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3.7.10 Curculioninae Latreille, 1802

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Distribution. The subfamily as here composed (see Phylogeny and Taxonomy below) includes approximately 350 genera and 4500 species (O’Brien & Wibmer 1978; Thompson 1992; Alonso-Zarazaga & Lyal 1999; Oberprieler *et al.* 2007), provisionally divided into 34 tribes. These are geographically generally restricted to a lesser or larger degree, only two—Curculionini and Rhamphini—being virtually cosmopolitan in distribution and Anthonomini, and Tychiini only absent from the Australo-Pacific region. Acalyptini, Cionini, Ellescini, Mecinini, and Smicronychini occur mainly in the Old World, from Africa to the Palearctic and Oriental regions, with Ellescini, Acalyptini, and Smicronychini also extending into the Nearctic region and at least the latter two also into the Australian one. Styphlini are restricted to the Palearctic region and the seemingly related Itini and the monobasic Acenetrusini to only its western part. Ancylocnemidini, Microstylini, Nerthopini, and Ochyromerini are largely African but extend into the Oriental region, the last extensively so and just reaching into Australia, whereas the small tribes Diabathrariini, and Ulomascini are entirely African. Nine tribes only occur in the New World, Camarotini, Ceratopodini, Otidocephalini, Piazorhinini, Thecesternini, Erodiscini, Prionobrachiini, Pyropini, and Sphaeripopoeini, the last four restricted to the Neotropical region. Cranopoeini, Cryptoplini, Storeini, and Viticiini are limited to the Australo-Pacific region, and the last two reaching north into Indonesia and southern Japan. Only two tribes appear to have a Gondwanan distribution, Eugnomini occurring in Australia and South America and Derelomini in Africa and South to Central America, but the composition of these tribes as including genera from these disparate regions needs verification.

Biology and Ecology. Adults of Curculioninae are usually found on flowers, fruits, leaves, and branches of many and various herbaceous plants and trees in nearly all habitat types, ranging from low plains to high mountains and from deserts to tropical pluvial forests. The larvae are predominantly endophytic in reproductive plant parts such as flower and fruit buds, seeds, and fruits, but some develop in shoots (in which some incite galls) or mine in leaves. The slimy, slug-like larvae of Cionini are exceptional in the subfamily for being ectophytic. No species, however, live in aquatic habitats. The biology of the subfamily varies considerably between the tribes, and sometimes also between their genera, but several tribes are associated with only one or a few plant families and some genera can be highly host-specific on a single plant genera or even species. Patterns of host association are, however, often confused by the uncertain

composition of many of the tribes and by the unreliability of some published host records. Curculionine weevils may often be found on flowers or foliage of plants on which their larvae do not develop, and such fortuitous occurrences must be distinguished from true host associations in which the plants serve as substrates for oviposition and larval development. The lists of plants on which weevils were only collected, without established evidence of a reproductive interaction, may portray false patterns of host association that are perpetuated over time and can have serious implications for applied fields of research, such as biological control. The known biology and host associations of the various tribes are summarized under their treatment below, but some of these associations are subject to verification.

Two particular lifestyles are more common in Curculioninae than in other subfamilies, namely mining in leaves and inciting galls. The bionomics of leaf-mining insects was reviewed by Hespeneheide (1991), who mentioned some aspects of the biology of the best-known curculionine leaf miners, the Rhamphini, but did not cover the habit comprehensively. The knowledge of leaf mining among European weevils is well covered by Scherf (1964), who recorded it to occur in the tribes Anoplini, Rhamphini, and Styphlini, whereas May (1993) provided an account of known leaf-mining genera of Storeini in New Zealand. The habit further occurs in the small South American tribes Camarotini, Piazorhinini, and Prionobrachiini and in the Australo-Pacific Vitiini, although it is poorly documented in these groups. Nothing appears known about this habit in Africa. Leaf-mining weevil larvae tend to be flat, with the head prognathous, deeply excised posteriorly and with reduced numbers of setae, and the body tapered caudally and with dorsal and ventral or lateral ambulatory ampullae and/or covered with fine asperities that enable the larva to crawl in its mine. May (1993) sketched a progression of increasing specialization in New Zealand leaf-mining storeine genera, from the largely unmodified larva (with a normal head capsule) of *Phorostichus linearis* (Broun) via *Peristoreus flavitarsis* (Broun) and *Hypotagaea concolor* (Broun), in which the head is weakly emarginate, to that of *Neomycta rubida* Broun, in which the epicranium is deeply excised except for the median endocarina. A similar head capsule occurs in the genus *Geochus* Broun (see Molytinae: Phrynixini) as well as in Rhamphini (*Ixalma* Pascoe, *Rhamphus* Clairville, *Rhynchaenus* Clairville; van Emden 1938; Scherf 1964; Lee & Morimoto 1996), in which a comparable cline of increasing morphological regression appears to occur (May 1993). The flat larva of the undescribed Australian vitiine genus *Austrocis* is similarly adapted to leaf mining, the head also deeply V-shaped posteriorly (but without a protruding endocarina) and the body segments each carrying a lateral pair of strong ampullae. Leaf mines are generally of two types, linear or round

(blotched), with the pattern often intricate and species diagnostic (Scherf 1964). Generally there is only one mine per leaf, but several larvae of the small *Rhamphus* species may mine in the same leaf (Scherf 1964). Pupation occurs either in the mines (Rhamphini, Styphlini) or in litter on the ground or in soil (Storeini). The larvae of *Anoplus* Germar and some *Rhamphus* and *Rhynchaenus* species cut out pieces of leaf, which they stick together and in which they fall to the ground and pupate (Scherf 1964). Larval habits associated with leaf mining are probably as varied and intricate in other leaf-mining groups.

The induction of galls appears to be more common in Curculioninae than in other subfamilies, with the exception of the Ceutorhynchini (Conoderinae). Korotyaev *et al.* (2005) compiled a useful summary of galling habits in the subfamily, discussing also ecological and evolutionary aspects that seem to make this habit more prevalent in Curculioninae than in other subfamilies. Galling appears to occur more commonly on herbaceous, short-lived plants and in rapidly growing organs (mainly young, slender stems but also roots), attributes characteristic of nonwoody plants growing in temperate or arid regions with short growing seasons. The lifestyle seems to be derived from stem boring (no transition from leaf-mining known) and enables a species to exploit very slender stems and similar plant organs that it could not utilize otherwise. The larvae of some *Smicronyx* Schoenherr, on completion of their development, leave their galls on the stems of parasitic dodder (*Cuscuta*) and tunnel into the stem of its *Vernonia* host for pupation (Anderson 1970). Generally, the closest relatives of gall incitants develop in flowers or seed capsules of the same plant species, and no instances are known of closely related species inducing galls on different host organs. Galling thus enables a greater number of related species to exploit the same host but does not form a definite feeding niche in any group. In central Europe, approximately 10% of the weevils whose larval habits are known incite galls (Scherf 1964), and weevils (as Coleoptera as a whole) never form a major component of gall-forming faunas. Some weevils also live as inquiline in galls induced by other insects, such as cecidomyid flies and cynipid and tenthrinid wasps, in which they may live as commensals or pseudoparasites. The examples of curculionine gallers provided by Korotyaev *et al.* (2005) largely comprise Palaearctic species of the tribes Meciniini, Smicronychini, and Tychiini, but galling is also known to occur in other tribes and in the southern hemisphere, for instance, in Anthonomini, Camarotini, Cryptoplinae, Curculionini, Eugnomini, Otidoccephalini, Rhamphini, Storeini, Thecesternini, and *Sidomenia* Laporte, as detailed in the sections on these tribes below. Whether galling may be as common in tropical and in southern temperate regions as is in northern temperate ones remains to be investigated.

Curculionine weevils are important pollinators of several plants, in particular palms and basal

angiosperms (magnoliids), in which cantharophily is the dominant pollination system. Weevil pollination of palms has been reported or indicated for the genera *Acanthococos*, *Acrocomia*, *Astrocaryum*, *Attalea*, *Bactris*, *Butia*, *Catoblastus*, *Chamaerops*, *Cocos*, *Cryosophila*, *Elaeis*, *Hydriastele*, *Phoenix*, *Phytelephas*, *Rhaphidophyllum*, *Rhapis*, *Sabal*, *Salacca*, *Serenoa*, *Socratea*, *Syagrus*, and *Wettinia* (Henderson 1986; Silberbauer-Gottsberger 1990; Meekijjaroenroj & Anstett 2003) and, given the close association of Derelomini with several other palm genera (Franz & Valente 2005), is probably more widespread in the family. In Africa and America, the weevils involved in palm pollination belong to the tribe Derelomini, whereas those in Asia and the Australo-Pacific region all seem to be Acalyptini (Kojima & Morimoto 2005). The best-known case of weevil pollination of palms is that of the African oil palm, *Elaeis guineensis*, which is pollinated by the derelomine *Elaeidobius kamerunicus* (Faust), which was introduced to Asia in 1981 to improve seed set in oil palms planted there (Krantz & Poinar 2004). Weevils also pollinate several species of Cyclanthaceae and some Araceae (Franz 2003 a, b, 2004, 2006, 2007 a, b; Franz & Valente 2005). Weevil pollination in magnoliids has been shown to occur in the families Annonaceae, Eupomatiaceae, Myristicaceae, and Winteraceae and is likely to occur also in other basal angiosperm families. In Annonaceae, Momose *et al.* (1998) reported species of *Endaenidius* Morimoto and *Endaeus* Schoenherr (Ochyromerini) to visit flowers of *Uvaria* (*Cyathostemma*) in Malaysia, evidently pollinating these plants (Zhou *et al.* 2009), and Ratnayake *et al.* (2006, 2007) similarly found *Polyalthia* and *Xylopia* species in Sri Lanka to be pollinated by weevils identified as *Endaeus*. Kojima & Morimoto (1995 a) described species of *Endaeus* and *Endaenidius* from flowers of *Polyalthia* in Malaysia and further species of *Endaenidius* from those of *Enicosanthum* and *Fissistigma*, of the same family, whereas similar undescribed species of Ochyromerini are indicated to pollinate the annonaceous vine *Melodorum leichhardtii* in Australia. In Japan, species of *Endaeus* and *Endaenidius* also occur in flowers of *Magnolia* (Magnoliaceae) and *Illicium* (Schizandraceae) (Kojima & Morimoto 1995 d), indicating that Ochyromerini may be involved in the pollination of several basal angiosperm families. The monobasic family Eupomatiaceae, restricted to eastern Australia and New Guinea, and the apparent sister group of Annonaceae are pollinated exclusively by weevils of the genus *Elleschodes* Blackburn, currently placed in the tribe Storeini (*q.v.*) (Armstrong & Irvine 1990), the flowers emitting fragrances consisting of short-chain fatty esters that attract the pollinators (Bergström *et al.* 1991). In the nutmeg family Myristicaceae, *Myristica insipida* in Australia is also pollinated by weevils (Armstrong 1997), and apparently several species are involved (Armstrong & Irvine 1989 a, b), but none of them are described and their taxonomic affinities are as yet unclear, whereas Kojima

& Morimoto (1995 a) described a species of *Endaenidius* from flowers of *Knema* in Malaysia. In Winteraceae, the genus *Exospermum* in New Caledonia is exclusively pollinated by a species of *Palontus* Kuschel (Pellmyr *et al.* 1990), also currently placed in Storeini (Kuschel 1990 a), but the taxonomy of all these weevil pollinators needs attention. Weevils have also been reported to be involved in the pollination of Amborellaceae (Thien *et al.* 2003), the most basal lineage of angiosperms, but their identity (given as “Cryptorhynchinae”) is in need of verification; they more likely also belong to a curculionine tribe such as Ochyromerini or Storeini. At least in *Eupomatia* and *Myristica*, the association between plant and weevil seems to be a nursery pollination mutualism, the pollinator breeding solely in the ovules of the host and thus being as dependent on the plant, as the latter is on the weevil for its pollination; also dubbed a system of pollination by deceit (Armstrong 1997), this is similar to weevil pollination in cycads and palms.

Due to their generally high host specificity, curculionine weevils also constitute important control agents of weedy plants throughout the world. O’Brien (1995) summarized the role of weevils generally in the biological control of weeds but used examples mainly from the subfamilies Brachycerinae, Conoderinae, and Molytinae, as species of especially the first group have achieved singularly spectacular control of major aquatic weeds in several regions of the world. The various species of Curculioninae currently used to control weeds, as enumerated by Julien & Griffiths (1998), mostly belong to the tribes Mecinini, Smicronychini, and Storeini. Mecinini make very successful biocontrol agents of European species of toadflax (*Linaria*, Plantaginaceae) in North America. The seed-feeding *Rhinusa antirrhini* (Paykull) and *R. neta* (Germar) were accidentally introduced from Europe into Canada and the United States in the early 20th century and exert some biological control of yellow toadflax (*Linaria vulgaris*) and Dalmatian toadflax (*L. genistifolia*). Their effort was boosted in the early 1990 s by the release in both countries of the stem-boring *Mecinus janthinus* Germar and the root-galling *Rhinusa linariae* (Panzer), the former now well established but the latter less so. In contrast, Smicronychini have proved less successful in weed control. *Smicronyx roridus* Marshall and *S. rufovittatus* Anderson failed to establish on dodders (*Cuscuta*, Convolvulaceae) in the Bahamas, Barbados, and Bangladesh (Julien & Griffiths 1998), whereas the stem-galling *S. guineanus* Voss and *S. umbrinus* Hustache have more of an impact on the parasitic witchweed *Striga hermonthica* (Scrophulariaceae) in Africa (Anderson & Cox 1997) and *S. dorsomaculatus* Cox similarly so on *Alectra vogelii*, although they are not able to control these weeds sufficiently (Sauerborn & Müller-Stöver 2009). The Mexican *Smicronyx lutulentus* Dietz, established in a small area in Australia on *Parthenium hysterophorus* (Asteraceae), has also not had a major impact on this weed

Q: “deceit” was changed to “deceit”. Correct?

(Dhileepan & Strathie 2009). Similarly, *Sibinia fastigiata* Clark (Tychiini), released from 1997 to 2002 against *Mimosa pigra* (Fabaceae) in northern Australia, failed to establish (Ostermeyer & Grace 2007), whereas *Anthonomus santacruzi* Hustache (Anthonomini) is deemed to be the most promising biocontrol agent of *Solanum mauritianum* (Solanaceae) in South Africa (Olckers 2009). Species of Storeini released in South Africa to control the invasive Australian shrub *Hakea sericea* (Proteaceae) have also been highly successful. The seed-feeding *Erytenna consputa* Pascoe, released in 1972, caused a reduction in seed production of up to 90%, whereas the shoot-boring *Cydmaea binotata* Lea, released in 1979, initially established but failed to have any long-term impact and appears to have largely died out (Gordon 1999). A third species, the flowerbud-feeding *Dicomada rufa* Blackburn, was released in 2005 to augment the biological control of the plant (Kluge & Gordon 2004). A recent comparison of *Hakea sericea* infestation levels in 1979 and 2001 (Esler *et al.* 2010) revealed that, together with the seed-feeding moth *Carposina autologa* Meyrick and mechanical eradication, *Erytenna consputa* caused a 64% decrease in the distribution of this weed in South Africa and a significant decrease in its overall density. When the impact of an introduced plant is ambivalent, weevils may function both as biocontrol agents and as pests. Thus, the seed-feeding *Ochyromera ligustri* Warner (Ochyromerini) is regarded as harmful to Chinese privet (*Ligustrum sinense*, Oleaceae) in North America, where the plant is used in landscaping, but beneficial in southeastern states where it is considered an invasive weed (Cuda *et al.* 2008).

Morphology, Adults (Fig. 3.7.10.1–3.7.10.4). Length 1–12 mm (rostrum excluded). Body broadly ovate to globular (e.g., Anthonomini, Camarotini, Cionini, Derelomini: *Anchylorhynchus* Schoenherr, Microstylini, Ochyromerini) to narrowly elongate (e.g., Erodiscini, Mecinini, Otidocephalini), slightly flattened to markedly convex. Integument black to brown to reddish to pale yellowish, rarely metallic blue (Cionini: *Nanomicrophyes* Pic, Mecinini: *Mecinus* Germar, Pyropini: *Pyropus* Schoenherr), covered with more or less adpressed, recumbent to erect, hair-like to rounded scales, which vary in color (white, yellowish, reddish, brown); color uniform in some taxa; species of other taxa with contrasting scale patterns, sometimes with metallic sheen, or scales regularly arranged in one to two series on each elytral interstria.

Head with rostrum mostly long to very long and slender, in lateral view more or less curved and narrowed from base to apex, at base dorsally sometimes concave (e.g., Anthonomini, Curculionini, Ochyromerini) to distinctly set off from head (Smicronychini), mostly sexually dimorphic with female rostrum longer, narrower, and smoother, rarely short, broad, flattened to flared (e.g., Diabathrariini, Microstylini, Ulomascini); scrobes oblique to parallel to long axis of rostrum and

ending before anterior margin of eyes, very short in Rhamphini, almost vertical in Microstylini. Eyes usually large, rounded to elliptical, flat to distinctly convex, sometimes nearly contiguous dorsally (e.g., Ancylocnemidini: *Ancylocnemis*) or ventrally (e.g., Acentrusini, Nerthopini: *Nerthops* Schoenherr, Smicronychini), frons slightly wider than rostrum at base to very narrow (e.g., Cionini, Rhamphini, Ochyromerini). Antennae usually inserted near middle of rostrum but often more basally in female than in male (at base of rostrum in Rhamphini); funicles five- (e.g., Cionini, Mecinini) to seven-segmented, usually with first two segments distinctly longer than others. Mouthparts generally phanero-gnathous (e.g., Ting 1936; Franz 2006). Mandibles without deciduous processes; sometimes moving vertically (some Curculionini); typically with two or three teeth; outer margin with or without setae. Maxillae with galea, lacinia, and palpifer fused; outer margin with one or more “lacinial teeth”, palps two- or three-segmented. Labium variously shaped, with or without setae along lateral and apical margins; ligula absent to projecting beyond labial palps, palps two- or three-segmented.

Pronotum slightly to distinctly convex, sometimes tuberculate (e.g., some Anthonomini, Cionini), at base slightly to distinctly narrower than elytral bases; sides more or less curved, usually widest at basal half, rarely carinate (some Derelomini), rarely with ocular lobes (some Storeini), sometimes abruptly restricted at apex to form a narrow neck or at base to become pedunculate (Erodiscini, Otidocephalini). Prosteronum with apical margin regularly transverse, sometimes more or less concave (e.g., Cionini, Storeini *sensu lato*) or with weak to deep canal into which the rostrum fits in repose (e.g., Smicronychini, Storeini *sensu stricto*, some Cionini, Mecinini, and Rhamphini), in this case, fore coxae separated, walls of canal in Storeini *sensu stricto* excised to form a cleft of “peep-hole” (Fig. 3.7.10.2 A and B), through which the weevil may be able to see when the rostrum is folded down. Scutellum usually clearly visible but sometimes indistinct (e.g., Smicronychini, some Storeini). Elytra with interstriae usually wider than striae, flat to moderately convex, sometimes at least in part distinctly convex (e.g., Cionini, Derelomini), rarely with tubercles (some Anthonomini, Cionini, Cryptoplini, Storeini); striae usually well defined and with deep punctures (obscure in some Cionini), sutural flanges unequal. Hind wings usually well developed, rarely reduced [e.g., Styphlini, Cionini: *Nanomicrophyes*, and Tychiini: *Tychius* (*Apeltarius* Desbrochers)]. Metanepisternal sutures without sclerolepidia. Legs with femora weakly to distinctly clavate, often with weak to very robust tooth, hind femora with apodeme for jumping in Rhamphini; tibiae with apex dorsoventrally oblique, usually without spurs (except *Nothofaginus* Kuschel), fore and middle tibiae at inner apex usually clearly imperfectly uncinately (Thompson 1992) or mucronate, especially in male, fore tibiae

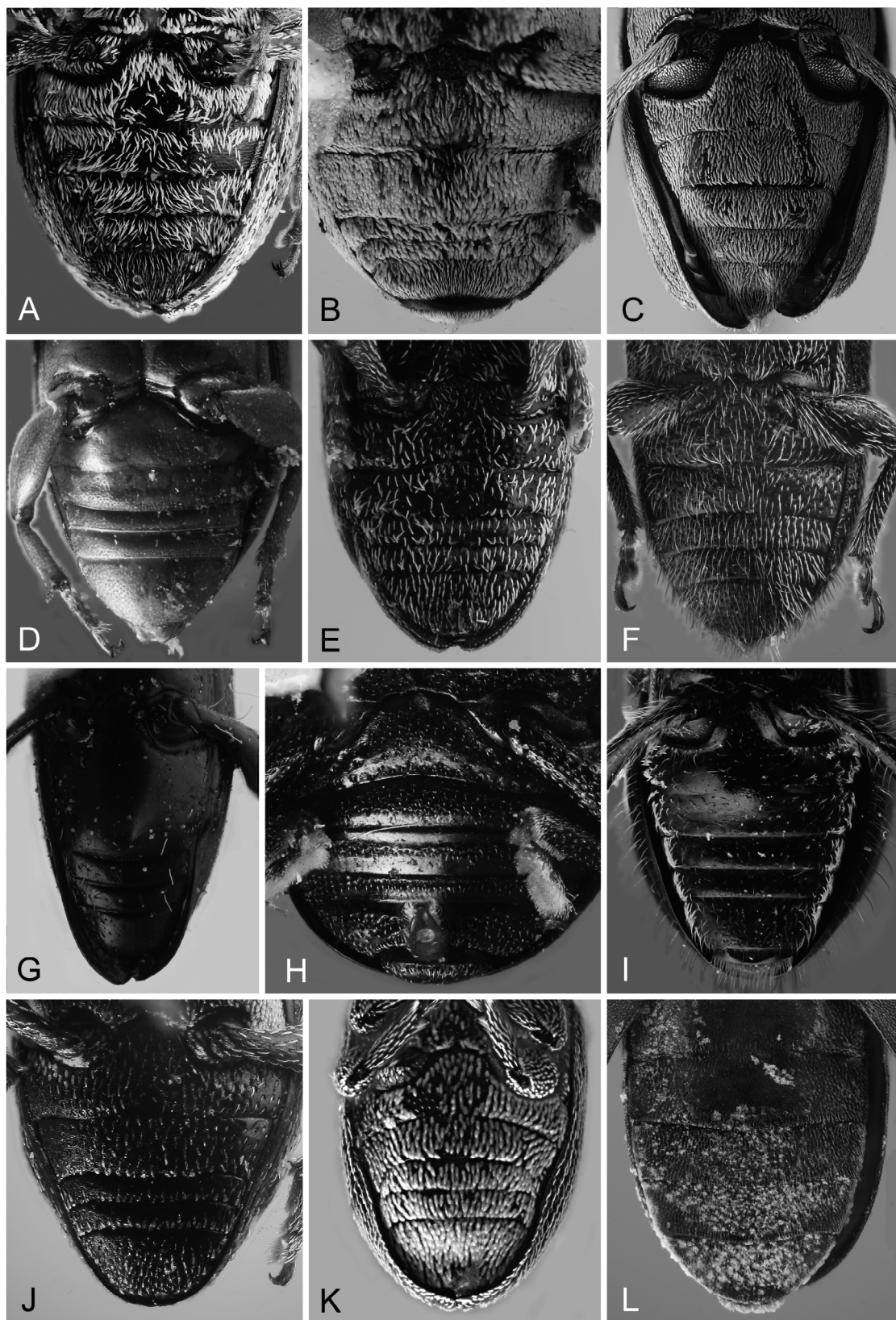


Fig. 3.7.10.1 Ventrites. A, *Anthonomus* sp. (Anthonomini); B, *Cionus* sp. (Cionini); C, *Curculio caryae* (Horn) (Curculionini); D, *Perelleshus carludovicae* (Günther) (Derelomini); E, *Ellescus ephippiatus* (Say) (Ellescini); F, *Mecinus pyraeter* (Herbst) (Mecinini); G, *Sicoederus* sp. (Erodiscini); H, *Pyropus pusillus* Pascoe (Pyropini); I, *Myrmex* sp. (Otidocephalini); J, *Smicronyx* sp. (Smicronychini); K, *Sibinia* sp. (Tychiini); L, *Ulomascus marshalli* Ghesquiére (Ulomascini). Not at the same scale.

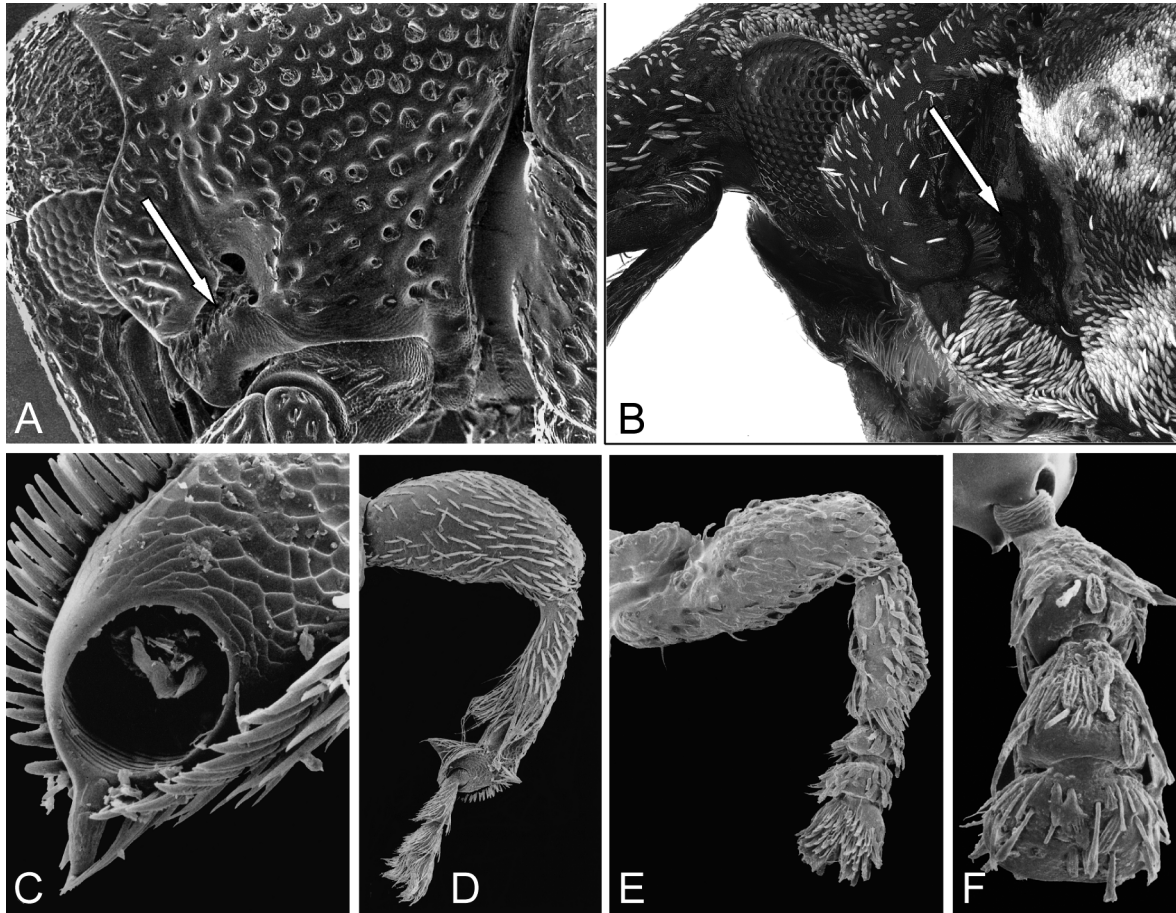


Fig. 3.7.10.2 Structural details. A, *Storeus* sp. (*Storeini sensu stricto*); cleft wall (arrow) of prosternal canal, lateral view; B, *Aporotaxus kanalensis* Perroud (*Storeini sensu stricto*); setiferous hole (arrow) in wall of prosternal canal, lateral view; C, *Leucomelacis quadrinotatus* Lea (*Storeini sensu stricto*), left hind tibia, apical view; D, *Sellechus tibialis* Lea (*Storeini sensu lato*), foreleg of male, caudal view; E, *Cratoscelocis foveicollis* Lea (*Cranopoeini*), left hind leg, ventral view; F, *Micraonychus casuarinae* Lea (*Storeini sensu lato*), tarsus, dorsal view. Not at the same scale.

sometimes sexually dimorphic (Fig. 3.7.10.2 D), hind tibiae with unci often small or absent, especially in female (in some Cionini and Derelomini unci absent on all tibiae) (Fig. 3.7.10.2 C, E, and F), unci sometimes displaced outward and inner apical angle then with praemucro flanked by tufts of long setae (e.g., Mecinini, Microstylini); tarsi with tarsomere 3 usually bilobate and wider than 2, onychium (tarsomere 5) usually long, sometimes short, reduced, or fully lost (some Anoplini, Diabathrariini, Storeini, Viticiini); claws simple to appendiculate to toothed or bifid, divergent to divaricate, mostly separate but often connate at base (e.g., Cionini, most Mecinini and Smicronychini, various other genera) to one claw reduced (Cionini, some Mecinini) or fully fused (single) (some Cionini, Cryptoplini: *Haplonyx* Schoenherr) to variously reduced or fully lost (e.g., Cryptoplini: *Cryptoplus* Erichson, Viticiini: *Aviticis* Kojima & Morimoto). Proventriculus generally well developed, with eight strong basal plates and paired rows of internal brushes, but weakly developed in, e.g., Rhamphini and absent in Cryptoplini.

Abdomen (Fig. 3.7.10.1) with posterior margin of ventrites 2, 3, and 4 straight to concave, sometimes laterally extended caudad (angled) (2–4 in Cionini, Mecinini, 2–3 in Ellescini, Ochyromerini, Rhamphini, Tychiini; Lignyodina, only 2 in Tychiina), 5 sometimes with median fringe of hair-like scales and/or fovea (Mecinini, Tychiini) and seldom with teeth (Mecinini: *Miarus* Schoenherr). Tergites VII and VIII usually hidden by elytra but sometimes clearly visible as pygidium (e.g., Acalyptini, Curculionini, Mecinini, Microstylini; males only in some Derelomini, and Tychiini); tergite VII in some taxa with plectrum consisting of one or more pairs of raised, setiferous tubercles scraping against inner apical file on underside of elytra (elytro-tergal stridulation system 1 of Lyal & King 1996), as far as studied present in both sexes in Camarotini: Prionomerina, Ellescini: *Ellescus* Dejean, Erodiscini, Otidocephalini, Rhamphini, and Smicronychini but apparently only in males in Acentrusini (*Acentrus* Desmarest), Ellescini: *Dorytomus* Germar, Prionobrachiini, Storeini, Tychiini, and *Pachytychius* Jekel (Lyal & King 1996), system 2

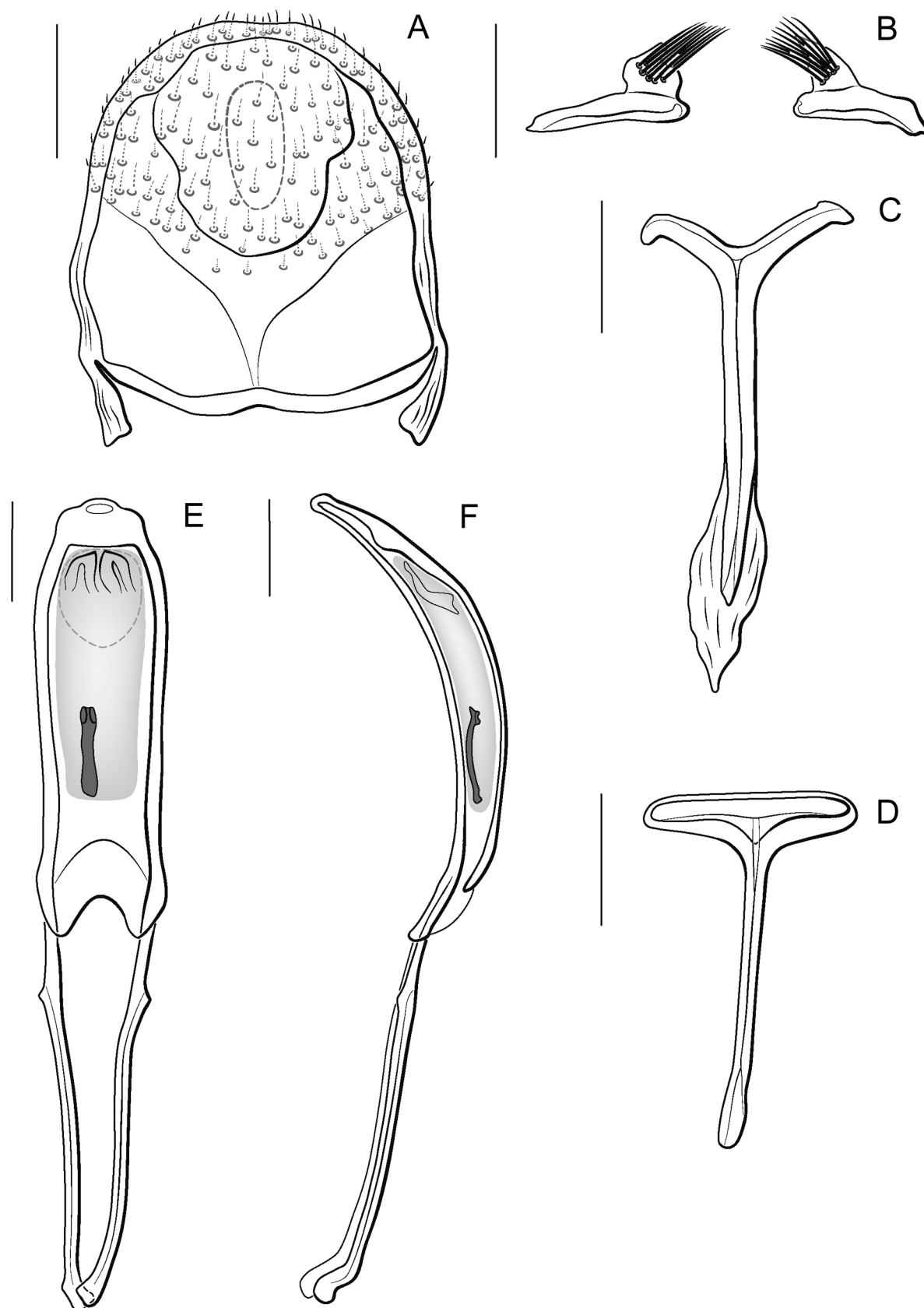


Fig. 3.7.10.3 Male terminalia of *Cyclanthura laticola* Franz (Derelomini). A, Tergum VIII, ventral view; B, sternum VIII, ventral view; C, Spiculum gastrale, ventral view; D, tegmen, ventral view; E, aedeagus, ventral view (with dark ampullate sclerite); F, aedeagus, lateral view. Scale bars 0.1 mm.

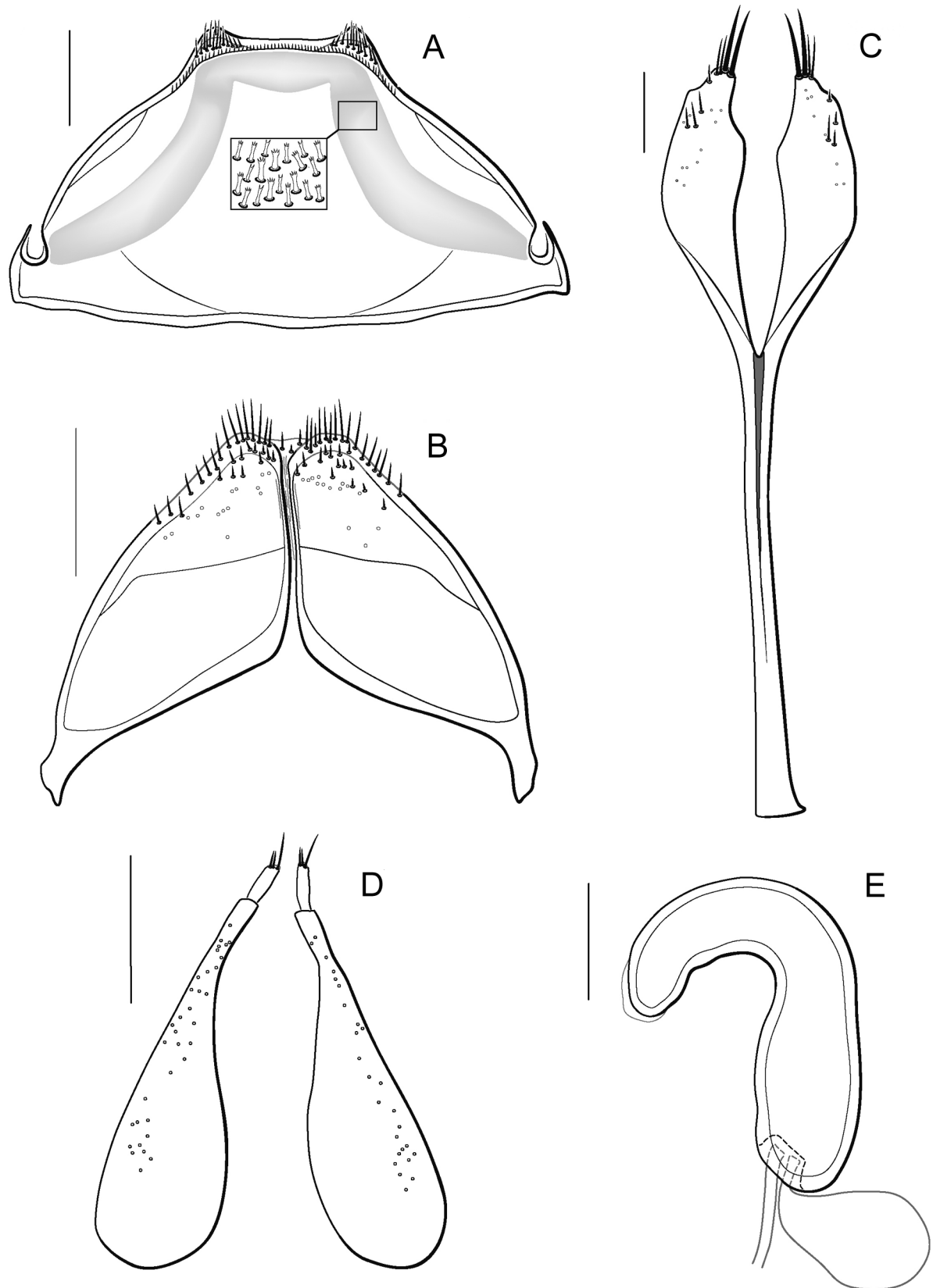


Fig. 3.7.10.4 Female terminalia of *Cyclanthura laticola* Franz (Derelomini). A, Tergum VIII, ventral view; B, tergum IX, ventral view; C, sternum VIII, ventral view; D, gonocoxites + styli, ventral view; E, spermatheca + gland, lateral view. Scale bars 0.1 mm.

(positions of plectrum and file reversed) reported in Anoplini, and Derelomini (*q.v.*). Aedeagus subcylindrical to flattened (strongly modified in Mecinini: *Miarus*), usually symmetrical (distinctly asymmetrical in some Rhamphini and Tychiini: Lignyodina), with long apodemes (temones) usually fused to aedeagus (articulated in Tychiini), endophallus without or with sometimes complex internal sclerites, occasionally with more or less long flagellum. Tegmen usually with complete ring (clearly incomplete in Lignyodini and Tychiini), with distinct apodeme and basal plate usually consisting of two lateral sclerotized parts. Sternite VIII of female with long apodeme, with basal plate usually sclerotized at sides. Bursa copulatrix membranous, rarely sclerotized (e.g., in Mecinini: *Miarus*). Spermatheca usually falciform, sometimes with body distinctly globose (e.g., Anthonomini, Cionini), spermathecal duct usually membranous (partially sclerotized, e.g., in Mecinini: *Gymnetron* Schoenherr), base of spermathecal gland sclerotized (funnel-shaped) in Cryptoplinae, and Tychiini: *Sibinia* Germar (*Microtychius* Casey) (various sources, supplemented by the authors' studies of relevant characters of numerous curculionine taxa).

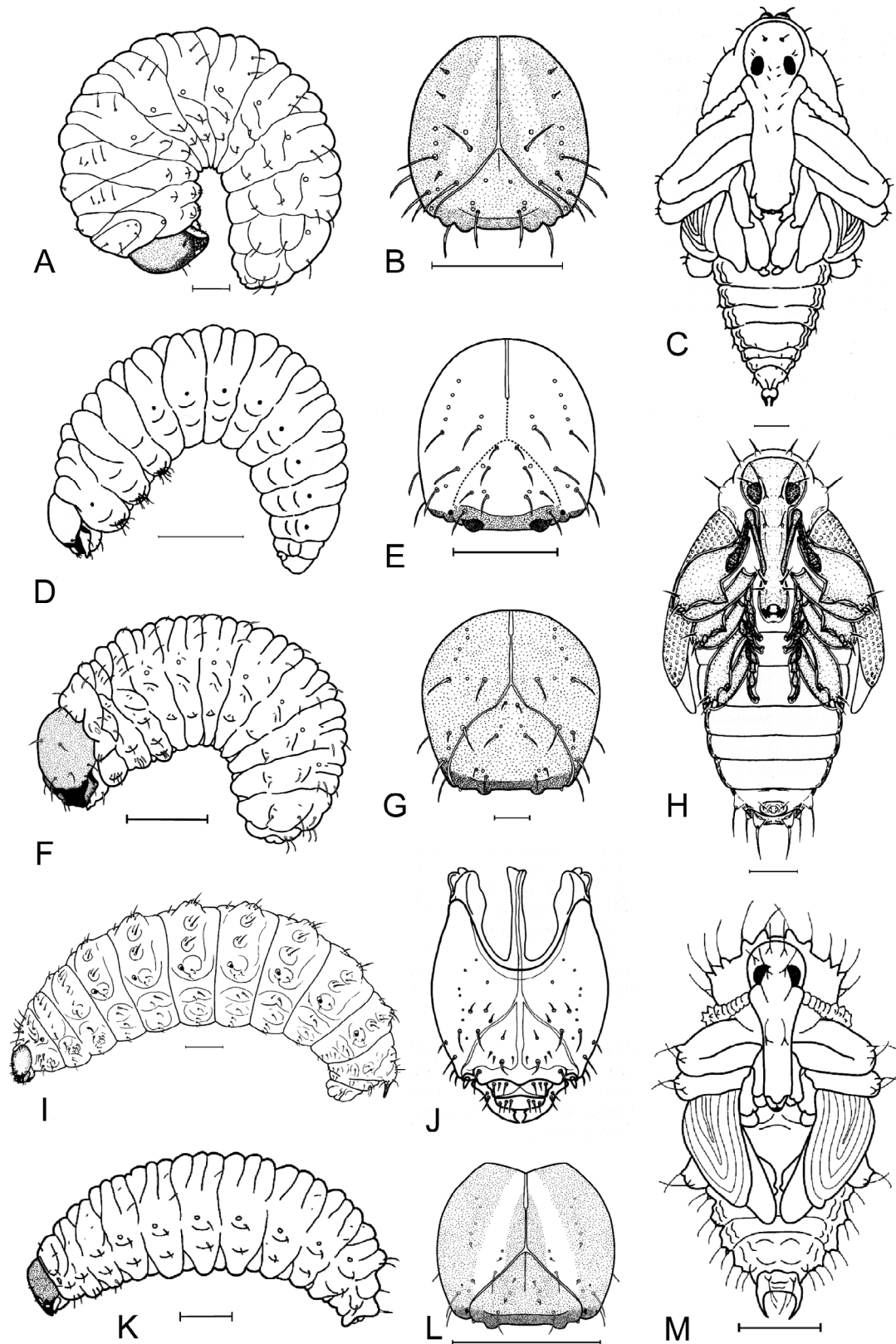
Morphology, Larvae (Fig. 3.7.10.5). Body slender to robust, elongate, slightly to strongly curved; integument usually white, rugulose to smooth; tuberculate to spinose asperities usually distributed over entire body, sometimes more conspicuous on thorax and abdomen. Head free, pale yellow to dark brown to black; usually wider than long, broadly rounded or narrowing dorsally or ventrally, posteriorly emarginate in leaf-mining taxa; anterior stemmata present, black to transparent (lacking pigmentation); posterior stemmata vestigial to absent. Frontal sutures usually distinct throughout length, closed anteriorly by fronto-epicranial bridge (bracon). Epicranial suture about half as long as head capsule, short when head posteriorly emarginate. Median endocarina almost always distinct, sometimes widest at apex, occasionally very short or absent (e.g., Eugnomini). Epicranium with four to five pairs of dorsal setae (*des*), *des1* often short, *des2* and *des4* sometimes minute to absent, *des3* and *des5* longest, with one pair of sensilla behind *des1* and another between *des4* and *des5*; laterally usually with one or two pairs of short to long setae (*les*), one pair of sensilla usually in front of *les1*; ventrally with two pairs of short to moderately long setae (*ves*); posteriorly with two to four pairs of minute setae (*pes*) and one pair of sensilla. Frons with three to five pairs of frontal setae (*fs*), *fs1* and *fs2* sometimes absent, *fs3* minute, *fs4* long, *fs5* long or short to vestigial; with two pairs of frontal sensilla, one laterally or posteriorly of *fs3* and the other between *fs3* and *fs4*. Clypeus wider than long, with two pairs of short setae (*cls*) and two sensilla located between or just in front of *cls*. Labrum with three pairs of setae (*lms*) of various lengths, paired sensilla present but median

sensillum sometimes absent; epipharynx with three to six pairs of anteromedian setae (*ams*), four pairs of median spines (*msp*), two to three pairs of anterolateral setae (*als*); labral rods (tormae) short to long, separated to united posteriorly. Antennae with membranous basal segment bearing a conical, blunt to elongate sensorium and several minute sensory processes. Mandibles short to elongate, more or less triangular, brown, each with two apical teeth, one pair of mandibular setae and one sensillum. Maxillary palps two-segmented, segments variable in length, bearing one to two sensilla, basal segment with one short lateral seta, apical segment with minute papillae. Labium with more or less complete premental sclerite, anterior and posterior median extensions mostly pronounced; prementum with one pair of long setae, two pairs of short ligular setae and two pairs of sensilla; postmentum with two or three pairs of more or less long setae; palps one- or two-segmented.

Thorax narrower than or as wide as abdomen. Thoracic spiracles unicameral or bicameral. Pronotum with 9–11 pairs of minute to long setae, prodorsum, and epipleural lobes of mesothorax and metathorax each with one pair of short to long setae. Pleural areas of prothorax with two to five pairs of short to long setae, of mesothorax and metathorax each with one pair of long setae. Sternum of each thoracic segment with two to four pairs of setae.

Abdomen with eight pairs of lateral unicameral or bicameral spiracles, spiracle VIII located on elongated dorsal protuberances in Ochyromerini. Segments I–VII, each with three dorsal folds, sometimes segment I with only two folds (e.g., Mecinini, Rhamphini); segment VIII, if present, always with two folds; all segments with one short to long pair of antedorsal setae and two to five pairs of postdorsal setae. Epipleuron with one long seta and one short seta. Pedal areas each with one long seta. Eusternum with two long setae. Segment IX with five to seven pairs of short setae. Anus subterminal to terminal, anal folds with several pairs of minute setae (Ahmad & Burke 1972; Anderson 1973; Clark *et al.* 1978; Cussigh 1992; May 1993, 1994; Marvaldi 2003).

Morphology, Pupae (Fig. 3.7.10.5). Color white to occasionally yellowish, sometimes with several darker regions. Head with distirostral setae absent or arranged in one or two pairs, short, two or three pairs of basirostral setae and one pair of interorbital setae; pair of supraorbital setae present or absent; frons with one or two pairs of setae. Pronotum with one pair of anteromedian setae, two to three (rarely one) pairs of anterolateral setae, one pair of discal setae, one pair of posteromedian setae, one to four pairs of posterolateral setae. Mesonotum and metanotum with anteronotal setae usually absent, with one to three pairs of posteronotal setae. Abdomen with or without one pair of anterotergal setae, one to five pairs of discotergal setae, one pair of



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Fig. 3.7.10.5 Pre-imaginal stages. A, *Curculio* sp. (Curculionini), larva, lateral view; B, *Curculio* sp. (Curculionini), larva, head, anterior view; C, *Cryptoplus* sp. (Cryptoplini), larva, lateral view; D, *Cryptoplus* sp. (Cryptoplini), larva, head, anterior view; E, *Myossita banksiae* Lea (Eugnomini), larva, lateral view; F, *Myossita banksiae* (Eugnomini), larva, head, anterior view; G, *Daeneus annae* Oberprieler (Ochyromerini), larva, lateral view; H, *Daeneus annae* (Ochyromerini), larva, head, anterior view; I, *Elleschodes* sp. (Storeini *sensu lato*), larva, lateral view; J, *Elleschodes* sp. (Storeini *sensu lato*), larva, head, anterior view; K, *Haplonyx maximus* Lea (Cryptoplini), pupa, ventral view; L, *Daeneus annae* (Ochyromerini), pupa, ventral view; M, *Storeus albosignatus* Blackburn (Storeini *sensu stricto*), pupa, ventral view (G, H, and L after Oberprieler 1993, all others after May 1994). Scale bars 1 mm except 0.5 mm for B, D, F, H, and J.

laterotergal setae on tergites I–VII, sometimes also on VIII; tergum IX with or without a pair of short to long, more or less sharply pointed, contiguous or widely separated posterior processes (urogomphi). Abdomen lacking ventral setae (Burke 1968; Clark *et al.* 1978; Cussigh 1992; May 1993, 1994).

Phylogeny and Taxonomy. In its various current taxonomic circumscriptions, the subfamily Curculioninae is a morphologically and biologically highly diverse group of weevils, without any clear concept yet of it representing a natural (monophyletic) taxon either in its widest sense (Kuschel 1995) or in a narrower one as adopted here. No attempt has yet been made to subject a meaningful number of curculionine tribes to a modern phylogenetic analysis with adequate taxon sampling, and also, molecular analyses spanning all subfamilies of Curculionidae (McKenna *et al.* 2009) so far have not shown clear monophyly of and between tribes of Curculioninae. Considerably larger sets of taxa and characters need to be analyzed to begin the understanding of proper tribal delineations and relationships. As a result, the classification of the subfamily and its tribes remains tentative and may change significantly in future.

The traditional concepts of most curculionine groups date back to Lacordaire's (1863, 1866) classification system, which was very comprehensive at its time but reflects the poor contemporary knowledge of especially the taxa of the southern hemisphere. As a major revision of these concepts, Morimoto (1962 b) published a tentative higher-level phylogenetic reconstruction of weevils based mainly on differences in the shape of the metendosternite and ovipositor. His scheme posits six main groupings within Curculioninae (i.e., Acalyptini, Anthonomini, Curculionini, Mecinini, Rhamphini, and Tychiini), whereas two other tribes, Cionini and Smicronychini, were placed in a separate subfamily Hyperinae. Being focused on the fauna of Japan, Morimoto's system did not, however, consider the various curculionine groups more or less restricted to Africa, Australia, and South America.

From a study of some key morphological characters, Thompson (1992) assembled many of the tribes here included in Curculioninae in an informal group named *Curculiones longirostres*, which spanned the former subfamilies Anthonominae, Ceutorhynchinae, Cioninae, Curculioninae, Derelominae, Gymnetrinae, Hyperinae, Rhamphinae, Smicronychinae, Storeinae, Tychiinae, and Xiphaspidae. He distinguished this group from the *Curculiones mediirostris* (here subfamilies Molytinae, Cossoninae, and Conoderinae) by the tibiae being imperfectly uncinata and from the *Curculiones brevisrostris* (here subfamilies Entiminae and Cyclominae but also Eugnomini and Ulomascini) by the head being relatively small, subspherical, the eyes relatively large, ovate, forwardly placed, contiguous with the base of a slender rostrum and separated

dorsally by a distance similar to or less than its basal width. Moreover, the *Curculiones longirostres* possess phanerognathous mouthparts, antennal scapes not passing the anterior margin of the eyes, the tibiae lacking spurs, and the body length seldom exceeding 10 mm. Even though this concept lacked a clear definition (autapomorphic characters), it was an important first step in gathering the various taxa of "flower weevils" into a larger group.

In the first morphological phylogenetic analysis of all higher weevil groups, Kuschel (1995) went further and formally subsumed all the taxa of Thompson's *Curculiones mediirostris* and *Curculiones longirostres* as tribes in a larger subfamily Curculioninae. This concept, however, also included the Erirhinae, a group possessing the ancestral pedotectal type of male genitalia and therefore treated as a separate family by Thompson (1992) and included in the subfamily Brachycerinae by Oberprieler *et al.* (2007). However, even without the erirhinines, a subfamily Curculioninae in Kuschel's (1995) wide sense is also not demarcated by any autapomorphic characters.

In their catalogue of weevil genera, Alonso-Zarazaga & Lyal (1999) adopted an eclectic systematic arrangement of curculionid subfamilies and tribes, based in part on Thompson's (1992) classification and composing a subfamily Curculioninae of 30 tribes. Although this catalogue was intended essentially as a nomenclatural work, its classification system has also become a standard taxonomic reference. Anderson (2002) thus adopted Alonso-Zarazaga & Lyal's (1999) concept of Curculioninae in his treatment of the North American weevil genera, yet concluding that "this subfamily [...] is now a large conglomerate of taxa of questionable relationships". He reviewed a suite of possibly distinctive features for the subfamily, i.e., apex of hind tibiae with small or no tooth (uncus); eyes rounded; rostrum usually elongate and cylindrical, distinctly longer in female than in male; antennae with scape at least reaching anterior margin of the eye and inserted more basally in female than in male. However, none of these characters are present in all tribes of Curculioninae, and all of them occur also in other curculionid subfamilies. Indeed, the Curculioninae are diagnosed in four different parts of Anderson's (2002) key to the Nearctic curculionid subfamilies. Despite the current absence of unambiguous and unreserved diagnostic features, it is apparent that many curculionine tribes are more closely related to each other than to members of tribes placed in other subfamilies such as Conoderinae and Molytinae (see Oberprieler *et al.* 2007), lending a measure of support to the present arrangement.

Molecular data and analyses have to date not provided any resolution of this dilemma. Marvaldi *et al.* (2002) published a phylogeny of the superfamily Curculionoidea based on both molecular (18S ribosomal RNA) and morphological characters (imaginal and larval) but including representatives of

only six curculionine tribes (Anthonomini, Camarotini, Curculionini, Derelomini, Mecinini, Rhamphini). The analysis of the combined data placed these taxa on different branches of the cladogram and the molecular data alone did not resolve any relationships among the “higher” Curculionidae. More recent molecular analyses (Hundsdoerfer *et al.* 2009; McKenna *et al.* 2009) based on more genes and including also more curculionine tribes (11 and 13, respectively) did not fare much better, although the latter recovered a well-supported clade including Curculioninae together with Molytinae, Conoderinae, Cossoninae, and Scolytinae. It is evident that analyses of relationships in Curculioninae and these other subfamilies of “higher” Curculionidae need to be based on much larger sets of taxa and characters.

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The larvae of Curculioninae are similarly difficult to diagnose. Van Emden (1938) provided diagnoses of the larvae of Mecinini and Rhamphini and their European genera and species. Scherf (1964), in a comprehensive treatment of the morphology and ecology of the larvae of central European weevils, distinguished the genera and species of Curculioninae in a key based largely on their host-plants, developmental sites, and feeding pattern, with morphological differences occasionally in support but made no attempt to diagnose the larvae of higher (tribal) groups. May (1993, 1994) provided diagnoses of and keys to the larvae of some Australo-Pacific tribes – Cryptoplini, Eugnomini, Storeini (as Curculionini) – but in most cases, these were based only on few representatives. In a key to the South American larvae of Curculionoidea, Marvaldi (2003) placed Curculioninae near Lixinae, from which they were distinguished by the reduction in overall size and the number of cephalic setae, in addition to a posteriorly emarginate head (not in all taxa) and often distinctive feeding styles (in flowers, fruits, seeds, etc.). According to van Emden (1938) and Marvaldi (2003), only larvae of the tribes Mecinini, Rhamphini, and Anthonomini are readily diagnosed, the first two by having abdominal segments with only two (instead of three) dorsal folds and expanded pedal lobes and the last by having four (instead of six) epipharyngeal sensilla and by lacking the setal pair 2 on the frons. In their treatment of Anthonomini, Ahmad & Burke (1972) presented the most complete study of larvae of any large tribe of Curculionoidea, identifying the following diagnostic features: (1) most abdominal segments with three dorsal folds, (2) frontal setae 2 absent, (3) anus subterminal. Burke (1968) and Ahmad & Burke (1972) have described and illustrated the larvae of 63 species and the pupae of 58 species of Anthonomini, covering 12 and 15 genera, respectively. Clark *et al.* (1978) discussed the immatures of nearly 15 species of *Tychius*, concluding that they seem to support some groupings previously postulated on adult morphology, but that the phylogenetic signal was not strong. Gibson

(1985) illustrated and keyed the larvae of 15 species of *Curculio* Linnaeus. More comparative and phylogenetic studies of curculionine larvae are needed to elucidate the monophyly and relationships among tribes in the subfamily on larval characters (see also May 1993).

Curculioninae are poorly represented in the fossil record, most specimens having been described from Eocene deposits at Florissant and Green River in the United States (e.g., Scudder 1890, 1893, Wickham 1911, 1912, 1917) and Havighorst in Germany (Zherikhin 1995) and from Miocene deposits at Shanwang in China (Zhang 1989) and the Simnicel Valley in Romania (Marinescu & Proches 1999). Most were placed in the extant genera *Anthonomus*, *Curculio* (“*Balaninus*”), and *Tychius*, but their true identities are generally unclear and all of them are in need of critical assessment. A much older fossil, *Arariperhinus monnei*, was recently described from the late Lower-Cretaceous Crato Formation in the Ararape Basin, Brazil, and interpreted as belonging to Curculioninae (and tentatively to the tribe Anthonomini) (Santos *et al.* 2011), based on its strongly convex body, rounded eyes, slender rostrum, and absence of a prosternal canal and tibial spurs. However, these characters do not distinguish the fossil from extant South American stenopelmene Brachycerinae such as *Argentinorhynchus* Bréthes, *Cyrtobagous* Hustache and *Onychylis* LeConte, and it may equally well represent this subfamily.

Given the uncertain concept of a subfamily Curculioninae, the taxon is here necessarily treated in a pragmatic sense, largely following Alonso-Zarazaga & Lyal (1999), Alonso-Zarazaga (2002), Korotyaev (2002), Marvaldi & Lanteri (2005), Elgueta & Marvaldi (2006), Oberprieler *et al.* (2007), Oberprieler (2010), and Bouchard *et al.* (2011), who considerably restricted its scope in comparison with classifications proposed by earlier authors, such as Hoffmann (1954; as Calandrinae), Kuschel (1995), and Marvaldi & Morrone (2000). Most of its tribes as considered here were assigned subfamily status in the past (e.g., Morimoto 1962 b; Thompson 1992; Marvaldi *et al.* 2002), but very few of them as currently composed (e.g., in the nomenclatural catalogue of weevil genera by Alonso-Zarazaga & Lyal 1999) can be regarded as natural. The treatment of the tribes below corrects some of the most glaring misplacements of genera and thus attempts to provide a more robust taxonomic foundation of the various taxa for future studies, but the delimitations of essentially all the tribes are in need of critical assessment. A number of genera remain of uncertain placement, although the majority of the ones so listed by Alonso-Zarazaga & Lyal (1999) can be provisionally accommodated in Storeini (*q.v.*).

Acalyptini (Fig. 3.7.10.6 A and B). This tribe includes a number of palm flower weevils, but its composition remains unclear despite some recent

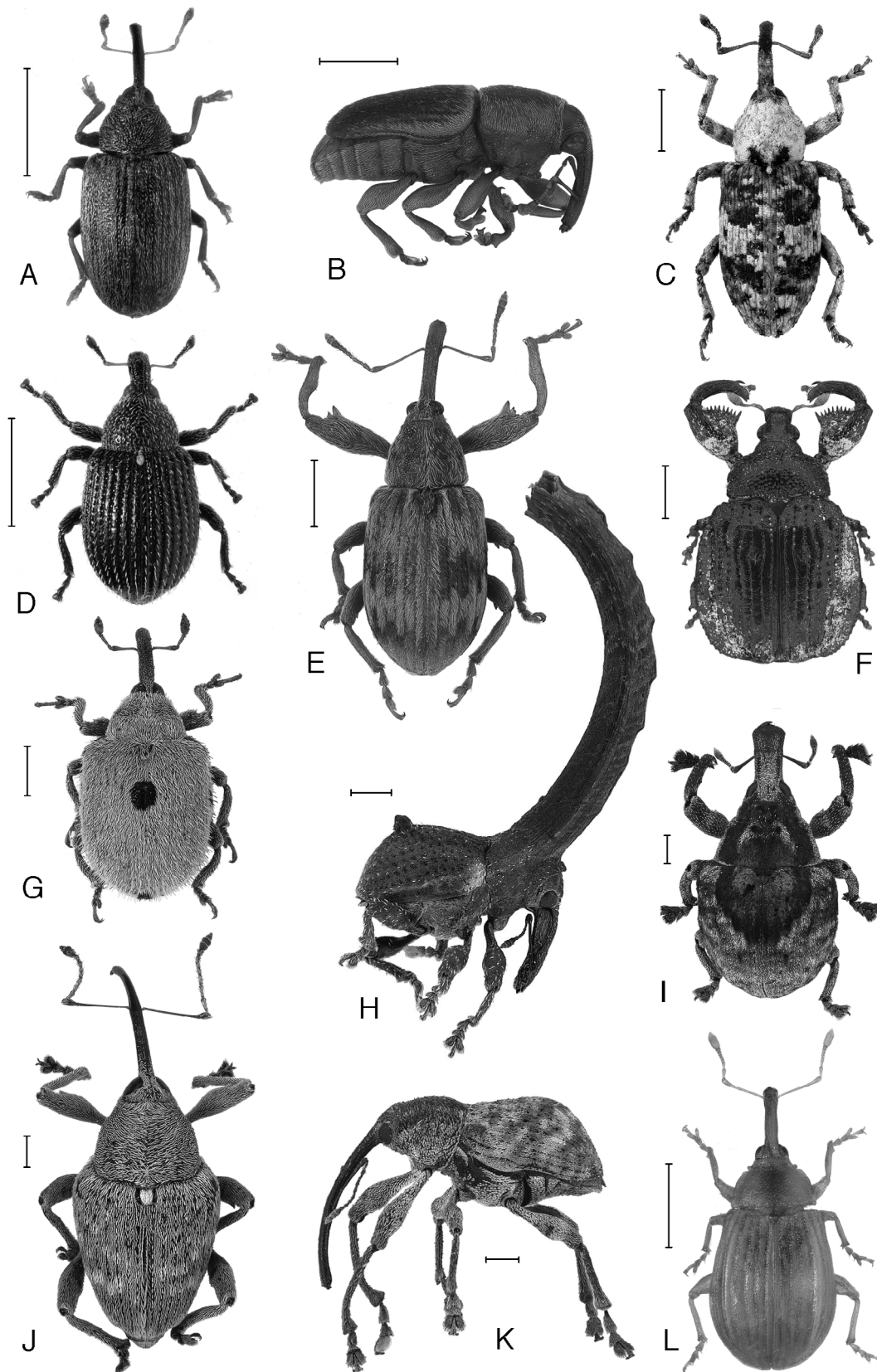


Fig. 3.7.10.6 Habitus, adults. A, *Acalyptus carpini* (Schoenherr) (Acalyptini); B, *Eudelodes bicolor* (Faust) (Acalyptini); C, *Acentrus histrio* (Schoenherr) (Acentrusini); D, *Anoplus roboris* Suffrian (Anoplini); E, *Anthonomus rectirostris* (Linnaeus) (Anthonomini); F, *Camarotus* sp. (Camarotini); G, *Cionus olivieri* Rosenschöld (Cionini); H, *Ceroctenus extremus* Kuschel (Cranopoeini); I, *Sigastus fuscodorsalis* (Heller) (Cryptoplini); J, *Curculio glandium* Marsham (Curculionini); K, undescribed genus from Australia with horizontal mandibles, seven funicles, divaricate claws, and trochanteral setae (Curculionini); L, *Derelomus piriformis* (Hoffmann) (Derelomini). Scale bars 1 mm.

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studies. Kojima & Morimoto (2005) distinguished the predominantly Australo-Asian genera of Acalyptini from the African Derelomini, based crucially on a unique configuration of the pygidium of the males in the former (representing tergite VII, with tergite VIII hidden under it) and also on their non-carinate prothorax, two-segmented labial palps, unarmed tibiae, simply truncated elytra, absence of wing folding and elytro-tergal stridulation structures, and some genital differences. Most of these features are, however, homoplasious or plesiomorphic with respect to the New World lineages included in Derelomini by Franz (2006). Based on a morphological cladistic analysis of 115 taxa and 155 characters, Franz (2006) included Acalyptini as a subtribe in Derelomini (but the name of the latter is the junior one; see Alonso-Zarazaga 2007). The analysis yielded a number of homoplasious but nevertheless unambiguously optimized morphological features for Acalyptini in such an expanded sense as well as for less inclusive clades incorporating the traditionally recognized acalyptine genera (*Acalyptus* Schoenherr, *Amorphoidea* Motschulsky, *Nodocnemus* Marshall, *Parimera* Faust), involving *inter alia* losses mostly of setae in mouthpart structures. However, the configuration of the pygidium was not included as a character in the analysis, and the antennal club is four-segmented in all acalyptine genera (rather than this condition representing a reversal in only *Nodocnemus* and *Parimera*). There is therefore no strong evidence supporting a merger of Acalyptini and Derelomini into a single tribe (Acalyptini *sensu lato*). In its narrow sense (Kojima & Morimoto 2005), it currently includes 14 genera, *Acalyptus* (ca. 4 species), *Amorphoidea* (ca. 14), *Derelomorphus* Marshall (1), *Epamoebus* Blackburn (4), *Eudela* Pascoe (1), *Eudelodes* Zimmerman (2–3), *Imera* Pascoe (4), *Meredoloides* Kojima (1), *Meredolus* Marshall (1), *Niseida* Pascoe (1), *Nodocnemus* (2), *Orsophagus* Roelofs (2), *Parimera* (ca. 6), and *Tithene* Pascoe (11), ranging from the Palaeartic to the Oriental and Australo-Pacific regions. A suitable definition of the tribe in this sense and an overview of the genera (except *Epamoebus* and *Meredoloides*) were provided by Kojima & Morimoto (2005). However, a plethora of undescribed genera and species occurs at least in Australia, mostly associated with palm flowers, and further study of the group is necessary.

Kojima & Morimoto (2005) summarized the information available on the biology of Acalyptini. The larvae of *Acalyptus* develop in flower catkins of *Salix* (Salicaceae) and those of the closely related *Orsophagus* and *Epamoebus* in flowers of *Melia azedarach* (Meliaceae) and *Acacia* (Fabaceae), respectively. *Amorphoidea* lives in flowers of Malvaceae such as *Hibiscus*, *Thespesia*, and *Gossypium* (cotton), several species becoming pests on the latter, and also, *Eudelodes* breeds in flowers of *Hibiscus tiliaceus* along the east coast of Australia and the Torres Strait islands.

Derelomorphus, *Meredoloides*, *Meredolus*, *Nodocnemus*, *Parimera*, *Tithene*, and several undescribed genera in Australia occur on palms (Arecaceae), which they are indicated to pollinate (Essig 1973; Mogeia 1978; Cock 1985; Henderson 1986), although the larvae and life cycles have not been studied in detail.

Acentrusini (Fig. 3.7.10.6 C). Hoffmann (1958) and Alonso-Zarazaga (2005) provided a diagnosis of this monobasic tribe, the latter author regarding it to be related to Styphlini but without identifying specific shared characters. The distinctive characters of the tribe are: body densely covered with broad scales; funicles seven-segmented; eyes almost contiguous ventrally; frons as wide as rostrum at base; prosternum with rostral canal; femora unarmed; tibiae with small uncus; claws simple, free, divaricate.

The larvae of *Acentrus histrio* (Fig. 3.7.10.6 C), the single representative of the tribe (Alonso-Zarazaga 2005), tunnel in the roots and basal parts of the stems of *Glaucium* (Papaveraceae), pupating inside the tunnels or in the soil (Hoffmann 1958).

Ancylocnemidini. Comprising the single genus *Ancylocnemis* Marshall (7 species), this tribe is also of uncertain affinity and taxonomic status. *Ancylocnemis* occurs mainly in Africa, from South Africa to Ethiopia, but two species have been described from India and at least one undescribed species occurs in southern China (M. Alonso-Zarazaga, personal communication). Marshall (1920) originally described the genus in Anthonomini but later transferred it to the molytine tribe Trachodini (Marshall 1943, 1948). Such a relationship was, however, disputed by Voss (1962) and Zimmerman (1964), the former proposing a separate tribe for it, placed near Rhamphini. The character of laterally angled ventrites 2–4 might support a relationship to this and allied tribes such as Ochyromerini and Tychiini, but the exact relationships of the genus are as yet unclear. Its salient characters are the following: body densely squamose, with tufts of elongate scales on pronotum and odd elytral interstriae; rostrum narrow, subcylindrical, straight; funicles seven- or (in subgenus *Epimerogrypus* Heller) six-segmented, thus club four- or five-segmented; eyes moderately large, frontally positioned, and dorsally almost contiguous; fore coxae contiguous or separate; prothorax without ocular lobes; mesoventrite steeply declivous (almost vertical); middle coxae close together; femora dentate, hind femora often very strongly so, the flattened tooth bearing a row of curved setae at its posterior edge; tibiae imperfectly uncinata, internally with median tooth and externally with apical and sometimes additional subbasal tooth; tarsal claws divaricate, slightly to strongly appendiculate; ventrites 2–4 laterally usually slightly angled; tegmen dorsally membranous, without parameroid lobes. Some seemingly related undescribed small South African species agree with *Ancylocnemis* in most of these characters but have large, round erect setae,

the fore coxae broadly separated by a pectoral canal ending in a shallow receptacle on the metaventricle, the femora adentate and the tibiae bearing a two-pronged uncus.

Ancylocnemis appears associated with Capparaeae, Marshall (1943) recording *A. sternalis* Marshall from *Capparis sepiaria* (Wild Caper Bush) in India and some *Ancylocnemis* and the undescribed species with a pectoral canal living on *Boscia foetida* in South Africa (R. Oberprieler, personal observation). The larvae probably develop in the fruits (Zimmerman 1964).

Anoplini (Fig. 3.7.10.6 D). The concept of this tribe is unclear. In the catalogue of Alonso-Zarazaga & Lyal (1999), it includes only two genera, the Palaearctic *Anoplus* Germar (5 species) and the Madagascan *Paranoplus* Hustache (1), characterized by the absence of the onychium of the tarsi. However, this loss has occurred independently numerous times in Curculioninae and other subfamilies and cannot be used as a tribal characterization. Zherikhin & Egorov (1991) and Kojima & Morimoto (2000) also placed the eastern Palaearctic genus *Sphinxis* Roelofs (ca. 15) in Anoplini, and Kojima & Morimoto (2002) added the mainly African *Thamnobius* Schoenherr (ca. 10), which they recorded from the Oriental region but which is evidently a composite genus (Oberprieler 1993). Several other Afrotropical genera, specifically the Madagascan *Cionesthes* Fairmaire, *Lepidoops* Hustache, *Parandoeopsis* Hustache, and *Semicardius* Hustache but also the continental *Acalyptops* Hartmann, *Neosphinctocraerus* Hustache and *Pansmicrus* Schoenherr, appear to belong to this tribe as well (Kojima & Morimoto 2002), and its proper composition and definition are in need of study. Alonso-Zarazaga (2002) placed the tribe in Molytinae, without comment or supporting evidence. The detection in *Anoplus*, *Sphinxis*, and *Thamnobius* of an elythro-tergal stridulation system 2 (Kojima & Morimoto 2000, 2002), otherwise recorded only in a few Molytinae and Cossoninae (Lyal & King 1996), may lend support to such a placement, but the feature was interpreted as independently evolved in Acalyptini by Kojima & Morimoto (2000) and has recently also been reported to occur in Derelomini (Kojima & Morimoto 2005). Elythro-tergal stridulation systems in general are in need of wider study in Curculioninae.

Little is known about the biology of Anoplini. The larvae of *Anoplus* mine in leaves of *Alnus* and *Betula* (Betulaceae); on completion of their development, they cut out pieces of leaf to form a pupal covering, in which they drop to the ground for pupation (Scherf 1964). Zherikhin & Egorov (1991) recorded *Sphinxis* to be associated with *Polygonum* (Polygonaceae), but Kojima & Morimoto (2000) doubted this because *Sphinxis* generally inhabits broad-leaved trees of the families Elaeocarpaceae, Lauraceae, and Sapindaceae. *Thamnobius* in Africa has been collected on Anacardiaceae (*Rhus*),

Combretaceae (*Terminalia*), Geraniaceae (*Geranium/Pelargonium*), and Penaeaceae (*Penaea*), but again, nothing is recorded about its larvae and their hosts (Oberprieler 1993).

Anthonomini (Fig. 3.7.10.6 E). As currently composed (Clark 2010), this tribe includes 43 genera and 826 species, the majority of species (558, of which 395 are Neotropical, 121 Nearctic, and 58 Palaearctic) classified in the large and widespread genus *Anthonomus* Germar. Almost all other genera comprise fewer than ten species, except for *Atractomerus* Duponchel & Chevrolat (45 species), *Bradybatus* Germar (20), *Huaca* Clark (26), and *Pseudanthonomus* Dietz (35). The classification of the tribe remains partially unresolved, as the constituent genera vary significantly in their morphological characters and the composition of the tribe has changed considerably over the past 20 years. Dieckmann (1968) last revised the western Palaearctic genera, whereas Clark (1988, 1989, 1990) clarified the phylogenetic relationships among several genera of Neotropical anthonomines and provided a wealth of taxonomic information on known and new species. Kojima & Idris (2004) diagnosed the tribe as follows: eyes more or less convex; rostrum cylindrical; procoxal cavities generally contiguous; tibiae usually uncinata (at least on fore and middle legs); tarsal claws not widely divergent, generally sharply bifid, and with one seta each; posterior margin of abdominal ventrites 2–4 straight, not laterally angled; aedeagus narrowed or emarginate at base in lateral aspect and with apodemes articulating at ventral surface; sternite VIII of male paired, devoid of setae along caudal margin; sternite IX of male bilobed, with apodeme more or less curved and oblique to axis of aedeagus; spermatheca with lateral lobe indefinite, spermathecal gland long, linear.

Anthonomini utilize more than 40 plant families as hosts (H. Burke, personal communication), including both herbaceous groups such as Asteraceae, Euphorbiaceae, Malvaceae, and Solanaceae and woody ones such as Rosaceae, Sapindaceae, and Ulmaceae (Scherf 1964; Dieckmann 1968; Burke 1976; Anderson 1993; Clark & Burke 1996). Individual species, however, tend to have much more restricted host ranges, spanning a small number of species in one plant genus or a few closely related genera (e.g., Scherf 1964; Burke 1976; Burke *et al.* 1986). Nearly all Palaearctic and several North American species of *Anthonomus* live on Rosaceae, causing serious damage to fruit trees in the genera *Cerasus* and *Prunus* and to shrubs of the genera *Fragaria* (strawberries) and *Rubus* (blackberries, dewberries) (Burke 1976). The North American cotton boll weevil, *A. grandis* Boheman, is a serious pest of cotton plants (e.g., Cross *et al.* 1975) and one of the most extensively studied species of weevils. Scataglioni *et al.* (2006) inferred that South American populations of *A. grandis* represent multiple ancient and more recent invasions from the United States.

In contrast to such pest species, the South American *Anthonomus santacruzi* Hustache, which develops in flower buds of *Solanum mauritianum*, has been identified as the most promising biocontrol agent of this seriously invasive weed in South Africa (Olckers 2009). It is noteworthy that two Palaearctic species of *Anthonomus*, *A. phyllocola* (Herbst) and *A. pinivorax* Silfverberg, and also *Brachonyx indigena* Schoenherr and *Macrobrachonyx gounellei* Pic live on conifers of the genera *Picea* and *Pinus* (Pinaceae) (Scherf 1964; Dieckmann 1968; Alonso-Zarazaga, personal communication). Larvae develop mainly in flower buds or flower heads and also in leaf buds, fruits, and seed capsules, in which they also pupate (Burke 1976), but some species live as inquiline in galls produced by fungi, nematodes, and several insect orders, sometimes in obligate relationships (see Gates & Burke 1972). In Africa, the genera currently placed in Anthonomini live on *Acacia* (Fabaceae) and *Ziziphus* (Rhamnaceae) (Oberprieler 1993).

Camarotini (Fig. 3.7.10.6 F). This small Neotropical tribe currently includes six genera (for the Australian *Meripherinus* Lea see Eugnomini) and is generally divided into two subtribes, Camarotina and Prionomerina (Alonso-Zarazaga & Lyal 1999). However, the prionomerines previously included also *Piazorhinus* Schoenherr, often split off into its own higher taxon (Piazorhinina) (e.g., O'Brien & Wibmer 1982), whereas Kuschel (in Wibmer & O'Brien 1986) proposed a larger concept of Camarotini that included not only Prionomerina and Piazorhinina but also Prionobrachiina. Lyal & King (1996) similarly included both the latter taxa in Prionomerinae (thus in Camarotini), and it appears that all these taxa may represent a single lineage, characterized by mostly strongly inflated fore femora carrying a large, serrate tooth on the anterior side, a short broad rostrum with short, compact antennae, and leaf-mining larvae. Reichardt (1971) revised the genus *Camarotus* Germar (40 species), broad, flat weevils characterized by having weakly geniculate antennae, widely separated fore coxae, strongly inflated fore femora with a large, serrate tooth and appendiculate claws. Reichardt (1971) recognized three species groups in *Camarotus*, based on differences in the structure of the elytra. The five genera of Prionomerina, *Camptocheirus* Lacordaire (6), *Ectyrsus* Pascoe (3), *Odontopus* Say (44), *Pristimerus* Schoenherr (2), and *Themeropsis* Pascoe (9), have not been studied recently, *Ectyrsus* also having been moved from Camarotini to Anthonomini by Wibmer & O'Brien (1986).

The larvae of *Camarotus* mine in parenchymous tissue of leaves of Melastomaceae and other dicotyledonous angiosperms (Reichardt 1971, based on Bondar 1945) and also the larvae of several Prionomerina are leaf miners on various plant families, e.g., *Odontopus* on Annonaceae, Hamamelidaceae, Lauraceae, and Meliaceae (Anderson 1993). Rosado-Neto & Lima (2002) recorded the larva of *Odontopus brevirostris* (Hustache) to feed on the parenchyma between the epidermal layers of the leaf, where

it also pupates in a spherical cocoon protected in a pupation chamber. A Costa Rican species of *Camptocheirus* induces galls on *Cinnamomum cinnamomifolium* (Lauraceae), where it is parasitized by a braconid wasp (Fortier & Nishida 2004).

Ceratopodini. Another small Neotropical tribe of uncertain status and affinity, the Ceratopodini presently include only three genera, *Aetiomerus* Pascoe (1 species), *Catiline* Champion (3), and *Ceratopus* Schoenherr (ca. 20). The Madagascan *Anthomelus* Hustache (8) and the New Guinean *Stelechodes* Faust (1), as listed in the tribe by Alonso-Zarazaga & Lyal (1999), almost certainly do not belong in it, although their proper placements are in need of assessment. Marvaldi & Lanteri (2005) regarded Ceratopodini as closely related to Camarotini, Piazorhinini, and Prionobrachiini, with which they share the large, triangular, often serrate tooth of the fore femora. A comprehensive revision of all these groups is needed.

Pakaluk & Carlow (1994) reported the larvae of *Ceratopus* to develop in fruits of *Ficus* and *Helicostylus* (Moraceae).

Cionini (Fig. 3.7.10.6 G). This tribe currently comprises seven genera occurring predominantly in the Palaearctic region. The largest genus is *Cionus* Clairville (ca. 100 species), which is also represented in southern Africa, whereas the other genera include fewer than 10 species (*Cleopus* Dejean, *Stereonychus* Suffrian) or are monobasic (*Cionellus* Reitter, *Nanomicrophyes* Pic, *Patialis* Pajni, Kumar & Rose, *Stereonychidius* Morimoto). Based on the Palaearctic species, Caldara & Korotyaev (2002) delimited the tribe as a monophyletic group identified by eight synapomorphies, i.e., frons between eyes narrower than half the width of the rostrum and narrower posteriorly than anteriorly; funicular segment 2 as long as or slightly longer than 1; median process of mesoventrite at least half as wide as a coxa; mucro on all tibiae absent in female; ventrites 1 and 2 much longer (at least 2.6 times) than 3 and 4; spermatheca with body markedly globose and ramus very short. Caldara & Korotyaev (2002) also analyzed the phylogenetic relationships of the genera, based mainly on the presence of a rostral canal and tibial mucrones and on features of the mesoventrite. A revision of the entire tribe is in progress, preliminary results indicating that most of the characters currently used to distinguish the seven genera are in need of reassessment with respect to the extra Palaearctic species (Caldara & Košťál, in preparation).

The larvae of Cionini are ectophagous, living externally on their host-plant or hidden between adjoining leaves and feeding on flowers and leaves. Although legless, they move nimbly on plant surfaces because they are covered with viscid mucus, which is secreted by a retractile tubular organ on the last segment. On completion of their development, the larvae secrete a substance containing chitinous microfibers from their midgut (Tris-tram 1978), with which they construct a spherical

translucent cocoon generally on the underside of leaves or branches for pupation. *Cionus* and *Cleopus* live mainly on Scrophulariaceae (but see McNeill *et al.* 2005), but some species of *Cionus* and also *Stereonychus* occur on Oleaceae and *Cionellus* on Plantaginaceae (Hoffmann 1958; Scherf 1964; Gumovsky 1997; Caldara & Korotyaev 2002). The only species of the Indian *Patialus*, *P. tecomella* Pajni, Kumar & Rose, lives on Marwar Teak, *Tecomella undulata* (Bignoniaceae), and may seriously damage this economically important tree (Rose & Sidhu 1994; Gaur & Ahmed 1998).

Cranopoeini (Fig. 3.7.10.6 H). This tribe was only recently established by Kuschel (2009) for the *Cranopoeus* complex of genera that he had earlier recognized in Molytinae (Kuschel 1987). The previously known genera, *Cranopoeus* Marshall (6 species), *Cratoscelocis* Lea (1), *Fergusonella* Zimmerman (1), *Spanochelus* Marshall (4), and *Swezeyella* Zimmerman (1), were included in Cryptoplini in the catalogue of Alonso-Zarazaga & Lyal (1999), but Kuschel (2009) detailed a range of character differences between the two groups and added another six genera to the new tribe: *Blastobius* Kuschel (1), *Cerocranus* Kuschel (1), *Cranoides* Kuschel (2), *Docolens* Kuschel (1), *Enneaesus* Kuschel (1), and *Onychomerus* Kuschel (1). The Cranopoeini are most diverse in the Pacific region (8 of the 11 genera, 6 only in New Caledonia) but also present in Australia (*Cranopoeus*, *Cratoscelocis*, *Enneaesus*, and *Fergusonella*) and New Guinea (undescribed). The tribe was well characterized by Kuschel (2009), the most conspicuous feature being the waxy secretions of the thorax and elytra that harden to form solid structures, which reach an extreme form in the huge, curved, hollow thoracic “horn” or “helmet” of *Cerocranus extremus* Kuschel (Fig. 3.7.10.6 H).

Nothing precise is known about the biology of Cranopoeini, but Kuschel (2009) recorded *Eucalyptus* and *Syzygium* (Myrtaceae), *Glochidion* (Euphorbiaceae), *Nothofagus* (Nothofagaceae), *Sloanea* (Elaeocarpaceae), and Lythraceae (as Sonneratiaceae) as probable hosts. *Enneaesus bituberculatus* (Lea) in Australia is found on *Eucalyptus* and *Melaleuca*.

Cryptoplini (Fig. 3.7.10.6 I). This small Australo-New Guinean tribe comprises five genera, but its exact composition and distribution need further study. The genera *Cryptoplus* Erichson (ca. 30 species), *Haplonyx* Schönherr (ca. 64), *Zeopus* Pascoe (1), and *Sigastus* Pascoe (2–3) are confined to Australia, whereas *Menechirus* Hartmann (1), a close relative of *Sigastus*, occurs from northeastern Australia to New Guinea and Seram. The other genera listed in the tribe by Zimmerman (1994, as Haplonychini) and Alonso-Zarazaga & Lyal (1999) belong to a different tribe, the Cranopoeini (*q.v.*), except for *Brendamaya* Alonso-Zarazaga & Lyal, whose name is a synonym of *Atelicus* Waterhouse (see *Platyurus* in Zimmerman 1994), a genus tentatively placed in Cyclominae: Aterpini by Oberprieler (2010). The tarsi of Cryptoplini characteristically have the onychium and claws reduced, ranging from the

onychium being narrow and the claws simple, fine, subparallel (*Menechirus*) to the onychium short and largely withdrawn into the lobes of tarsomere 3 (*Sigastus*) to the claws being single, rarely bifid at apex (*Haplonyx*) to the onychium being minute and hidden in the narrow cleft of tarsomere 3 (*Cryptoplus*) to being completely absent (*Zeopus*). Other unusual features of Cryptoplini are the complete undifferentiation of the proventriculus, lacking the normal plates and paired brushes found in most higher curculionids and the presence of a dorsal plate (tectum) on the penis. An undifferentiated proventriculus is a feature of more primitive weevil groups (Calder 1989), and the only other Australian genera of Curculionidae so far known for this condition are *Strongylorhinus* Schoenherr and *Atelicus*, formerly classified in Diabathrariini (Oberprieler *et al.* 2007; Oberprieler 2010). However, a weakly developed proventriculus occurs in some other curculionid genera as well (see Calder 1898). A dorsal plate on the penis (the pedotectal type of aedeagus) is also characteristic of more primitive weevils, in Curculionidae, occurring only in the subfamily Brachycerinae. The dorsal plate of Cryptoplini is, however, basally broadly fused to the pedon and the temones show no sign of a dorsal (tectal) arm at their bases, as is the condition in the typical pedotectal aedeagus. The phylogenetic significance of this character in Cryptoplini remains to be investigated. Other characters of the tribe are the following: body densely squamose; rostrum stout and straight, sometimes apically flattened; prementum mostly transverse; maxillary and labial palps three-segmented; scrobes apically not visible from above; funicles seven- or (in *Cryptoplus* and *Zeopus*) six-segmented; clubs short, four- or five-segmented; fore coxae contiguous or narrowly separate, middle coxae closer together than hind ones; all femora dentate; tibiae two-pronged, with inner uncus and praemucro above it; endophallus sometimes with large basal sclerite; gonocoxites without styli; base of spermathecal gland funnel-shaped sclerotized (Kuschel 2009).

Cryptoplini are mostly associated with Myrtaceae. The larvae of *Haplonyx*, and *Cryptoplus* develop in flower and fruit buds of *Eucalyptus*, *Melaleuca*, and *Leptospermum*, the adult female generally severing the stem of a flowering or fruiting terminal so that it falls to the ground, where the larvae feed and pupate in the wilting buds. Some species of *Haplonyx* have been reared from fleshy and woody galls on *Eucalyptus* and *Leptospermum*, in which they may develop both as incitants and inquilines. Nothing is recorded of the biology of *Zeopus*, but it probably also lives on *Eucalyptus* or other Myrtaceae. The larvae of *Sigastus* develop in flowers and fruits of *Syzygium* but have also been reared from woody homopteran galls on *Eucalyptus* and *Allocasuarina* (Casuarinaceae) (Juniper & Britton 2010), whereas an undescribed species has become a pest in fruits (nuts) of planted *Macadamia* (Proteaceae) in northern Australia (Fay *et al.* 2001). *Sigastus*

fuscodorsalis (Heller) (Fig. 3.7.10.6 I), originally described in *Menechirus*, was imported in fruits of *Syzygium suborbiculare* from Darwin in Australia to the Philippines (Heller 1921). *Menechirus* has been reared from *Syzygium* fruits but also collected from *Rhodomyrtus macrocarpa* in Australia.

Curculionini (Fig. 3.7.10.6 J and K). This cosmopolitan tribe contains approximately 15 genera, although a number of others may belong in it as well. The almost cosmopolitan genus *Curculio* Linnaeus (ca. 500 species) is the largest, several smaller ones – *Archarius* Gistel (ca. 10), *Carponinus* Heller (ca. 50), *Ergania* Pascoe (17), *Indocurculio* Pajni, Singh & Gandhi (10), *Koreoculio* Kwon & Lee (2), *Labaninus* Morimoto (14), *Pagumia* Kwon & Lee (1), *Pimelata* Pascoe (1), *Pseudoculio* Pelsue & O'Brien (7), and *Shigizo* Morimoto (14) – occurring in the Palaearctic and Oriental regions. In the east, the distribution of the tribe extends southward to New Guinea and Australia, from where approximately 16 species of *Curculio* are known as well as *Pycnochirus* Berg (ca. 2), a genus classified in Trigonocolini by Alonso-Zarazaga & Lyal (1999) but agreeing with Curculionini in most characters, especially the structure of its tarsi, venter, and pygidium. It was originally described from New Guinea but redescribed from Australia as *Balanerhinus* Lea (Heller 1925; Rheinheimer 1994). Several undescribed genera occur in Australia (Fig. 3.7.10.6 K) and New Guinea. Three genera are known from the Afrotropical region, *Timola* Pascoe (ca. 30) from continental Africa and *Aviranus* Fairmaire (ca. 20) and *Pseudobalaninus* Faust (ca. 40) from Madagascar, but some other Madagascan genera may belong in the tribe as well. Pelsue & O'Brien (2011) recently described a genus *Megaoculus* based on two South American species, but it does not convincingly fit into Curculionini and may represent a different tribe. Gibson (1969, 1977) revised the North and Central American species of *Curculio*, whereas Morimoto (1960 a, b, 1981) treated the Japanese and Pelsue & Zhang (2000 a, b, 2002, 2003) treated the Chinese ones. An exploratory molecular phylogeny of 22 species of *Curculio* (Hughes & Vogler 2004) supported two previously recognized European species groups but remained inconclusive with regards to the monophyly of the American groups. Pelsue (2004, 2005, 2007, 2009) revised the Oriental genera *Indocurculio*, *Labaninus*, and *Shigizo*.

Curculionini are traditionally characterized by their smoothly triangular, vertically moving mandibles, but this character only occurs in the derived genera such as *Curculio*, *Carponinus*, *Indocurculio*, *Koreoculio*, *Labaninus*, and *Shigizo*. In *Ergania*, *Pimelata*, and some *Timola* species, the mandibles articulate in a more or less oblique plane, the sockets positioned lateroventrally, and a gradual transition in the plane of the mandibles can be traced from a horizontal position as in *Pycnochirus*, and some undescribed forms (Fig. 3.7.10.6 K) via the oblique one as in *Ergania* to a fully ventral one in

Curculio and allies. Similar vertically articulating mandibles occur in Belidae: Oxycoryninae (*Oxycorynus* Chevrolat, *Parallocorynus* Voss, and *Rhopalotria* Chevrolat) and in Brentidae: Antliarhinini (females of the seed-feeding *Antliarhinus zamiae* (Thunberg); mandibles articulating obliquely in other *Antliarhinus* species) and appear to be convergent adaptations for drilling very fine oviposition holes. Other characters of Curculionini include a long to very long, slender rostrum (especially in the female), seven-segmented funicles (six-segmented in *Ergania* and *Pimelata*), ten-striate elytra without stridulatory file and mostly narrowly impressed around the scutellum, often large and ascending mesepimera, contiguous fore coxae, dentate femora, broad flat tarsi, divaricate and appendiculate claws (simple in *Timola*; parallel but not connate in *Ergania*, *Pimelata*, and *Pycnochirus*), often exposed pygidium (especially in male), and ventrite 5 in male generally with median to apical depression flanked by tufts or rows of dense, long setae. *Ergania*, *Pimelata*, *Pycnochirus*, and some other genera (Fig. 3.7.10.6 K) also retain a strong trochanteral seta and appear to be generally less derived than the other genera. After Heller (1925, 1927), the tribe is generally divided into three subtribes, Curculionina, Pseudobalanina, and Timolina, but Pelsue & O'Brien (2011) recently proposed three additional ones, Archariina for *Archarius*, *Koreoculio*, and *Pagumia*, Erganiina for *Ergania* and *Pimelata*, and Labaninina for *Labaninus*, *Pseudoculio*, and *Shigizo*. However, none of the distinguishing characters of these subtribes appear to constitute suitable synapomorphies for defining them as monophyletic groups, and the entire tribe is in need of revision and phylogenetic analysis to determine its proper delineation and the relationships between the genera.

The biology of many species of Curculionini is relatively well known. Their host-plants mostly belong to the families Betulaceae, Fagaceae, Juglandaceae, Moraceae, and Salicaceae (Hoffmann 1954; Scherf 1964; Gibson 1969, 1977; Rasplus *et al.* 2003). The larvae generally develop in flower buds or fruits and pupate in the soil, but some, especially in the genus *Archarius*, incite galls or live asinquilines in galls produced by Hymenoptera (Hoffmann 1954; Scherf 1964; Cussigh 1992). The pecan weevil, *Curculio caryae* Horn, is the most extensively studied and economically by far the most important species of the tribe (see Neel 1985). In Japan, the rostrum length of *Curculio camelliae* Roelofs is closely linked to the pericarp thickness of its host, *Camellia japonica* (Theaceae), across multiple varying populations, yielding a pattern of adaptation suggestive of a co-evolutionary arms race (Toju & Sota 2006). In Australia, most species of *Curculio* appear to develop in figs (Moraceae) (Zimmerman 1994), but Howden (1995) recorded *C. niveopictus* Lea ovipositing in ripe fruits of *Syzygium tiernayanum* (Myrtaceae), whereas *Pycnochirus fuscovarius* (Faust) has been

collected from fruits of *Alectryon coriaceus* (Sapindaceae) (Rheinheimer 1989). In Africa, *Curculio* also develops mostly in figs (Marshall 1907; Perrin 1992), whereas *Timola* is associated with Ebenaceae, *T. posticata* Marshall developing in fruits of *Diospyros lycioides*, and other species living on, e.g., *D. austro-africana* and *Euclea* species (R. Oberprieler, personal observation).

Derelomini (Fig. 3.7.10.6 L). In a comprehensive cladistic analysis of more than 30 genera and 90 species in the in-group, Franz (2006) diagnosed the Derelomini as follows: segments 1 and 2 of maxillary palps lacking mediolateral setae; tibial apices unarmed; adults feeding and reproducing only on angiosperm flowers and inflorescences, typically acting as pollinators; and predominantly associated with inflorescences of Araceae. Franz (2006) proposed five subtribal concepts to accommodate the major lineages in this morphologically and biologically heterogeneous tribe, including the predominantly Old World (Asian) Acalyptina, which were nested within Derelomini (though see Acalyptini above). Members of Anthonomini, Ellescini, and Trypetidini were identified as the most immediate out-group, the last taxon, however, now considered part of the molytine tribe Petalochilini (see Chapter xx.x). Kojima & Morimoto (2005) identified the unusual elytra-tergal stridulation system 2 (Lyal & King 1996) occurring in typical Derelomini (the Old World *Deleromus* Schoenherr and *Elaeidobius* Kuschel), whereas the New World genus *Anchylorhynchus* Schoenherr has the more common system 1 (Lyal & King 1996).

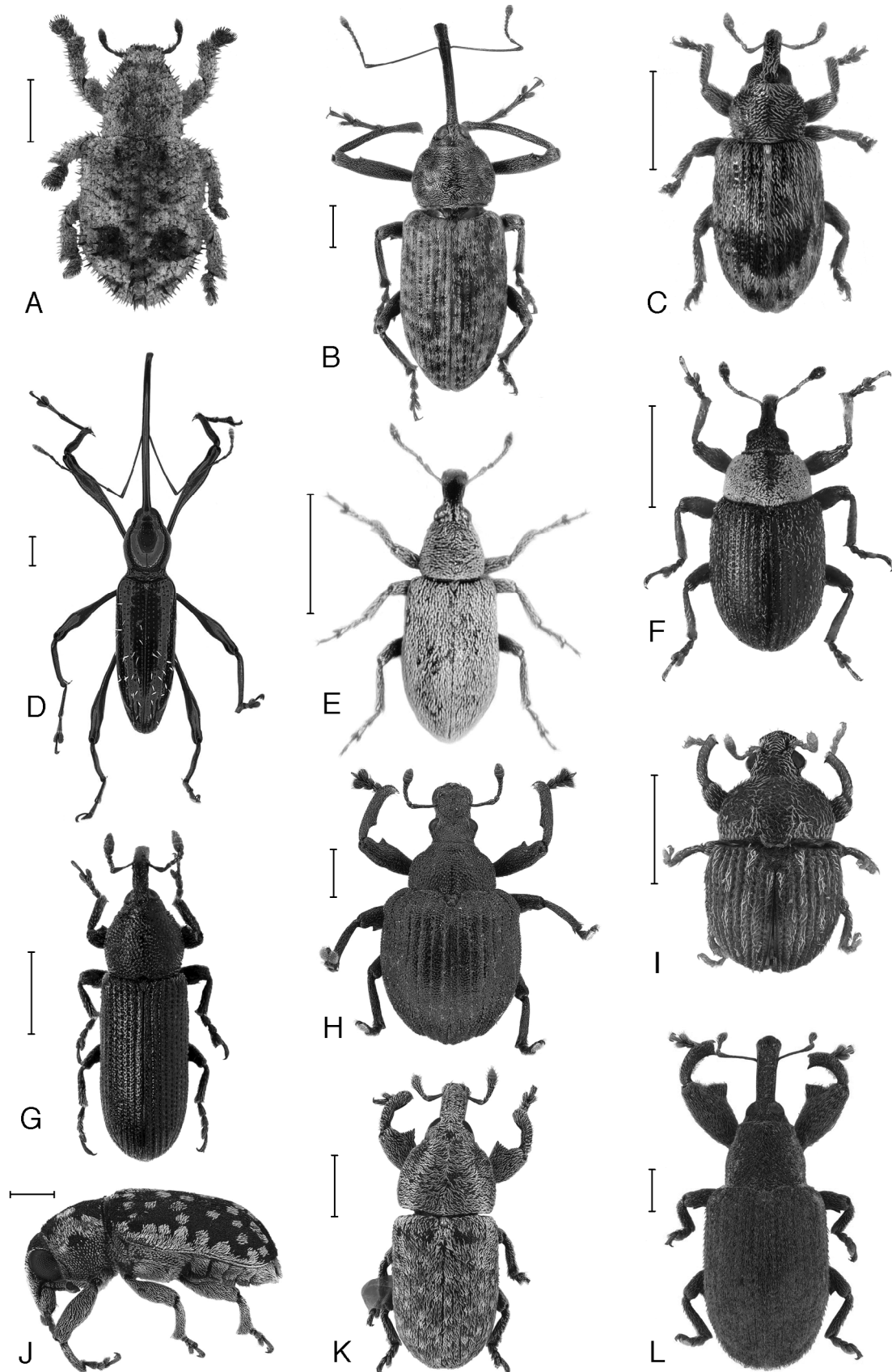
Derelomini, generally known as “palm flower weevils” or “derelomine flower weevils” (Franz 2006), are primarily associated with the reproductive organs of monocotyledons belonging to the families Araceae and Cyclanthaceae (Henderson 1986; Franz & Valente 2005). According to Franz & Valente (2005), certain lineages inhabiting temperate regions or higher-elevation habitats have secondarily shifted onto dicotyledons, including members of the Acalyptina (Dieckmann 1988; Kojima & Morimoto 2005) and the genus *Phyllotrox* Schoenherr in the Phyllotrogina. Larvae vary considerably in life habits because they may be detritivorous or herbivorous, often feeding on parts of the floral structures that are dispensable for the hosts (e.g., *Celetes* Schoenherr; Valente 2005) but sometimes destroying the seeds (e.g., *Systemotelus* Anderson & Gómez 1997). In certain lineages, morphological adaptations and reproductive strategies are closely correlated with those of their host-plants (Franz 2003 a, 2004). Notable derelomine lineages include the Staminodeina, in particular *Staminodeus* Franz, whose seven species are associated with the staminodes of the inflorescences of cyclanths (Franz 2003 a). The males have a row of 6–10 teeth along the margin of the fore tibiae, whereas the females have a small, curved spine on the frons. Upon arriving at an inflorescence, a

female detaches a staminode with her mandibles, falls to the ground with it, transports it to a site in leaf litter using her frontal spine as a point of resistance against the substrate and then oviposits in it. Meanwhile, males associate with the moving staminode and fight each other with their forelegs, executing fast blows until their tibial teeth cling and dislodge competitors from the staminode. A phylogeny of *Staminodeus* hypothesizes that female transporting behavior evolved before male fighting behavior (Franz 2003). Other Neotropical lineages with potentially more than 100 species remain almost entirely undescribed yet constitute the primary pollinators of Cyclanthaceae (Franz 2007 a). Pollinating members of the related phyllotrogine genus *Cyclanthura* Franz, in turn, have shifted onto species of Araceae, in particular *Anthurium* (Franz 2003, 2007 b).

Diabathrariini (Fig. 3.7.10.7 A). As limited by Oberprieler *et al.* (2007) and Oberprieler (2010), this small group only includes three African genera, *Aphanonyx* Marshall (2 species) and *Diabathrarius* Schoenherr (4) in southern Africa and Madagascar and *Onychogymnus* Quedenfeldt (ca. 14) in central Africa and Madagascar. All have entirely lost the onychia, a condition rare among African weevils but more common in Australia. The weevils are stocky with short, stout legs; densely covered in broad, fluted, overlapping scales; the rostrum short and broad, sometimes apically strongly flared, fitting into a shallow depression or deep excavation (in *Aphanonyx*) of the prosternum; the scrobes narrow, deep, and curving onto the venter of the head before the eyes; the funicles seven-segmented and the clubs short; the maxillary and labial palps large, three-segmented; the femora unarmed; the tibiae with a strong uncus and smaller praemucro above it; the proventriculus strongly developed; the elytra without stridulatory file; the pointed aedeagus with two pairs of apical setae and the tegmen with long parameres. The group is in need of revision, and its taxonomic affinities are unclear.

Little is known about the biology of Diabathrariini, but *Diabathrarius variegatus* Boheman has been reared from seedpods of *Schotia afra* in South Africa (S. Naser, personal observation), and *Aphanonyx setulosus* Marshall is there regularly collected on *Pterocarpus rotundifolius* (R. Oberprieler, personal observation) and may develop in its fruits as well (both hosts Fabaceae).

Ellescini (Fig. 3.7.10.7 B and C). Generally divided into subtribes Ellescina and Dorytomina, this tribe was included in Tychiini (as a subfamily) by Clark *et al.* (1977) based on the latero-posteriorly angled ventrites and the direction of the pronotal scales. However, its composition and status are unclear. The genera *Minyrus* Schoenherr and *Ontoctetorus* Faust, listed in Ellescina by Alonso-Zarazaga & Lyal (1999), are now considered to belong in Anthonomini (Clark 2010), the Australian *Sellechus* Lea is



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Fig. 3.7.10.7 Habitus, adults. A, *Aphanonyx latesetosus* (Hustache) (Diabathrariini); B, *Dorytomus longimanus* (Forster) (Ellescini); C, *Ellescus bipunctatus* (Linnaeus) (Ellescini); D, *Ludovix fasciatus* (Gyllenhal) (Erodiscini); E, *Ita chavanoni* Meregalli & Borovec (Itini); F, *Gymnetron beccabungae* (Linnaeus) (Mecinini); G, *Mecinus janthinus* Germar (Mecinini); H, *Galloisia inflata* Hustache (Microstylini); I, *Microstylus rufus* Schoenherr (Microstylini); J, *Nerthops guttatus* Schoenherr (Nerthopini); K, *Acallopistus* sp. (Nerthopini); L, *Teinomphasus robustus* Oberprieler (Ochyromerini). Scale bars 1 mm.

currently best classified in Storeini (*q.v.*), and the placement of the Asian *Bathrorygma* Marshall and *Minyrophilus* Voss in Ellescini is questionable. No genera of Ellescina have been recently studied, but many species of the Holarctic genus *Ellescus* Dejean are well known. The species of *Dorytomus* Germar in North America, Japan, and Siberia were taxonomically revised by O'Brien (1970), Morimoto & Enda (1962) and Korotyaev *et al.* (1976, 1996), and Colonnelli (2003), respectively, synonymized all the subgenera as listed by Alonso-Zarazaga & Lyal (1999) with *Dorytomus* because they were shown to be polyphyletic.

Ellescini, in particular *Dorytomus* (ca. 100 species) and *Ellescus* (7), are generally associated with *Populus* and *Salix* (Salicaceae) (Hoffmann 1958; Morimoto & Enda 1962; Scherf 1964; O'Brien 1970; Dieckmann 1988; Fjellberg & Böcher 2006). The biology of some Palaearctic species of these genera is well known. The larvae develop in the axis of mainly female catkins and penetrate the ovaries and pollen masses, which causes the catkins to atrophy early in their development and drop to the ground, the larvae pupating in the soil (Hoffmann 1958; Scherf 1964). The larvae of *Dorytomus* appear earlier in the season in *Salix* catkins than those of *Ellescus* (Scherf 1964).

Erodiscini (Fig. 3.7.10.7 D). This small Neotropical tribe was comprehensively revised by Vanin (1986), who recognized 8 genera and 98 species in it, and proposed a genus-level phylogeny with two principal clades (excluding *Sicoderus* Vanin). Anderson (1999) added three further species to *Sicoderus*, which comprises more than half (59) of all species of the tribe. The other genera are much smaller, *Ecnomorhinus* Vanin (1), *Erodiscus* Schoenherr (5), *Hammatostylus* Champion (9), *Lancearius* Vanin (2), *Ludovix* Laporte (2), *Pimelero dius* Vanin (12), and *Prosicoderus* Vanin (11). The Indonesian *Pseuderodiscus* Heller, listed in Erodiscini by Alonso-Zarazaga & Lyal (1999), belongs to the molytine tribe Trachodini (H. Kojima, personal communication). Erodiscini appear closely related to Otidocephalini (Vanin 1986; Marvaldi & Lanteri 2005), and the two groups are sometimes combined (e.g., Anderson 1993). Erodiscini are characterized by the following features (after Vanin 1986): body narrow, elongate; prothorax posteriorly distinctly constricted; integument shiny, often with bronze sheen, largely glabrous with sparse long setae, rarely with scales; head hemispherical; eyes flat; rostrum mostly strongly elongate (up to twice the body length), down-curved; prementum quadrate to strongly bilobed, labial palps three- to one-segmented; antennae long, slender, funicles seven-segmented, segment 2 often elongate, clubs long, slender; elytra 10-striate; ventrites 1 and 2 fused; legs long and slender, femora clavate, ventrally usually dentate, tibiae with uncus and praemucro, tarsi long with strongly elongate tarsomere 1, claws free, simple, or toothed. *Erodiscus* is exceptional in the tribe (as

in weevils overall) by possessing an elytro-femoral stridulation system, consisting of a row of lateral elytral tubercles and a sharp keel on the inner face of the hind femora.

Vanin (1986) and Anderson (1999) summarized the available information on the biology and host associations of the tribe. Adults are often found on inflorescences, particularly of aquatic or semi-aquatic plants, but the larvae appear to tunnel in branches of various plants. *Ludovix fasciatus* (Gyllenhal) (Fig. 3.7.10.7 D) is seemingly unique among weevils for being predacious, both adults and larvae feeding on eggs of the grasshopper genus *Cornops* (Acrididae) deposited inside stems of water hyacinth, *Eichhornia crassipes* (Pontederiaceae) (Zwölfer & Bennett 1969). Judging from the even more extremely elongated rostrum of some other species of Erodiscini, Vanin (1986) speculated that entomophagy may be more common in this tribe.

Eugnomini. In the catalogue of weevil genera (Alonso-Zarazaga & Lyal 1999), this tribe contains 23 genera, mainly from Australia and New Zealand but also occurring in New Caledonia and South to Central America. Its precise composition and distribution, however, remain in contention. Kojima & Morimoto (1993) transferred the Oriental *Api-nodes* Marshall from Anthonomini to Eugnomini, but Alonso-Zarazaga & Lyal (1999) placed it back in Anthonomini (as a synonym of *Pseudopoophagus* Voss). There are, however, also other Eugnomini in Indochina, similar to the undescribed Australian genus pictured by Zimmerman (1992, pl. 511) (H. Kojima, personal communication). Alonso-Zarazaga & Lyal (2002) also referred the New Zealand *Oropterus* White to Eugnomini, whereas Leschen *et al.* (2003) listed this genus in Storeini and two other New Zealand genera in Eugnomini, *Colabotelus* Broun and *Philacta* Broun, which were placed in Erihiniinae by Alonso-Zarazaga & Lyal (1999). Franz (2006) transferred the American genus *Pedetinus* Faust from Derelomini to Eugnomini and presented four putative synapomorphies and two additional diagnostic features for the three American genera of the tribe, although this outcome was not a focus of the study. In addition, the Australian *Meripherinus* Lea belongs in Eugnomini rather than in the New World tribe Camarotini, and several further, undescribed genera occur in Australia and New Guinea. The group was last studied by Cawthra (1966), who detailed its distinguishing characters and provided a definition for it, although no single character can be used to unequivocally identify all genera as belonging to it. Typical features are the generally long and stout rostrum; often exodont mandibles; flexible maxillae with long palps; large eyes; elongate head with distinct neck; conical, contiguous fore coxae; large, flat, smooth tooth on at least the hind femora; mucronate tibiae (except the American genera; Franz 2006); free, simple to appendiculate tarsal claws; and ventrites with straight posterior

margins. The Australian genera *Meriphus* Erichson, *Myossita* Pascoe, and *Orpha* Pascoe possess extraordinary mouthparts, with the epistome produced into a triangular process extending over the mandibles, which are flat with two large, exterior teeth and can open far outward and backward in a horizontal plane. The function of these outwardly cutting mandibles is not clear.

Cawthra (1966) and May (1993) summarized what is known about the biology of Eugnomini. The adults are generally found on flowers, feeding on pollen and probably nectar, whereas the larvae mostly develop under bark of dead branches and logs of a variety of plant species. A few, however, develop in living plant tissues and appear to be more host specific. In New Zealand, *Gonoropterus* Broun develops in fruits of *Nestegis* (Oleaceae), *Nyxetes* Pascoe in galls on *Clematis* (Ranunculaceae), *Hoheria* (Malvaceae), and also *Nestegis*, the latter seemingly in symbiotic relationships with mealybugs (Coccidae), and *Oreocalus* May in stems and galls of *Hebe* (Scrophulariaceae) (May 1993). In Australia, *Myossita* breeds in the confluences and infructescences ("cones") of *Banksia* (Proteaceae) (Scott 1982), whereas *Omoides* Boheman in Argentina and Chile is associated with several plant families, mainly Flacourtiaceae (Morrone & Roig Juñent 1995), and South American species of *Udeus* Champion may occur on palms (Arecaceae), as some species of this genus have been misplaced in *Celetes* (N. Franz, personal observation).

Itini (Fig. 3.7.10.7 E). This small tribe was included in Curculioninae by Alonso-Zarazaga & Lyal (1999) but was transferred to Molytinae by Alonso-Zarazaga (2002). However, in a recent revision Meregalli & Borovec (2011) again placed the tribe in Curculioninae, based mainly on the different structure of the apex of the hind tibiae and of sternite VIII in the males of *Ita* Tournier, and they regarded this genus to be closely related to Styphlini, from which it differs in having very short scrobes and the antennae inserted near or before the middle of the rostrum (at the apex in Styphlini). These characters also occur in *Geranorhinus* Chevrolat, which Meregalli & Borovec (2011) consequently (but tentatively) transferred from Styphlini to Itini. In contrast, Legalov (2011) placed *Geranorhinus* in Hyperini: Coniatina, and it appears that the affinities of this genus are in need of further study.

Ita (15 species) occurs in stable halophytic habitats around the Mediterranean Sea, from Macaronesia in the west to Turkmenistan and Uzbekistan in the east (Meregalli & Borovec 2011). The adults are associated with Amaranthaceae (Chenopodioideae, Salicornioideae, and Salsoloideae) and represent the dominant weevil component of halophytic coenoses on flat, warm, or hot plains with saline soil or at the margins of brackish marshes. The weevils crawl along the stems of their apparent hosts during the day, feeding on the succulent stems and leaves or hiding in debris at the base of the shrubs. It is very likely that goosefoots are the hosts also of

the larvae, although these have not yet been found. *Geranorhinus* (ca. 16) similarly occurs in Palaearctic halophytic habitats, from Algeria to Mongolia, although its species live on *Tamarix* (Tamaricaceae), the larvae apparently forming galls and constructing cocoons for pupation.

Mecinini (Fig. 3.7.10.7 F and G). This tribe comprises six genera, *Cleopomiarus* (ca. 40 species), *Gymnetron* (100), *Mecinus* (50), *Miarus* (20), *Rhinumiarus* Caldara (4), and *Rhinusa* Stephens (40). Caldara (2001) performed a phylogenetic analysis of the genera, with Cionini, Ellescini, and Tychiini as out-group taxa. This analysis suggested a sister group relationship existing between Mecinini and Cionini, based on the shared characters of a five-segmented funicle, only partially visible tarsal sockets, and basally connate claws, and yielded three synapomorphies for Mecinini: ventral margin of scrobes in dorsal view convex and slightly protruding; posterior margin of ventrites 3 and 4 generally laterally angled; tergite VII more or less uncovered. Phylogenetically informative characters between the genera were found to occur on the rostrum (position of antennal insertion), antennae (number and length of funicular segments), prosternum (presence of a rostral canal), elytra, claws, tergites (presence of a pygidium), aedeagus, and spermatheca (shape, location of gland). Vahtera & Muona (2006) confirmed the monophyly of the closely related genera *Miarus* and *Cleopomiarus* from COI and ITS2 sequence data. *Miarus*, *Gymnetron*, and *Rhinusa* have also been subjected to phylogenetic analyses (Caldara 2007, 2008; Caldara *et al.* 2010), with particular attention given to the disjunct Mediterranean-South African distribution of *Gymnetron* and also *Cleopomiarus* Pierce (Caldara *et al.* 2008). The Afrotropical species of *Gymnetron*, currently placed in 13 apparently endemic groups, seem very closely related to the Palaearctic species (distinguishable only by few subtle differences), but it is as yet unclear whether they represent the same or a different lineage (Caldara 2008). The Afrotropical species of *Cleopomiarus*, in contrast, form three groups based on characters of their genitalia, two groups including also all the Palaearctic species but the third being endemic to the Afrotropical region (Caldara 2005). In *Rhinusa*, ten groups assembled in three clades could be identified (Caldara *et al.* 2010), one clade including all species living on Scrophulariaceae and divided into two groups associated with the closely related genera *Scrophularia* [*R. bipustulata* (Rossi) group] and *Verbascum* [*R. tetra* (Fabricius) group], whereas the other two clades encompass the species occurring on Plantaginaceae of the tribe Antirrhineae. These results indicate that host associations in this genus are narrow and conservative as well as partly congruent with the phylogenetic pattern among their hosts, the two plant families being closely related.

The larvae of Mecinini develop in roots, shoots, leaves, and flowers, many causing their host organs

to swell or develop into galls. The latter habit occurs in several genera and often in unrelated species, and some species of *Rhinusa* are inquiline in galls produced by other species of the same genus (Hoffmann 1958; Arzanov 2000; Caldara 2001, 2003, 2005, 2007, 2010; Korotyaev *et al.* 2005). Mecinini are predominantly associated with the families Scrophulariaceae (tribe Scrophularieae), Plantaginaceae (tribes Antirrhineae and Plantagineae), and Campanulaceae. *Mecinus* species live on Plantagineae and *Rhinusa* species on both Scrophulariaceae and Plantaginaceae as presently circumscribed (Olmstead *et al.* 2001; Albach *et al.* 2005), as association supporting the close relationship between these families as indicated by recent molecular studies. Several species of *Mecinus* and *Rhinusa* have recently become the subject of detailed ecological studies (Toševski & Gassmann 2004) investigating their potential use as additional biological control agents of Palearctic species of toadflax (*Linaria* spp., Plantaginaceae) that have become invasive in North America. The Palearctic species of *Gymnetron* live on *Veronica* (Caldara 2008), currently included in Plantaginaceae (Olmstead *et al.* 2001; Albach *et al.* 2005), whereas those in the Afrotropical region (Caldara 2003; Caldara *et al.* 2010), where Plantaginaceae are poorly represented, appear to live on various genera of Scrophulariaceae distributed mainly in the southern hemisphere, i.e., *Diascia*, *Hemimeris*, and *Nemesia* (Hemimerideae), *Hebenstreitia*, *Selago*, *Sutera*, and *Tetrasselago* (Selagineae), and *Buddleja* (Buddlejaceae), all closely related to Scrophulariaceae, as well as on Stilbaceae, i.e., *Anastrebe*, a family very closely related to Scrophulariaceae (Olmstead *et al.* 2001). The Palearctic species of *Miarus*, and *Cleopomiarus* are associated with genera of Campanulaceae in the subfamily Campanuloideae (*Adenophora*, *Campanula*, *Jasone*, *Phyteuma*), whereas species of *Cleopomiarus* in South Africa and Mexico live on genera of the subfamilies Campanuloideae (*Lightfootia*, *Roella*, *Wahlenbergia*) and Lobelioideae (*Lobelia*) (Caldara 2005, 2007).

Microstylini (Fig. 3.7.10.7 H and I). The genera included in this tribe, proposed by Lacordaire (1865) for *Microstylus* Schoenherr, were generally placed in several others, namely Galloisiini, Metatygini, and Nerthopini, but the classification of these groups has been controversial and confusing and remains somewhat unclear. Voss (1962) grouped all of them in a subfamily Nerthopinae, distinguishing four tribes on the different combinations of separate or contiguous fore coxae and free or connate tarsal claws: Nerthopini with *Nerthops* Schoenherr, *Microstylus* and *Teluropus* Marshall; Metatygini (as Omophorini) with *Omophorus* Schoenherr, *Physarchus* Pascoe, *Sternechosomus* Voss, and *Zantes* Pascoe; Galloisiini with *Galloisia* Hustache and *Microgalloisia* Voss; Acalloplastini with only *Acalloplastus* Schoenherr. Marshall (1935), however, had placed the Oriental *Galloisia* in Nerthopinae near *Microstylus* despite the difference

in the position of their fore coxae, whereas Morimoto (1962 a) proposed a separate subfamily, Galloisiinae, for it but evidently did not know the relevant African taxa in detail. Kuschel (1987) included Metatygini and Galloisiini in Molytinae but gave no specific reasons for this placement, and Alonso-Zarazaga & Lyal (1999) followed it in their generic catalogue. None of these genera have been studied in detail, however, and several of them share characters that contradict Voss' superficial group differences and classification as well as that of Alonso-Zarazaga & Lyal (1999). The distinction between *Microstylus* and *Zantes* is obscure, with their species agreeing in a number of characters (e.g., *Zantes* also possesses separate fore coxae (Pascoe 1888), *contra* Voss' classification, and several having been moved between these two genera in the literature. Microstylini, and Nerthopini are here treated in Curculioninae, whereas the tribe Metatygini is retained in Molytinae (*q.v.*).

The tribe Microstylini is here taken to include the genera *Microstylus* (ca. 5 species), *Zantes* (ca. 22), *Microgalloisia* (1), *Menesinus* Faust (1), and *Galloisia* (2), the first three African, *Menesinus* Indian and *Galloisia* Oriental (one species each in Japan and China). *Microstylus* species are peculiar subglobular weevils with a short, broad rostrum; bulging eyes and a definite neck; the head with a pair of deep, posteriorly convergent furrows between the eyes; the mandibles flat, adentate, with broadly rounded apices; the prementum large with labial palps absent; the postmentum with a median tooth or ridge in the male; the fore coxae narrowly separated; the fore femora with two small teeth; the tibiae shallowly grooved on the inside and apically with an inner praemucro and a large, sharp outer uncus; the claws strongly appendiculate; the scutellum triangular to pentagonal, centrally depressed to sometimes forming lateral carinae; the elytra with ten striae and interstria 10 strongly costate, without stridulatory file; ventrite 1 posteriorly broadly emarginate in the middle; the pygidium exposed; the aedeagus flat, with very short temones; and the tegmen without apodeme. In fresh specimens, the body is covered by a reddish waxy secretion. The very similar *Menesinus* differs in not having the rostrum separated from the head by a pair of oblique grooves, the fore femora with a single tooth, the tibial apices with only an uncus, and ventrite 1 posteriorly straight (after Faust 1898). Legalov (2006) discovered that the African *Archolabus* Voss, described and long treated as a representative of an ancestral attelabine lineage, is very similar to *Menesinus*; it is in fact congeneric with *Microstylus*, and its type species, *A. methneri* Voss, may be the same as *M. hypocritus* Hustache (R. Oberprieler, personal observation). *Zantes* also agrees with *Microstylus* in most characters, in particular, the two-pronged tibiae, appendiculate claws, male postmental tooth, and similar scutellum, but it has a longer rostrum that in the female may be ventrally

inflated in front of the almost vertical scrobes. *Microgalloisia* was considered by its author (Voss 1962) to be close to both *Microstylus* and *Zantes* but differs most conspicuously by having connate claws. *Galloisia* is similar to *Microstylus* and *Zantes* in habitus and vestiture (very fine, sparse setae and reddish waxy secretion) and the absence of labial palps (see Morimoto 1962 a), but it differs in having the femora with a single large tooth, the tibiae internally carinate and with only an uncus, and the claws connate. The rostrum in the female is ventrally similar but more spectacularly inflated than in *Zantes*.

Nothing has been reported about the biology of any genus of Microstylini. *Microstylus* appears associated with fabaceous trees, *M. rufus* Schoenherr (Fig. 3.7.10.7 I) living on *Acacia nigrescens* and *Dalbergia obovata* and *M. hypocritus* on *Pterocarpus rotundifolius* in South Africa (R. Oberprieler, personal observation). The stout, subglobular body shape of this genus and also its similarity in some other characters (dentate fore femora, double-pronged tibial apex, toothed claws, laterally costate elytra) with the American genus *Camarotus* suggest that its larvae may also be leaf miners or leaf gillers, and the same probably applies to *Menesinus* in India. *Zantes armatipes* has been collected feeding on leaves of *Lecaniodiscus cupanioides* (Sapindaceae) and fogged from *Terminalia ivorensis* (Combretaceae) in West Africa (records in Natural History Museum, London), whereas *Galloisia* appears to be associated with *Actinidia arguta* (Actinidiaceae) (H. Kojima, personal communication).

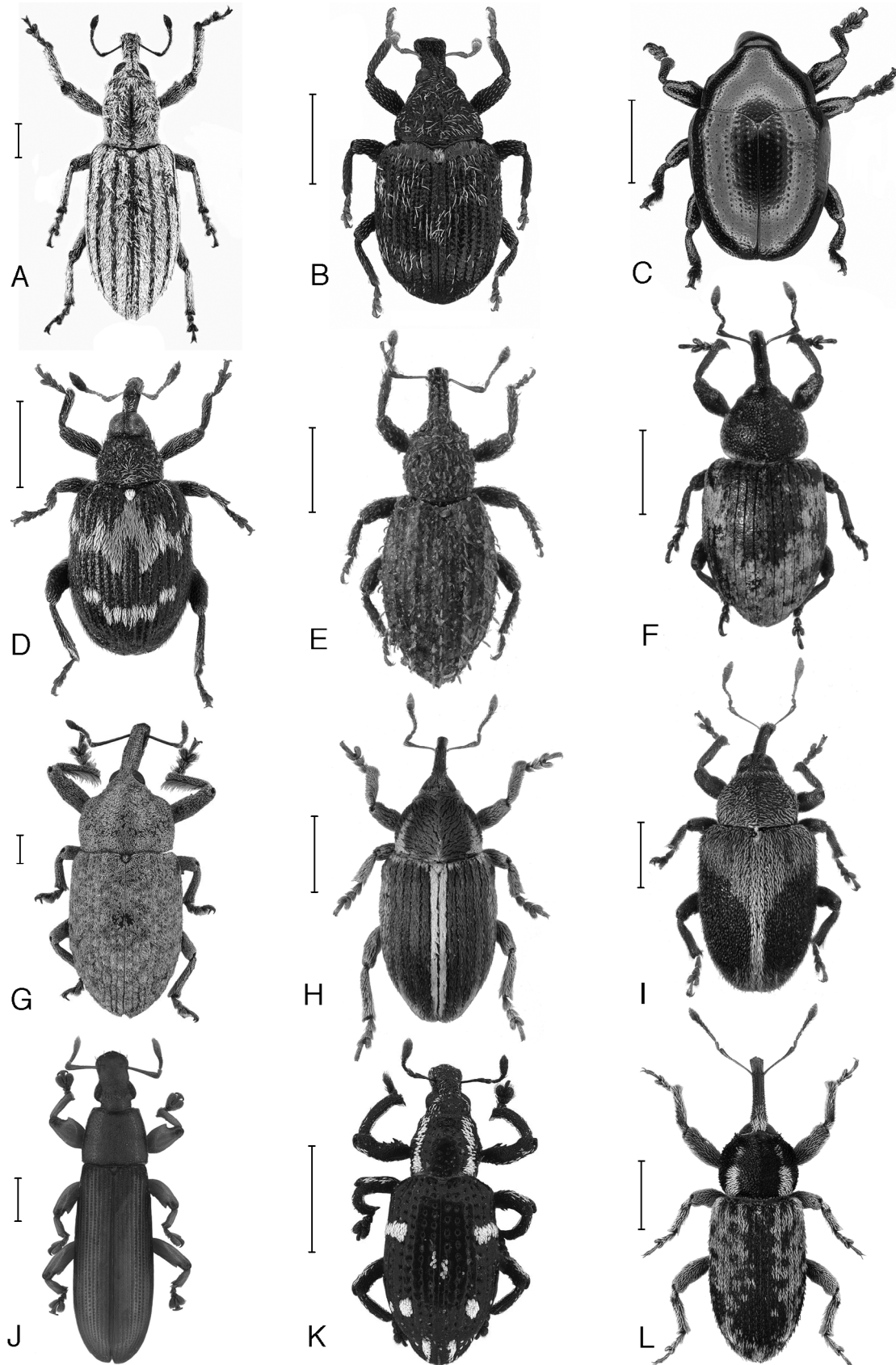
Nerthopini (Fig. 3.7.10.7 J and K). In its current composition (Alonso-Zarazaga & Lyal 1999), this tribe comprises eight African genera and one Indian genus, but there is no evidence that they together and exclusively form a natural (monophyletic) group. *Nerthops* (1 species in South Africa) agrees closely with *Acalloplastus* (ca. 11 species in Africa, also in India) in the structure of the antennae (seventh funicular segment closely fitting to club), the dentate fore femora, the uncinata tibiae with long, ascending talus, the strongly bifid claws, and the exposed pygidium, although *Nerthops* differs in having a shorter, tapering rostrum, large, ventrally contiguous eyes, and adelognathous mouthparts. The two genera appear closely related, but further study of both is required. The relationships of the Madagascar genera *Acalloplastellus* Hustache, *Achynius* Fairmaire, *Helaeniella* Hustache, *Paranerthops* Hustache, and *Pseudodesmidophorus* Hustache to *Acalloplastus* and *Nerthops* are in need of verification, whereas *Microstylus*, and *Menesinus* represent a different group (Microstylini).

All recorded hosts of Nerthopini belong to the family Malvaceae. *Acalloplastus* develops in fruits of *Abutilon*, both in Africa – *A. abutilonis* in Sudan and *A. maculithorax* Hustache in Kenya and Uganda (Marshall 1950), *A. fallax* Boheman of *Abutilon angulatum* in Namibia (S. Nesar & R. Oberprieler,

personal observation), and evidently also *A. malvae* Boheman in South Africa – and in India – an undescribed species on *Abutilon indicum* (Pajni & Nanda 1992). *Nerthops guttatus* Schoenherr (Fig. 3.7.10.7 J) develops in the seed capsules of *Hibiscus aethiopicus* and *H. microcarpus*, and adults have also been found feeding in flowers of cotton (*Gossypium*) (R. Stals, personal communication).

Ochyromerini (Fig. 3.7.10.7 L). Often treated as a subtribe of Tychiini (Clark *et al.* 1977; Oberprieler 1993), this group currently contains approximately 28 genera of flower weevils generally characterized by the robust fore femora carrying a large median anterior tooth, although this does not occur in all the genera. The majority of the genera occurs in Asia and was well studied by H. Kojima and coauthors in a series of papers (Kojima & Morimoto 1995 a–e, 1996 b–c; Kojima 1997; Kojima & Matoba 2002). One genus, *Neochyromera* Heller, has been described from New Guinea (Setliff 2007), but further undescribed taxa occur there as well as in northeastern Australia, some of the latter related to *Hexeria* Pascoe, which was uncertainly placed in Eirrhiniinae by Alonso-Zarazaga & Lyal (1999). Five genera are known from Africa, which were last treated by Oberprieler (1993). Two genera listed in the tribe by Alonso-Zarazaga & Lyal (1999), *Sphinxis* and *Thamnobius*, were transferred to Anoplini (*q.v.*) by Kojima & Morimoto (2000, 2002). A definition of Ochyromerini was provided by Kojima & Morimoto (1995 d); salient features are the uncinata tibiae (uncus often reduced to lost in the hind tibiae), femora generally with large flat tooth flanked on outside by a row of long erect setae, appendiculate tarsal claws, elytro-tergal stridulation structures in both sexes, endophallus with a pair of elongate sclerites, and tegmen without parameres. *Katsurazo* Kojima has spectacularly modified and inflated antennal funicles. However, the exact concept and composition of the group remains unclear.

Biological information for the Ochyromerini was summarized by Oberprieler (1993) for the African fauna and is included for the Oriental genera in the papers by Kojima & Morimoto (1995 a–e, 1996 b, c). The adult weevils are associated with many plant families (e.g., Anacardiaceae, Celastraceae, Clusiaceae, Combretaceae, Ebenaceae, Geraniaceae, Hamamelidaceae, Fabaceae, Lauraceae, Moraceae, Oleaceae), but the habits of the larvae are much less well known. The larvae of the Oriental *Drepanoscelus* Marshall and *Ochyromera* Pascoe and the African *Daeneus* Oberprieler have the spiracles of segment VIII located on elongated dorsal protuberances (Gardner 1938; Cuda *et al.* 2008; Oberprieler 1993, respectively), an apparent adaptation for breathing when developing in the mostly fleshy fruits of *Machilus* (or *Persea*, Lauraceae), *Ligustrum* (Ebenaceae), and *Bequaertiendron* (Sapotaceae), respectively. This modification also occurs in undescribed Australian species and



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Fig. 3.7.10.8 Habitus, adults. A, *Myrmex scutellaris* (Sharp) (Otidocephalini); B, *Piazorhinus scutellaris* (Say) (Piazorhinini); C, *Pyropus cyaneus* (Herbst) (Pyropini); D, *Tachyerges salicis* (Linnaeus) (Rhamphini); E, *Orthochaetes setiger* (Beck) (Styphlini); F, *Smicronyx discoidus* LeConte (Smicronychini); G, *Storeus maximus* Lea (Storeini); H, *Tychius uralensis* Pic (Tychiini); I, *Lignyodes enucleator* (Panzer) (Tychiini); J, *Ulomascus parallelus* Marshall (Ulomascini); K, *Tivicis* sp. (Viticini); L, *Pachytychius simillimus* Desbrochers des Loges (Curculioninae incertae sedis). Scale bars 1 mm.

probably more widely in the tribe. The larvae of the South African *Teinomphasus robustus* Oberprieler (Fig. 3.7.10.7 L) develop in the fleshy fruits of *Hexalobus monopetalus* (Annonaceae), pupating in fallen fruits on the ground (R. Oberprieler, personal observation). *Ochyromera ligustri* Warner, the ligustrum weevil, is a pest as well as a possible natural control agent of Chinese privet (*Ligustrum sinense*, Oleaceae) in North America (Cuda *et al.* 2008), the larva feeding in the seeds, and *Ochyromera miwai* Kôno is considered a pest of *Diospyros kaki* (Oleaceae) in Taiwan, the larvae mining in the leaves (Kojima & Morimoto 1996 b, c). The larvae of *Endaenidius* and *Endaeus* appear to develop in flowers of various magnoliids, with the adults shown or indicated to be the main pollinators of several basal angiosperm families (see Biology and Ecology above).

Otidocephalini (Fig. 3.7.10.8 A). This American tribe, comprising only the five genera *Laemomerus* Kirsch (2 species), *Micromyrmex* Sleeper (10), *Myrmex* Sturm (>100), *Oopterinus* Casey (8), and *Ptinopsis* Champion (2), appears closely related to Erodiscini (Vanin 1986; Marvaldi & Lanteri 2005) and is sometimes combined with the latter group (e.g., Anderson 1993). The species are similarly characterized by a narrow, pedunculate prothorax and often mimic ants. Ivie & Sikes (1995) commented on the taxonomic challenges regarding the large genus *Myrmex* and presented a key to the genera.

Larvae and adults of *Myrmex* are associated with numerous plant families including Araceae, Asteraceae, Fagaceae, Platanaceae, Santalaceae, Sapotaceae, Smilacaceae, and Ulmaceae, with the larvae mining in stems and in several instances associated with galls of cynipid wasps (Burke *et al.* 1975; Anderson 1994). The larvae of *Micromyrmex asclepia* Ivie & Sikes develop in the stems of Asclepiadaceae (Ivie & Sikes 1995).

Piazorhinini (Fig. 3.7.10.8 B). This tribe includes only the American genus *Piazorhinus* (ca. 30 species). Often included in Prionomerini (thus Camarotini, *q.v.*), e.g., by O'Brien & Wibmer (1982), Anderson (1993), and Lyal & King (1996), its fore femora, however, carry only a small tooth. A key to most of the species of *Piazorhinus* was provided by Hustache (1939) and Voss (1940, 1944).

Piazorhinus is associated with *Quercus* (Fagaceae) and *Coccoloba* (Polygonaceae) (Anderson 1993, 2002), the larvae mining in leaves (Marvaldi & Lanteri 2005).

Prionobrachiini. Another American tribe of uncertain status, the Prionobrachiini comprise only two South American genera, *Chelotonyx* Waterhouse (5 species) and *Prionobrachium* Faust (ca. 10). Anderson (1993) included the group in Prionomerini and regarded also *Macrorhoptus* LeConte as belonging in it, sharing the host family (Malvaceae) with *Chelotonyx*. The adults are again characterized by the fore femora carrying a large, serrate tooth.

A key to the species of *Prionobrachium* was given by Hustache (1938).

Prionobrachiine larvae appear to be leaf miners as well, with one species of *Chelotonyx* living on Malvaceae (Anderson 1993).

Pyropini (Fig. 3.7.10.8 C). This very small tribe is characterized by a thin, angled lateral carina separating the pronotum from the pleuron of the prothorax (Marvaldi & Lanteri 2005) and composed of two genera from central and southern America, *Craspedotus* Schoenherr (5 species) and *Pyropus* Schoenherr (3).

Adults of *Craspedotus* and *Pyropus* have been collected on Brassicaceae and Capparaceae, respectively (Silva *et al.* 1968; Anderson 1993; Pakaluk 1996), the larvae of the former genus forming galls on leaves and shoots of Rubiaceae or developing in seeds pods of Lamiaceae and those of the latter tunneling in stems and leaf petioles of *Brassica* (Anderson 1993; Pakaluk 1996).

Rhamphini (Fig. 3.7.10.8 D). This large, almost cosmopolitan tribe contains about 20 genera and is presently divided into three subtribes, Ixalmina, Rhamphina, and Tachygonina. All the Holarctic genera, among them *Orchestes* Illiger (ca. 80 species), *Pseudorchestes* Bedel (ca. 35), *Rhamphus* (ca. 15), *Rhynchaenus* (ca. 10), and *Tachyerges* Schoenherr (ca. 12), are included in the first subtribe. In the Afrotropical region, in addition to these, there are two monobasic, apparently endemic genera, *Macrorhynchaenus* Hustache from Madagascar and *Rhamphonyx* Voss from Sudan. *Orchestes* and *Rhamphus* also occur in Australia – the species of the former placed in *Rhynchaenus* by Zimmerman (1992), but their characters agreeing with those of *Orchestes* as differentiated by Kojima & Morimoto (1996 a) – and several further unidentified or undescribed genera are known from the region (Zimmerman 1992). The tribe is not represented in New Zealand, however; the sole genus listed there by Leschen *et al.* (2003), *Geochus*, displays features of phrynixine Molytinae (*q.v.*) rather than of Rhamphini. Its larva mines in dead leaves of *Weinmannia* (Cunoniaceae) and is similarly adapted to this lifestyle (May 1992, 1993), but leaf mining has evolved numerous times in Curculionidae and does not represent direct evidence of relationship. The subtribe Ixalmina comprises only one genus, the Oriental *Ixalma* (ca. 15 species), whereas the three genera of Tachygonina, *Laemorches* Champion (1), *Tachygonidius* Champion (4), and *Tachygonus* Guérin-Méneville (ca. 40), occur only in the New World. Morimoto (1984) studied the phylogenetic relationships among the Japanese genera of Rhamphini and Kojima & Morimoto (1996 a) those of the Oriental fauna, establishing the monophyly of the tribe on the basis of two synapomorphies (maxillary palps one- to two-segmented and hind femora with an apodeme, modified for jumping). The sister group of the tribe is, however, not established. Anderson (1993) sketched

the evolution of the North American genera, and Hespeneide (1992) reviewed the North American species of *Tachygonus*.

Larvae of Rhamphini generally mine in young leaves of broad-leaved trees belonging to many families, e.g., Anacardiaceae, Betulaceae, Caprifoliaceae, Fagaceae, Myricaceae, Rosaceae, Salicaceae, and Ulmaceae, feeding on the parenchyma in winding tunnels and often causing serious damage by defoliation, but those of *Pseudorchestes* live on herbaceous Asteraceae (Hoffmann 1958; Scherf 1964; Anderson 1989; Hespeneide 1992; Kojima & Morimoto 1996 a; Lee & Morimoto 1996). Pupation generally occurs in the mines, but some species drop to the ground in pieces of leaf, in which they pupate. The larvae of *Orchestes hustachei* Klima develop in aphid galls, feeding on the aphids as the primary source of food (Tomisawa & Akimoto 2004). In Australia, *Orchestes australiae* Lea has been reared from seedpods of *Brachychiton populneus* (Malvaceae) and an undescribed *Orchestes* species from leaf mines on *Argyrodendron trifoliolatum* (Malvaceae), whereas *Rhamphus* lives on *Acacia* (Fabaceae), where the larvae presumably mine in leaves (although some adults have been reared from galls). A number of *Rhamphus* species also occur on *Acacia* in southern Africa, which is remarkable because the African and Australian acacias are not closely related and do not normally share any weevil taxa. The larvae of *Ixalma* feed in blotch-like mines along the edge of leaves of *Euptelea* (Eupteleaceae) and *Kadsura japonica* (Schisandraceae) in Japan, hibernating and, in spring, pupating in the mines (Morimoto 1984; Lee & Morimoto 1996). In North America, larvae of *Tachygonus* mine in leaves of *Quercus* (Fagaceae), and adults occur on Fabaceae (*Coursetia*, *Robinia*), Rhamnaceae (*Berchemia*), and Ulmaceae (*Ulmus*) (Hespeneide 1992), whereas Melo da Silva *et al.* (2007) recorded a *Tachygonus* species mining in leaves of *Erythroxylum* (Erythroxylaceae) in Brazil. Also in Brazil, larvae of *Tachygonidius* mine in leaves of Ochnaceae (Vanin & Mermudes 2007).

Smicronychini (Fig. 3.7.10.8 F). This tribe of five or six genera is clearly differentiated from other Curculioninae by a basally constricted rostrum and connate claws. Most species belong to the widespread, mainly Holarctic genus *Smicronyx* (ca. 140 species), whereas the smaller *Sharpia* Tournier (ca. 15) occurs in the Palaearctic region, *Promecotarsus* Casey (4) in North America, *Afrosmicronyx* Hustache (5), and *Topelatus* Hustache (6) in Africa, and *Hedychrous* Marshall (1) in India. Anderson's (1962) monograph of North American *Smicronyx* is the latest comprehensive treatment of the group, whereas the taxonomy of the numerous Palaearctic species of this genus as well as that of the closely related *Sharpia* is still confused. *Smicronyx* is generally divided into five subgenera, three restricted to North America and one to western Europe, and *Afrosmicronyx* is sometimes also treated as a

subgenus of *Smicronyx* (Anderson & Cox 1997). The nominate subgenus *Smicronyx* extends its distribution into northern Australia, with two species described but several more present in collections, although it is unclear whether any of them is truly native there.

The larvae of *Smicronyx* develop in seeds or stems of herbaceous plants in numerous families, including Asteraceae, Convolvulaceae (*Cuscuta*), Fabaceae, Malvaceae, and Scrophulariaceae. In some cases, they incite galls in the stems or seeds of their hosts and pupation occurs in infested plant tissues or in the soil (Hoffmann 1958; Anderson 1962; Scherf 1964; Anderson & Cox 1997; Anderson *et al.* 2006). Several species have been used as biological control agents of weeds, e.g., the seed-feeding Mexican *S. lutulentus* Dietz of *Parthenium hysterophorus* (Asteraceae) in Australia (Dhileepan & Strathie 2009) and the galling *S. (Smicronyx) guineanus* Voss, *S. (Afrosmicronyx) dorsomaculatus* Cox, and *S. (Afrosmicronyx) umbrinus* Hustache of parasitic witchweeds, *Striga hermonthica* and *Alectra vogelii* (Scrophulariaceae), in Africa (Anderson & Cox 1997), all with only moderate success. Adults of *Smicronyx squalidus* Casey appear to be the only weevil recorded to feed on nectar, from extra-floral nectaries of *Desmanthus* (Fabaceae) (Davis 2007).

Sphaeriopoeini. This monobasic tribe was recently proposed for a single Chilean genus and species, *Sphaeriopoeus faber* Kuschel, with a most unusual biology (Kuschel 2003). It is a small (2–3 mm long), broad, compact species with appressed pubescence and erect sensory dorsal hairs; a short, stout rostrum with large, broad, tooth-like ventral process locking behind the fore coxae; coarsely faceted eyes; seven-segmented funicles; three-segmented maxillary and labial palps, the latter contiguous; anteriorly toothed fore coxae; toothed femora; uncinata tibiae, the fore and middle ones in female with long praemucro; thin, basally connate tarsal claws; ten-striate elytra without stridulatory files, infrolateral flange extending to middle of length; rudimentary proventriculus; ring-like rectal valve; sternite IX of male asymmetrical and tegmen with complete parameres; sternite VIII of female well sclerotized but gonocoxites weakly so, without styli. Kuschel (2003) placed the tribe Sphaeriopoeini near Molytinae in his larger concept of a subfamily Curculioninae (Kuschel 1995), but Elgueta & Marvaldi (2006) included it in Curculioninae in the narrower sense as adopted here.

Sphaeriopoeus faber lives in the canopy of the deciduous *Nothofagus obliqua* (Nothofagaceae), where the female rolls and folds whole new leaves into tight balls, without incising the leaf lamina as attelabids do. A single egg is laid into each roll, apparently before the rolling commences, and on completion of the rolling, the leaf ball is cut off and falls to the ground, where the larva consumes the

contents. This leaf-rolling method is apparently unique in weevils (Kuschel 2003).

Storeini (Fig. 3.7.10.8 G). The concept of this tribe is unclear and contentious. In a narrow sense, it includes those genera with a pectoral canal in front of the fore coxae and the walls of the canal being incised to form a narrow cleft to large “window” or “peep-hole” (Fig. 3.7.10.2), which may be lined with dense setae and in some species come to lie over the eyes when the head and rostrum are folded down and through which the weevil may then be able to see (Lea 1927). On this rather unique structure, Storeini *sensu stricto* include the large but composite genera *Storeus* Schoenherr (ca. 50 species) and *Emplesis* Pascoe (ca. 100) and also *Leucomelacis* Lea (2), *Microberosiris* Lea (2), *Placorrhinus* Marshall (1), and *Pseudostoreus* Lea (1) in Australia as well as *Aporotaxus* Perroud (1) and *Griphosternus* Heller (1) in New Caledonia and *Diomia* Pascoe (1) in New Guinea (the last misplaced in Molytinae: Ithyporini by Alonso-Zarazaga & Lyal 1999). Zimmerman (1992, 1994) used an expanded concept of Storeini by including also the Australian genera *Arthriticosoma* Lea, *Cycloporopterus* Lea, *Euthebus* Pascoe, *Hybomorphus* Saunders & Jekel, *Hybophorus* Waterhouse, *Lybaeba* Pascoe, *Melanterius* Erichson, *Moechius* Pascoe, *Neomelanterius* Lea, *Rhinidotasia* Lea, and *Teutheria* Pascoe, which do not have the “peep-hole” type of pectoral canal and also differ in several other features from *Storeus* and allies, most importantly in possessing uncinuate tibiae and sclerolepidia and appear to be Molytinae of a cleogonine affinity (except *Euthebus*, *Hybomorphus*, and *Rhinidotasia*). Kuschel (1990 a) tacitly used yet another broader concept of Storeini, loosely characterized by the possession of divaricate claws and, in the male, of elytral stridulatory files and a broadly angulate, asymmetrical sternite IX, and he included in it genera such as *Palontus* from New Caledonia, *Aneuma* Pascoe from New Zealand and *Elleschodes* and *Rhinidotasia* from Australia, which either have a pectoral canal without an incision in its walls or no canal at all. This concept includes another 14 genera of New Zealand “flower weevils” (Leschen *et al.* 2003) as well as approximately 47 Australian genera classified in Tychiini by Zimmerman (1992) but later placed without tribal assignment in Curculioninae (Zimmerman 1994; Alonso-Zarazaga & Lyal 1999). Of the latter, *Imathia* was transferred to Storeini by Kojima & Morimoto (1998). These Australian genera are a diverse group, however, including besides many genera with divaricate claws also others with simple, divergent claws (such as *Abethas* Zimmerman, *Lexithia* Pascoe, *Olbiodoros* Blackburn, *Paryzeta* Pascoe, *Plaesiorhinus* Blackburn) or with strongly toothed to bifid ones (*Agestra* Pascoe, “*Ellescus*”, *Hibberticola* Lea) as well as several without onychia (*Anarciarthrum* Blackburn, *Cenchrena* Pascoe, *Micraonychus* Lea, *Misophrice* Pascoe, *Thechia* Pascoe). *Cenchrena*, *Ethadomorpha* Blackburn,

Notionomus Erichson, and *Symbothynus* Blackburn have strongly imbricate to agglutinated scales and appear to all live on sedges in semi-aquatic habitats, suggesting that they may not be closely related to the other genera. All of these Australian genera are in need of study to assess both their proper generic delineations and their taxonomic affinities. Both in the narrow and the wide sense, Storeini appears to be a purely Australo-Pacific group, in the narrow one extending from Australia, New Caledonia, and Fiji north to the Philippines, and Taiwan and in the wider sense also including New Zealand and probably other Pacific islands as far north as the Ryukyus. The four African genera listed in Storeini by Alonso-Zarazaga & Lyal (1999) most probably do not belong in this tribe; *Anchonocranus* Marshall appears related to the *Phacellopterus* Schoenherr group of Anthonomini (Oberprieler 1993) and *Pansmicrus* to Anoplini (*q.v.*), whereas the identities and affinities of *Australafer* Alonso-Zarazaga & Lyal and *Merocarater* Hustache require investigation. Also, the placement of the only two Palearctic genera in Storeini, *Aubeonymus* Jacquelin du Val and *Pachytychius* (previously in Eriirrhinae), is highly doubtful (González 1968; Caldara 1978), and they are here treated as *incertae sedis*.

Biological information on Storeini is mostly limited to host-plant records, although not all of these necessarily reflect true (larval) hosts. Among Storeini *sensu stricto*, *Aporotaxus* develops in figs (Kuschel 1990 a) and also some *Storeus* species in Australia occur on *Ficus* (Moraceae), whereas *Storeus albosignatus* (Blackburn) lives on various *Acacia* species (Fabaceae) both in Australia and in New Zealand, where it is adventive, and *Storeus baedontus* Lea has been collected on *Dodonea cuneata* (Sapindaceae) (Rheinheimer 1989). It is, however, uncertain whether these species are congeneric. *Emplesis* Pascoe is generally found on *Eucalyptus*, and *Emplesis bifoveata* Lea – misidentified as *Storeus majusculus* (Blackburn) by Rheinheimer (1989) and redescribed as *Storeus acmenae* by Rheinheimer (1996) – occurs on *Syzygium smithii* (Myrtaceae) also in New Zealand where it is adventive. *Leucomelacis quadrinotatus* Lea has been reared from *Syzygium* fruits and *Placorrhinus placitus* Lea collected on *Doryphora* (Monimiaceae).

Biological records for several New Zealand genera of Storeini *sensu lato* (*Alloprocas* Broun, *Aneuma*, *Hypotagaea* Pascoe, *Neomycta* Pascoe, *Oropterus*, *Peristoreus* Kirsch, *Phorostichus* Broun, *Praolepra* Broun, *Simachus* Broun) are given by May (1987, 1993) and Kuschel (1990 b); the larvae often are leaf miners but also develop in stems, flower buds, young fruits, and seeds of families spanning conifers (Podocarpaceae) to monocotyledons (Asteliaceae) and various dicotyledons (Asteraceae, Ericaceae, Fabaceae, Nothofagaceae, Malvaceae, Myrtaceae, Onagraceae, Pittosporaceae, Polygonaceae, Rubiaceae, Scrophulariaceae). Of the Australian genera, *Cydmaea* Pascoe, *Dicomada* Pascoe, and *Erytenna* Pascoe breed in stems

or fruits of *Hakea* and *Grevillea* (Proteaceae), the larvae feeding on the seeds to the extent that several species have been used as biological control agents against the invasive *Hakea sericea* in South Africa (Gordon 1999; Kluge & Gordon 2004). The clawless *Micraonychus*, *Misophrice*, and *Thechia* live on *Allocasuarina* (Casuarinaceae) and *Misophricoides* Rheinheimer on *Callitris* (Cupressaceae), whereas *Agestra*, and *Plaestorhinus* develop in seedpods of *Bossiaea* and *Daviesia* (Fabaceae) and *Hibberticola* in galls on *Hibbertia* (Dilleniaceae). Some *Elleschodes* species, such as *E. hamiltoni* Blackburn, pollinate *Eupomatia* (Eupomatiaceae) (Armstrong & Irvine 1990), whereas *E. compactus* Lea and some other species live on *Pultanea* (Fabaceae) but are not evidently congeneric with the former. *Eniopea* Pascoe, *Epacticus* Blackburn, *Eristinus* Lea, *Myllorhinus* Boisduval, and *Paryzeta* are associated with Myrtaceae (*Eucalyptus*, *Leptospermum*, *Melaleuca*), *Myllorhinus* boring in shoots of *Eucalyptus* (Jones & Potts 2000). *Symbothynus* lives on *Gahnia* sedges (Cyperaceae), and *Cenchrena*, *Ethadomorpha*, and *Notionomus* occur in similar habitats and are likely to have similar hosts.

Styphlini (Fig. 3.7.10.8.E). This Palaearctic tribe, generally included in Eriurhininae until 15 years ago, is mainly characterized by having a stout rostrum, the scrobes directed toward the anterior margin of the eyes, the antennae inserted near the apex of the rostrum, small eyes, the humeral area of the elytra constricted, all or the odd-numbered interstriae usually distinctly convex, and the legs distinctly stout with short tarsi. It currently comprises ten extant genera: *Orthochaetes* Germar (ca. 15 species), *Paraphilernus* Desbrochers (1), *Paroryx* Reitter (1), *Philernus* Schoenherr (1), *Pseudostyphlus* Tournier (5), *Salsolia* Bajtenov (1), *Styphlidius* Penecke (1), *Styphlus* Schoenherr (20), *Trachystyphlus* Alonso-Zarazaga & Lyal (3), and *Turanostyphlus* Davidian & Savitsky (1). Of the two other genera listed in the tribe by Alonso-Zarazaga & Lyal (1999), *Geranorhinus* was recently transferred to the closely related tribe Itini (*q.v.*) by Meregalli & Borovec (2011), whereas the Madagascan *Madecastyphlus* Richard, as the only African genus, is most unlikely to belong in it. Several genera were partially taxonomically revised (González 1967; Osella 1981; Osella & Zuppa 1994; Davidian & Savitsky 2000), but none of these papers treated the genera phylogenetically. Most species have a limited distribution, and some of them [*Orthochaetes alpicola* Daniel, *Styphlidius corcyreus* Reitter, and *Trachystyphlus alpinus* (Penecke)] were divided in one or more subspecies (Osella 1981; Osella & Zuppa 1994).

The biology of Styphlini is poorly known. Atypically for Curculioninae, the adults are usually found under stones or by sifting mosses, dead leaves, and marcescent roots in bare patches or at the margins of woods both in plains and at high altitudes (some *Orthochaetes*, *Trachystyphlus*) or in sandy and dry soil (some *Styphlus*). *Orthochaetes* lives on a wide range of plants, including

unrelated taxa such as *Allium* (Amaryllidaceae), *Aquilegia* and *Clematis* (Ranunculaceae), *Cyclamen* (Primulaceae), *Myosotis* (Boraginaceae), *Plantago* (Plantaginaceae), and *Viola* (Violaceae), but appears to prefer Asteraceae, on which the larvae mine in leaves before pupating in the soil (Scherf 1964; Dieckmann 1986; Osella & Zuppa 1994). *Styphlus* and *Pseudostyphlus* also live on Asteraceae (the genera *Barkhausia*, *Hedypnois*, and *Matricaria*), where the larvae develop in flower heads, seeds, or roots (Hoffmann 1958; Scherf 1964; Dieckmann 1986; Bland & Nelson 1997; Ostoja-Starzewski 2002; Knutelski 2005). *Trachystyphlus* appears to live on Caryophyllaceae (*Cerastium*, *Heliospermum*) (Franz 1974). Interestingly and seemingly unique in Curculioninae, some species, e.g., *Orthochaetes setiger* (Beck) and *O. insignis* (Aubé), are parthenogenetic at least in part of their distribution range (González 1967; Osella & Zuppa 1994).

Thecesternini. Both the composition and the classification of this small tribe have been confused in the literature. In the catalogue of Alonso-Zarazaga & Lyal (1999), it was placed in Entiminae and included four genera; however, the Palaearctic genus *Herpes* Bedel belongs in Hyperini (Alonso-Zarazaga & Lyal 2002) and the New Caledonian *Cyphomastax* Marshall in Storeini (G. Kuschel, personal communication). Thus, Thecesternini comprise only the two New World genera *Thecesternus* Say (ca. 6 species) and *Arodenius* Heller (2). They are characterized by having the prosternum anteriorly deeply and sharply excavate (the canal closed off before the fore coxae), the prementum deeply excavate, the tibiae with two apical spines (in *Thecesternus* representing a mucro and an apparently fused spur, in *Arodenius* a praemucro and uncus), the elytra fused in *Thecesternus* but separate, with unequal flanges, in *Arodenius*, the aedeagus dorsally solid at its base and with loosely attached temones, the ovipositor with the distal gonocoxites short, cylindrical, with a large apical stylus, the tergite above it with the apex produced into two flat, upcurved processes (for pushing into soil), and the proventriculus with eight long, internal processes ending in a flat scoop with serrated margins (Kissinger 1963), similar but not identical to those of Gonipterini. Marvaldi (1997) related *Thecesternus* to various tribes of Entiminae and Cyclominae because the mandibular thecae of its pupa also carry setae, but it does not belong in Entiminae due to its phanerognathous mouthparts and absence of deciduous mandibular cusps in the adult and conical antenna in the larva, and it also does not fit into the current concept of Cyclominae (see Oberprieler 2010) due to the epicranial position of setae *des3* in the larva (Marvaldi 1997; Oberprieler 2010). For the moment, it is therefore here dealt with in Curculioninae.

The larva of the Mexican *Thecesternus hirsutus* Pierce feeds semi-ectophytically in gall-like growths on the roots of *Parthenium* (Asteraceae)

(McClay & Anderson 1985) and the species has been considered for biological control of *P. hysterothorus* in Australia (McFadyen 1992), where this plant is a severe weed of crops and pastures, but it was not released (Dhileepan & Strathie 2009).

Tychiini (Fig. 3.7.10.8 H and I). This concept of this tribe is complex and contentious. In its traditional status as a subfamily, Clark *et al.* (1977) divided it into four tribes, Ellescini, Lignyodini, Ochyromerini (as Endaeini), and Tychiini, and defined it by two apparent synapomorphies, laterally angled ventrites and mesadly directed pronotal scales or setae. Morimoto (1962 b) and Oberprieler (1993) pointed out, however, that both these characters occur in several other curculionid groups and cannot be used to identify a group as composed by Clark *et al.* (1977) as monophyletic. In a series of subsequent papers on the Asian ochyromerines, H. Kojima and coauthors (Kojima & Morimoto 1995 a–e, 1996 b–c; Kojima 1997; Kojima & Matoba 2002) treated these as a distinct tribe, and Ochyromerini and Ellescini are therefore also here regarded as tribes separate from Tychiini, the latter comprising Demimaeina, Lignyodina, and Tychiina as subtribes (as in Alonso-Zarazaga & Lyal 1999). Oberprieler (1993) discussed the difficulties of properly delineating these groups as well as the tribe Tychiini, and a larger phylogenetic study of all curculionine genera with angled ventrites is required to elucidate natural groups in this complex.

Q: "or" was changed to "of". Correct?

All three subtribes of Tychiini comprise only two genera. In Demimaeina, *Demimaea* Pascoe (ca. 25 species) is largely Oriental but also occurs in Africa (Voss 1962; Oberprieler 1993), whereas the monobasic *Pseudocionus* Marshall is only known from South Africa. The Lignyodina, comprising the largely Holarctic genus *Lignyodes* Dejean (ca. 25 species) and the American *Plocetes* LeConte (ca. 35), were studied by Clark (1980, 1982), whose phylogenetic analyses divided the former genus into three groups (subgenera). Kojima & Morimoto (2003) recently recorded *Lignyodes* also from Japan. Both genera of Tychiina, *Sibinia* Germar and *Tychius* Germar, are very large (ca. 240 species each) and widespread. About 50 species of *Sibinia* occur in the Palaearctic region (Caldara 1979, 1984 b), 130 in the New World, mainly South America (Clark 1978), and 60 in subsaharan Africa, mainly South Africa (Caldara 1989 b, 1993). The genus is tentatively divided into three subgenera, *Dichotychius* Bedel, *Microtychius* Casey, and *Sibinia sensu stricto*. The almost entirely American *Microtychius*, distinguishable by the cup-shaped, sclerotized base of its spermathecal gland and its host-plants (Fabaceae: Mimosoideae), was subjected to a preliminary phylogenetic analysis by Clark (1978). No clear apomorphies have been identified for the Palaearctic *Dichotychius* so far (Caldara 1979), but the taxon may be characterized by its different host plants (Plumbaginaceae: Statioideae), whereas species of *Sibinia sensu stricto* live on several sub-

families of Caryophyllaceae. The Afrotropical species, divided into eight groups of which seven are considered endemic to the region (Caldara 1989 b, 1993), appear to be closely related to both *Sibinia sensu stricto* and *Dichotychius* but seem to live on different plant families, especially Aizoaceae, which is closely related to Caryophyllaceae, and their relationships are still unclear (Caldara *et al.* 2008). In *Tychius*, most species (180) occurs in the Palaearctic region, with the remainder in the Nearctic (10) and Afrotropical (ca. 45, mainly in South Africa) regions and on the Indian subcontinent (3). The Palaearctic species are arranged in two subgenera, *Apeltarius* Desbrochers and *Tychius sensu stricto*, the latter divided into 22 species groups (Caldara 1990). The North American species possibly belong to four of the Palaearctic groups (Clark 1971), whereas the southern African species fall into six groups, four apparently endemic but the other two including also several Palaearctic species (Caldara 1989 a, 1996). However, the four endemic groups also appear closely related to some Palaearctic ones, from which they can be distinguished only by a few subtle characters (Caldara *et al.* 2008). In India, three groups are represented, only one of them endemic, the *T. eremita* Caldara group (Caldara 1989 a, c). Phylogenetic analysis of all the groups of *Tychius* was so far unsuccessful due to the extreme uniformity of the species and the absence of clear synapomorphies. No Tychiini appear to occur in the Australo-Pacific region, the various genera listed in this tribe by Zimmerman (1994) belonging in *Storeini sensu lato* (*q.v.*) and the New-Guinean *Sibiniella* Voss probably in that group as well. A species of *Sibinia* (*S. fastigiata* Clark) has been introduced for the biological control of the weed *Mimosa pigra* (Fabaceae) in northern Australia but evidently failed to establish (Ostermeyer & Grace 2007).

Host associations are relatively narrow in Tychiini. The larva of *Demimaea* tunnels in green stems of *Ficus* (Moraceae) (Gardner 1934), but no biological information is available for *Pseudocionus*. *Lignyodes* lives on Oleaceae (Clark 1980) and *Plocetes* on Rubiaceae (Clark 1982), the larvae feeding in the seeds and pupating in the soil. The Palaearctic species of *Sibinia* develop in seeds of mainly Caryophyllaceae and Plumbaginaceae (Hoffmann 1958; Scherf 1964; Caldara 1979, 1984), and the Afrotropical ones are at least partly associated with the related family Aizoaceae (Caldara 1989 b), whereas the American species (subgenus *Microtychius*) breed in seeds of Fabaceae [Clark 1978; see also Anderson (1993) for a discussion of host-mediated speciation in *Sibinia*]. *Tychius* has an even narrower host range, all known hosts belonging to Fabaceae (Scherf 1964; Clark 1971, 1977, 1978; Clark & Burke 1977; Clark *et al.* 1978; Caldara 1989 a, 1990; Anderson 2002; Oberprieler *et al.* 2007) and certain lineages appearing to have phylogenetically highly conservative host associations. Most species are seed predators, but a few form galls on leaves, flowers, or pods (Scherf 1964; Clark & Burke 1977; Korotyaev

et al. 2005). When mature, seed-feeding larvae typically leave the pods and enter the soil to pupate (Clark & Burke 1977).

Ulomascini (Fig. 3.7.10.8 J). This small tribe comprises three genera of most bizarrely shaped weevils, *Buttikoferia* Roelofs (1 species), *Cratopechus* Marshall (3), and *Ulomascus* Fairmaire (9). They are only known to occur in central Africa, from Sierra Leone in the west to Kenya in the east. The weevils are flat and long, with a broad, spatulate rostrum; flat, calliper-like, non-overlapping mandibles; seven- or six-segmented funicles and often greatly elongate antennal clubs; large coxae and trochanters; strongly inflated, flattened, dentate femora often densely adorned with long hairs; short stout tibiae folding against or under the flat, broad femoral tooth; flat tarsi with large, deeply lobed third tarsomeres and strong, widely divaricate but simple claws; elytra with eight or nine punctate striae. In *Ulomascus insolitus* Hoffmann, the onychium of the hind tarsi is in the female extremely elongate (as long as a tibia) and carries a single, equally long claw folded back onto the onychium, a most extraordinary feature of unclear function. The females of *Ulomascus* and *Cratopechus* also have a large, tapering tergal pouch situated under a very large, tergite-like apodeme that is extended by a large membrane with a bundle of tendon-like fibers between apodeme and pouch, and the pouch itself ends in similar hardened fibers from which powerful muscles extend to the extraordinary long genitalia, which, when unfolded, are nearly twice as long as the body of the weevil (Kuschel 1987). The taxonomic affinities of the group are unclear.

Nothing specific is known about the biology of Ulomascini, except that the adults are apparently nocturnal (usually collected at lights) and the Kenyan *Cratopechus arundinarum* Marshall and *C. gedyei* Marshall have been found on reeds. Because of the long, golden hairs on the femora and sides of the prothorax and elytra of some species of *Ulomascus*, a myrmecophilous or termitophilous habit has been surmised for the group (Marshall 1928; Ghesquière 1932), but the flat, long, strong body shape and the occurrence on reeds of *Cratopechus* suggest that all genera probably live on large grasses or perhaps palms, where they may hide or push into tight spaces between leaves and stems. The very long and complex ovipositor also indicates that the eggs may be laid into deep, narrow spaces, perhaps covered with a secretion from the tergal pouch.

Viticiini (Fig. 3.7.10.8 K). This group is based on *Viticis* Lea, small weevils lacking onychia and distributed throughout the Pacific islands. The genus was associated with the entimine tribe Ottistirini by Lea (1930) and subsequent authors, until Morimoto (1983) recognized that its mouthparts are phanerothous and proposed a separate tribe for it and a closely related genus, *Tivicis* Morimoto, which has short onychia and basally connate but apically divergent claws. Kojima &

Morimoto (2007) added another genus to the tribe, *Aviticis*, which retains very small onychia but without claws. Oberprieler (2010) recently also included the Samoan *Samoacis* Zimmerman and the Australian *Euphlocis* Lea, *Peliocis* Lea, and *Platynotocis* Lea as well as Zimmerman's (1992, Plate 561) undescribed genus *Austrocis* (a *nomen nudum*) in the tribe, based in part on a study of the group commenced by E. C. Zimmerman before his death in 2004. In this composition, the Viticiini comprise two groups, one including *Viticis*, *Tivicis*, *Aviticis*, and *Euphlocis*, characterized by having six-segmented funicles, separated fore coxae, and dentate femora, the other including the closely related *Austrocis*, *Platynotocis*, and *Samoacis* as well as *Peliocis*, which have seven-segmented funicles, contiguous fore coxae, and unarmed femora. A number of other similar but undescribed genera occur in Australia and New Guinea, and the precise composition and delineation of the tribe require further study. Morimoto's (1983) definition of Viticiini therefore only applies to the former group. *Viticis* (6 species), redescribed by Kuschel (2008), occurs from Guam south to New Caledonia and from Amboina east to the Marquesas Islands. *Tivicis* (2) is presently known only from the Ryukyu Islands of Japan, but *Euphlocis maculatus* Lea from New Britain evidently also belongs to it as well as at least one undescribed species from southern New Guinea and northern Australia. *Aviticis* (1) is only known from Taiwan and *Euphlocis dentipes* Lea from northern Queensland. *Austrocis*, *Platynotocis*, and *Peliocis* (1 species each) are recorded from northeastern Australia, but a large species of or near *Peliocis* occurs in southwestern Western Australia.

The available biological information of Viticiini was summarized by Oberprieler (2010). *Viticis* appears associated with *Ficus* (Moraceae), whereas *Austrocis bicaudatus* Zimmerman (undescribed, a *nomen nudum*) mines in leaves of *Elaeocarpus* (Elaeocarpaceae) and *Platynotocis bicaudatus* Zimmerman (the species also undescribed, a *nomen nudum*) in leaves of *Polyosma cunninghamii* (Escalloniaceae) and *Peliocis* lives on *Allocasuarina* (Casuarinaceae). Other than probably *Peliocis*, the larvae of all genera may be leaf miners.

Genera of Uncertain Placement (*Incertae Sedis*) (Fig. 3.7.10.8 L). A number of genera cannot be currently placed in any of the above tribes, although the list is not as long as that given by Alonso-Zarazaga & Lyal (1999). The largest group of such genera of uncertain placement occurs in Madagascar, owing both to their generally inadequate descriptions and to the fact that the Madagascan weevil fauna has not been studied in recent times. Although these genera are mostly placed into tribes in the catalogue of Alonso-Zarazaga & Lyal (1999) and tentatively left there in this work, their placements need scrutiny in nearly all cases. Some genera in continental Africa are also currently unplaced, e.g., the closely related

South African genera *Hypsomus* Schoenherr and *Pachytrichus* Schoenherr (Alonso-Zarazaga & Lyal 2002; Oberprieler 2010), the former apparently associated with grasses (one species introduced in Western Australia, often found there in wheat fields) and the latter with *Moraea* (Iridaceae). Also of unclear affinity are the South African genera *Sidomenia*, and *Stenotypus* Marshall, both described in Erihinae but transferred to Curculioninae *incertae sedis* by Alonso-Zarazaga & Lyal (2002), the former an apparent inquiline in cecidomyid galls on *Aspalathus* (Fabaceae) (S. Naser, personal observation) and the latter breeding in stems of *Arctotheca* and *Senecio* (Asteraceae) (R. Oberprieler, personal observation). The classificatory position of the Indian *Teluropus ballardi* Marshall, reported from leaves of jackfruit (*Artocarpus*, Moraceae) (Marshall 1917; Jha & Sen-Sarma 2008) but intercepted in the United Kingdom in association with fruits of *Syzygium jambos* (Lyal 1996), is also unclear; it certainly does not belong in Molytinae: Metatygini. In the New World, the important genera of uncertain affinity are *Macrorhoptus*, which appears to be oligophagous on Malvaceae (Burke 1973; Anderson 1993) and was associated with the prionobrachiine genus *Chelotonyx* by Anderson (1993), and a group of Chilean genera mostly associated with *Nothofagus* (Nothofagaceae) – *Epaetius*, *Epembates*, *Nothofaginoides*, *Nothofaginus*, and *Wittmerius*, all described by Kuschel (1952) – as well as *Malaiserhinus* Kuschel, associated with *Kageneckia* (Rosaceae). Regarded as a “special group of Curculioninae” by Kuschel (1987), these genera may represent a distinct tribe. The classification of the South American fauna of Curculioninae generally needs attention, as nearly all of its typical tribes are poorly delineated. In the Palaearctic region, the main genera in need of placement are *Aubeonymus* and *Pachytychius* (Fig. 3.7.10.8 L). *Aubeonymus mariaefranciscacae* Roudier is considered a pest of *Beta vulgaris* (Amaranthaceae) in Spain, adults and larvae feeding on beetroot and sugar beet (Marco *et al.* 1998), while *Pachytychius* lives on Fabaceae (such as *Astragalus* and *Sarothamnus*) and Poaceae (Caldara 1978), with *P. avulsus* Faust able to cause serious damage to wheat in the eastern Mediterranean region (Martelli *et al.* 1960).

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