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2.7.5 Chrysomelidae: Cryptocephalinae Gyllenhal 1813

Maria Lourdes Chamorro

Distribution. Worldwide approximately 5300 species are classified in 127 genera in three tribes. Fulcidacini (most commonly and until recently treated under the name Chlamisini), Clytrini, and Cryptocephalini, with the highest diversity occurring in the tropical and subtropical regions. Of the three tribes, Fulcidacini, the warty leaf beetles, is the least diverse with an estimated 500 species in 11 genera. The only genus not present in the New World is *Hymetes* Lacordaire (3 spp.) from Asia; four genera

are endemic to the Neotropical region (*Melittochlamys* Monrós, 13 spp.; *Fulcidax* Voet, 7 spp.; *Kakita* Chamorro & Konstantinov, 1 sp., and *Carcinobaena* Lacordaire, 1 sp.); three genera extend their range into the Nearctic region [*Diplacaspis* Jacobson, 6 spp.; *Neochlamisus* Karren, 17 spp.; *Pseudochlamys* Lacordaire, 5 spp.] and three genera exhibit broader patterns of distribution into the Oriental, Australasian, Afrotropical and/or Palearctic regions [*Exema* Lacordaire, 26 spp.; *Aulacochlamys* Monrós, 32 spp.; and *Chlamisus* Rafinesque, 400+ spp.]. The second most diverse tribe is Clytrini with more than 1300 species in six subtribes and 62 genera. All 38 genera in the subtribe Clytrina, with the exception of *Anomoea* Agassiz, occur in the Old World; 11 genera are endemic to Africa, and only *Smaragdina* Chevrolat is cosmopolitan. The subtribes Babiina (13 genera), Megalostomina (seven genera), Ischiopachina (one genus), and Arateina (one genus; Brazil) are restricted to the New World. The subtribe Eoclytrina (one genus) and the *incertis sedis* genus *Parantipa* Medvedev are endemic to Africa. Cryptocephalini consists of more than 3500 species in five subtribes and 54 genera distributed worldwide. The most species rich genus is *Cryptocephalus* Geoffroy with more than 1700 species. The subtribe Achaenopina (one genus) is endemic to southern Africa. Stylosomina (three genera) is absent from the New World, whereas Pachybrachina (10 genera), Monachulina (16 genera), and Cryptocephalina (21 genera) are found in all biogeographic regions. [Monrós 1951, 1953; Crowson 1967; Seeno & Wilcox 1982; Masutti 1960; Reid 1990, 1991, 1995, 1998; Moldenke 1970; Watts 2005; Schöller 2002, 2007; Chamorro-Lacayo & Konstantinov 2009; Bezděk 2010.]

Biology and Ecology (Fig. 2.7.5.1 C–F, J, K). A detailed account of Camptosomata (Cryptocephalinae + Lamprosomatinae) biology was presented by Erber (1988). Brown & Funk (2005) described in detail case-making behavior and other aspects of *Neochlamisus* life history (Fulcidacini). Cryptocephalini larvae are saprophagous, feeding on decomposing leaves in litter and on vegetation growing on rocks, but also remove the outer layer of twigs and fruits; some feed on fresh leaves and seedlings. Adults are usually found on flowers where they feed on pollen and petals, but also on fresh leaves. Camptosomata exhibit complex case-building and oviposition behaviors. Their unique biology involves fecal enclosures provided by the female to her offspring in the form of an egg-case or scatoshell, which the larvae retain and progressively build upon to create a portable dwelling. Each egg is individually coated by the female with a mixture of her own feces and rectal secretions. During oviposition and during the coating process of each egg, the adult female rests her body forward onto her fore- and mid-legs, while her hind tarsi hold and rotate each egg within a small fovea, or depression, in abdominal ventrite 5. The process of placing and arranging the shingles, or fecal plates, around the egg to form the scatoshell may take approximately 20–30 minutes. Eggs resemble small seed pods. In the northern hemisph e105.]

Morphology, Adults (Fig. 2.7.5.1 A, I, L, M, N, Q, R, S). Length 0.8 mm–10.0 mm, with the largest species occurring in Holarctic clytrines and Neotropical Fulcidacini (e.g., *Fulcidax* Voet); the smallest species belong to Cryptocephalini (*Triachus* LeConte, *Diachus* LeConte, and some *Lexiphanes* Gistel). Body 2 times longer than wide,1.5 times longer than wide (cylindrical), or rarely as long as wide; in dorsal view parallel-sided with prothorax as wide as combined elytral bases; or rarely rounded; anteriorly and posteriorly blunt for most Cryptocephalini, some anteriorly and posteriorly rounded, in transverse plane almost round; multicolored and patterned, particularly Cryptocephalini, black with red humeri commonly in Clytrini, brown, black, straw-yellow and some with velvet spots in Fulcidacini, glabrous to pubescent, particularly Clytrini, but some Cryptocephalini (e. g., *Mylassa* Stål).

Head not declined, anteriorly flat; retracted into prothorax up to frons or almost completely, with compound eyes completely to barely visible from above; without transverse occipital ridge or stridulatory file. Frontal region rarely with median groove. Compound eyes entire, not protuberant to strongly protuberant; finely facetted, with interfacetal setae; weak to deep canthus present. Antennal insertions not exposed from above; subantennal grooves absent. Frontoclypeal transverse strengthening ridge prominent to absent; clypeus variously shaped, usually trapezoidal. Labrum well developed, square, apex commonly truncate, but variably shaped. Antennae 11-segmented, longer than pronotum and filliform in Cryptocephalini (sometimes antennomeres distally dilated and flattened), shorter than pronotum and dentate in Clytrini, and clavate in Fulcidacini; beginning of club variable; scape subglobular to elongate and longer than pedicel. Mandibles usually deltoid, moderately elongate, gradually curved mesally, rarely asymmetrical in males (e. g., *Megalostomis* Chevrolat); from uni- to quadridentate, lacking mola and prostheca. Maxillae each with elongate, setose galea; lacinia variably shaped sometimes bilobed in Clytrini; apical maxillary palpomere digitate. Mentum transverse; ligula bilobed; apical labial palpomeres digitate, apically truncate in some. Gular sutures widely separated and short. Tentorium with anterior arms and bridge absent. Cervical sclerites reduced.

Pronotum about 0.75–1.0 times as long as wide, widest basally; sides slightly rounded or sinuate; base slightly narrower or as wide as combined

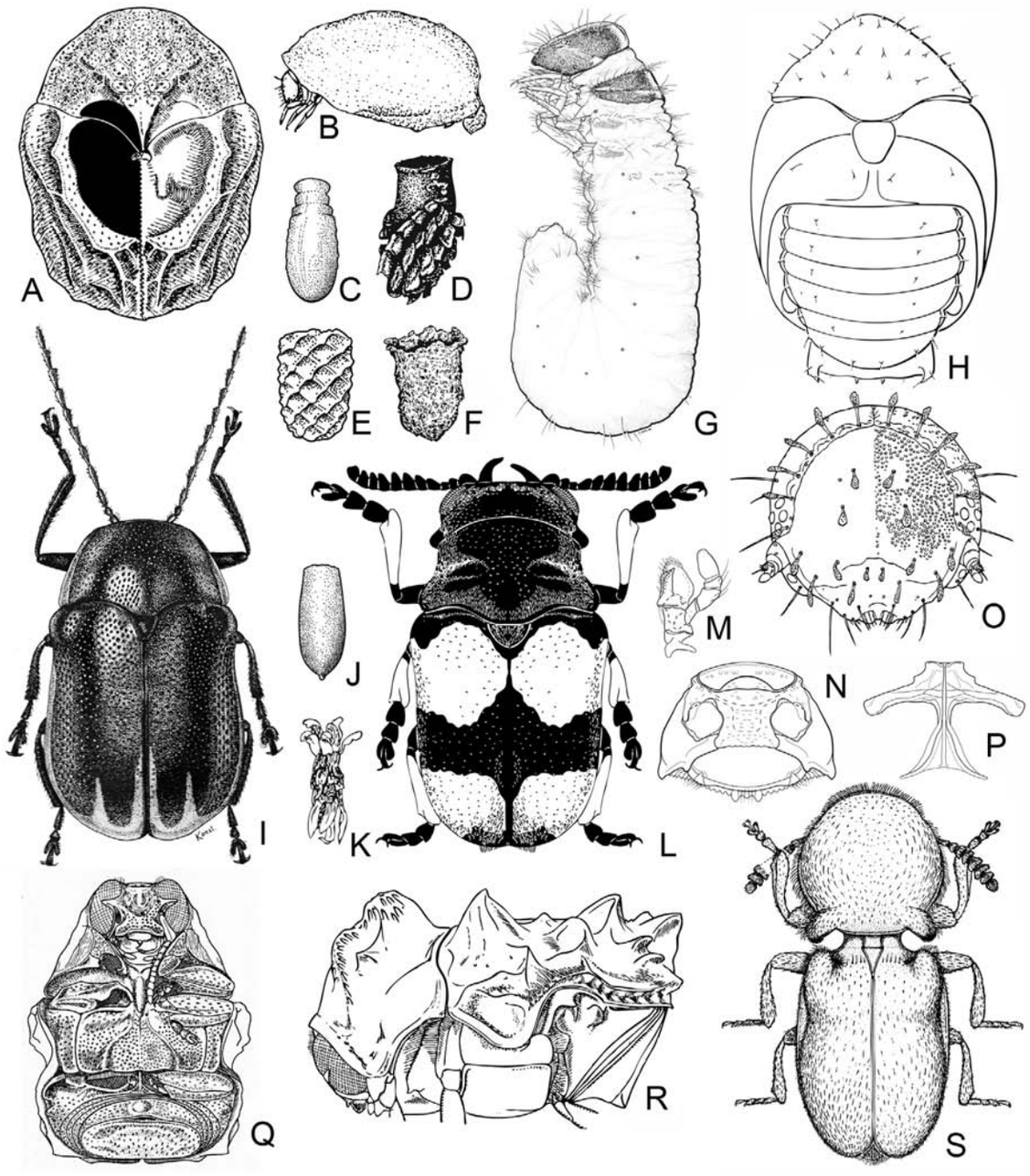

Fig. 2.7.5.1 Cryptocephalinae. A, *Chlamisus perforatus* Monrós adult, dorsal view, right side drawn without velvety spot (after Monrós 1952); B, *Exema canadensis* Pierce larva within fecal case, lateral view (after Erber 1988); C, *Chilotoma* scatoshell (after Medvedev 1962); D, *Cryptocephalus bipunctatus* (Linneaus) young larval case (after Erber 1988); E, *Smaragdina* scatoshell (after Medvedev 1962); F, *Exema canadensis* scatoshell (after Erber 1988); G, *Pachybrachis* larva, lateral view (reproduced with permission of LeSage (LeSage 1985); H, *Lexiphanes* pupa, dorsal view (after LeSage, 1984); I, *Cryptocephalus* adult, dorsal view (reproduced with permission from Konstantinov); J, *Labidostomis* scatoshell (after Medvedev 1962); K, *Metallactus* scatoshell (after Erber, 1988); L, *Megalostomis bubalus bubaloides* adult (after Monrós 1953); M, *Cryptocephalus* sp., right maxilla; N, *Cryptocephalus* sp. prothorax, ventral view; O, *Lacnabothra baccata* larval head, anterior view (after Reid 1990 as *Cadmus);* P, *Cryptocephalus* sp. met-endosternite, dorsal view; Q-R, *Fulcidax bacca* (Kirby) adult, Q, ventral view, R, lateral view (after Monrós 1952); S, *Hockingia curiosa* Selman dorsal view (after Selman 1988).

elytral bases; lateral pronotal carinae present or absent, rarely weakly explanate; anterior and posterior angles rounded or pointed, bearing large seta; posterior edge straight to medially produced, margined or not; disc entire in Cryptocephalini and Clytrini to greatly sculptured and sometimes with plateaued projections in Fulcidacini. Prosternum in front of coxae usually narrow and shorter

than shortest diameter of a single coxal cavity, flat to moderately convex, sometimes produced to conceal mouthparts. Prosternal process complete, usually parallel-sided; males with median projection in some Cryptocephalini (e. g., *Bassareus* Haldeman), apex (posterior margin) truncate, broadly produced (e. g., *Pachybrachis* Chevrolat), to bilobed (*Cryptocephalus*), flat on same plane with mesothorax or not. Antennal grooves present along prosternal process in Fulcidacini. Notosternal sutures distinct. Hypomera of different surface sculpture, almost always smooth and concave to accommodate forelegs. Procoxae not projecting below prosternum, without concealed lateral extensions; trochantins exposed within coxal cavity. Procoxal cavities subcircular, very narrowly (e. g., *Clytra* Laicharting) to widely separated (more than widest diameter of coxa, e. g., *Stegnocephala* Baly), open to closed, without lateral extensions. Scutellar shield variously shaped to seemingly absent (i. e., *Adiscus* Gistel) abruptly elevated or not, anteriorly convex to emarginate, posteriorly concave in Fulcidacini to obtusely angulate in some Cryptocephalini; stridulatory device present on concealed part of mesoscutellum. Elytra about 1–1.5 times as long as wide and 1–3 times as long as pronotum; regularly (with eight to ten distinct puncture rows and elevated or flat sutural striae) or irregularly punctate, punctures of varying size; disc greatly sculptured in Fulcidacini; humeri well-developed or not, abrupt basal edge usually present; elytral apices often meeting at median suture, concealing all tergites, but independently rounded, exposing greatly pigmented pygidium; epipleura well-defined, disappearing apically; stridulatory device (Clytrini) present on underside of elytra as basolateral rounded patch and apicolateral narrow strip; elytral base (posterad of scutellar shield) rarely exposing metascutellum; elytral serration entire to acutely serrate and interlocking in Fulcidacini. Mesoventrite separated by complete sutures from mesanepisterna; anterior edge on same plane as metaventrite, without procoxal or prothoracic rests. Mesocoxae not conical and projecting, with exposed trochantins. Mesocoxal cavities narrowly to broadly separated (greater than widest diameter of mesocoxa); subcircular, slightly oblique or not; partly closed laterally by mesepimera and slight portion of mesanepisterna. Metaventrite with discrimen as long as entire sclerite (extending to metaventral process; katepisternal (transverse) suture absent; metanepisternum moderately elongate and moderately narrow; sometimes bearing white setae. Metacoxae narrowly to widely separated, horizontally oriented, extending laterally to meet metanepisterna; plates absent. Metendosternite with stalk short to elongate, lateral arms long, laminae well-developed and broad; anterior process short to moderately elongate (almost as long as stalk), bearing variously separated anterior tendons. Hind wings with long apical field; each wing containing small distinct sclerite and anterior and posterior remnants of RP; radial cell triangular, well-developed to apically open (Radius-Median cross-vein missing); RP short to indistinct; media (M) short; subcubital fleck absent; three to four anal veins present and cross-veins forming two anal cells (distal 2AC and basal 1AC). Legs generally well-developed; short and stout with tibiae bearing grooves to accommodate tarsi in some Fulcidacini (*Carcinobaena*); trochanterofemoral joint strongly oblique with base of femur separate from coxa; pro- and metafemora may be enlarged, particularly in males; inner and external surfaces of tibiae may be keeled and bearing groove; tibial spurs present in some taxa; tarsi 5-5-5 in both sexes; penultimate tarsomere reduced and antepenultimate bilobed, all usually wider in males; tarsomere 3 densely clothed beneath with adhesive microtrichia; pretarsal claws simple to deeply bifid; empodium not visible.

Abdomen with five free ventrites and six tergites. Ventrite 1 more than twice as long as 2, usually longer than ventrites 2–4 combined, without postcoxal lines; intercoxal process narrowly rounded to almost truncate. Functional spiracles present on tergites I–VI. Tergite VI forming strongly pigmented pygidium, always exposed; anterior edge of sternite VIII in male without median strut. Ventrite 5 in females with variably-sized apical fovea. Males with segment IX membranous and spiculum gastrale Y-shaped. Aedeagus of cucujiform type; tegmen Y-shaped; struts (remnants of tergite IX) either present or absent; penis flattened to rounded, slightly to strongly curved apically; apically and/or laterally usually with tufts of setae. Sternite VIII in female lacking spiculum ventrale. Ovipositor short, rigid and oval with distinct proctigeral, paraproctal, and coxital baculi; paraprocts deltoid, slightly shorter than undivided coxites, sclerotized or less pigmented proximally, flattened, digitate lobes of variable form, apically setose; styli absent. Spermatheca strongly to moderately sclerotized, variably shaped, usually J-, C-, or S-shaped., Rectal sclerites ("Kotpresse") present in female; ventrally sclerite complete, without median section (two lateral sclerites), or with median section thickened (three sclerites apparent), variously shaped, laterally extended into plates; dorsal sclerites complete as longitudinal strip (one sclerite), without median section (two lateral sclerites), or with two lateral and one median section (three sclerites); additional sclerites and chitinpolsters present [Monrós 1951, 1953; White 1968; Reid 1990; Chamorro-Lacayo *et al*. 2004, 2006; Schöller 2008].

Morphology, Eggs and Scatoshell (Fig. 2.7.5.1 C–F, J, K). Oval, with or without chorionic stalk. Color milky-white to yellowish-white. Surface

of chorion micropustulate. Scatoshell of various shapes and with various surface sculpture; resembling seeds, buds, etc. A detailed description of fecal case architecture is given by Chaboo *et al*. (2008) [LeSage & Stiefel 1996; Lee & Cheng 2007].

Morphology, Larvae (Fig. 2.7.5.1 B, G, O). Body strongly J-shaped in lateral view, with last five abdominal segments bent anterad; head, pronotum, and legs strongly sclerotized; abdomen lightly pigmented. Larvae partly contained within bell-shaped case made of own feces and debris, but head and legs exposed; setation sparse.

Head hypognathous; anteriorly usually flattened to concave, sometimes with distinct circular ridged margin; entire head capsule resembling flattened cork (usually in Cryptocephalini and Clytrini) or in anterior view oblong in some Fulcidacini, to circular in Cryptocephalini and Clytrini. Epicranial suture Y-shaped, with long epicranial stem (= coronal suture); frontal arms enclosing a broad U-shaped frontal area, or straight and frontal area V-shaped; extending to antennal insertions anteriorly. Median endocarina ending before frontal arm-epicranial stem junction or absent[1]. Rugosity and microsculpture present on surface of head in some Clytrini and Cryptocephalini. Six stemmata clustered in two groups on each side: two pairs of posterior stemmata above antennae, one pair of anterior stemmata below antennae. Frontoclypeal suture partially visible or absent, lateral fourth or weak depression visible (usually Fulcidacini). Labrum fused; clypeolabral fusion line weak; anterior clypeolabral margin concave to acutely sinuate. Antennae short, appearing two-segmented in both Clytrini and Fulcidacini; three-segmented in Cryptocephalini and sensorium similar in size and width to three antennal segments combined; sensorium weakly sclerotized, located apically on antennomere 2 in Fulcidacini and Cryptocephalini, absent in Clytrini. Mandibles symmetrical, tri- quad-, or quinquedentate, without mola; each with pronounced globate basolateral condyle. Ventral mouthparts retracted; maxillary articulating area slender to apparently obsolete. Cardines moderately oblique, undivided; stipites distinctly longer than wide; outer lobe (mala) digitate, setose; inconspicuous inner lobe fused to stipes bearing two or three stout setae; maxillary palps three-segmented, each with well-developed palpifer; palpomere 3 with digitiform sensillum in groove on outer surface. Labium consisting of narrow, poorly defined prementum and prominent mentum and submentum; paramental sclerites present; ligula digitate, simple, membranous, apically bearing three pairs of spiniform setae; shorter than two-segmented palps; palpomeres of same length, segment 1 broader than 2; palpiger transverse to elongate. Hypopharyngeal sclerome and bracon absent. Gular sutures separated. Tentorial bridge narrow.

Prothorax as long as meso- and metathorax combined or slightly shorter; with distinct sclerotized plates; prosternum without armature. Meso- and metathorax with asperities; egg-bursters on tubercle with long seta and spine present in first instar. Quadrate sclerites associated with legs present. Legs well-developed, five-segmented, of equal size; pretarsus (tarsungulus) long, acute, claw-like; strongly curved in Fulcidacini or arched, with single seta; mesocoxae relatively widely separated. Spiracles annular uniforous, not placed at ends of spiracular tubes.

Abdomen more than twice as long as thorax, with segments of similar length. Terga without sclerotized plates, not extending laterally beyond edges of sterna. Asperities present throughout. Segments IX simple, not enclosed by sternum VIII. Last five to six segments curved anterad. Anal opening transverse. Spiracles similar to those of thorax; spiracular-peritreme diversely-shaped among taxa.

Chaetotaxy of head and body diagnostically and taxonomically important; setae from simple and elongate to clavate distally with minute spicules and appearing serrate; in Fulcidacini, distal setae on tibia elongate, apically flattened, enlarged, and curved. Reid (1990 and references therein) offer detailed discussion on chaetotaxy nomenclature for Camptosomata (Cryptocephalinae + Lamprosomatinae) [Monrós 1951, 1953; LeSage 1982, 1984 a, b, 1985, 1986; LeSage & Stiefel 1996; Reid 1990; Medvedev 1998; Agrain & Marvaldi 2009; Jerez & Briones 2010].

Morphology, Pupae (Fig. 2.7.5.1 H). Exarate, white to yellowish. Head not visible from above. Pronotum bell-shaped. Setae on tubercles present or absent on head (epicranium), pronotum, mesanotum, metanotum, femora, and abdominal segments I–V, VI. Shape of tergites VI–VII variously shaped. Posterior podothecae bare. Laterally posteriorly directed projections on tergite VII absent or fleshy usually with subapical seta and or spinose. Elytrothecal lobe and urogomphi present or absent [LeSage 1984; Reid 1990].

Phylogeny and Taxonomy. Cryptocephalinae tribes and genera have remained essentially unchanged since their establishment by Chapuis (1874), with the exception of incorporating the former subfamilies Fulcidacini and Clytrini under Cryptocephalinae following the results of a higher-level phylogenetic analysis of Chrysomelidae by Reid (1995). The monophyly of Cryptocephalinae is well supported based on morphological (Reid 1995, 2000; Schmitt 1996)

[1] Agrain & Marvaldi (2009) indicated it being absent.

and molecular analyses (Farrell 1998; Duckett *et al*. 2004; Gomez-Zurita *et al*. 2007, 2008) of higher-level relationships in the Chrysomelidae. Tribes within Cryptocephalinae are morphologically uniform and each is undisputedly monophyletic. However, relationships of the taxa within the subfamily have not been confirmed by any published phylogenetic analysis. The dissertation by Reid (1990) inferring the phylogeny of mostly Australian Cryptocephalinae remains unpublished. Approximately half of all genera of Cryptocephalini (21 genera in four subtribes) are restricted to Australia and surrounding areas. However, generic synonymies may reduce the total number of Australasian genera to approximately 15. Evidence suggests Lamprosomatinae to be the sister-taxon to a monophyletic Cryptocephalinae (Reid 1995, 2000; Gomez-Zurita *et al*. 2008), a clade known as the Camptosomata. Earlier studies hypothesize Fulcidacini and Lamprosomatinae as sister taxa (Monrós 1960; Suzuki 1988, 1994, 1996; Kasap & Crowson 1976), or Lamprosomatinae as sister-taxon to a monophylum Clytrini + Cryptocephalini (Lee 1993); however, these relationships remain uncorroborated. Circumscription of generic limits with precise and reliable diagnostic features is lacking. Modern revisions and cladistic analyses are sorely needed to address over- and under-splitting of natural groups [Crowson 1967; Reid 1995; Suffrian 1866, 1863].

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