiini and Anthiini (Bily 1975; Capogreco 1989; Arndt & Paarmann 1999), which is regarded as an adaptation to an arid environment, and four or five larval instars respectively in members of Lebiini and Brachinini (Erwin 1967, 1975), which is regarded as an adaptation to an ectoparasitic way of life. Pseudomorphini are ovoviviparous (Liebherr & Ka-

vanaugh 1985; Baehr 1997). Brood care occurs in some species of Pterostichini, were the females guard their eggs (Kavanaugh 1998) and in some species of Harpalini, where the female lay eggs in individual soil cells prepared with food stores. Pupation usually takes place in moist soil. The full-grown last instar larvae dig a pupal chamber using their head and legs. In one species (*Thermophilus sexmaculatum*) the first instar larva digs the pupal chamber, and the final second instar remains inactive in this chamber (Arndt & Paarmann 1999). The life span in the field is up to four years; at least carabids of the temperate regions live usually longer than one year.

Adults and larvae have a partial extraoral digestion. During the manipulation of the prey, mandibles and maxillae rotate the food item while digestive fluids are expelled onto it. Adults of most species are omnivorous (Larochelle 1990; Thiele 1977), even though carnivorous nutrition seems to prevail. A few groups are specialised herbivores, e.g., *Zabrus* and some representatives of Harpalini; even arboreal species of *Agra* were found to feed on flowers and nectar (Arndt *et al.* 2001). Much less is known on the feeding preferences of larvae, but carnivorous habits of the majority of species is likely. Larvae of several taxa are specialised on specific prey such as snails (Cychrini, Licinini), springtails (Nebriini, Notiophilini, Loricerini), ants, or ant brood (Anthiini, Graphipterini, Metriini, Ozaenini). Larvae of Paussini and Pseudomorphini are probably fed by ants and those of Lebiini and Brachinini are ectoparasitic on insect eggs and pupae as far as known. Larvae of Cicindelinae and Ozaenini live in burrows and lie in ambush for prey at the entrances. Larvae of several Harpalini are specialised on seeds (Brandmayr 1975; Zetto Brandmayr 1990; Arndt *et al.* 1996). Only very few ground beetles are known as pest insects. The grain ground beetle (*Zabrus tenebrioides*) is the only species of a certain economic importance, but it became known as serious pest only in a restricted period and restricted area in eastern Germany, Moravia and the Ukraine.

The ecological importance of the extremely diverse family Carabidae is not well understood. The ground beetles represent a major part of the invertebrate predator guild of the soil fauna, e.g., in temperate forests and agrocoenoses. Due to their abundance and ubiquitous occurrence, the importance of the role of carabids in these ecosystems can be safely assumed.

Insectivores, bats, rodents, birds, amphibians, reptiles, ants, Asilidae, and Aranea are known as predators of ground beetles. Sporozoa (Gregarinida), Nematoda (*Mermis*, *Hexameris*), Nematomorpha (*Gordius*) are endoparasites, and several taxa of mites (Trombidiformes, Sarcoptiformes) are known as ectoparasites on carabids.

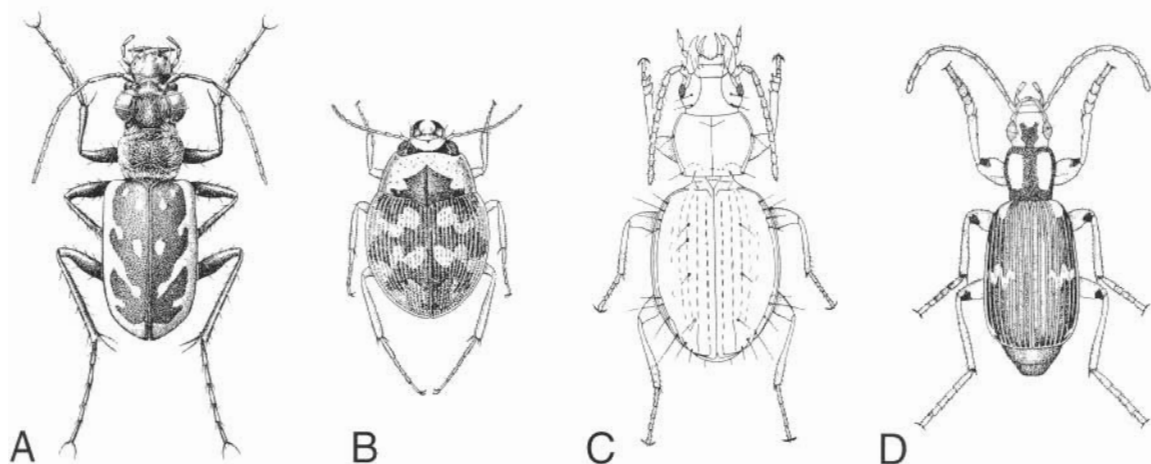


Fig. 7.8.1. Carabidae, habitus of adults of different subfamilies. A, *Lophyra sumlini* (Cicindelinae) (Cassola 1976); B, *Omophron aequale* (Omophroninae); C, *Trechus kurentzowi* (Trechinae); D, *Pheropsophus javanus* (Brachininae) (B–D Lafer, 1989).

Several other representatives of Acari (e. g., *Parasitus*) occur frequently on Carabidae but they are phoretic. Parasitoids of carabid larvae include the hymenopteran taxa *Proctotrupes* spp (Proctotrupidae; on Harpalinae and Carabinae), *Microtonus* spp (Braconidae; on Harpalinae), *Methocha* spp (Tiphidae; on Cicindelinae) and representatives of the dipteran families Larvaevoridae (on several subfamilies) and Bombyliidae (*Anthrax* spp; on Cicindelinae). Besides non-specific insect parasitizing fungi (Entomophthorales, Hypomycetes) 16 genera with several hundreds of species of Laboulbeniales (Ascomycota) infest carabids.

The following references summarise information on the biology of these beetles: Den Boer (1977), Thiele (1977), Laroche (1990), Lindroth (1992), Turin (2000).

Morphology, Adults (Figs. 7.8.1–7.8.3). 1–85 mm long. Usually flattened and elongate, with distinct pronoto-elytral angle, rarely with distinctly convex dorsal side and laterally evenly rounded (e. g., *Omophron*). Cuticle usually smooth and shiny. Colour black or dark in most species, sometimes metallic. Depigmentation of parts of the integument can result in conspicuous colour patterns (e. g., *Cicindela*, *Eurynebria*, Omophroninae, *Lebia*). Microsculpture usually present as a fine polygonal meshwork. Strongly impressed microsculpture decreases brilliance of cuticular surface. Long articulated setae (= 'macrochètes' *sensu* Jeannel 1941–42; fixed setae) distributed with regular patterns (chaetotaxy). Small articulated hairs with irregular distribution present or absent, sometimes forming pubescent surfaces.

Head (Figs. 7.8.2 A, 7.8.3.A) prognathous, relatively elongate, moderately retracted. Without distinct neck region. Frontal furrows present or absent. Compound eyes usually well developed

and protruding, but different degrees of reduction and total loss occur. Clypeus trapezoid, with two pairs of fixed setae. Supraocular area with one or two pairs of fixed setae and subocular genal area with one pair of setae. Gula fairly elongate, moderately broad, distinctly delimited by gular sutures, always glabrous, without fixed setae. Median gular apodeme present or absent. Tentorium with all parts well developed, usually with median laminatentorium. Labrum variable in shape, transverse, medially emarginate, bilobed or rarely trilobed. Anterior margin with six or eight fixed setae. Anterolateral margin usually with shorter curved setae. Ventral side largely unsclerotized and covered with sensorial structures, with shallow excavations adapted to the convex dorsal surface of the mandibles. Antennae almost always filiform and 11-segmented, usually inserted below lateral frontal projection, rarely inserted on dorsal side of head capsule (Cicindelinae). Pubescence present on antennomeres 4–11 or 3–11, sometimes also on basal segments but then less dense than on distal antennomeres. Mandibles with basic form of a triangular pyramid, with dorsal, ventral and external surface, moderately to strongly (e. g., *Lecanomerus*; Acorn & Ball 1991: Fig. 16) elongate. Primarily with distinct apical tooth, terebral tooth, anterior retinacular tooth, posterior retinacular tooth, premolar or molar tooth, incisor ridge, terebral ridge, retinacular ridge, ventral groove with row of microtrichiae and basal brush (Acorn & Ball 1991). Maxillae composed of transverse, short cardo, which articulates with well developed fossa maxillaris, triangular basistipes, mediostipes, elongate triangular palpifer with several fixed setae, lacinia, galea and 4-segmented palp. Lacinia basally fused with mediostipes, hook-shaped, with dense row of mesally directed strong setae and thin hairs. Galea 2-segmented, palp-like. Palpomere I very short. Palpomeres 3 and 4 vary strongly in size, usually

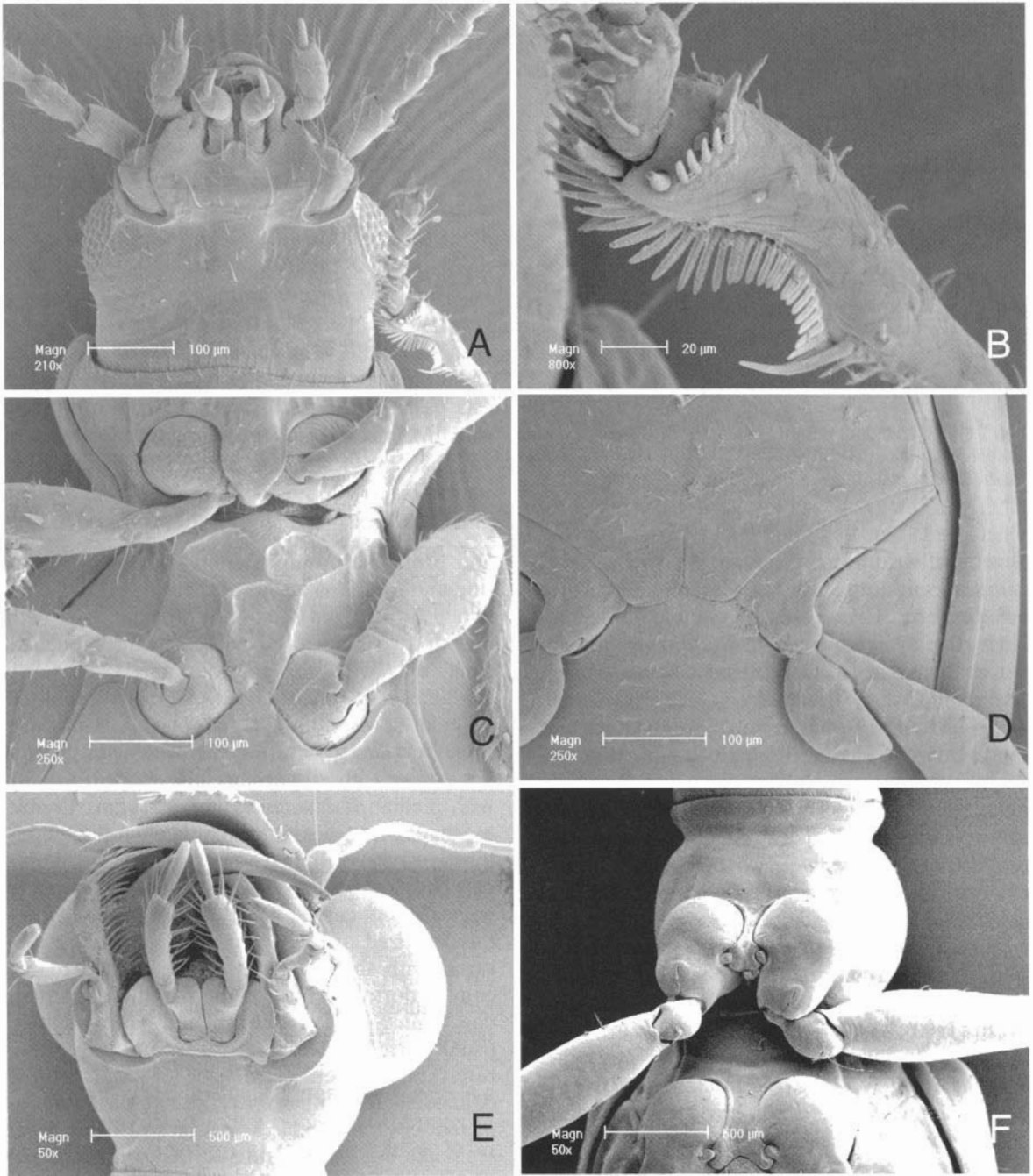


Fig. 7.8.2A–D, *Gehrungia olympiaca*, adults. A, head, ventral view; B, protibia with antenna cleaning organ; C, mesoventrite; D, metacoxae; E–F, *Therates waagenorum* Horn, 1900 (Cicindelinae), adult. E, head, ventral view; F, meso- and metaventrite.

in correlation with labial palpomeres 2 and 3. Submental part of labium T-shaped, fused with gula posteriorly. Transverse anterior part mesally delimits fossa maxillaris, with two or more pairs of fixed setae. Mentum with distinct lateral lobes and often with a more or less projecting median bifid or simple process, with one pair of fixed setae. Prementum variable in shape but usually roughly quadrangular, with sclerotized median part and more or less distinct, less strongly sclerotized lateral lobes (paraglossae). Anterior margin with one pair of long, fixed setae close to median line and sometimes additional shorter

lateral setae. Parallel-sided palpigera inserted between emargination of mentum and prementum. Palp, 3-segmented, with very short palpomere 1. Preoral cavity usually with well developed filter apparatus composed of rows of hairs on mandibles, maxillae, and hypopharynx.

Prothorax (Fig. 7.8.3 C) rounded laterally and more or less strongly narrowed posteriorly, distinctly narrower than elytra at posterior margin (with few exceptions, e.g., *Omophron*, Pseudomorphinae). Pronotum medially divided by longitudinal line, usually with raised lateral margin (indistinct or absent in *Dyschirius* and *Apotomus*)

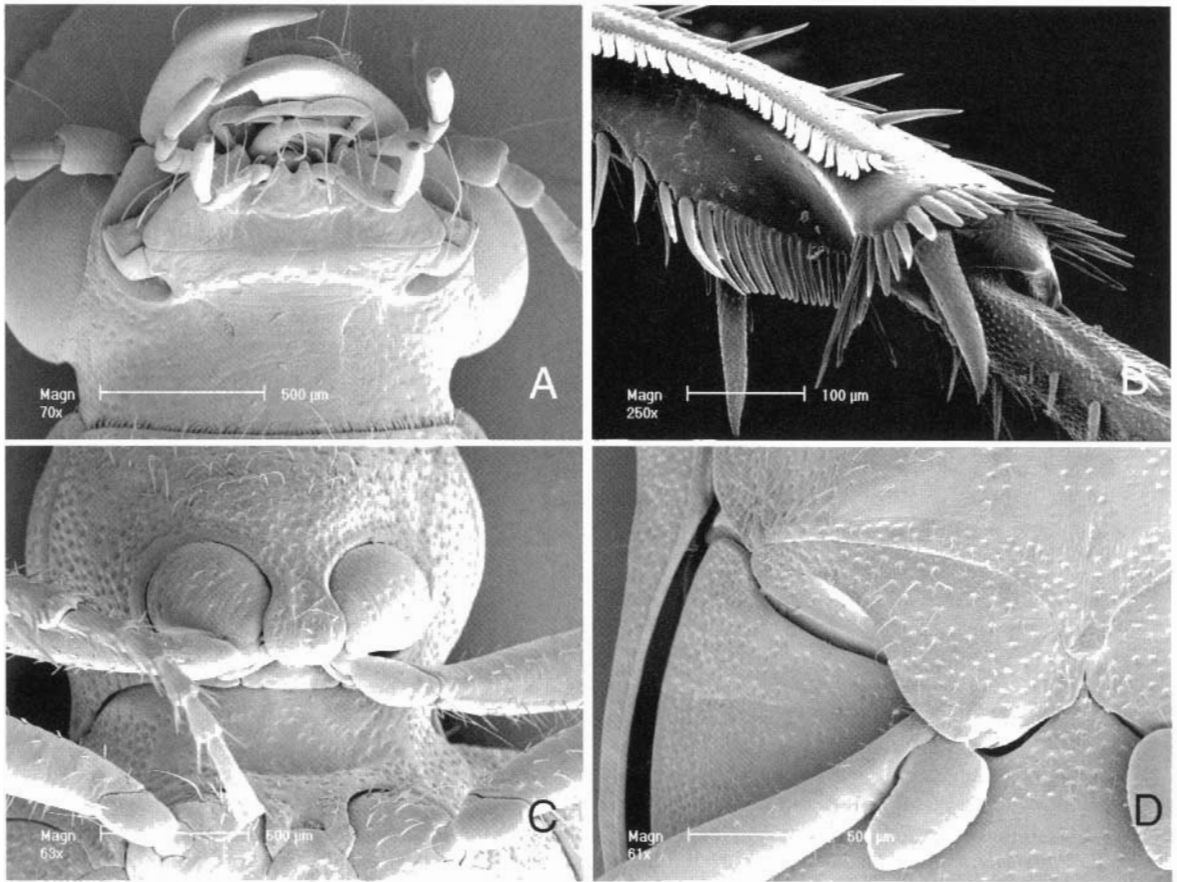


Fig. 7.8.3 A–D. *Elaphrus* sp., adults. A, Head, ventral view; B, protibia with antenna cleaning organ; C, Pro- and mesoventrite; D, Metacoxae.

and distinct basal impression. Lateral margin with two or more pairs of fixed setae, one of them located close to posterior margin. Prosternal process either narrow and short (*Gehringia*), strongly developed, projecting beyond the hind margin of the procoxae and tapering posteriorly (*Metrius*, Carabinae, Hiletinae), or shortened and posteriorly truncate (Paussinae excl. *Metrius*, Cicindelinae, Omophroninae, Elaphrinae, Loricarinae etc.). Procoxal cavities open, without internal postcoxal bridge (*Gehringia*, Carabinae, Hiletinae) or externally closed. Protibiae usually with two apical spurs, both inserted apically (Paussinae [= "Isochaeta"], Cicindelinae, Opisthiini, Carabini) or one spur shifted proximally ("Anisochaeta"). Antennal cleaning (Figs. 7.8.2 B, 7.8.3 B) organ restricted to apical part of tibia (Cicindelinae, Opisthiini, Carabini) or extended towards base (Pausinae, *Gehringia*, Omophroninae, Hiletinae etc.). Scutellar shield enclosed by elytral bases or shifted anteriorly (e.g., *Brosicus*). Mesoventrite of Gehringiini (Fig. 7.8.2 C), Carabinae and Hiletinae short, with hexagonal groove and anterolateral grooves for reception of procoxae (= carabine type). Mesoventrite of other groups (Figs. 7.8.2 F, 7.8.3 C) moderately elongated, without hexagonal groove and anterolateral grooves, rounded

in cross section, with smooth collar region and articulating with prothorax in a ball-and-socket manner (Figs. 7.8.2 F, 7.8.3 C; Paussinae [excl. *Metrius*], Cicindelinae, Loricarinae, Elaphrinae, Migadopinae, Scaritinae, Trechinae, Harpalinae, Brachininae, Pseudomorphinae) (= harpaline type). Mesocoxal cavities laterally open, i.e. bordered by mesepimeron ('disjunct type') or closed ('conjunct type') (Trechinae, Harpalinae, Brachininae, Pseudomorphinae). Elytra usually covering abdominal tergites completely, apically truncate in some groups (Paussinae excl. *Metrius*, Gehringiinae, Lebiini, Odacanthini, Galeritini, Brachininae). Basal margin present or absent. Disc primarily with eight striae and nine interspaces. Setae generally present in interspaces 3, 5 (discal setae), and 9, but sometimes also in 1 and 7. Sutural stria usually not recurrent at apex. Epipleura broad at humeral region, gradually narrowing posteriorly, usually ending at apical external angle of elytra, not reaching sutural angle. Always without setae but sometimes with pubescence. Metanotum usually of generalised adepagan type but shortened and strongly simplified in forms with completely reduced flight organs (e.g., *Omus*). Anepisternum does not reach mesocoxal cavity. Epimeron exposed, narrow and parallel-sided (Gehringiinae,

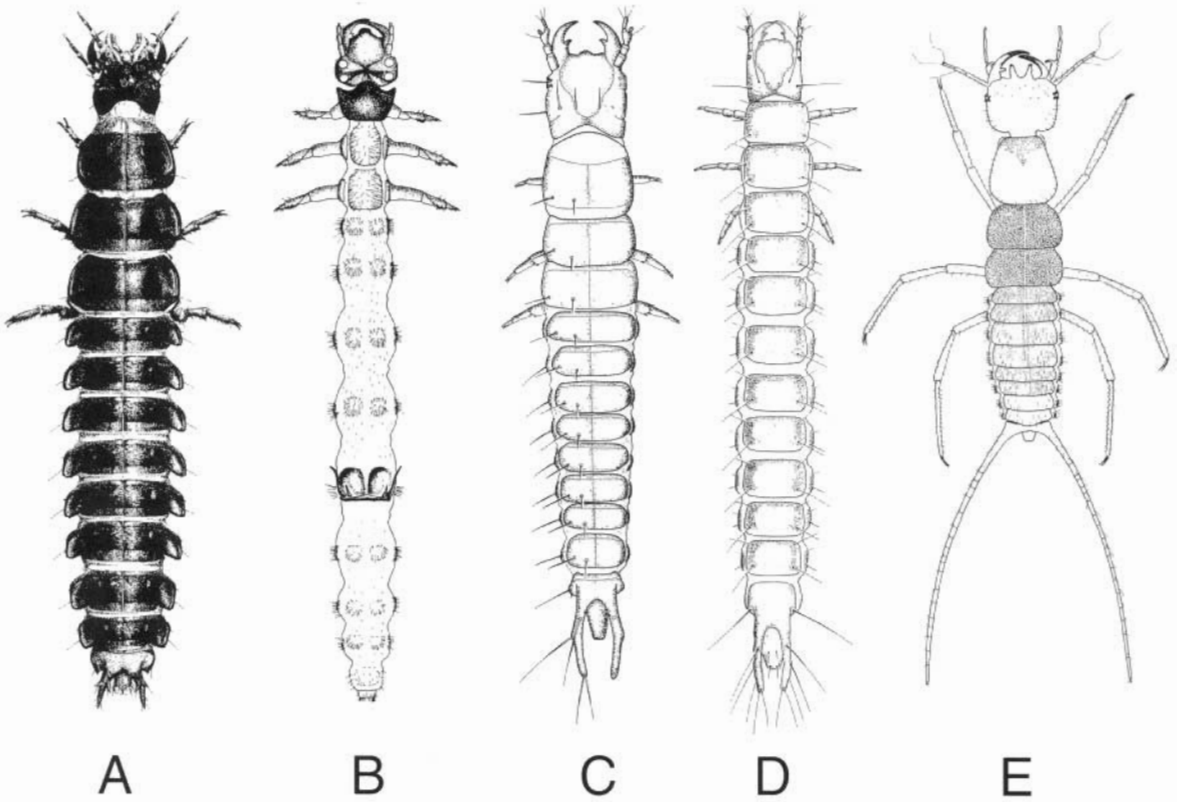


Fig. 7.8.4. Habitus of larvae of different subfamilies. A, *Carabus exaratus* (Carabinae) (redrawn from Arndt & Makarov 2003); B, *Platychile pallida* (Cicindelinae) (Arndt 1998 b); C, *Lindrothius* sp. (Harpalinae, Platynini) (Arndt & Hurka 1992); D, *Lionychus quadrillum* (Harpalinae, Lebiini) (Arndt 1989); E, *Trichognathus marginipennis* (Harpalinae, Galeritini) (Arndt & Drechsel 1998).

Omophroninae, Elaphrinae, Loricerinae, Migadopinae, Scaritini), concealed (Opisthiini, Carabinae), or lobate (Hiletinae, Trechinae, Harpalinae). Metaventricle (7.8.2 D, F, 7.8.3 D) with discrimen and complete transverse suture separating preepisternum from katepisternum. Metacoxae (7.8.2 D, F, 7.8.3 D) not extended cranially, medially not fused and not fused to katepisternum, mobility partly retained (c. 5°). Laterally scarcely broader or as broad as posterior margin of ventrite, not reaching elytral epipleura laterally. Metafurca well developed. Mm. furca coxalis anterior and posterior present. Alae sometimes reduced, if well developed with oblongum but without katastigma (subcubital setal binding patch).

Abdomen usually with six visible sternites. Sternite II only visible laterally in most groups. Large median piece of sternite II usually present in species with distinctly separate metacoxae (*Metrius*, *Ozaenini* part.). Sternites III + IV fused. Terminal sternite VII posteriorly acuminate, rounded, or truncate with rounded lateral edges. Tergites I–VIII with spiracles. Posterior segments invaginated and strongly modified. Aedeagus usually with asymmetric parameres. Coxosternum VIII only exposed in Brachininae. Gonocoxae relatively short, probably primarily

unsegmented, but divided into proximal and distal part in most representatives.

Morphology, Larvae (Figs. 7.8.4–7.8.10). campodeiform, moderately flattened, subparallel. Sclerotized parts brownish to black. Head prognathous, rounded laterally (Paussinae, Cicindelinae) or roughly quadrangular (Fig. 7.8.5 A); cervical groove present laterally in most taxa but absent in basal groups (e.g., Paussinae, Carabinae, Cicindelinae, Omophroninae). Head laterally with six stemmata arranged in two rows. Ocular groove present posterior to the stemmata in many taxa but absent in basal groups (e.g., Paussinae, Carabinae). Frontal suture almost always sinuate; posterior part of frontale (pars aboralis frontalis) usually with pairwise egg bursters; coronal suture usually present, often strongly shortened or absent. Anterior clypeolabral margin primarily with four nasal teeth (Fig. 7.8.5 A), each with one small ventrally directed microseta; ventral side of clypeolabral region with row of teeth. Antennae 4-segmented, anteriorly directed. Antennomeres 1 and 2 subcylindrical, antennomere 3 with bulb-like sensorial appendage laterally, antennomere 4 smaller, rounded apically. Mandibles with retinaculum; terebrum usually with two cutting edges; penicillus present or absent. Maxillae articulated with

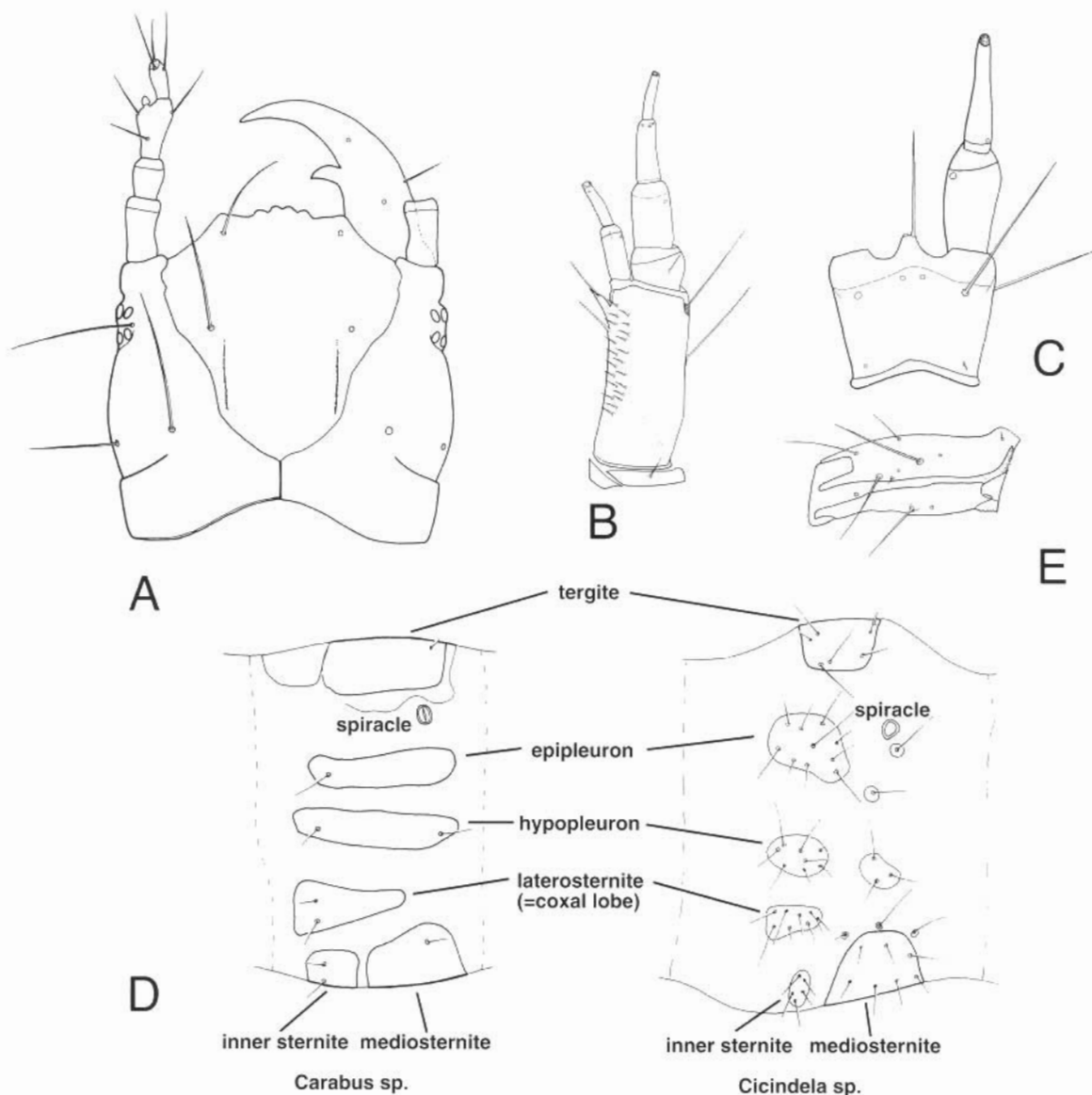


Fig. 7.8.5 A, *Lindrothius horsti*, head capsule with mandible and antenna, first instar, dorsal aspect (Arndt & Hurka 1992); B, C, *Agonum mülleri*. B, maxillary palpus, dorsal aspect (Arndt 1993); C, labium and labial palpi, dorsal aspect (Arndt 1993); D, abdominal tergite III, lateral aspect, *Carabus nemoralis* (left) and *Cicindela campestris* (right) (Arndt 1997); E, *Agonum mülleri*, pygopod, lateral aspect (Arndt 1993).

anteroventral margin of head capsule, moveable in all directions; maxillary groove completely reduced; cardo small, with or without separate mesal sclerite; stipes usually elongate; mobility between both parts strongly restricted; lacinia usually short (elongate and hook-shaped in *Metrius*, *Ozaenini* and *Omophron*), absent in some groups; galea 2-segmented; palpi 4-segmented (or 3-segmented and inserted on palpifer, Fig. 7.8.5 B). Maxillae moved by four longitudinally arranged extrinsic muscles; craniostipital muscle (levator of maxilla) probably homologous with *M. craniolacinalis*. Submentum completely fused with remaining parts of head capsule; mentum short and membranous; prementum usually with ligula and 2-segmented palpi (Fig. 7.8.5 C). Prementum retracted by two pairs of muscles with tentorial origin. *M. submentopraementalis* ab-

sent. Hypopharynx with dense field of microtrichiae, separated from dorsal surface and bulging or completely flattened. *M. tentoriohypopharyngalis* primarily present, but absent in larvae with flattened hypopharynx (e.g., *Pterostichus*, *Brachinus*). Gula usually elongate, represented by a narrow area enclosed by paired gular sutures, rarely broad (e.g., *Loricarinae*; *Licinus*). Functional mouth open but narrow, in close contact with anterior hypopharyngeal margin. Preoral filter apparatus formed by hypopharyngeal trichiae and trichiae on the mandibular (penicillus) and maxillary bases. Prepharyngeal tube always present. *M. clypeopalatalis* always represented by several bundles. Pharynx fairly narrow, primarily with well developed ventral dilator (*M. tentoriohypopharyngalis*) and postcerebral dorsal dilator (*M. verticopharyngalis*), but both muscles

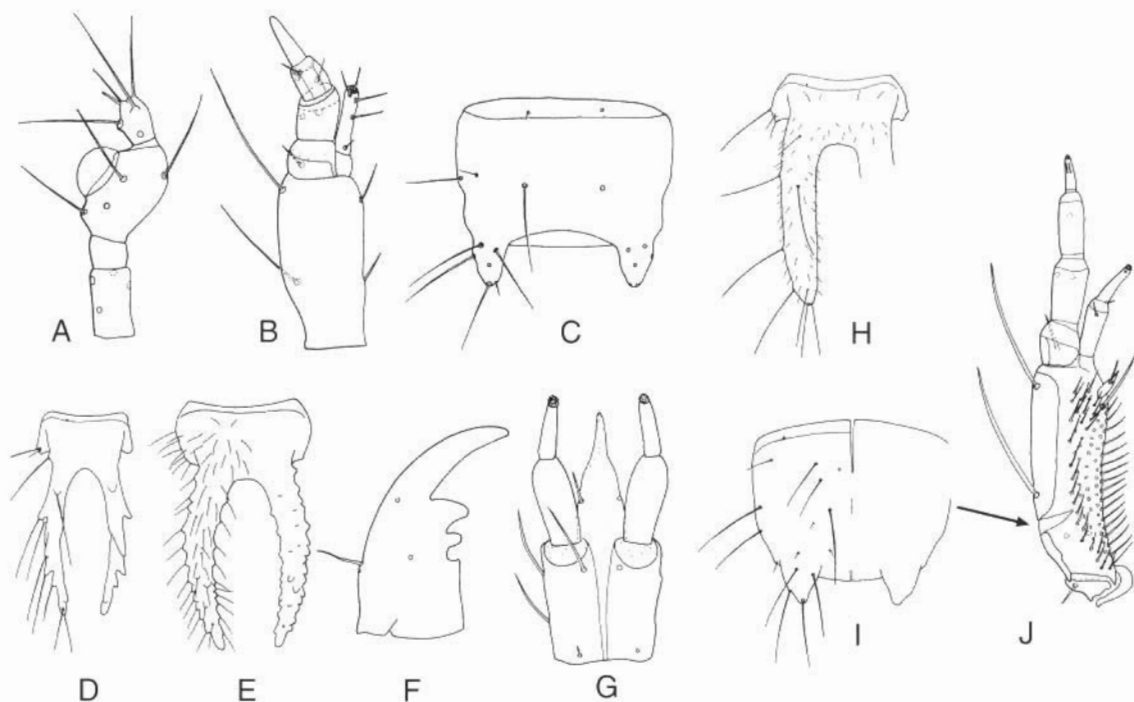


Fig. 7.8.6 A–C. *Brachinus crepitans*, first instar, dorsal aspect; A, antenna; B, maxilla; C, tergite IX with urogomphi; D, *Elaphrus* sp., urogomphi, third instar; E, *Blethisa multipunctata*, urogomphi, third instar; F–G, *Omophron limbatum*, dorsal aspect, F, mandible; G, labium; H, *Clivina fossor*, third instar, urogomphi; I, *Dyschirius* sp., third instar, urogomphi; J, *Pterostichus* sp., maxilla, dorsal aspect; arrow: lateral membranous notch; (A–G, Arndt 1991; H–J, Arndt 1993).

reduced or absent in many groups (e. g., Harpalinae, Brachininae).

Thorax with tergites medially divided by narrow median ecdysial suture; mesonotum and metanotum with anterior keel; pronotum larger than following segments. Large spiracle present between pro- and mesothorax. Legs 5-segmented (coxa, trochanter, femur, tibia, tarsus), usually with two claws. Four small sclerites present laterally and dorsally of coxal base (episternum, epimeron, trochantin, pleurite, the latter two are lacking on the prothorax). Abdominal tergites I–VIII similar in structure, with anterior keel and median ecdysial suture; ventral and lateral sides with sternites, epipleuron, hypopleuron and a lateral spiracle; sternites consisting of one large (medio-) sternite and smaller paired anterior, inner and outer (latero-) sternites (Fig. 7.8.5 D). Abdominal segment IX smaller, with fused sternites; tergite IX usually with a pair of urogomphi (Fig. 7.8.6 C–E, H, I); urogomphi long and slender, moveably attached to tergite and unsegmented, or segmented and/or fused with tergite, or reduced. Tergite X (pygopod) cylindrical, directed downwards (Fig. 7.8.5 E).

First instar larvae with characteristic chaetotaxy (Bousquet & Goulet 1984; Arndt 1993). Epicranial sclerites with ten dorsolateral and seven ventral setae; frontale with eleven setae, two on anterolateral margin and one very distinctive long seta in anterolateral angle. Antennomere III with three long setae, antennomere IV with four long apical setae. Mandible with

one strong seta on outer margin. Cardo with one distinctive seta; stipes with two large setae on outer side and a field of setae on inner side; lacinia with one seta subapically (even distinct on strongly reduced lacinia); palpifer with a distinctive seta on the ventral side; setae on galea and palpi very small. Prementum including ligula primarily with seven pairs of setae, but number almost always reduced or increased; ventral side with a pair of very small basal setae, a large central seta, and a pit on the apical part of the ligula (distinctive in most species). Urogomphi with five long setae in first instar and nine long setae in the following instars.

Larvae of several groups of Carabidae are strongly modified morphologically (e. g., legs reduced, hyperprognathous, physogastric; see below).

The following references summarise information on the larval morphology of Carabidae: van Emden (1942), Bousquet & Goulet (1984), Arndt (1991 a, 1993), Beutel (1993), Luff (1993).

Paussinae (= Metriinae + Ozaeninae + Protopaussinae + Paussinae)

Distribution. All zoogeographic regions, but most diverse in the tropics. Only few species occur in southern parts of the Northern Hemisphere. The Metriini are restricted with one genus and two species to western North America. Ozaenini occur with about 14 genera pantropical and in southern North America, the Protopaus-

sini are restricted with one genus and seven species to the eastern Oriental region. The Paussini are the most diverse and widespread tribe.

Biology and Ecology. Higher paussines (= Proto-paussinae + Paussinae) are characterized by their advanced myrmecophilous habits, at least in the larval stage. This unusual life style may have originated from specialised predatory habits of larvae, which are a groundplan feature of the subfamily (Nagel 1979). Larvae of *Metriini* (*Metrius*) and *Ozaenini* produce gland secretions at their highly modified terminal abdominal segments, which attract other insects. These secretions are apparently also attractive for ants, and may have enabled paussine larvae to enter ants nests as parasites. Adults of Paussini are adapted to these hostile environments in different ways (defiant type, symphilous type). Myrmecophilous habits have independently evolved in *Physeae* (*Ozaenini*).

Morphology, Adults (Darlington 1950; Nagel 1997). Colour black (e.g., *Metrius*) or brown (most *Ozaenini*, *Protopaussini* and *Paussini*). Body laterally rounded (*Metrius*, *Mystropomus*) or parallel-sided. Fixed setae (i.e., long mechanoreceptive setae) present or absent in *Ozaenini*, always absent in *Protopaussini* and *Paussini*. Antennae filiform or moniliform in *Metrius*, *Ozaenini*, *Protopaussus* and *Megalopausus*. Strongly modified in other subgroups of Paussini, with pedicellus very small, deeply sunken into apex of scapus, connected with antennomere 3 by rigid wedging, and flagellomeres broadened and often transformed into a compact club. Procoxal process elongate and tapering posteriorly in *Metrius*, more or less truncate and posterolaterally connected with pleural process or strongly reduced in other paussines. Procoxal cavities always closed. Both protibial spurs in apical position if present, usually obsolete or absent in Paussini. Antenna cleaning organ extended towards base of tibia or reduced (Paussini). Hind walls of procoxae contact anterior excavations of mesoventrite in *Metrius*. Connection between pro- and mesoventrite of harpaline type in all other paussines, with smooth anterior collar of mesoventrite and without hexagonal groove. Mesocoxae separate or contiguous. Metacoxae separate in *Metrius* and *Ozaenini* (almost contiguous in *Physeae*), contiguous in *Protopaussini* and *Paussini*. Terminal abdominal segment covered by elytra (*Metrius*, most *Ozaenini*, *Protopaussus*), exposed in *Dhanya* and most Paussini. Specialised abdominal defense secretion delivery system present. Subapical elytral flange present in Paussinae excl. *Metrius*.

Higher paussines with labrum often extended laterally or longitudinally. Mandibles comparatively small and simple. Maxillary and labial

palpi very variable. Mentum usually reduced in size and retracted or obliterated medially. Prothorax usually strongly modified. Prothoracic glands almost always present, usually associated with concavities or clefts and trichome systems. The trichome system is specialised in *Protopaussus* (Nagel 1997) and absent in *Arthropterus* and some other genera (e.g., *Homopterus*, *Carabidomemmus*). Prosternal process fairly broad and posteriorly truncate in *Protopaussus*, distinctly or completely reduced in Paussini. Procoxae usually very prominent and contiguous or almost contiguous (Paussitae *sensu* Nagel 1997). Femora and tibiae of fore-, middle- and hind legs usually broadened and flattened (not in *Pleuropterus*). Protibial antenna cleaning organ vestigial or absent. Protarsomeres usually cylindrical, in some cases partly or completely retractile (*Homopterus*). Elytra without lateral edge. Meta-ventrite usually without discrimen and transverse suture. Median cell of alae usually triangular (not in *Protopaussus*). Abdominal sternites II–IV fused, sutures between sternites faintly indicated or absent. Stridulatory file on the ventral abdominal base present or absent. Terminal abdominal segments partly exposed and sclerotised. Parameres slender and asymmetric in advanced paussines.

Morphology, Larvae (Fig. 7.8.7A–G). Larvae live in burrows in soil or in ants nests and are strongly modified morphologically. Head and posterior part of body bent upwards (dorsad) (Fig. 7.8.7.G). Head capsule slightly or distinctly rounded laterally; stemmata reduced to one ocellus or lacking; coronal suture absent (Fig. 7.8.7A); posterior tentorial grooves represented by a single narrow cleft immediately adjacent to a deep posteromedian emargination of the ventral wall of the head capsule in Paussini (Arndt & Beutel 1994); nasale present in *Metrius* but absent in other groups; frontale with membranous anterior margin in Paussini (Arndt & Beutel 1994); mandible (Fig. 7.8.7B) broad at base, with slightly sclerotized appendage (*lacinia mobilis*) proximal to retinaculum in Paussini; maxillae with 4-segmented palpi in *Metriini* but 3-segmented palpi in *Ozaenini* and Paussini; palpomere I more or less completely fused with stipes in the latter group; galea 1-segmented (Arndt & Beutel 1994), blade-like in *Metriini* (Beutel 1992); *lacinia* absent in Paussini but long and blade-like in *Metriini*. Prementum elongate, with tubercles. Paussini with posterior tentorial arms originating from narrow, common median stalk, immediately adjacent with posteromedian emargination of head capsule, with dorsal arms strongly flattened and exceptionally short (Arndt & Beutel 1994). Regular fringe of longer hairs absent from cranial part of hypopharynx in

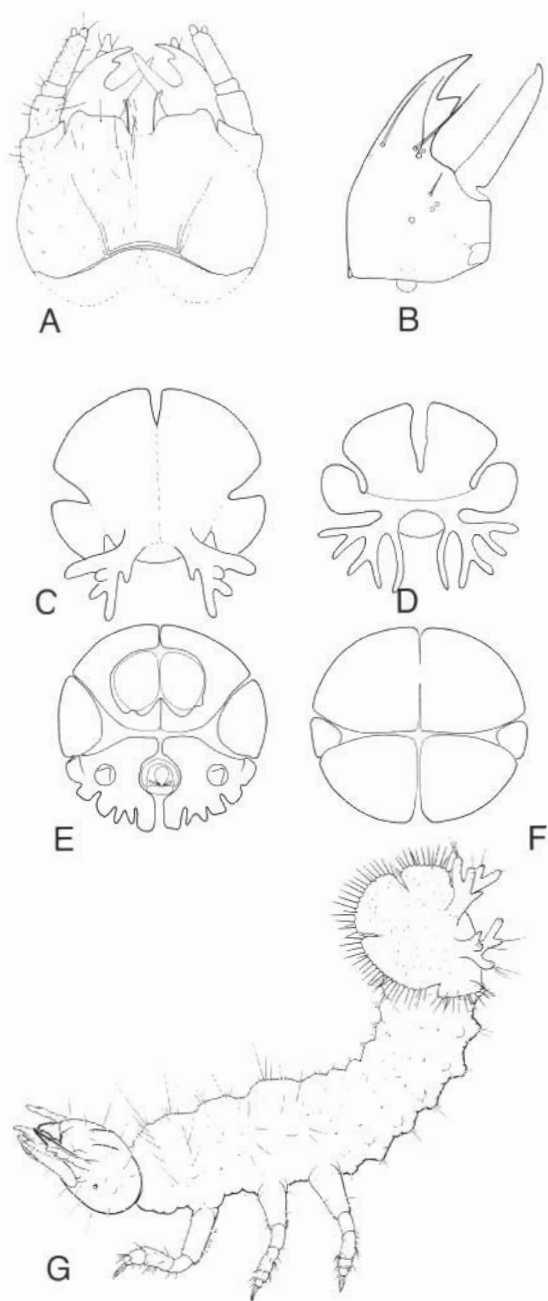


Fig. 7.8.7A, *Paussus* sp., head capsule, dorsal aspect (Arndt & Beutel 1995); B, *Paussus* sp., mandible, dorsal aspect (Arndt & Beutel 1995); C–F, Transformation series of posterior part of abdomen in representatives of Paussinae. C, *Metrius contractus* (redrawn from Bousquet 1986); D, *Pachyteles* sp. (redrawn from Costa *et al.* 1988); E, *Physea setosa* (redrawn from Bousquet 1986); F, *Paussus* sp. (Arndt 1998 a); G, *Metrius contractus*, habitus, first instar (Bousquet 1986).

Paussini (specialised feeding habits); present but sparse in Metriini.

Legs primarily 6-segmented with two claws (anterior claw longer in Metriini and Ozaenini); tibia and tarsus fused to one strongly sclerotized segment with numerous strong setae on the ventral side and a single small hook-like claw in Paussini. Posterior abdominal segments and urogomphi strongly modified. Epipleurites IX

greatly enlarged and forming a vertically oriented anal plate together with tergum VIII. Urogomphi branched (Metriini, Ozaenini) or flattened, triangular and integrated into anal plate (Paussini) (Fig. 7.8.7C–F) (Bousquet 1986; Arndt & Beutel 1994; Vigna-Taglianti *et al.* 1998).

Gehringiinae

Distribution. The only known species, *Gehringia olympiaca*, was described by Darlington (1933). It occurs in north-western North America.

Biology and Ecology. *G. olympiaca* occurs on gravel banks of small to moderate mountain brooks with cold water. It lives in the moist gravel and coarse sand and avoids coming to the surface. Oviposition takes place in early summer.

Morphology, Adults (Fig. 7.8.2 A–D; Lindroth 1969; Beutel 1992). 1.6–1.7 mm long, black, upper surface covered with scattered setigerous punctures. Compound eyes with large, convex facets. Antennae short, moniliform, pubescent except on scapus. Distal antennomeres transverse. Ultimate maxillary palpomere small, subulate. Pronotum distinctly narrowed posteriorly. Prosternal process short and narrow, not extending beyond hind margin of procoxae posteriorly. Procoxal cavities open. Protibial cleaning organ present, elongated towards proximal part of tibia. Spurs both in terminal position. Protarsi not dilated in males, proximal three tarsomeres with sparse adhesive setae. Mesoventrite of carabine type. Mesocoxal cavity disjunct. Elytra with underlapping edges (Lindroth 1961–69), with deep sutural (and often faintly suggested 2nd and 3rd) stria, otherwise with sparse punctures arranged in irregular rows. Apex truncate, exposing last tergite. Metaventrite broad, with short discrimen and laterally obsolete transverse suture. Metepimeron parallel-sided and exposed, not lobate. Metacoxae distinctly separate. Alae well developed, with marginal fringe of hairs. Abdomen without separate sclerite between metacoxae. Terminal sternite VII with almost truncate, very slightly convex hind margin. Parameres slightly asymmetric.

Morphology, Larvae. Length of specimen described by Lindroth (1960) 1.2 mm. Habitus of larvae and characters generally very similar to those of Trechinae. Body slightly sclerotized, abdominal tergites and sternites not apparent. Head almost square, parallel-sided; sutures indistinct. Frontale distinctly extended posteriorly; coronal suture short; postocular groove absent; cervical groove absent. Egg-bursters consist of two rows of 5–7 minute tubercles on posterior frontale. Stemmata absent. Nasale with slightly

bisinate anterior margin, slightly produced in advance of inconspicuous adnasale, with four small teeth alternating with minute setae. Antenna with three stout basal segments and slender antennomere IV; antennomere III with mesal spine and stalked, globulose sensorial appendage. Mandible sickle-shaped, with one lateral seta and well developed pointed retinaculum; penicillum absent; mesal edge of stipes with only one seta; 2-segmented galea with very slender distal segment; lacinia absent; basal palpomere with twisted seta. Prementum subquadrate; palpi slender, widely separated; ligula absent. Hypopharynx completely flattened. Prothorax distinctly larger than meso- and metathorax. Legs short, with equal claws. Urogomphi fused with tergite IX, unsegmented, number of setae reduced (as in Trechinae). Pygopodium longer than urogomphi.

Omophrinae

Distribution. Represented by one genus with 60 species in the Holarctic, Oriental and Afrotropical regions, as well as Central America.

Biology and Ecology. All species are strongly hygrophilous and restricted to the immediate vicinity of water. The adults are nocturnal and run very rapidly when hunting at night. Like the larvae, they spend the day in burrows in sand or clay.

Morphology, Adults (Fig. 7.8.1 B; Lindroth 1969; Beutel 1992). Characterised by an almost circular outline, long and slender antennae and legs, and an unusual colour pattern with a pale ground colour and darker, often metallic markings. Head short and transverse. Prosternal process broad and apically truncate, covering the mesoventrite entirely, thus joining the prothorax immovably to the pterothorax. Procoxal cavities closed, but procoxae contact the anterolateral concavities of the mesoventrite. Protibia of anisochaetous type, antennal cleaner distinctly elongated towards proximal part of tibia. Two proximal protarsomeres of males strongly dilated. Proximal mesotarsomere moderately dilated. Scutellar shield concealed. Elytra with 14–15 striae, but without abbreviated sutural stria. Metepimeron indistinct. Alae well developed. Median lobe sclerotized only in ventral half. Parameres moderately asymmetric.

Morphology, Larvae (Fig. 7.8.6 F–G). With fossorial adaptations. Body tapering posteriorly. Head capsule comparatively large and pronouncedly wedge-shaped, with strongly protruding, triangular nasale. Stemmata large. Postocular and cervical grooves lacking. Antennae conspicuously held upward, inclined towards me-

dian line, forming part of a prey-grasping basket. Mandible with single cutting edge and bidentate retinaculum; penicillus absent (Fig. 7.8.6 F). Preepipharynx with V-shaped, sclerotized bar; hypopharyngeal bulge reduced. *M. tentoriohypopharyngalis* medialis absent. Maxilla with very long lacinia and almost equally long 2-segmented galea. Prementum small; ligula long, moderately wide at base and extended as digitiform projection apically (Fig. 7.8.6 G). Ligula and labial palps subequal in length. Posterior tentorial grooves V-shaped, shifted to posterior margin of head capsule. Tentorial bridge absent. Prothorax broad basally, narrowed toward head, wider than other segments. Legs rather long, with shortened tibia; trochanter, femur and tibia with apical whirls of stout setae; claws subequal, each with a long seta. Abdominal segments with numerous long setae. Hypopleurites not apparent in first instar. Urogomphi fused to tergite IX, not segmented, about 3 times longer than tergite IX. Apex of urogomphi formed by a hyaline appendage in first instar (Landry & Bousquet 1984).

Cicindelinae

Distribution. World-wide, with five tribes, approximately 130 genera and 2000 species. The Ctenostomatini comprise two genera, *Pogonostoma* in Madagascar, and *Ctenostoma* in tropical South America. The Collyrini are restricted with few genera to India and South East Asia, the Manticorini are restricted with two genera to Southern Africa. Megacephalini and Cicindelini are the most diverse and widespread tribes.

Biology and Ecology. Adults of several genera are characterised by diurnal habits, very rapid terrestrial locomotion, and excellent flying abilities. The larvae live in vertical or horizontal burrows in soil, sandy substrates or rotten wood and are predators with a highly specialised ambush strategy and unusual morphological adaptations.

Morphology, Adults (Fig. 7.8.1 A, 7.8.2 E–F). 10–70 mm. Body black in basal groups (e. g., *Omus*, *Amblycheila*), with comparatively stout legs. Other genera with conspicuous colour pattern, metallic areas and long and very slender legs (*Cicindela*, *Megacephala*) or a very slender, ant-like body (arboricolous genera). Compound eyes large and protruding in diurnal cicindelinae (e. g., *Cicindela* auct.). Labrum large and broadened. Antennae inserted on dorsal side of head. Mandibles with several pointed apices, long, intercrossing in resting position. Prothorax elongated, prosternal process and postcoxal bridge unusually broad. Antennal cleaner and protibial spurs terminal. Elytra without stria. Alae completely reduced (*Omus*) or well developed. Oblongum absent. Thoracic segments otherwise

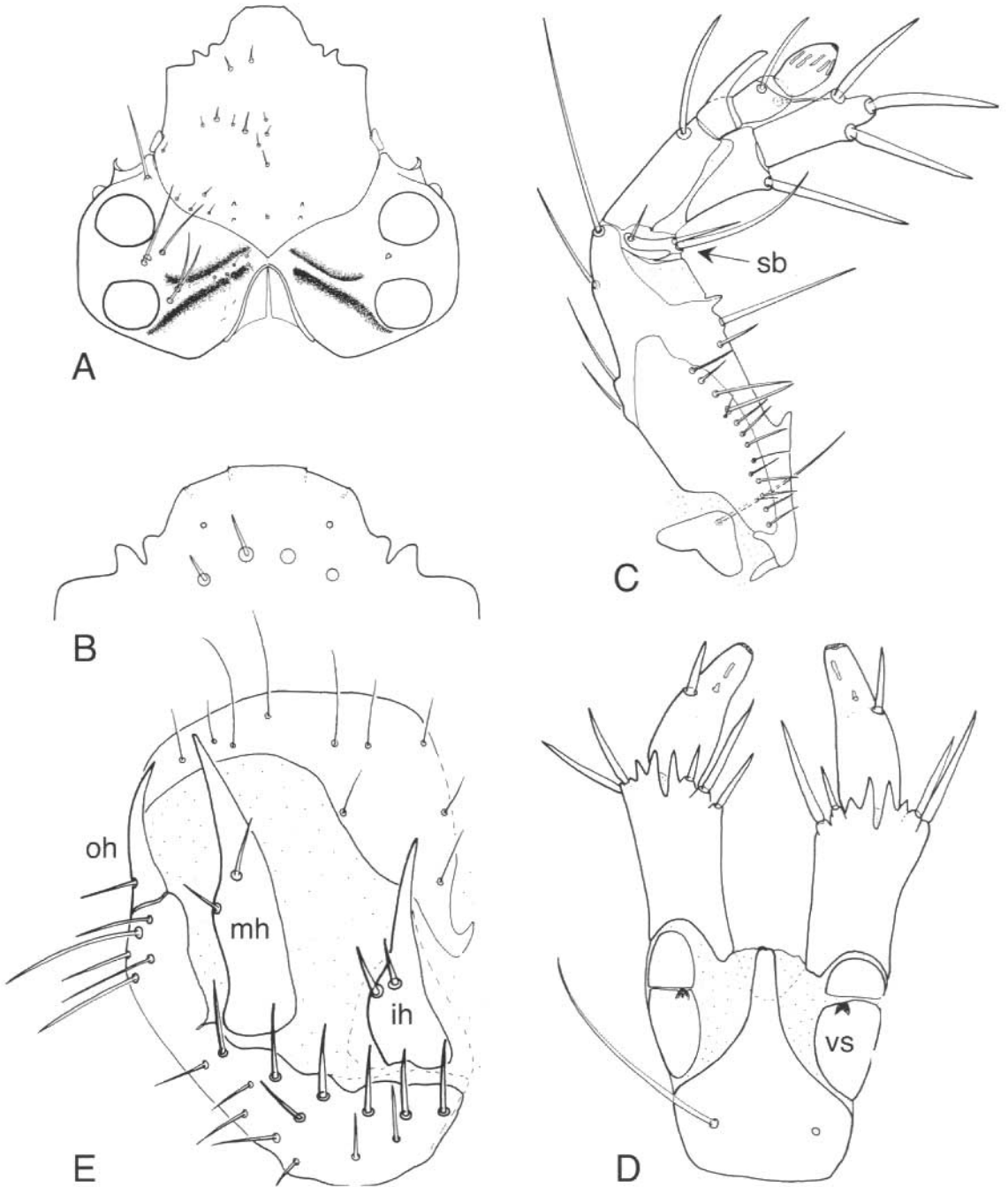


Fig. 7.8.8A–C. *Platychile pallida*, first instar, dorsal aspect (Arndt 1998 b). A, head capsule; B, nasale; C, maxilla, sb – sclerotized bar; D–E. *Eucallia boussingaultii* (redrawn from Arndt *et al.* 1996). D, labium; E, abdominal tergite V, ih – inner hook, mh – median hook, oh – outer hook.

similar to Elaphrinae and Loricerinae. Parameres symmetrical, connected by jugal sclerite.

Morphology, Larvae (Arndt 1998 b; Arndt & Putschkov 1997; Breyer 1989; Hamilton 1925; Knisley & Pearson 1984; Putschkov & Arndt 1994) (Fig. 7.8.8). Strongly modified morphologically in correlation with their life habits. Head and pronotum strongly enlarged and strongly sclerotized in contrast to long and slender rest of body. Dorsal side of hyperprognathous head and protergum form a functional unit. Both parts together form a lid of the bur-

rows prior to the capture of prey. Head strongly rounded laterally; ventral side strongly convex. Six stemmata of different size present; two pairs on dorsal side of head strongly enlarged (Fig. 7.8.8A). Frons distinctly extended posteriorly, coronal suture very short or absent. Posterodorsal margin of head capsule emarginate, thus nearly reaching or reaching posterior margin of frontale. Ridge on caudal part of parietale connected with ridge on caudal part of frontale in Manticorini and Megacephalini, but separate in other taxa. Nasale (Fig. 7.8.8B) strongly protruding, shovel-shaped, with anterior margin

smooth and subtruncate or sinuate. Antennae with elongate, nearly equally sized antennomeres 1–3. Antennomere 4 slightly shorter. Sensorial appendage of antennomere 3 replaced by small field of pores. Mandible slender; apical part longer than basal part including triangular retinaculum; penicillus absent. *M. craniomandibularis internus* unusually large and complex. Additional protergal muscle inserts on adductor tendon (*Cicindela*; Breyer 1989). Cardio triangular; stipes slender, curved, strongly sclerotized, with one or more spines on mesobasal margin and a membranous field on dorsal side; lacinia small or absent; strongly sclerotized bar with three bristles present between stipes and palpomere 1; palpomere 1 large, fused with or at least attached to galeomere; galea as large as maxillary palp; both galeomeres with thick bristles (Fig. 7.8.8 C). Prementum dorsally covered by multisetose hypopharynx; ligula prominent, with two pairs of setae; bipartite ventral sclerite between prementum and labial palpomere 1 (Fig. 7.8.8 D) present or absent (Megacephalini and Manticorini). Premental retractors very strong, arranged in an unusual manner (*Cicindela*; Breyer 1989). Dense preoral filter present, apparently arising from upper part of ligula (*Cicindela*; Breyer 1989; Fig. 5). Hypopharynx separated from dorsal premental surface by a distinct fold but almost completely flattened. *M. tentoriohypopharyngalis* absent. Gular suture anteriorly limited by an Y-shaped posterior tentorial groove in Cicindelini; posterior tentorial groove T-shaped in all other taxa. Most parts of tentorium strongly flattened (dorsal arms) or thin; posterior arms basally fused; thin U-shaped tentorial bridge with attached to posterodorsal margin of head capsule by thin processes; anterior arms strongly developed, broadly connected with head capsule (*Cicindela*; Breyer 1989). Pronotum rhomboid (Fig. 7.8.4 B), distinctly different from smaller, laterally rounded meso- and metanota. Legs stout, with very short tarsus; anterior claw larger than posterior claw. Abdominal segments I–IV and VI–IX subequal, but segment V distinctly modified, dorsally enlarged as an “abdominal hump”, with separate anterior-, lateral- and caudal sclerites and 2–3 hooks inserted between them (Fig. 7.8.8 E). Urogomphi absent; pygopod short, conical and multisetose. Chaetotaxy strongly modified. Unusual, flattened, split setae on head and pronotum present in many taxa.

The following characters distinguish Manticorini from other larvae of Cicindelinae: antennal base inserted anteroventrad of stemmata and separate from base of mandible by wide sclerotized area; antennomere I very thin; tibia distinctly curved with a field of numerous short setae on posterolateral side; number of stemmata reduced, two enlarged stemmata situated on prominent region of head capsule (Oberprieler &

Arndt 2000). Larvae of Collyrini and Ctenostomatini live in the rotten wood contrary to all other groups and are characterised by several apomorphies: width of nasale reduced, body flattened, and (except in *Pogonostoma*) claws fused with tarsus (Arndt & Putschkov 1997).

Carabinae

The subfamily comprises 9 tribes, four of which (Carabini, Ceroglossini, Pamborini, and Cychrini) contain large and colourful species. The adults, especially of the largest genus *Carabus*, are often characterised by metallic cuticle with conspicuous elytral patterns. The group is para- or polyphyletic, comprising with Cicindini, one of the most peculiar and enigmatic tribes.

Distribution. World-wide, but the great majority of species live in the Northern Hemisphere. The monotypic Notiokasiini are restricted to the warm-temperate Neotropical region, Ceroglossini to the Neotropical Andes, Pamborini to Australia and New Zealand. The Cicindini contain two monotypic genera, *Cicindis* from Argentina and *Archeocindis* from Persian Gulf.

Biology and Ecology. Most representatives including *Carabus* and *Ceroglossus* live on the ground as more or less generalized predators, and nearly all of them are flightless. Adults and larvae of Cychrini are specialized predators of snails. Adults and larvae of *Calosoma* are very active predators of caterpillars and adults and larvae of some species climb trees. Mass flights to caterpillar outbreaks are recorded e.g., for *Calosoma frigidum*. Larvae of *Notiophilus* are highly specialised predators of springtails.

Morphology, Adults. Size ranging from small (e.g., *Notiophilus*) to very large (e.g., *Carabus* subgenus *Procerus*). Protibial spurs and antenna cleaning organ terminal (Opisthiini, Carabini, Cychrini) or one spur subterminal and antenna cleaning organ slightly prolonged proximally. Prosternal process distinctly extending beyond hind margin of procoxae and apically tapering. Procoxal cavities open. Mesoventrete of carabine type. Metepimeron concealed.

Morphology, Larvae (Fig. 7.8.4 A, 7.8.5 D). Larvae of Carabinae are remarkably diverse morphologically. None of the features which characterize the subfamily as a whole are autapomorphic: cervical and ocular grooves absent; hypodon (central tooth) usually present (absent in *Opisthius*); antennal muscles not intercrossing; mandible usually with penicillum; hypopharynx distinctly bulging, with preoral filter; *M. tentoriohypopharyngalis* medialis usually present (ten-

torial bridge interrupted and M. 42m absent in *Nebria*); Mm. verticopharyngalis and tentorio-pharyngalis well developed (Beutel 1992).

Ceroglossini, Carabini, Pamborini and Cychrini are characterised by strong sclerotization, reduced number of setae on tergites and sternites, a remarkably increased number of pores, and a reduced sensorial appendage of antennomere 3 (Arndt 1998a; Prüser & Arndt 1995). The urogomphi are markedly sclerotized, shortened, fused with tergite IX and increasingly reduced in the latter three taxa. The tergites are often extended laterally (e.g., Cychrini). Nasal teeth and setae FR_{10,11} are absent in Cychrini and many species of *Carabus* (Arndt & Makarov 2003). Larvae of Nebriini, Opisthiini, and Notiophilini are characterized by reduced setae TE₆, PR₈ and ME₂, and the presence of a roughly pointed microsculpture on all tergites. The urogomphi are thin, straight and moveably attached to tergite IX (Arndt 1993). Antennomere III is enlarged and multisetose in Opisthiini (Bousquet & Smetana 1991). A strongly protruding nasal region with long, sharp and prominent teeth is characteristic for Notiophilini and some taxa of Nebriini. A sclerotized bar is present between the stipes and maxillary palpomere I in Notiophilini (as in Cicindelinae; Arndt 1993).

Hiletinae

Distribution. Hiletinae (Hiletini) are a tropical group considered as rare and enigmatic (Erwin & Stork 1985). Approximately 20 known species are arranged in 2 genera, *Hiletus* and *Eucamaragnathus*. *Hiletus* species occur in tropical Africa and species of *Eucamaragnathus* in Africa, Madagascar, south-eastern Asia, and in South America east of the Andes from Ecuador to lowland eastern Brazil (Erwin & Stork 1985).

Biology and Ecology. All species frequent latosolic soils in broadleaf evergreen and deciduous forests or in grassland savannahs with scattered trees.

Morphology, Adults (Erwin & Stork 1985; Beutel 1992). Head large and robust in proportion to pronotum, with transverse sulcus which connects the sulcate frontal furrows. Antennae geniculate, with scapus as long as antennomeres 2–4. Scapus fits in groove below compound eyes. Mandibles large and markedly downturned distally, creating a hollow concavity beneath. Each mandible with eight or nine triangular teeth, which increase in size distally. Lacinia enlarged laterally, resembling an asymmetric club. Dorsal edge with numerous spatulate spiculae. Galea long and finger-like. Mentum with deep median concavity, anteromesally produced into simple (*Eu-*

camaragnathus) or bifurcate (*Hiletus*) projections. Profemora of males almost always with ventral tooth (not in Southeast Asian *Eucamaragnathus*). Protibia of anisochaetous type. Antennal cleaner poorly developed. Tarsi of all legs slender and distally tapering. Adhesive setae present on protarsomeres 1–3 and mesotarsomeres 1–2. Prosternal process long and narrowing posteriorly. Procoxal cavity open. Mesoventrite with hexagonal and anterolateral grooves (carabine type). Mesocoxal cavities of disjunct type. Elytral pattern diverse. Metepimeron lobate. Alae well developed, with anterior sector cell much larger than 3rd radial cell. Median lobe unspecialised. Parameres asymmetric, usually brushy or multisetiferous (not in *E. brasiliensis*).

The thoracic structures display a unique combination of "primitive" (prosternal process, procoxal cavity, mesoventrite) and derived features (lobate metepimeron).

Larvae. unknown

Loricerae

Distribution. One tribe with two genera, the Holarctic *Loricera* (9 spp.) and the monotypic *Elliptosoma* (Madeira).

Biology and Ecology. Species of *Loricera* are more or less hygrophilous and characterised by specialised prey-catching techniques of larvae and adults, which involve the modified antennae or maxillae, respectively. They feed on springtails.

Morphology, Adults (Jeannel 1941–42; Lindroth 1961–69). In general outline resembling a middle-sized *Agonum* (*Loricera*). Frons with 2 large foveae and a posterior median sulcus, emanating from a deep transverse constriction behind the eyes. Antennae with long scapus and very long, erect setae on pedicellus and antennomeres 3–6. Protibia of anisochaetous type. Procoxal cavity posteriorly closed by narrow bridge. Prothoracic-mesothoracic connection of harpaline type. Mesocoxal cavity of disjunct type. Elytra with 12 regular stria (without abbreviated sutural stria). Metepimeron parallel-sided and narrow. Copulatory organ short and oval, median lobe with wide open basal orifice and elongated, asymmetric apical part. Parameres apically rounded, without fringes of hairs. Left paramere longer.

Morphology, Larvae (Arndt 1993, Luff 1993) (Fig. 7.8.9 A–B). Head capsule rounded laterally. Cervical and ocular grooves absent. Nasal region with two acute teeth and a row of small sharp teeth beneath them. Antenna 2 × longer than mandibles. Mandible sickle-shaped; retina-

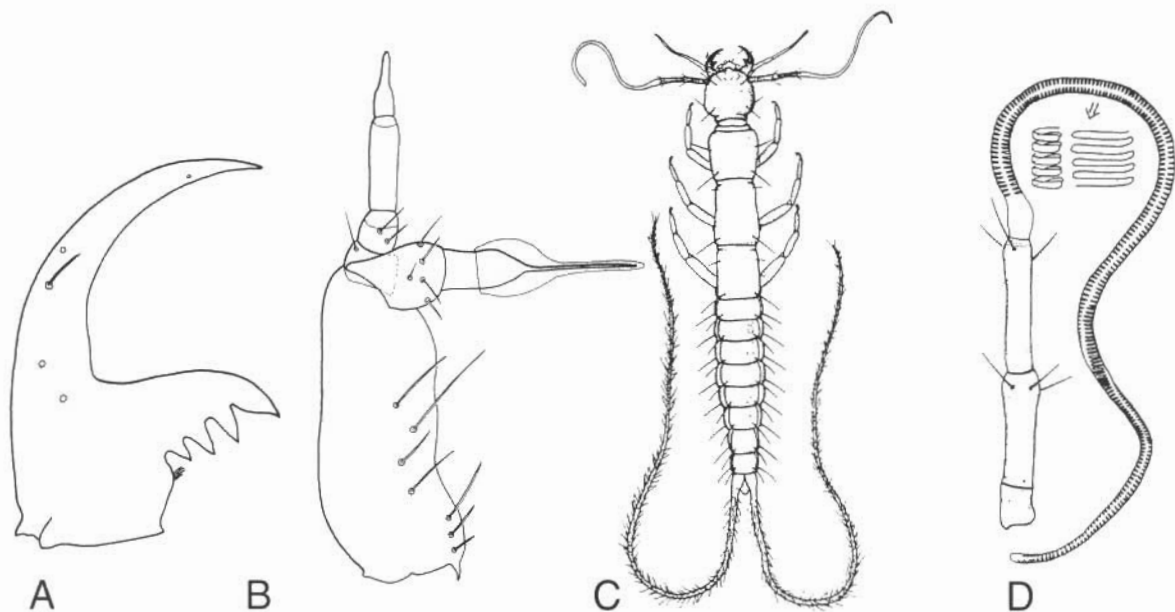


Fig. 7.8.9 A–B. *Loricera pilicornis*, third instar (redrawn from Arndt 1991). A, mandible; B, maxilla; C–D, *Siagona* sp. (Grebennikov 1999 a); A, habitus. B, antenna.

culum large, serrate along inner edge; penicillum present (Fig. 7.8.9 A). Stipes very large, almost entirely sclerotized; galea mesally directed at right angle to stipes, longer than maxillary palp; apical galeomere with divided into a swollen, finely granular basal portion and a long, whip-like apical portion; distal part covered by hyaline secretion (Fig. 7.8.9 B); field of setae on maxillary palp reduced; stipital field of setae reduced, its vestiges shifted to the middle of the inner margin. Labial palp slender, with secondarily subdivided apical palpomere (*Loricera* sp.; Thompson 1979); ligula unusually large, broadly rounded anteriorly, multisetose. Chaetotaxy of frontale and tergites modified; flattened, split setae on pronotum, mesonotum and metanotum present (see Cicindelinae). Legs long; tarsi elongated, with 2 unequal claws; anterior claw larger, with basal seta; seta absent from posterior claw. Urogomphi slender and nearly as long as head and thorax combined, fused to medially divided tergite IX, in later instars with numerous setiferous nodes. Pygopod short and conical.

Elaphrinae

Distribution. One tribe comprising 3 genera, *Diacheila*, *Blethisa* and *Elaphrus*, restricted to the Holarctic region.

Biology and Ecology. Elaphrines are usually strongly hygrophilous, and often riparian and very active during the daylight.

Morphology, Adults (Fig. 7.8.3; Jeannel 1941–42; Lindroth 1961–69; Beutel 1992). Middle-sized, always with metallic lustre. Eyes large and prominent. Prothorax with coarse punctuation.

Protarsomeres I–IV or I–III dilated in males. Elytral striae feeble, irregular, usually disturbed by fovea or tubercles. Thoracic structures otherwise similar to Loricerinae. Copulatory organ with a long sclerotized stylet protruding through the basal orifice of the median lobe when in repose. Parameres with fringes of hairs at the apex and ventral edge, less dense on the left paramere in *Elaphrus*.

Morphology, Larvae (Goulet 1983, Luff 1993) (Fig. 7.8.6 D–E). Body slender and subcylindrical (Luff 1993; Fig. 21). Head without ocular and cervical grooves (Luff 1993; Fig. 22). Coronal suture distinct, moderately long or short. Nasale centrally produced, triangular, with serrate (*Elaphrus*) or smooth (*Blethisa*) lateral edges. Mandible with large retinaculum and penicillus. Cutting edge of mandible finely serrate in many species. Lacinia reduced, very short or ring-shaped. Prothorax largest segment of body; pronotum quadrangular. Other segments laterally rounded. Equal claws elongate, more than 0.5 as long as tarsus. Urogomphi fused with tergite IX, in second and third instars multisetose with setae inserting on small tubercles or with 10 long setae on very large nodes (Fig. 7.8.6 D–E).

Migadopinae

Distribution. A relatively small group of two tribes with 15 genera mainly distributed in the subantarctic region (Andes, southern part of South America, Falkland Islands, southern Australia and Tasmania, Southern New Zealand, Auckland Islands) (Jeannel 1938; Moret 1990; Baehr 1999).

Biology and Ecology. Most species of this tribe live in cool and south temperate rain forests and moorland. They live on the ground, and are flightless with the exception of one species.

Morphology, Adults (Jeannel 1938). Medium sized beetles ranging from 6–20 mm, with glabrous surface. Almost always with one supra-orbital seta (absent in *Aquilex diabolicola*; Moret 1990). Pronotum and elytral disc without setae. Elytra with one additional stria between 1st and 2nd primary striae. Wings always absent. Thoracic structures otherwise similar to Loricerinae. Parameres well developed, at least right paramere fringed with hairs.

Morphology, Larvae (Johns 1974). Three different larvae of *Loxomerus* and the larva of an undetermined genus were described so far (Johns 1974). Internal features are unknown. Head with more or less constricted neck region. Ocular and cervical groove absent. Coronal suture very long. Nasale with three or five teeth including a hypodon; mandible straight and slender, with large retinaculum; retinaculum with additional subbasal tooth; penicillus present; maxilla with stipes, palpi and galea long and slender; lacinia absent. Prementum wide; ligula small. Legs with two claws, the anterior longer than the posterior one. Urogomphi short, articulating on membranous region of tergite IX. Hypopleurite with cap-like gland on dorsal margin in second and third instar larvae (absent in first instar).

Siagoninae

A small group comprising two tribes, Enceladini represented by the monotypic genus *Enceladus* (northern South America) and Siagonini represented by the genera *Siagona* (southern Palaearctic including Malay Archipelago and Philippines, Africa; 80 species), *Cymbionotum* (southern Palaearctic excluding Malay Archipelago, Africa) and *Luperca* (Africa, India; two species) (Darlington 1967; Erwin 1978).

Biology and Ecology. Species of *Cymbionotum* and *Siagona* live on the ground in wet areas with decaying vegetation or like *Enceladus* under bark. Some occur on mud and in soil clefts of desiccating waters. *Luperca* were found in termittaria.

Morphology, Adults (Jeannel 1941–42). Moderately depressed and glabrous (*Enceladus*, *Luperca*) or strongly depressed and pubescent (*Siagona*). Body always strongly constricted between pro- and mesothorax. Mandibles short, without seta. Palps short and narrow. Prothorax strongly narrowed posteriorly. Prothoracic-mesothoracic connection of harpaline type. Mesocoxal cavities

disjunct. Elytra distinctly flattened, without basal margin, with 8 stria (indistinct in *Siagona*). Metepimeron parallel-sided, not lobate. Aedeagus large, laterally compressed. Parameres devoid of hairs in *Luperca* and *Enceladus*.

Morphology, Larvae (Fig. 7.8.9 C–D) (Grebennikov 1999 a). The larvae of Siagoninae are characterised by many apomorphic features. Head with more or less constricted neck; cervical groove absent (*Siagona*, Fig. 7.8.9 C) or completed to a dorsal parietal keel (*Enceladus*); ocular groove lacking; coronal suture long; 6 stemmata present or number of stemmata reduced to two or one. Nasal region protruding, serrate, shovel-shaped; adnasale with a dense group of setae. Antennomere III without sensorial appendage; antennomeres III and IV multisetose with membranous area on ventral side or extremely elongate and whip-like (Fig. 7.8.9 D). Mandible with large retinaculum; subapical seta MN₂ longer than retinaculum; penicillus and seta MN₁ on outer mandibular margin absent. Maxillary and labial palpi strongly elongate (*Siagona*), or of normal size but with terminal segments enlarged and with extended sensorial fields (*Enceladus*). Lacinia present. Ligula broadly rounded. Legs slender, with two claws; setae of claws shifted to pretarsal sclerite. Abdominal tergite IX distinctly reduced, divided medially, fused with multisetose and extremely elongate urogomphi (Fig. 7.8.9 C). Urogomphi about 0.5–1.0 as long as remaining body.

Scaritinae

Scaritinae, which are probably not monophyletic (s. below), comprise small to very large species. They are always strongly constricted between the pro- and mesothorax.

Biology and Ecology. Scaritinae are mainly characterised by their habits of burrowing in soil or sandy substrates.

Distribution. Scaritini (*sensu lato*) occur world wide, but most of taxa are concentrated in the Southern Hemisphere. Promecognathini with five genera are restricted to southernmost Africa and northwestern North America. Salcediini occur with three genera in the pantropical region.

Morphology, Adults (Jeannel 1941–42). Distinctly depressed (e. g., *Scarites*) or almost cylindrical (e. g., *Dyschirius*). Prothorax strongly narrowed posteriorly, thus body distinctly constricted between pro- and pterothorax. Prothoracic-mesothoracic connection of harpaline type. Mesocoxal cavities disjunct. Metepimeron parallel-sided, not lobate.

Morphology, Larvae (Fig. 7.8.6H, I). One of the most heterogeneous groups concerning larval morphology (Thompson & Allen 1974; Peyrieras 1976; Thompson 1979; Nichols 1986; Bousquet & Smetana 1986; Arndt 1991a; Luff 1993; Moore & Lawrence 1994).

Promecognathini: Only the first instar larva of one species of *Promecognathus* is known and differs strongly from all other taxa in this subfamily (Bousquet & Smetana 1986). Head quadrangular, parallel-sided; stemmata reduced; cervical groove absent; coronal suture absent; posterior angles of frontale bulging, extended to posterior margin of head. Nasale straight, smooth, not protruding; antenna slender; antennomere III without sensorial appendage but with sensorial field apically on ventral side; mandible slender, with small retinaculum; penicillus lacking in contrast to other known scaritine larvae; lacinia and ligula lacking; palpi short and stout, urogomphi club-like, attached to tergite IX by a membranous area; body and urogomphi multisetose even in first instar.

Scaritine subtribe Carenina: Body strongly sclerotized; lateral margins of head subparallel; six stemmata present; coronal suture long; cervical groove present; anterior margin of frontale smooth, straight, nasale not protruding; antennae extremely short; mandible stout, without retinaculum; lacinia elongate, as long as galea; maxillary palpi modified, only penultimate article of normal shape; ligula present; labial palpi short and wide, with very large terminal sensorial field; epipleurites and hypopleurites fused on all abdominal segments; urogomphi absent (Moore & Lawrence 1994).

Subtribe Pasimachina: Body slender, subparallel, strongly sclerotized and dark; head wider than long; six stemmata present; cervical groove lacking; coronal suture short; nasale protruding, shovel-shaped, with smooth anterior margin; antenna long and slender, with sensorial appendage absent from article III; mandible slender with small retinaculum; lacinia and ligula absent; both palpi of normal structure; urogomphi fused to tergite IX, turned inside, longer than pygopod (Thompson & Allen 1974).

Subtribe Scaritina: Larvae strongly sclerotized, slender, elongate, subparallel; head quadrangular; coronal suture very long; cervical groove shallow; nasale trapezoid; antenna long and slender with antennomere 3 flattened latero-apically, sensorial field present but appendage absent on antennomere III; mandible long and slender; lacinia absent; galea and palpi slender, of normal structure; ligula present; urogomphi slender, fused with tergite IX (Peyrieras 1976; Thompson 1979; Nichols 1986; Arndt 1991a).

Clivina and related groups: Body yellowish, not strongly sclerotized; stemmata absent; coronal suture and cervical groove present; nasale

wide, with several teeth, slightly protruding; antenna short and stout; antennomere III with sensorial appendage; mandible slender, with small retinaculum; finely serrate on inner margin; lacinia and ligula present; legs as in *Dyschirius* and in contrast to all other known Scaritinae with single claw; urogomphi fused with tergite IX, as long as pygidium, but flattened in dorso-ventral direction (Fig. 7.8.6H); multisetose in second and third instars or urogomphi and pygopod with several large horns (Thompson 1979).

Dyschirius and related groups: Larvae strongly sclerotized, brown to black coloured, only head sometimes red. Head wider than long with six stemmata, nasale protruding, crown-like, posterior angles of frontale wide or slender and long; antenna stout but sensorial appendage on antennomere III present; mandible slender with retinaculum present; lacinia absent; legs with a single claw; urogomphi short and stout, much shorter than pygopod or tergite IX (Fig. 7.8.6I; Arndt 1991a; Luff 1993).

The larvae of several subtribes and of the tribe Salcediini are still unknown.

Trechinae

Trechinae are a much disputed problematic group and probably a paraphyletic assemblage (see below). It is unclear whether Patrobini, *Apotomus*, Broscini and Psydrini should be included. The inclusion of Melaenini and Cymbionotini (Lawrence & Newton 1995) is also problematic.

Distribution. World wide, a very diverse group.

Biology and Ecology. Highly variable, s. above.

Morphology, Adults. (Fig. 7.8.1C; Jeannel 1941–42). Male protarsi often with unilaterally dilated proximal tarsomeres. Mesepimeron broad or narrow. Otherwise harpaline type character combination of thoracic sclerites, i. e. closed procoxal cavities, apically truncate prosternal process, harpaline type mesoventrite, conjunct mesocoxal cavities, lobate metepimeron.

Morphology, Larvae. The larvae of Trechinae are close to the ground plan of "higher Carabidae" (Arndt 1993). Body moderately flattened, parallel-sided. Head roughly quadrangular; cervical groove present; head laterally with 6 stemmata arranged in two rows, number reduced in cave dwelling taxa. Ocular groove present; frontal suture sinuate; egg bursters consisting of a keel, isolated teeth or microspines. Nasale serrate, protruding. Antennomeres I and II subcylindrical; antennomere III with bulb-like sensorial appendage inserted laterally; antennomere IV smaller, rounded apically. Mandibles with retinaculum; terebrum with single cutting edge,

smooth, or serrate in some taxa of Anillini and Bembidiini; penicillus present or absent. Stipes slender; lacinia absent. Prementum with ligula. Hypopharynx separated from dorsal surface, flattened, with dense field of microtrichiae. Antennal muscles arranged crosswise (Beutel 1993).

Thorax with large pronotum and smaller, subequal meso- and metanotum, the latter two with anterior keel. Legs slender, with single claw in all taxa except *Perileptus*, *Amblystogenium*, *Thalassophilus*, and Patrobini (s. Psydrini, Gehringiini). Lateral and dorsolateral area above coxal base with four small sclerites (episternum, epimeron, trochantin, pleurite, the latter two are lacking on prothorax). Abdominal tergites I–VIII similar in structure; tergites with anterior keel and median ecdysial sutures; sternites consisting of one large median plate and smaller paired anterior, inner and outer (latero-)sternites. Abdominal segment IX smaller, with fused sternal plates; tergite IX fused with urogomphi. Abdominal tergite X cylindrical, directed downwards (pygopod). Number of setae on urogomphi in second and third instars reduced, seta UR_β always lacking. Setae TA_{3–6} lacking in Trechini, Zolini, Bembidiini (incl. Anillina), and Pogonini (Arndt *et al.* 1999, Grebennikov 1999b; Arndt 2000; Grebennikov & Maddison 2000). Larvae of Apotomini, Melaenini and Cymbiotonini are unknown.

Harpalinae

Distribution. World wide, the most diverse group with more than 30 tribes and 20000 species.

Biology and Ecology. Highly variable, s. above.

Morphology, Adults (Jeannel 1941–42). Mandibles without scrobal seta. Male protarsi never with unilaterally dilated proximal tarsomeres. Procoxal cavities uni- or biperforated. Elytra complete or apically truncate (e.g., Odacanthini, Lebiini).

Morphology, Larvae (Figs. 7.8.4C–E, 7.8.6J). The tremendous number of species and supra-specific taxa included in this subfamily is reflected by an extreme diversity of larval characters. Taxa which are presumably close to the ground plan of the subfamily, such as some Pterostichini and Platynini, are similar to Trechinae in most features described above, but have a short lacinia and double claws. All larvae of this subfamily are characterised by the reduction of the second ligular seta to a pore (Arndt 1993). The antennal muscles are arranged crosswise as in larvae of Trechinae and Brachininae (Beutel 1993). A membranous band is present ventrolaterally on the stipes in many representatives (Morrionini, Pterostichini, Zabrinini, Panagaeini, Peleciini, Callistini, Oodini, Licinini, Harpalini;

Arndt 1993; Fig. 7.8.6J). The membranous notch is regarded as rudiment of a complete transverse division of stipes as occurring in *Cnemalobus* (Roig-Juñent 1993).

The subgroups with most derived larval characters are the Licinini, Panagaeini and related groups (van Emden 1942; Liebherr & Ball 1990; Arndt 1991b), and the so-called “Truncatipennia”, e.g., Anthiini (Arndt & Paarmann 1999), Helluonini, Orthogoniini (Makarov 1998), Graphipterini (Zetto Brandmayr *et al.* 1993), Dryptini (Habu & Sadanaga 1965), Galeritini (Arndt & Drechsel 1998), and Lebiini (part.) (Lieftinck & Wiebes 1968; Arndt 1989; Capogreco 1989; Arndt *et al.* 2001).

Pseudomorphae

Distribution. An unusual group of carabids distributed in the Oriental region, Australia (*Adelotopus*, *Cryptocephalomorpha*, *Cainogenion*, *Pausotropus*, *Sphallomorpha*) and the New World (*Pseudomorpha*).

Biology and Ecology. Pseudomorphine adults are mainly found under bark (Baehr 1994). The known larvae (except *Sphallomorpha*) are physogastric due to their myrmecophilous habits. The known larvae of *Sphallomorpha* dig holes in the ground around ant nests and prey on ants in a similar manner like cicindelinae larvae. Pseudomorphines are the only known carabids with ovoviviparity (Liebherr & Kavanaugh 1985).

Morphology, Adults (Notman 1925; Baehr 1992). Body form elongate and more or less parallel and moderately convex (*Pseudomorpha*), very elongate and cylindrical, resembling Scolytidae (*Adelotopus* part.), or broadly oval and depressed (*Sphallomorpha*). Colour dark piceous to nearly black (*Sphallomorpha* part.) or variegated with maculae, vittae or pale margins. Head deflexed (*Cryptocephalomorpha*) or horizontal, with deep antennal grooves. Compound eyes on dorsal side of head (*Adelotopus*, *Cainogenion*) or lateral, continuous border beneath eye present in *Adelotopus*. Scapus partly visible from above. Mandibles without visible scrobes, very small in *Cryptocephalomorpha*. Maxilla with (*Cainogenion*, *Pausotropus*) or without a large lateral lobe in most genera. Submento-mental suture absent. Prosternal process present or absent (*Pausotropus*). Legs short, with strongly developed femora. Configuration of thoracic sclerites of harpaline type (see above). Six abdominal sternites visible. Parameres setose or glabrous, fairly symmetrical or highly asymmetrical but not ‘balteate’ (Baehr 1992).

Morphology, Larvae (Fig. 7.8.10) (Erwin 1981, Baehr 1997). Larvae with abdomen curved in lateral view and rows of spines on tergites V–VII

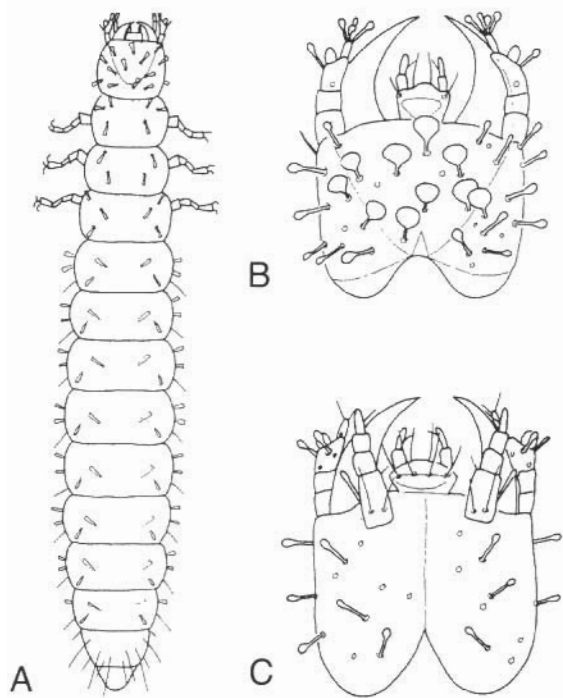


Fig. 7.8.10 A. *Adelotopus dytiscoides*, habitus, first instar; B, *Adelotopus rubiginosus*, head, first instar, dorsal aspect; C, ventral aspect (A–C, Baehr 1997).

(*Sphallomorpha*, Moore 1974) or physogastrical with membranous, poorly sclerotized body (Fig. 7.8.10A). Head subquadrate (Fig. 7.8.10B–C) or elongate and slightly narrowing anteriorly, without stemmata and egg bursters. Frontale very wide, frontal suture not sinuate, broadly reaching posterior margin of head; coronal suture, ocular and cervical groove absent. Nasale flat, convex or triangular, smooth, without teeth. Mandible without retinaculum or penicillus. Lacinia absent; galea 1- or 2-segmented, more or less reduced; maxillary palp 4-segmented, large in relation to other maxillary parts, longer than stipes. Ligula broadly rounded or absent. Pronotum sclerotized; other tergites largely or entirely membranous. Legs with double claws of different length. Urogomphi absent. Chaetotaxy strongly modified, larvae often multisetose or with large club-like, flattened or split setae on head (Fig. 7.8.10 B–C), dorsal head appendages, thoracic and abdominal tergites (Baehr 1997; Erwin 1981).

Phylogeny and Taxonomy. A branching pattern (*Sphallomorpha* + (*Pseudomorpha* + (*Cryptoccephalomorpha* + (*Adelotopus* + (*Cainogenion* + *Paussotropus*)))) was proposed by Baehr (1994).

Brachininae

Mainly characterised by a complex abdominal explosive mechanism. A comparable apparatus is only present in Paussinae. However, distinct structural differences in both groups were

pointed out by Forsyth (1972) and others (see below).

Distribution. Crepidogastrini with 7 genera (more than 100 species) are distributed in tropical and southern Africa, two species of *Tyronia* occur in India and Sri Lanka. Brachinini with 8 genera (and more than 500 species) occur world wide, but most of the species are distributed in tropical and subtropical regions.

Biology and Ecology. The known larvae of Brachininae are parasitic.

Morphology, Adults (Fig. 7.8.1 D; Erwin 1970, Jeannel 1941–42; Lindroth 1961–69; Liebherr & Will 1998). Mandibles with a long seta at the anterior part of the external scrobe. Prothorax narrow, not or only slightly wider than head. Elytra very broad, abruptly truncate at apex, with (*Brachinus*) or without a pale, narrow membrane. Other thoracic features of harpaline type, with narrow mesepimeron. Abdomen with 7 visible sternites in females and 8 visible sternites in males. Copulatory apparatus with the median lobe often deformed, the right paramere strongly reduced, and the left paramere strongly sclerotized. Female genital tract with appended spermathecal gland, segmented gonocoxae, gonocoxal rami absent, and in some taxa, a digitiform diverticulum of the spermathecal duct present (Liebherr & Will 1998).

Morphology, Larvae (Fig. 7.8.6 A–C). There is little known about larvae of Brachininae. Only Brachinini are known in the larval stage. Few first instar larvae are described (see Arndt 1993 for a review), and a single species is known in all instars (Erwin 1967).

Following characters distinguish Brachininae from the ground plan of Carabidae and are regarded as autapomorphic character states: anterior margin of frontale membranous, teeth and setae lacking. Posterior angle of frontale very slender, V-shaped, egg bursters lacking in first instar. Setal group gMX lacking, Lacinia absent (7.8.11 B). Ligula and setae LA_{3,4,6} lacking. Urogomphi reduced or absent (7.8.11 C). Later instar larvae physogastrical, legs and head appendages ± reduced (Arndt 1993). The antennal muscles are arranged crosswise, a feature shared by larvae of Brachininae, Harpalinae and Trechinae (Beutel 1993). Other internal head structures are similar to those of harpaline larvae examined. Hypopharynx completely flattened. Functional mouth narrow. Mm. tentoriohypopharyngalis, verticopharyngalis and tentoriopharyngalis absent. The shift of the brain to the prothorax (Beutel 1993: Fig. 27) is a result of miniaturisation.

Phylogeny and Taxonomy. Phylogenetic hypotheses for Carabidae, originally simply the classification of presumed natural groups, have continued to develop and be refined as advances in technology have permitted researchers to use more and finer details of behaviors, morphology, chemistry and gene sequence data. The extensive knowledge of carabid beetles makes them well suited to cladistic methodology, which is more frequently being used to rigorously test hypotheses of relationships previously posited. Ball (1979) and Ball *et al.* (1998) provide an excellent detailed review of the history of classification and phylogenetics for the family. Brief and useful synopses with notes on relationships and distribution of each tribe were published by Bousquet & Laroche (1993).

Recent phylogenetic analyses that bear on relationships within Adephaga, affecting our understanding of the root for the family, or for exemplars from across many tribal level taxa in carabids, include a variety of character systems. Notably, 18S rDNA sequence data (Maddison *et al.* 1998, 1999; Shull *et al.* 2001), female reproductive tract (Liebherr & Will 1998), larval morphology (Arndt 1993, 1998), cuticular and muscular morphology (Beutel 1992, 1993; Beutel & Haas 1996) have all been analysed. Each of these studies, with their strengths and limitations, has provided some insight into the evolutionary history of the family.

The placement of Trachypachidae relative to Carabidae and Hydradephaga has varied over time and among authors. Some analyses have favoured a sister-group relationship to Dytiscoidea (e.g., Arndt 1993, 1998; Beutel 1993; Arndt & Beutel 1995; Beutel & Haas 2000) while others place them as sister to Carabidae, including rhyssodines (e.g., Kavanaugh 1986; Beutel 1998). Given the conflicting results from analyses based on both adult and larval characters, Shull *et al.* (2001) used 18S rDNA sequence data to attempt to resolve the relationships among the families of Adephaga. In all but one alignment and analysis strategy used by Shull *et al.* (2001) Trachypachidae was associated with the remaining Geadephaga and not Dytiscoidea. Ultimately, 18S rDNA sequence data, additional sequence data from other regions and characters from morphology should be combined in a single analysis to see if sufficient overall agreement can be found among character sets. Although analyses thus far do not unequivocally establish the relationships among adephagan families, all reinforce the distinctness of the trachypachid lineage, its great age and relictual nature.

Rhyssodidae is treated in this volume as a separate family from Carabidae, however, many authors have treated them as a subfamilial member of Carabidae, potentially related to some group of Clivinini (Bell 1998) (s. 1–7.9). Many authors

have noted that their extraordinary life history involving wedging through wood and feeding on slime-molds has likely resulted in members of this group being highly apomorphic both as adults and larvae. The apparent deviation from the primitive form makes it difficult or impossible to clearly assess the homology of many adult and especially larval structures. Rhyssodines are generally separate from Carabidae because of their distinctly divergent form, however, little evidence exist that Carabidae excluding Rhyssodidae is a monophyletic group. The arrangement of prehypopharyngeal setae in the larva (Beutel 1993) and development of pubescence of the antennomeres in adults (Beutel 1995) have been suggested as possible synapomorphies for Carabidae not including rhyssodines. These characters were presented to support a working hypothesis that excludes rhyssodines from carabids. Unfortunately, neither can be considered very convincing given the variation involved in these structures.

Various external structures found in adult rhyssodines such as the form of the medial septum that separates the procoxal cavities, the closure of the procoxal cavities and so-called anisochaete form of antennal cleaner, seem to indicate a placement within Carabidae (Bell 1967; Beutel & Haas 1996). This is consistent with characters of the female reproductive tract (Liebherr & Will 1998), though this character system did not provide any decisive synapomorphies for a specific sister-group relationship, the preferred phylogenetic hypothesis placed rhyssodines within Carabidae in a grade with Clivinini. The shared condition of a divided gonocoxite IX is the only evidence that supports the inclusion of rhyssodines within anisochaetous carabid taxa.

Bell (1998) concluded that rhyssodines, and what he considered a subtribe of scaritines, the salcediines (Clivinini), were sister taxa. However, Scaritini is most likely not monophyletic, clivinines may only be distantly related to Scaritini *sensu stricto*, with some evidence supporting a closer relationship of rhyssodines to Scaritini than to Clivinini (see below). Molecular sequence evidence from the 18s gene (Maddison *et al.* 1998, 1999; Shull *et al.* 2001) are problematic due to likely convergence of several potentially aberrant sequences including rhyssodines, scaritines, cicindelines and paussines. Although the authors view these associations as potentially spurious, additional taxon sampling and various methods over the course of the several papers has not altered this result. None of these analyses have associated rhyssodines and clivinines nor has any placed rhyssodines outside of Carabidae. As noted (Maddison *et al.* 1999) it is likely that this particular sequence cannot properly place basal carabid taxa. It is also possible that some of these taxa are in fact related. A relationship be-

tween Rhysodini and Scaritini, exclusive of Clivinini, should not be discounted as these taxa also share a peculiar structure, the vesicula seminalis (referred to as "mesidemia" by Smrž (1981, 1985)), not found in any other carabid tribe (Smrž 1981, 1985; Will unpubl.).

The larval form is strikingly different in rhysodines, unlike any carabid taxon and salcediines have apparently typical carabid larvae (Arndt, pers. obs.). Bell's (1998) proposed association of rhysodines and salcediines (Clivinini), or any association with a particular tribe within Carabidae, is not supported by larval characters (s. 1-7.9).

Subdivisions within Carabidae have been placed at a variety of levels over the years (Ball 1979; Ball *et al.* 1998). The subfamilies used by Lawrence & Newton (1995), which have been adopted for use in this volume, vary greatly in the type and relative support for their monophyly. Several of the subfamilies contain relatively few species and only one or a small number of genera, e. g., Gehringiinae, Omophroninae, Hiletinae, Loricarinae, Elaphrinae and Siagoninae. Each of these is well supported by apomorphic characters and are distinct in form, but their relationships to other subfamilies are not well understood. Other subfamilies have many more taxa and vary considerably in regard to the support for their monophyly and evidence for sister-group relationships.

Although the monophyly of Cicindelinae is well supported, the position of tiger beetles in Carabidae is still a question as contentious as the relationships for the families Trachypachidae and Rhysodidae discussed above. Although no character analysis has placed them outside of Carabidae, they are still frequently classified that way, with some authors maintaining them as a separate family. However, this issue in particular, and the phylogenetic structure of Carabidae in general, is dependent on the choice of the rooting point for the family. Recently it was proposed (Pearson & Vogler 2001) that Cicindelinae be maintained as a family separate from Carabidae given results from studies by Bils (1976) and Nichols (1985). However, neither Bils nor Nichols tested the monophyly of Carabidae excluding Cicindelidae. Rather they chose Cicindelinae (-idae) as the outgroup and so fixed the rooting point between tiger beetles and other carabids. Therefore these analyses provide no evidence for the exclusion of Cicindelinae. In fact, re-rooting the phylogenies presented by Bils and Nichols using Trachypachidae, Gyrinidae or Haliplidae, as suggested by results of recent studies on adephagan families (Beutel 1998; Beutel & Haas 2000; Shull *et al.* 2001), places Cicindelinae well within the family Carabidae. Adult morphological structures consistently place tiger beetles within Carabidae and often associate them with

some Carabinae (Carabini, Cychrini, Pamborini) (Beutel 1998; Liebherr & Will 1998) a relationship that suggests the unique form of the tiger beetle female abdomen is derived from the carabine type (Liebherr and Will 1998). Additionally, both Cicindelinae and some carabines (*Calosoma*) produce aromatic aldehydes as a major constituent of their defensive secretions (Moore & Wallbank 1968; Schildknecht *et al.* 1968). However, pygidial gland secretory cell aggregation type and structure are more similar to the typical hydradephagan form (Forsyth 1970). Larval characters suggest a close relationship of Cicindelinae and Loricarinae (Arndt 1993). Combined analysis of adult and larval characters places them as a member of a more derived grade than carabines together with loricarines, elaphrines and scaritines (Beutel & Haas 1996).

Published analyses of 18S ribosomal DNA (Maddison *et al.* 1999; Shull *et al.* 2001) are problematic with regard to the placement of cicindelinae within carabids, and their study suggests that the 18S rDNA sequence is probably not sufficient for resolving relationships of the subfamily. Results of these analyses of sequence data are consistent with a placement of cicindelinae within Carabidae, but are not considered conclusive as the sequence divergence of Cicindelinae is likely to strongly effect results due to convergence.

Paussinae is a very well supported monophyletic group based on morphological characteristics including aspects of the pygidial glands and substantial larval characters (Beutel 1995). They share with Brachininae similar chemical compounds and delivery of these defensive secretions by crepitating. However, the form of the glands, details of the secretory cells and mode of delivery differs dramatically between these groups (Eisner *et al.* 2000, 2001). Paussinae is generally considered adelphotaxon to the remaining carabid subfamilies or one of the basal-most lineages, however, evidence for this is limited. This basal position is supported by female reproductive track and larval characters (Arndt 1993; Liebherr & Will 1998). However, DNA sequence data (Shull *et al.* 2001) consistently places Paussinae as a much more derived group and never as sister to the remaining Carabidae. Shull *et al.* (2001) suggest the intriguing, and only slightly less parsimonious, possibility that a clade of Paussinae + Brachininae lies at or near the base of Harpalinae. This would, as pointed out by Shull *et al.*, require the reversal of a large number morphological characters thought to define the general pattern of relationships in the family.

Gehringiinae, like nebrinae and carabines, have what is thought to be the plesiomorphic thoracic configuration for Carabidae: confluent, internally unbridged and open procoxae, mesoventrite with anterolateral grooves for reception

of the procoxae and with a median hexagonal groove). As this is the plesiomorphic arrangement these structures do not provide grouping information and emphasis for classification has been placed on whether the arrangement of the protibial spurs and antennal cleaning organ represents an isochaete or anisochaete condition (Bell 1967; Beutel 1992; Beutel & Haas 1996). The condition of the Gehringiine tibia is not clearly assigned. If considered as isochaetous Gehringiinae is placed as sister to Paussinae (Beutel & Haas 1996), if anisochaetous, they could be sister to Nebriitae. Placement within anisochaete taxa and near nebriines is consistent with the dimerous condition of the gonocoxite and dual spermatheca in the female tract (Liebherr & Will 1998). Larval characters have not proven decisive for grouping Gehringiinae and no results have been published based on DNA sequence data.

The rounded body shape of species in Omophroninae immediately sets them apart from all other adaphagans. Details of their adult morphology are equally unique and this has resulted in a wide range of proposed relationships for the subfamily. Some authors have even placed them outside Carabidae with Hydradephaga (Bils 1976; Nichols 1985), but like Cicindelinae discussed above, re-rooting these phylogenetic hypotheses maintains Omophroninae as a member of Carabidae. Larval characters clearly support their inclusion within carabids (Beutel 1991; Arndt 1993) and suggest a position near the base of Anisochaeta or with Nebriitae. A close relationship between Nebriitae, Omophroninae and Gehringiinae was suggested by Liebherr and Will (1998) based on a hypothesised substitution of spermathecal function in these taxa. Analyses of 18S rDNA sequence data clearly place Omophroninae in Carabidae and in the basal grade of non-Harpalinae taxa (Maddison *et al.* 1998, 1999; Shull *et al.* 2001). However, no consistent sister-group relationships were found in the various analyses.

Carabinae as delimited by Lawrence & Newton (1995) is almost certainly not monophyletic. As discussed above Cicindelinae may be closely related to some carabine but there is no suggestion of a Carabinae + Cicindelinae clade that includes nebriite taxa. There is moderate support for the monophyly of Nebriitae from both DNA sequence data (Maddison *et al.* 1999) and morphological data (Kavanaugh & Nègre 1982; Kavanaugh 1996). However, there is no evidence beyond plesiomorphic similarity that Carabidae and Nebriitae form a monophylum. Additionally, female genital tract characters suggest that Siagoninae may be sister to the carabine + Cicindelinae clade, though this relationship is not supported by other character systems.

Several of the subfamilies (Hiletinae, Elaphrinae, Migadopinae, Siagoninae and Scaritinae) are taxa thought to occupy the mid-grade of the carabid phylogeny. Overall, these taxa show a trend of extensive reconfiguration of the thorax (Beutel 1992; but not in Hiletinae) and female abdomen (Deuve 1993; Liebherr & Will 1998) from the organisation found in the basal taxa leading up to the Harpalinae radiation. This set of taxa (excluding Clivinini from Scaritinae), Carabinae (excluding some Nebriitae), Cicindelinae and some members of Trechinae, have a sclerotized ramus mesad of the base of the female gonocoxite that is considered a significant synapomorphy. There is little agreement among various data set as to the relationships of this heterogeneous set of taxa. Certainly some of the subfamilies that fall along this grade are not likely to be monophyletic.

Scaritinae, excluding Promecognathini, is only weakly supported as monophyletic in some analyses of 18S rDNA sequence data (Shull *et al.* 2001) and thought to be polyphyletic based on female reproductive structures. Larval characteristics offer no synapomorphies for Clivinini + Scaritini (Arndt 1993). No recent analysis confirms the placement of Promecognathini with other members of Scaritinae as established by Lawrence & Newton (1995). As noted above, the peculiar form of the vesicula seminalis that is known from Scaritini *sensu stricto* but not found Clivinini is known from Rhyssodidae (Smrž 1981, 1985; Will unpubl.). This is consistent with a relationship of rhyssodines and scaritines found with 18S rDNA sequence data (Maddison *et al.* 1999; Shull *et al.* 2001), but interpreted as artefact by those authors.

As suggested by Erwin (1985) Migadopinae(ini) has not been supported as monophyletic in any recent analyses. Liebherr & Will (1998) placed Amarotypini as sister to Promecognathini while Migadopini was placed in a grade sister to Carabidae Limbata of Jeannel (1946). Based on 18S sequences data Maddison *et al.* (1999) found that *Amarotypus* was best placed near but not as sister to genera of Migadopini. A novel relationship of Loricerini + Migadopini (excluding *Amarotypus*) was strongly supported in those analyses.

The traditional arrangement of Trechinae (including Apotomini, Broscini, Melaenini, Psydriini, Bembidiini, Pogonini, Patrobini) or Styliifera of Jeannel (1941) is clearly not monophyletic. In addition to the various hypotheses for some of these taxa discussed above, Apotomines were included by Jeannel (1946) based on an incorrect assessment of the arrangement of the thoracic sclerites. Both morphological characters and 18S sequence data are in agreement that apotomines are not particularly closely related to these taxa, however, an alternate placement is

not clear. It has been demonstrated repeatedly that Psydrini is not monophyletic (Arndt 1993, 1998; Baehr 1998; Liebherr & Will 1998; Maddison *et al.* 1999; Shull *et al.* 2001). Psydrines fall out into at least two groups, neither thought to be closely related to other Trechinae taxa. A monophylum of Trechitae + Patrobini is quite plausible. Trechitae monophyly is supported by achiasmatic male meiosis (Serrano 1981) and a sister-group relationship of Patrobini is indicated by larvae (Arndt 1993), female abdominal structure (Deuve 1993) and molecular sequence data (Maddison *et al.* 1999).

Members of Brachininae like Paussinae, use an explosive discharge of hot quinones for chemical defence. Based on this alone it has been suggested that these two groups are closely related. However, as discussed above, they differ significantly in both adult and larval features. Brachininae larval characters have been interpreted as primitive (Arndt 1993), but no synapomorphies tying them to Paussinae have been identified (Arndt 1998). Although Arndt (1998) pointed out that there are no external synapomorphies in larvae for these two groups, Beutel (1993) identified an antennal musculature arrangement that was synapomorphic for Brachininae and Harpalinae. The female reproductive tract characters and form of the abdomen (Liebherr & Will 1998), thoracic structure and larval characteristics (Beutel 1992, 1993) all seem to place this group in or near Harpalinae. Confirmation of hypotheses from these morphological systems is found in 18S sequence data (Maddison *et al.* 1999), where moving Brachininae from sister of Harpalinae to a basal position adds forty-nine steps to the parsimony tree.

The great subfamily Harpalinae contains the bulk of species and greatest range of character variation. Despite considerable heterogeneity of the member taxa in terms of body form and life history, this is one of the most clearly monophyletic subfamilies in Carabidae based on a variety of character systems including the form of the female abdomen and reproductive tract (Deuve 1993; Liebherr & Will 1998), larvae (Arndt 1993), and molecular sequence data (Maddison *et al.* 1998, 1999; Shull *et al.* 2001). The only serious challenge to the monophyly is Brachininae as discussed above. Pseudomorphinae have a highly apomorphic form apparently in response to the group's evolution into myrmecophily. Its placement within Harpalinae, best treated as a tribe therein, has been confirmed in all recent analyses.

Relationships of taxa within Harpalinae, the presumed Cretaceous radiation of the majority of extant carabid taxa, remains delphic. No analysis of any significant number of harpaline taxa for a character system that is able to provide resolution among the included tribes has been

published. Some highly distinctive taxa are undoubtedly monophyletic but clearly some, perhaps most, of the major tribes are not. Arndt (1998) presents evidence for grouping some taxa based on larval characters. A group including Pterostichitae, Panagaeitae, Callistitae, and Harpalitae is supported by a shared condition of a membranous band on the lateroventral surface of the larval stipes. The villous canal extending along the common oviduct in the female reproductive tract was suggested as a possible synapomorphy for Orthogoniini, Panagaeini, Melanchitonini, Graphipterini, Licinini and Loxandriini. The presence of a basal sclerite of the spermatheca is synapomorphy from the female tract grouping Geobaenini, Pseudomorphini, Lachnophorini and Odacanthini (Liebherr & Will 1998).

Defensive chemical data and structures of the pygidial gland system may also provide clues to the affinities of Harpalinae tribes. Orthogonitae as circumscribed by Erwin (1985, 1991) is certainly a polyphyletic group with member taxa most likely related to a variety of tribes. Abdominal structures in *Catapiesis* Solier, *Brachidius* Chaudoir, *Oxyglychus* Straneo and *Cratocerus* Dejean are probably synapomorphic for these taxa, exclusive of Orthogoniini (Will *et al.* 2000). Defensive chemical data and molecular sequence data recently collected for *Catapiesis* (Will *et al.* 2000, unpubl.) and *Brachidius* (Will unpubl.) are consistent with a sister-group relationship of these taxa. Secondary chemical compounds support grouping these with members of Dryptitae and Perigonini.

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7.9. Family Rhysodidae Laporte, 1840 (= Rhysodini s. Bell)

Rolf G. Beutel

Distribution. World-wide, with a higher diversity in tropical regions. Especially prominent in insular faunas.

Leoglymniina Bell & Bell, 1978: confined to Australia

Dhysorina:

Tangarona Bell, 1982 substituted for *Tangaroa* Bell & Bell, 1978 (preoccupied): North Island of New Zealand

Dhysores Grouvelle, 1903: Africa

Neodhysores Bell & Bell, 1978: Brazil

Medisorina:

Medisores Bell & Bell, 1987: South Africa

Rhysodina:

Rhysodes Dalman, 1823: Europe, Asia

Kupeus Bell & Bell, 1982 substituted for *Kupoea* Bell & Bell, 1978 (preoccupied): North Island of New Zealand

Kaveinga Bell & Bell, 1978: Pacific islands from New Caledonia and New Zealand to Australia and Tasmania, westwards to Mindanao and Sulawesi

Angekiva Bell & Bell, 1979: Australia

Ingevaka Bell & Bell, 1979: North Island of New Zealand

Vakeinga Bell & Bell, 1979: North Island of New Zealand and New Caledonia

Kaveinga s. str.: Pacific islands from the Solomons and Australia (Cape York) to Mindanao and Sulawesi

Sloanoglymniina

Sloanoglymnius Bell & Bell, 1991: Australia
Clinidiina:

Grouvellina Bell & Bell, 1978: Madagascar, Mayotte (Comoro Islands)

Rhysodiastes Fairmaire, 1895: Oriental and Australian regions, eastern South America

Rhysotetrops Bell & Bell, 1985: Fiji

Rhysoarca Bell & Bell, 1985: New Caledonia, New Zealand, Australia

Temoana Bell & Bell, 1985: Taiwan, Pacific Islands, Australia westwards to Andamans, eastern India, western China

Rhysotrix Bell & Bell, 1985: northern South America

Rhysodiastes s. str.: eastern Brazil

Clinidium Kirby 1895: Holarctic region, Central America, northern South America

Mexiclinidium Bell & Bell, 1978: highlands of Mexico and Guatemala

Protainoa Bell & Bell, 1978: western Cuba

Tainoa Bell & Bell, 1978: Greater Antilles

Arctoclinidium Bell & Bell, 1978: Europe, Iran, Japan, western North America, eastern USA

Clinidium s. str.: Central America, West Indies, northern and western parts of South America

Omoglymniina

Xhosores Bell & Bell, 1978: Natal and extreme eastern part of Cape Province, South Africa

Yamatosa Bell & Bell, 1979 substituted for *Yamatoa* Bell & Bell, 1978 (preoccupied): Oriental Region, from the Himalayas to Japan and Java

Shyrodes Grouvelle, 1903: Burma

Srimara Bell & Bell, 1978: Vietnam

Plesioglymnius Bell & Bell, 1978: Greater Sunda Islands, Malay Peninsula, Mindanao, Brazil, Cuba

Ameroglymnius Bell & Bell, 1979: Cuba, Venezuela, southern Brazil

Juxtaglymnius Bell & Bell, 1979: Borneo, Malay Peninsula, Java

Plesioglymnius s. str.: Sumatra, Borneo, Celebes, Mindanao

Arrowina Bell & Bell, 1978: southern India, Sri Lanka, southern Japan

Omoglymnius (*sensu lato*) Ganglbauer, 1892: by far the largest genus of Rhysodidae, almost cosmopolitan, but absent from Madagascar and New Zealand

Hemoglymnius Bell & Bell, 1978: Greater Sunda Islands, Africa (1 species)

Boreoglymnius Bell & Bell, 1982: North America, Japan

Pyxiglymnius Bell & Bell, 1978: Oriental Region, from Japan to Java, Sumatra, Andaman Islands and Luzon

Laminoglymnius Bell & Bell, 1982: Malay Peninsula, Sumatra, Borneo, New Guinea

Navita Bell & Bell, 1978: Fiji, New Hebrides