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10.33. Coccinellidae Latreille, 1802

Adam Ślipiński and Wioletta Tomaszewska

Distribution. The family Coccinellidae, ladybird beetles or lady beetles, is the largest family in Cucujoidea and numbers about 6000 species and 360 genera classified in two subfamilies and 30 tribes (Ślipiński 2007). The family is abundant in tropics and subtropics with fewer species represented in temperate regions, especially in cool climate zones of the southern part of Chile (Tierra del Fuego) and northern Alaska. Only 42 species occur naturally in Great Britain (Majerus 1994), 83 species in the Russian Far East (Kuznetsov 1997), 27 species in the Arctic Zone of North America (Belicek 1976) and 93 species in Chile (Gonzales 2008), as compared to 481 species recorded from North America (Gordon 1985; Vandenberg 2002), 480 species from India (Poorani 2002) and approximately 500 species from Australia (Ślipiński 2007). Korschefsky (1931, 1932) published the only complete catalogue of world

Coccinellidae and summarized the distributions of all the then-known species of the family. Palaearctic species and these of the northern part of the Oriental Region were recently catalogued by Kovář (2007) and the world Epilachninae by Jadwiszczak & Węgrzynowicz (2003). Larger monographic or revisionary studies of Coccinellidae include: Bielawski (1963) [Epilachnini of New Guinea and Pacific], (1984) [Mongolia]; Chapin (1965 b) [Micronesia]; Sasaji (1971 b) [Japan]; Pang & Mao (1979) [China]; Hoang (1982, 1983) [Vietnam]; Iablokoff-Khnzorian (1982) [Palaearctic and Oriental regions]; Savoiskaya (1983) [Central Asia and parts of the former USSR]; Pope (1989) [Australian Coccinellini]; Gordon (1985) [North America]; Kuznetsov (1997) [Russian Far East] and Ślipiński (2007) [Australia].

Within Microweiseinae, the tribe Microweiseini includes seven New World genera, and about 50 species distributed from southern Canada to Chile (Gordon 1977, Gonzales 2008). The single species of *Microfreudea* Fürsch and the two known *Paracoelopterus* Normand (= *Diloponis* Pope) are known from southern Africa, the Mediterranean and Middle Asia, and the single species of *Hong* Ślipiński occurs in southern Queensland. Sukunahikonini includes five genera distributed in the world tropics, with most of the species classified in the pantropical genus *Scymnomorphus* Weise (= *Sukunahikona* Kamiya); few species belong to Indo-Australian genera *Paraphellus* Chazeau and *Pharellus* Sicard, while the monospecific *Hikonasukuna* Sasaji is known from Taiwan and *Orculus* Sicard from Central and West Africa (Kamiya 1960; Pope 1962; Gordon 1977; Fürsch 1985 a; Ślipiński & Tomaszewska 2005). Ślipiński & Burckhardt (2006) recognized three genera of mostly tropical Serangiini, *Serangium* Blackburn and *Serangiella* Chapin known from the Old World, and *Delphastus* Casey confined to the New World (Gordon 1994 a). Carinodulini includes three genera, *Carinodula* Gordon *et al.* and *Carinodulinka* Ślipiński & Tomaszewska from Mesoamerica, and *Carinodulina* Ślipiński & Jadwiszczak from northern Thailand. (Ślipiński & Jadwiszczak 1995; Ślipiński & Tomaszewska 2002 a.)

The subfamily Coccinellinae contains most of known species and is divided into many cosmopolitan tribes. Distinctive groups with limited distribution include the monogeneric Monocorynini (*Monocoryna* Gorham) distributed in Thailand, Indonesia and Malaysia [Miyatake 1988; Sasaji 1989; Ślipiński & Jadwiszczak 2000]. The exclusively Asian Aspidimerini comprises four genera *Aspidimerus* Mulsant, *Cryptogonus* Mulsant, *Acarus* Kapur, and *Pseudaspidimerus* Kapur distributed from Pakistan-India and Japan south to the Wallace's line [Kapur 1948 b; Poorani 2001]. Telsimini is a small tribe known from Old World with all species classified in *Telsimia* Casey except single Australian species of *Hypocyrema* Blackburn [Ślipiński *et al.* 2005]. Similarly, the Old World tribe Platynaspidini contains numerous species of *Platynaspis* Redtenbacher known from Europe, Africa and Asia and single species classified in *Crypticolus* Strohecker from Madagascar [Miyatake 1961; Ślipiński & Tomaszewska 2002 b]. Among the formerly recognized Sticholotidinae (Gordon 1977; Kovář 1996 b), several groups have limited distribution, like the New World tribes Cephaloscymnini extending from Arizona southward to Brazil and Chile (Gordon 1985), or Argentipilosini restricted to Brazil (Gordon & Almeida 1991). The Old World taxa of the former Sticholotidinae include primarily Oriental tribes, like Plotinini (Miyatake 1969; Kovář 1995 b), Shirozuellini (Sasaji 1967) and Limnichopharini (Miyatake 1994), and the nearly cosmopolitan Sticholotidini with no representatives in Europe and North America north of Mexico (Sasaji 1971 b; Gordon 1977; Miyatake 1994; Ślipiński 2004).

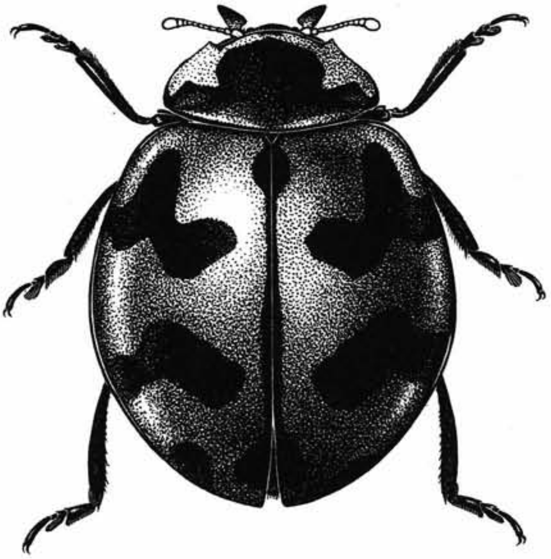

Fig. 10.33.1. *Coccinella transversalis* Fabricius, adult, dorsal (from Lawrence & Britton 1991; © CSIRO Australia), length = 5 mm.

Biology and Ecology. Various aspects of biology and ecology of Coccinellidae are covered by several thorough reviews of Clausen (1940), Hagen (1962), Hodek (1967, 1973), Majerus (1994), Hodek & Honek (1996) and Kuznetsov (1997). In addition to these Dixon (2000) covers ecology and population dynamics of predatory Coccinellidae and their interactions with various prey groups. In the following sections we will discuss in more detail various aspects of food preferences, aggregation and dormancy, interactions with ants and other invertebrates, structural color and defence, predators, parasites and pathogens and economic importance.

The predatory habit of adults and larval coccinellids is derived relative to their potential sister taxa Endomychidae and Corylophidae (Leschen 2000) that are mycophagous, and this diet is still dominant in the family. In addition to various predatory traits, species of ladybirds also feed on plant tissue or fungal material often supplemented by variable facultative food sources as honeydew, pollen, sap and nectar. Giorgi *et al.* (2009) argue that feeding on scales (coccidophagy) arose as the ancestral feeding preference of the family and there were multiple, independent shifts to feeding on various arthropods or plant tissue, and probably a single transition from aphidophagy to mycophagy and another one to leaf feeding (*Bulaea* Mulsant) within Coccinellini. They also stressed an importance of pollen as a primary larval food in transition from carnivory to leaf-feeding in *Bulaea* and from carnivory to mycophagy in other Coccinellini.

The majority of predacious species of ladybirds show a preference for Hemiptera, notably species of Sternorrhnycha, but they also prey on mites, nymphs of Thysanoptera, beetle larvae, and on early instar larvae of Lepidoptera, Hymenoptera, and Diptera (Schilder & Schilder 1928; Omkar & Pervez 2004). The predacious coccinellids have usually been classified according to their essential prey. However, there is substantial evidence that particular species may develop on prey other than the essential or preferred form, and that this preference may be seasonal (Clausen 1940; Ponsonby & Copland 1997). Hodek (1973, 1996 a) divided coccinellid prey into four categories: (a) essential prey allowing to complete development; (b) accepted prey that will prolong survival of the species but does not allow complete development; (c) rejected prey that is released immediately after attack and may not be touched again; and (d) toxic prey that will kill a ladybird if eaten or is deficient in nutritive value and causes death by starvation. There is a wealth of evidence that the same aphid or coccid species may be an essential prey for one coccinellid species but may be toxic to another (Hodek 1973, 1996 a).

Aphid feeders (aphidophages) mostly belong to Coccinellini but this food preference for ephemeral prey is probably shared by members of Platynaspidini, Aspidimerini, some Hyperaspidini and Coccidulini (*Apolinus* Pope & Lawrence, some *Scymnus* Kugellan). The feeding mechanism in aphidophagous species usually involves extra-oral digestion, with or without mastication of prey. Usually younger larval instars pierce their prey and inject digestive juices before sucking out the body contents and abandoning the empty exoskeleton. Mature larvae and adults not only consume body contents, but also chew the exoskeleton, usually consuming the entire aphid. Apparently larvae capable of masticating and chewing the prey are much more efficient from larvae using exclusively extra-oral digestion (Richards & Goletsos 1991). Aphids may be accepted essential prey for many Australian Coccinellini, but historically native aphids were scarce in Australia and most of these species developed on psyllids, and some still require psyllids for their development (Hales 1979). Aphid feeding Coccinellini are known to form larger batches of up to 100 eggs on leaf surfaces close to the colonies of aphids (Iperti 1999), and female lays between 150 and 920 eggs, depending on the aphid host and the ladybird species. [Kaddou 1960; Hagen 1962; Hodek 1972; Anderson 1982; Kuznetsov 1997.]

Coccidophages feed on stationary scales that may be ingested whole if small in size or in portions if the scale is large-bodied. Clearly the scale morphology and its structure has a strong bearing on its availability as prey to coccinellid species, affecting host preference and biology (Honda & Luck 1995). Significant groups of specialized scale feeders are among Microweiseini, Telsimini, Chilocorini, many Hyperaspidini and most Coccidulini. Most coccidophages lay their eggs singly or in small groups close to or directly on or beneath the female or immature scale. Females of *Rhyzobius ventralis* (Erichson) preying on *Eriococcus coriaceus* Maskel in Australia use their heavily sclerotized ovipositor to insert eggs singly or in groups directly to the ovisac of the scale and emerging larvae feed on the eggs, the crawlers and the female scale. [Hodek 1973; Richards 1981; Booth *et al.* 1995; Drea & Gordon 1990; Ponsonby & Copland 1997; Stathas 2001.]

Spider mite predators (acarophages) belong exclusively to species of the two genera *Stethorus* Weise and *Parastethorus* Pang & Mao (formerly tribe Stethorini, now Coccidulini) that feed on various species of Tetranychidae (spider mites). Both adults and larvae are voracious predators feeding on all development stages of tetranychids. The female lays eggs singly on the leaf, usually in the midst of the mite colony, and adult and larvae are capable of moving along the mite's webbing and use this to locate the prey along with other olfactory cues. Adult beetles chew and devour entire mites while larvae suck the mites dry using grooved mandibles for extraoral digestion. [Fleschner 1950; Chazeau 1979, 1985; Gutierrez & Chazeau 1972.]

Heteroptera or true bugs are preyed upon by few, relatively large members of Coccinellini. *Synona* Pope is known to prey on nymphs of the family Plataspidae (mostly of the genus *Coptosoma* Laporte) and Tessarotomidae (*Cumare pallida* Blote) (Monteith 2006; Poorani *et al.* 2008). Adults and larvae of the *S. melanaria* Mulsant in India are voracious and effective predators of nymphs of *Coptosoma ostensum* Distant. In favorable conditions the beetle can complete nine generations per year, and that, on average, a female may consume up to 6600 nymphs of *Coptosoma* during the 46 days of its life (Afroze & Uddin 1998). Complex interactions between species of two genera of plataspid bugs, *Camponotus* ants and the large predatory coccinellid *Anisolemnia tetrasticta* Fairmaire in Africa were studied by Dejean *et al.* (2002). They found that the *Anisolemnia* females lay eggs on branches of plants infested with colonies of plataspid bugs. The adult beetles and first instar larvae feed exclusively on bug eggs, but the larger larvae progressively attack bug nymphs, including final instars. Strongly sclerotized adult bugs were not attacked by lady beetles while nymphs show a characteristic defense behavior: approached by a coccinellid larva, a nymph will protect its soft venter by pressing its body tightly against the plant surface, but the ladybird larva slides its long forelegs under the nymph, lifts it from the plant surface and bites the nymph on the ventral surface.

Pollen and nectar are taken by various species and many predatory coccinellids utilize pollen as an important food source in early spring when their main insect prey is hard to find. Pollen and nectar are usually sufficiently nutritious for a beetle to survive, but not adequate for egg development. However, for *Bullaea lichatschovi* (Hummel) pollen is often an essential or principal food source (Savoiskaya 1983). A mixed or alternating diet is probably the rule for many Coccinellini, not the exception (Anderson & Hales 1983; Hawkeswood & Turner 2002). Larvae of *Tytthaspis sedecimpunctata* (Linnaeus) for example can collect and process grass pollen and powdery mildew spores (*Oidium* sp.) simultaneously (Ricci 1982). Adults of principally mildew-feeding *Illeis galbula* (Mulsant) often supplement its diet with *Acacia* or *Ligustrum* pollen (Anderson 1982). Interestingly, the same mixed diet (aphids, conidia, spores and pollen) was reported by Ricci (1986) for a Coccidulinae species, *Rhyzobius litura* (Fabricius) suggesting this may be more widespread strategy for many cocinellids.

Mycophagy. The principal mycophagous taxa belong to the coccinellid group often treated separately as the tribe Halyziini (= Psylloborini). All species of this group feed on conidia and hyphae of powdery mildews (Ascomycota: Erisyphales). Eggs are laid in small batches in vicinity or on patches of fungal growth. Adults and larvae graze fungal spores and hyphae from leaf surfaces using comb like structures on their mandibles. They can be cannibalistic, feeding on their own eggs but not on the larvae. [Strouhal 1926; Anderson 1981, 1982; Ricci 1986; Almeida & Milléo 1998.]

Aggregations and Dormancy. One of the most fascinating features of ladybird biology, especially common in the Northern Hemisphere Coccinellini, is their seasonal migration and aggregation combined with diapause. This behavior was once thought to be directly related to beetle survival in winter, but gradually it became clearer that the dormancy is more complex and involves climatic and environmental factors, primarily driven by the food availability. Many aphid feeding Coccinellini (especially *Semiadalia undecimnotata* [Schneider]) are known by their long migratory flights to a prominent landscape features (rocks, mountain tops, towers) where they hibernate in large clusters. Other species, like *Hippodamia convergens* Guerin, have a more complex behavior involving food induced diapause, periodical feeding on alternative food (pollen or nectar), smaller summer aggregations, and finally dispersal to large winter aggregations. [Hodek 1973, 1996 b; Anderson & Richards 1977; Ricci 1986 a.]

Interactions with ants are very complex and probably arose early in the evolutionary history of the group. Strong dependence of Coccinellidae on primary hemipteran prey, that are often tended by ants, brought these two groups together and has had a large impact on coccinellid evolution. There is a vast amount of literature discussing mutual benefits between aphids or coccids and ants tending their colonies, the ants gaining readily available rich food (honeydew), while protected hemipterans enjoy increased developmental rate, larger body size, fecundity and reproduction rate. Majerus *et al.* (2007) distinguish three types of interactions: (a) competitive interactions between the ants tending Hemiptera and the feeding coccinellids; (b) ladybird beetles preying upon ants; (c) ants feeding directly on ladybird beetles. Orivel *et al.* (2004) added yet another category to these interactions – ladybirds as obligatory myrmecophiles. They have discovered that larvae and pupae of a South American species, *Thalassa saginata* Mulsant, develop inside of colonies of *Dolichoderus bidens* (Linnaeus) and are tended by ants that move them around, and lick dorsal hairs and secretions from the anal gland. The relationship between the beetles and ants is species specific and the beetle larvae are well-integrated into the ants' colonies mimicking the cuticular patterns (hydrocarbons) of their hosts. Orivel and co-workers were unable to discover how the larvae find their way to the colonies (the adults are immediately attacked by the worker ants) or what the larvae feed on in the colony. From their observations it was apparent that the ladybird larvae did not feed on either the ants or their brood.

The tolerance of different species of ladybirds to ants depends on their behavioral, physical or chemical capabilities. Adult ladybirds, when molested by ants, may try to escape by running, flying away or dropping to the ground or may try to clamp down by attaching themselves firmly to the substrate while retracting all appendages under the body and withdrawing the head under, or fitting it firmly against, the pronotum. The clamping behavior is particularly common in the members of Chilocorini, Platynaspidini, Telsimini, and Serangiini that have short and easily retractable appendages and distinct fossae to contain flattened legs on the ventral surfaces. Larger species of Coccinellinae have been shown to adopt a "rolling motion" by dropping the side being attacked to make close contact of the body with the substrate. [El-Ziady & Kennedy 1956; Banks 1958; Bartlett 1961; Bradley 1973; Richards 1980, 1985; Jiggins *et al.* 1993; Majerus 1994; Pasteels 2007; Kaneko 2007.]

There are no records of Coccinellidae being associated with other social insects. The only true inquilinous species described in Coccinellidae – *Cleidostethus meliponae* Arrow (Arrow 1929) – is associated with stingless bees of the genus *Melipona* Illiger. However, it was transferred to Corylophidae by Bowestead *et al.* (2001).

Structural, Color, Chemical Defense. Defensive mechanisms among the Coccinellidae include bright warning colors, reflex bleeding, camouflage by wax secretions or cryptic colors, and by having a miniaturized body. When disturbed ladybirds often feign death and drop from the surfaces. Reflex bleeding involves secretion of a yellowish, reddish, or whitish fluid from the tibiofemoral articulation of the adults and from dorsal glands or intersegmental pores in of larvae (Kendall 1971). The secreted fluid is bitter, toxic and often has a strong smell (Hagen 1962), and has been regarded as a defence system against insect or vertebrate predators. The smell is due, at least in part, to a pyrazine (Al Abassi *et al.* 1998). Ladybirds exhibiting reflex bleeding are usually large and have bright warning or aposematic colors (mostly a combination of red, orange, yellow or blue with black or red patterns). The chemical defence system of ladybirds is based on a repellent, only rarely containing toxic alkaloids, some of which are known to be produced autogenously (Tursch *et al.* 1976; Ayr & Browne 1977). Each ladybird species usually contains a mixture of alkaloids but there is usually one major alkaloid such as for instance adaline in *Adalia* and coccinelline in *Coccinella* species. Alkaloids have been reported in Coccinellinae, Epilachninae, Chilocorinae and some Scymninae but only a fraction of the taxa have been studied so far (Daloze *et al.* 1995; Dixon 2000).

Natural enemies of Coccinellidae are numerous and some have severe impact on populations of particular species. Vertebrate predators commonly preying upon ladybirds include small mammals, birds and lizards. Among many invertebrate predators on ladybirds are spiders, mites, wasps, ants, carabid beetles, flies, and hemipterans. The adverse effect of vertebrate predation on Coccinellidae is best documented in reports on biological control studies using coccinellids. The Spanish sparrow *Passer hispaniolensis* (Temminck) devastated colonies of *Chilocorus cacti* (Linnaeus) imported into Algeria (Smirnoff 1957), while lizards have seriously limited populations of *Rhyzobius lophanthae* Blaisdel introduced to the Pacific islands (Cochereau 1969). Majerus (1994) considers spiders a major group impacting populations of ladybirds both by direct predation and by immobilisation on their webs. Of other important predators the ants, flies (adults of Asilidae and larvae of Syrphidae), neuropteran larvae and some entomophagous Hemiptera are of considerable importance, depending on ladybird species and its biology.

Richerson (1970) listed about 100 species of parasitic organisms found in Coccinellidae. Among other insects, Diptera (Phoridae and Tachinidae) and six families of Hymenoptera (Ichneumonidae, Braconidae, Pteromalidae, Encyrtidae, Eulophidae and Eupelmidae), have been recorded from Coccinellidae. Most of the parasites are found in the larval, pupal or adult stages, with very few eulophid or encyrtid Hymenoptera recorded as egg parasitoids. Some larval parasitoids of the genus *Homalotylus* Mayr (Encyrtidae) were reported to have devastating effects on ladybird populations, eliminating up to 95% of larvae of *Chilocorus* and in extreme cases up to 100 % of *Rodolia cardinalis*. Phorid flies are frequent ladybird parasites and in some conditions may parasitize up to 80% of populations (Disney *et al.* 1994). Phorids almost always attack freshly formed ladybird pupae, laying their eggs on its ventral side. The larvae hatch very quickly and the larva bores into the host, develops inside for short time, and then leaves the host to pupate in soil.

Pathogens of Coccinellidae include gut-dwelling sporozoan groups such as Gregarinida and Microsporidia, some nematodes and several fungal genera. Hurst *et al.* (1992, 1993) found a cytoplasmically inherited bacterium (*Rickettsia* spp.), present in about 7% of a Cambridge (United Kingdom) population of *Adalia bipunctata* (Linnaeus). The pathogen was responsible for killing male embryos. In many cases all surviving offspring were females. Majerus (1994) discussed the detailed biology of the pathogen and the evolutionary consequences of the male-killing bacteria phenomenon. Several hypotheses have been proposed, but the benefits of females vectoring the male killing bacterium and the long term effects on the population dynamics remain unclear. [Richerson 1970; Hodek 1973; Drea & Gordon 1990; Majerus 1994; Ceryngier & Hodek 1996; Ponsonby & Copland 1997.]

Economic importance. The value of ladybirds in destroying aphids in English gardens was well noted at the beginning of 19th Century. The modern history of biological control dates from the spectacular control of the cottony cushion scale (*Icerya purchasi*) by the introduced vedalia beetle *Rodolia cardinalis* (Mulsant) in citrus plantations in California in 1888 (Caltagirone & Doutt 1989). Since then many species of ladybirds have been used as biological control agents world wide, and in North America alone 179 species were imported and intentionally released over last 100 years, of which only 16 were established (Gordon 1985). Efficacy of Coccinellidae as biological control agents varies from highly efficient suppressors of various scales, mealybugs, spider mites or whiteflies to rather inefficient agents in controlling aphid populations. Except for a relatively few species of *Rodolia* Mulsant, *Rhyzobius* Mulsant, *Chilocorus* Leach, *Hyperaspis* Mulsant, and *Cryptolaemus montrouzieri* Mulsant used mostly against various hard scales or mealybugs in the field, the remaining successful ladybirds (*Stethorus* Weise, Serangiini) are mostly used in enclosed spaces (glass houses) to control spider mites and white flies. The augmentation methods with use of various aphidophagous Coccinellini (like *Hippodamia convergens*) harvested from their overwintering sites show very limited success because the beetles disperse from the release site very quickly. [Hodek 1973; Pope 1981; Samways 1984; Booth & Polaszek 1996; Hodek & Honek 1996; Obrycki & Kring 1998.]

Non-target impacts of imported biological control agents on other organisms besides the targeted pest is frequent, and best illustrated by the multicolored Asian lady beetle *Harmonia axyridis* (Pallas) with a long list of adverse effects on native insects, humans, and crops (Koch 2003). Rapid decrease of abundance of several native ladybirds in Florida following introduction of *H. axyrydis* and *C. septempunctata* (Linnaeus) shows an alarming trend now seen across most of the eastern and central North America. Other reported negative effects of *H. axyridis* in USA include feeding on ripening fruit crops and reducing yields (peaches, raspberries, and grapes), biting human skin causing minor bleeding, and causing a nuisance in households by aggregating in large numbers for overwintering (Hahn & Kovach 2004).

Pests among Coccinellidae all belong to exclusively phytophagous Epilachnini with some species considered one of the most economically important pests among beetles. Various *Epilachna* species feed mostly on leaves of various plants of Cucurbitaceae and Solanaceae. Species of other genera (e. g., *Dira* Mulsant, *Subcoccinella* Huber or *Cynegetis* Chevrolat) have a wider spectrum of host plants including grasses and legumes such as alfalfa (*Medicago sativa*) and various clovers (*Trifolium* spp.). Adult beetles and larvae may feed on the fruits and flowers of the plants, but generally prefer the leaves. They consume the tender parenchyma of the leaves from the underside, leaving the upper epidermis intact that dries out giving the leaf a lacy, "skeletonized" appearance. [Gordon 1985; Li & Cook 1961; Li 1993; Kuznetsov 1997.]

Morphology, Adults (Figs. 10.33.1–5). Length 0.8–28 mm. Body usually oval or rounded and distinctly convex dorsally; rarely elongate and almost flat (e. g., *Cranophorus* Mulsant, *Oryssomus* Mulsant, *Roger* Ślipiński); venter mostly flat, but sometimes distinctly convex. Dorsum polished and apparently glabrous or covered with short to moderately long setae, stiff hairs or a combination of both. Color from brown or black to bright red and yellow, often with contrasting pattern of spots, transverse bands or large maculae.

Head small, partly withdrawn into a prothorax and to varying extent covered from above by pronotum. Usually flattened and prognathous, sometimes hypognathous (Serangiini, Chilocorini) or deflexed and fitting closely underneath against the prosternum (some Sukunahikonini and Microweiseini). Appendages often short and inconspicuous. Head capsule quadrate to distinctly transverse, very rarely distinctly rostrate (Microweiseini, Carinodulini), not abruptly constricted posteriorly. Occipital region without transverse ridge or occipital file. Eyes large, convex and mostly finely facetted but facets often coarse and convex in many Coccidulini (eyes strongly reduced in *Carinodulinka*); interfacetal setae or stiff bristles rarely present (Noviini); anterior or inner margin of eye often indented by ocular canthus (eye almost completely divided in Telsimiini and some Chilocorini). Frontoclypeal suture always absent; clypeal region usually short, straight or arcuate anteriorly; laterally expanded forming ocular canthus in most Chilocorini, Platynaspidini and Telsimini. Labrum simple, transverse, about as wide as clypeus, except for Chilocorini, Platynaspidini and Telsimini where it is much narrower than the clypeus; usually exposed, rarely partially hidden; tormae poorly developed and labral rods always absent. Antennae very variable in length, 7- to 11-segmented, usually with weak antennal club; sometimes serrate or pectinate (e. g., *Discotoma* Mulsant). Antennal insertions usually exposed, situated near inner margin of eyes, but often completely hidden under expanded clypeus (Telsimiini, Chilocorini, Platynaspidini) or broadly separated from eye margins (Epilachnini, some Coccinellini, *Rhynchortalia*); rarely insertions nearly adjacent and distinctly in front of eye margins (Sukunahikonini, Microweiseini, Serangiini, some Carinodulini). Antennal groove usually present, short, often extending posteriorly to hind margin of eyes; rarely externally encircling the posterior margin of eye (some Coccidulini) or forming a pocket (*Platynaspis*). Mandible triangular, heavily sclerotized, usually bidentate apically (unidentate in several unrelated groups, multidentate in Epilachnini), with hyaline prostheca and smooth concave basal mola armed with sharp tooth; mola and prostheca absent in Serangiini, Sukunahikonini and Microweiseini; mola replaced by membranous process in Epilachnini; additional minute denticles or teeth present on apex or along incisor edge of mandible in mould-feeding genera of Coccinellini (formerly Halyziini). Maxilla large, with quadrate to strongly transverse cardo, elongate stipes, broad apically setose galea and often much smaller lacinia (strongly reduced in Microweiseinae); maxillary palp 4-segmented with terminal palpomere narrow and pointed apically to strongly securiform. Mentum transverse, distinctly narrowed posteriorly (parallel-sided or broadest and base in Epilachninae); labial palps usually 3-segmented (2-segmented in Noviini), situated on ventral side of prementum (in some Microweiseinae placed at anterior edge); ligula usually short and reduced but in many Coccinellini distinctly expanded. Gular sutures widely separated, usually long but strongly reduced in Serangiini. Tentorial arms simple, broadly separated, exceptionally (in some *Rhizobius* species only), with simple corpotentorium. Cervical sclerites present.

Prothorax transverse, usually widest at base, narrowing anteriorly, sides sometimes narrowly explanate and base usually distinctly narrower than elytral bases. Lateral pronotal carina complete and simple, with or without raised margin or bead;

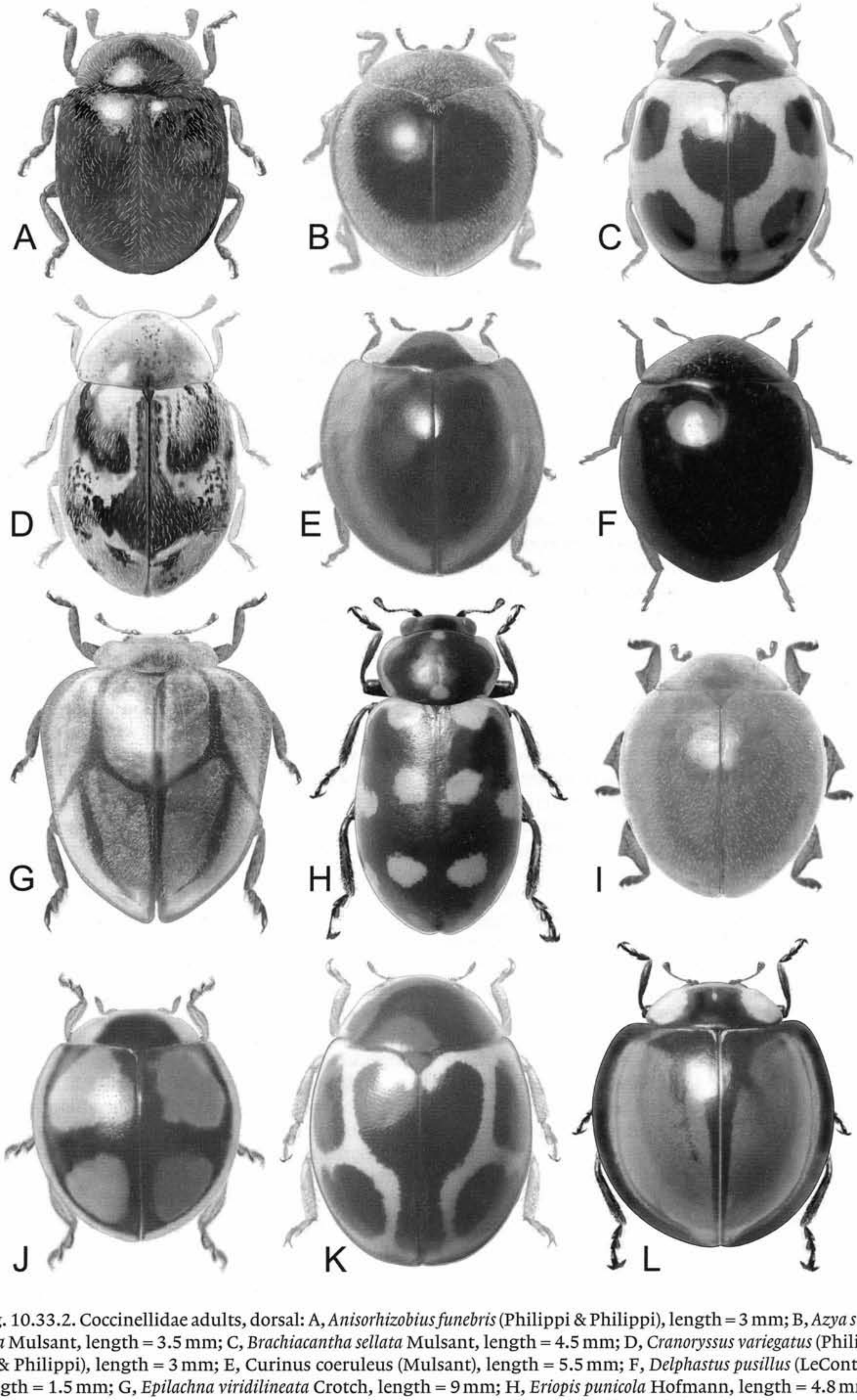

Fig. 10.33.2. Coccinellidae adults, dorsal: A, *Anisorhizobius funebris* (Philippi & Philippi), length = 3 mm; B, *Azya sulcata* Mulsant, length = 3.5 mm; C, *Brachiacantha sellata* Mulsant, length = 4.5 mm; D, *Cranoryssus variegatus* (Philippi & Philippi), length = 3 mm; E, Curinus coeruleus (Mulsant), length = 5.5 mm; F, *Delphastus pusillus* (LeConte), length = 1.5 mm; G, *Epilachna viridilineata* Crotch, length = 9 mm; H, *Eriopis punicola* Hofmann, length = 4.8 mm; I, *Exoplectra ruberima* (Erichson), length = 4.5 mm; J, *Harpasus quadrifolium* Gonzáles *et al.*, length = 3.0 mm; K, *Cyra loricata* (Mulsant), length = 4 mm; L, *Neda ostrina* Mulsant, length = 8 mm. All © Guillermo González.

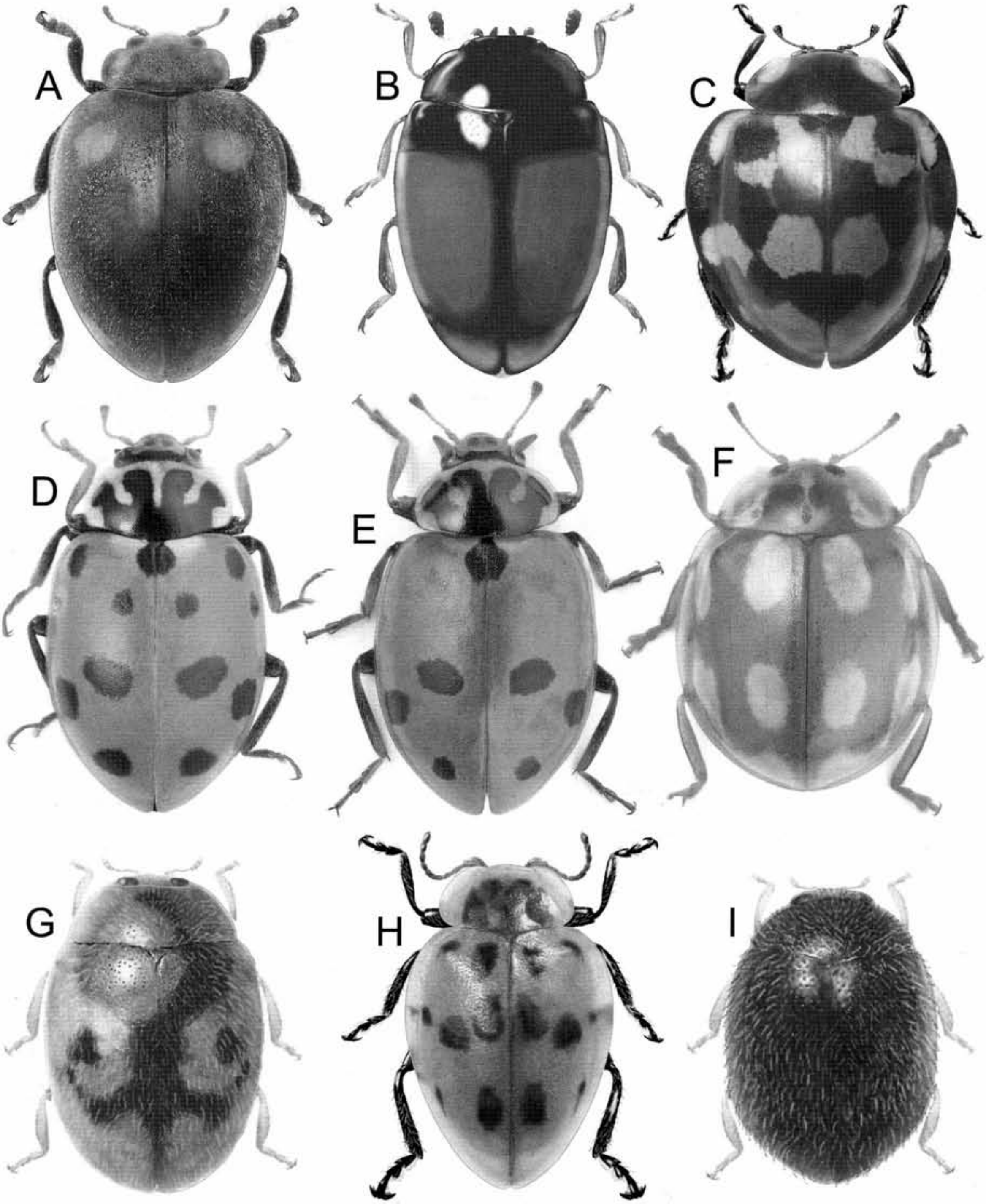

Fig. 10.33.3. Coccinellidae adults, dorsal: A, *Toxotoma venusta* (Erichson), length = 8 mm; B, *Parasidis porteri* Brethes, length = 1.5 mm; C, *Anaris lebasi* (Mulsant), length = 10 mm; D, *Thtthaspis sedecimpuncata* (Linnaeus), length = 2.5 mm; E, *Adinia variegata* (Goeze), length = 4 mm; F, Calvia decemguttata (Linnaeus), length = 6.3 mm; G, *Scymnobius galapagoensis* (Crotch), length = 1.8 mm; H, *Oxytela longula* Weise, length = 4.6 mm; I, *Stethorus peruvianus* Gonzáles *et al.*, length = 1.4 mm; (A–C, G–I © Guillermo González; D–F © Kirill B. Makarov).

anterior pronotal angles usually absent or not produced forward; posterior angles absent or broadly rounded; disk usually convex, simple, rarely with short carinae near anterior angles (Microweiseini, some Sukunahikonini), or almost complete sublateral carina associated with pits (some Sukunahikonini and Carinodulini). Prosternum in front of coxae usually as long as or longer than mid length of procoxal cavity (much shorter than mid length of cavity in Noviini); often with paired longitudinal carinae of variable length, originating on prosternal process; in several groups anterior edge produced forward to form chin-piece (Shirozuellini, Serangiini, *Bucolus* Mulsant). Notosternal suture

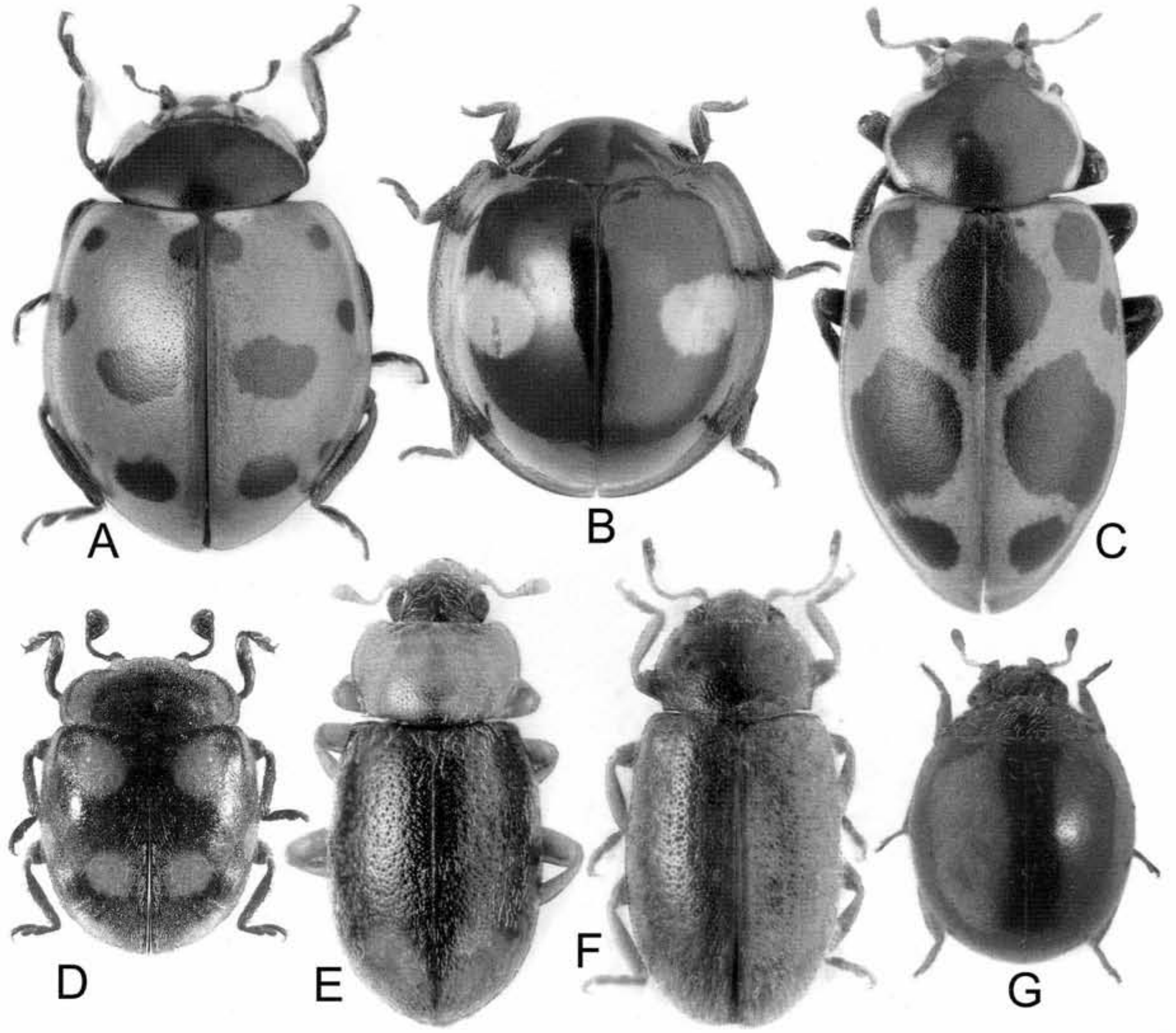

Fig. 10.33.4. Coccinellidae adults, dorsal: A, *Coccinella ainu* Lewis, length = 5.0 mm; B, *Chilocorus renipustulatus* Scriba, length = 4.0 mm; C, *Ceratomegilla ulkei* Crotch, length = 5.5 mm; D, *Monocoryna* sp., Borneo, length = 5 mm; E, *Tetrabrachys tauricus* (Semenov), length = 4 mm; F, *Coccidula rufa* (Herbst), length 3.0 mm; G, *Serangium lygaeum* Iablokoff-Khnzorian, length = 2.0 mm; A–C, E, F © Kirill B. Makarov; B © CSIRO Australia; G © M. E. Smirnov.

usually complete; hypomeron often modified to receive antennae and/or legs in repose. Prosternal process complete, 0.2–0.5 times the width of the procoxal cavity, parallel-sided or weakly expanded apically (narrowly carinate and narrowly separating coxae in some Sukunahikonini, very broad in Shirozuellini or Cephaloscymnini). Exposed portions of procoxae oval to transverse, not or only slightly projecting below prosternum, with long concealed lateral extensions; trochantins hidden. Procoxal cavities oval to strongly transverse, narrowly to moderately widely separated, externally always open and internally closed. Scutellar shield well-developed and visible, abruptly elevated, anteriorly simple, posteriorly acute to broadly rounded or truncate. Elytra usually less than two times as long as combined width, mostly irregularly punctate (some regular punctuation in Sukunahikonini), without scutellary striole; apices usually conjointly rounded and concealing all abdominal tergites; epipleura usually complete, often wide and inflexed or horizontal, sometimes bearing foveae housing tips of the femora in repose (e. g., Serangiini, Chilocorini); in *Scymnomorphus* Weise (Sukunahikonini) with short carina along elytral edge. Mesoventrite anteriorly usually on lower plane than metaventrite, almost always separated by complete sutures from mesanepisterna, which are broadly separated from one another; anteriorly with paired, procoxal rests and usually with deep median prosternal rest; mesocoxae not conical and projecting. Mesocoxal cavities moderately to widely separated, circular, open laterally, partly closed by mesepimeron; mesotrochantin always hidden. Mesometaventral junction simple, meeting as a straight or curved line (sometimes absent due to fusion of mesoventrite and metaventrite); in Diomini metaventrite extending anteriorly, overlapping mesoventrite from below. Metaventrite usually long without transverse suture but usually with discrimen of variable length; postcoxal lines almost always present; exposed portion of metanepisternum moderately elongate to very long and narrow. Metacoxae widely separated,

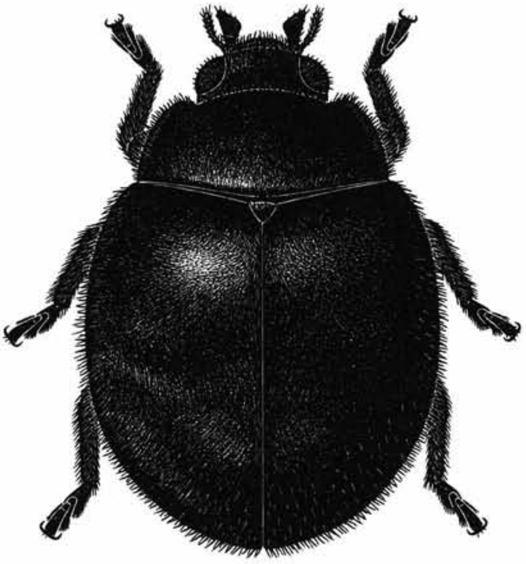

Fig. 10.33.5. *Scymnodes bellus* Pope & Lawrence, adult, dorsal (from Pope & Lawrence 1990; © CSIRO Australia), length = 4.0 mm.

not extending laterally to meet elytra; coxal plates absent. Metendosternite with stalk moderately long (short or absent in some Microweiseinae) and widely spread arms bearing moderately to broadly separated anterior tendons; laminae often reduced or absent. Hind wing usually present (absent in many Sukunahikonini, Carinodulini and Coccidulini), usually relatively narrow in smaller species with very long apical field; radial cell, medial fleck and wedge cell absent; R-M loop usually forming narrowly acute angle, sometimes absent; medial field without venation or with two veins; fringe of short or long setae usually restricted to posterior edge; anal notch usually present. All three pairs of legs similar; trochanterofemoral joint oblique; femora flattened and usually broad; tibiae usually simple, rarely strongly widened or with outer edge serrate or spinose, sometimes apically with a groove to receive the folded tarsus; tibial spurs double, single or absent. Tarsi 4-4-4 (sometimes 3-3-3), with tarsomeres 1 and 2 large and lobed beneath and 3 very small and simple; claws usually appendiculate, rarely simple or split apically; empodium absent or strongly reduced.

Abdomen with five or six ventrites. Ventrites 1 and 2 usually solidly fused; first ventrite often much longer than second, almost always with postcoxal lines (absent in *Epiverta* Mader, *Hippodamia* Mulsant, *Rynchortalia* Crotch and *Nat* Ślipiński), sometimes with associated pits or pores; intercoxal process broad and arcuate. Functional spiracles present on abdominal segments I–V. In male anterior edge of sternite VIII without median strut. Sternite IX with spiculum gastrale (strongly reduced in Telsimini); tergite IX in male always distinct. Aedeagus of complex cucujiform type, rotated on left side when retracted; tegminal phallobase forms ring around penis and projects forward forming penis guide (median lobe), it articulates with tegminal strut (trabes) posteriorly and setose parameres (lateral lobes) anteriorly; tegminal parts mostly symmetrical, but with strong asymmetry in Microweiseini, Sukunahikonini and Serangiini, and minor asymmetries in penis guide in many groups. Penis (sipho) simple and rod like (rarely divided into two or more moveable sclerites, usually enlarged at tbase forming a capsule; endophallus simple. Female segment VIII forms simple sclerotized ring; sternite VIII without spiculum ventrale. Ovipositor very short to moderately long and lightly sclerotized, usually without distinct baculi; styli usually well-developed and terminal. Internal female tract with sclerotized and variably shaped spermatheca and attached gland; large bursa copulatrix apically receiving sperm duct that sometimes thickens into a tube (infundibulum) or consists of two parts of variable diameter (Chilocorini, Chapin 1965 a); additional gland-like structures present in many groups including glands of unknown function associated with the ovipositor in all Coccinellini (Verhoeff 1895; Hemptinne *et al.* 1991; Ślipiński 2007). [Dobzhansky 1924, 1926; Hafez & El-Ziady 1952 a; Sasaji 1971 a, b; Gordon 1994 b, 1999; Kovár 1996 a, Ślipiński 2007.]

Morphology, Larvae (Figs. 10.33.6, 7 A–F). Length 1–30 mm. Body usually oblong or elongate, fusiform and slightly, with well-developed legs; broadly ovate, strongly flattened and disc-like in Platynaspidini and Aspidimerini and some Coccidulini. Dorsal surfaces sometimes covered by dense wax exudations (Pope 1979), usually in combination with soft and lightly pigmented integument; integument granulose or spinulose, often with distinct sclerotized plates on most of thoracic and on smaller parts of the abdominal tergites in larvae without waxy exudates; dorsal sclerotizations often associated with complex, cuticular armature and branched processes (see Gage [1920] and Rees *et al.* [1994]).

Head protracted and prognathous, sometimes concealed from above by pronotum (*Scymnodes bellus* Pope & Lawrence); usually transverse and slightly flattened, rarely elongate (Microweisenini). Posterior edge not or only slightly emarginate. Epicranial stem present or absent; frontal arms joined at base (absent in late instars of some Hyperaspidini and Coccidulini), V- or U-shaped (Epilachninae) or lyriform, rarely with paired endocarinae underneath (*Coccidophilus* Brethes); median endocarina present in *Microweisea* Cockerel. Stemmata three in a triangle behind antennal insertion (two stemmata much larger and approximate, third with lens reduced and positioned posteriorly in *Stethorus* and *Parastethorus*). Frontoclypeal suture usually absent (present in some Epilachninae). Labrum usually free. Antennae extremely variable, usually short, 3-segmented (2-segmented in many Coccinellini, 1-segmented in *Stethorus* and some Chilocorini); antennomere 3 reduced and shorter than conical sensory appendix; antennal insertions separated from mandibular articulation by a distance usually

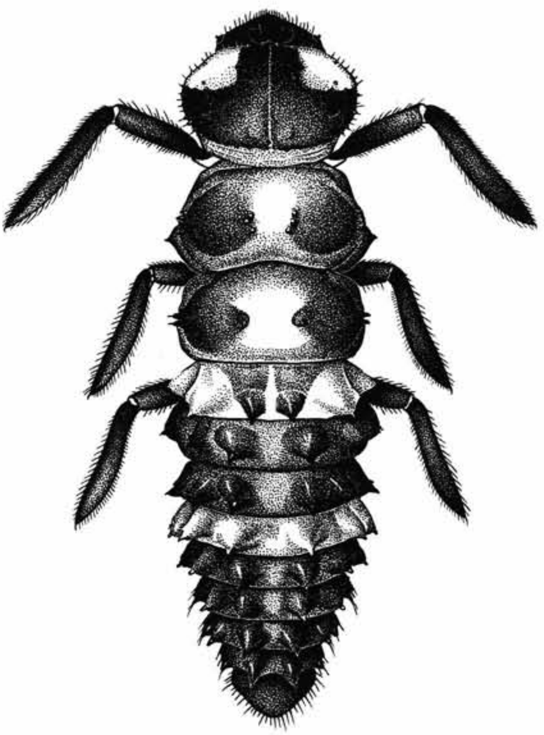

Fig. 10.33.6. *Coccinella transversalis* Fabricius, larva, dorsal (from Lawrence & Britton 1991; © CSIRO Australia), length = 6 mm.

broader than the antennal socket; antennae rarely long and clavate, with very long first antennomere (*Amida* Lewis and *Ortalistes* Gorham). Mandibles symmetrical, broad at base and apically narrowed, usually bidentate or unidentate (multidentate in Epilachninae), bearing additional teeth forming scoop like structure in some Coccinellini (*Illeis* Mulsant and related taxa); accessory ventral process absent; mola usually developed as a molar projection bearing microtrichia (absent in Epilachnini and Microweiseinae); prostheca always absent. Ventral mouthparts retracted; maxillary articulating area absent. Cardo indistinct, fused to stipes mala rounded to narrowly falcate without an uncus but often with a double stylus; palps almost always 3-segmented (2-segmented in *Rodolia*), usually with relatively long apical palpomere. Labium with submentum, mentum and prementum often fused to a plate-like structure; ligula short and usually only slightly expanded; labial palps usually 2-segmented (1-segmented in Hyperaspidini). Hypopharyngeal sclerome usually absent, but sometimes consisting of transverse bar. Hypostomal rods short and parallel or weakly divergent posteriorly; ventral epicranial ridges absent. Gular sutures separate; gula usually transverse.

Prothorax longer than meso- or metathorax, sometimes as long as both combined, slightly to strongly transverse; meso- and metathorax and abdominal segments I–VIII strongly transverse; thoracic and abdominal segments sometimes laterally expanded forming various processes. Prosternum without special armature. Legs well-developed (in Coccinellini front legs usually longer than remaining pairs), 5-segmented, including pretarsus, which is claw-like, with basal tooth bearing single simple seta; apex of tibiotarsus usually with specialized clubbed or flattened setae; coxae moderately to widely separated. Thoracic spiracles annular.

Abdomen usually about twice as long as thorax. Paired dorsal glandular openings often present on intersegmental membranes or on abdominal segments I–VIII (Chilocorini, Diomini, Shirozuellini, Sticholotidini). Tergum IX slightly longer and narrower than VIII and extending onto ventral surface, sometimes forming evenly rounded, flattened plate without urogomphi, but sometimes with slight median projection; sternum IX simple; segment X somewhat cylindrical and ventrally or posteroventrally oriented, forming adhesive pygopod. Abdominal spiracles annular, located dorsally or dorsolaterally. [Böving 1917; Binaghi 1930; Verhoeff 1895; Dobzhansky 1924, 1926; Kapur 1950; Hafez & El-Ziady 1952 a, b; Kamiya 1965; Sasaji 1968 c, 1971 a, b; Priore 1963; Ricci 1979; Kovár 1996 a; Gordon & Vandenberg 1995; Costa, Vanin & Casari-Chen 1988; Pope & Lawrence 1990; LeSage 1991; Ślipiński 2007.]

Morphology, Pupa (Figs. 10.33.7 G–J). Adecticous and exarate with all appendages free. Larval exuvium usually folded back and covering abdominal apex (enclosed in broken longitudinally larval exuvium in Chilocorini, Noviini and Hyperaspidini). Color yellow, white or brown, often with darker spots (most Coccinellini); surfaces sparsely to densely setose, smooth, covered with wrinkles or spines. Head hypognathous, always covered by pronotum in dorsal view. Eyes partially convered by pronotum and antennae in ventral view. Mouthparts well visible in ventral view. Antennae lying between eyes and first pair of legs.

Pronotum large, variably shaped like in adult beetles. Legs visible in ventral view, not covered by the wing pads which usually extend past the first or second ventrites. Wings membranous, bulbous and tapered apically; surface usually smooth and glabrous (setose in Serangiini, Microweiseini, Noviini, Scymnillini and *Rhyzobius*).

Abdominal terga I–VII in Coccinellini rather strongly sclerotized, with their much lower intersegmental membranes exposed, making pupal abdomen much more flexible, forming a gin trap to flick away parasites; in remaining groups all segments closely opposed to each other. Abdominal spiracles present on terga I–VIII (absent in Hyperaspidini), sometimes located on distinct pedunculate projections. Gland opening situated between abdominal tergum I and metanotum in Chilocorini. Tergum IX with pair of urogomphi (absent in Serangiini and Microweiseini). [Phuoc & Stehr 1974; Ślipiński 2007.]

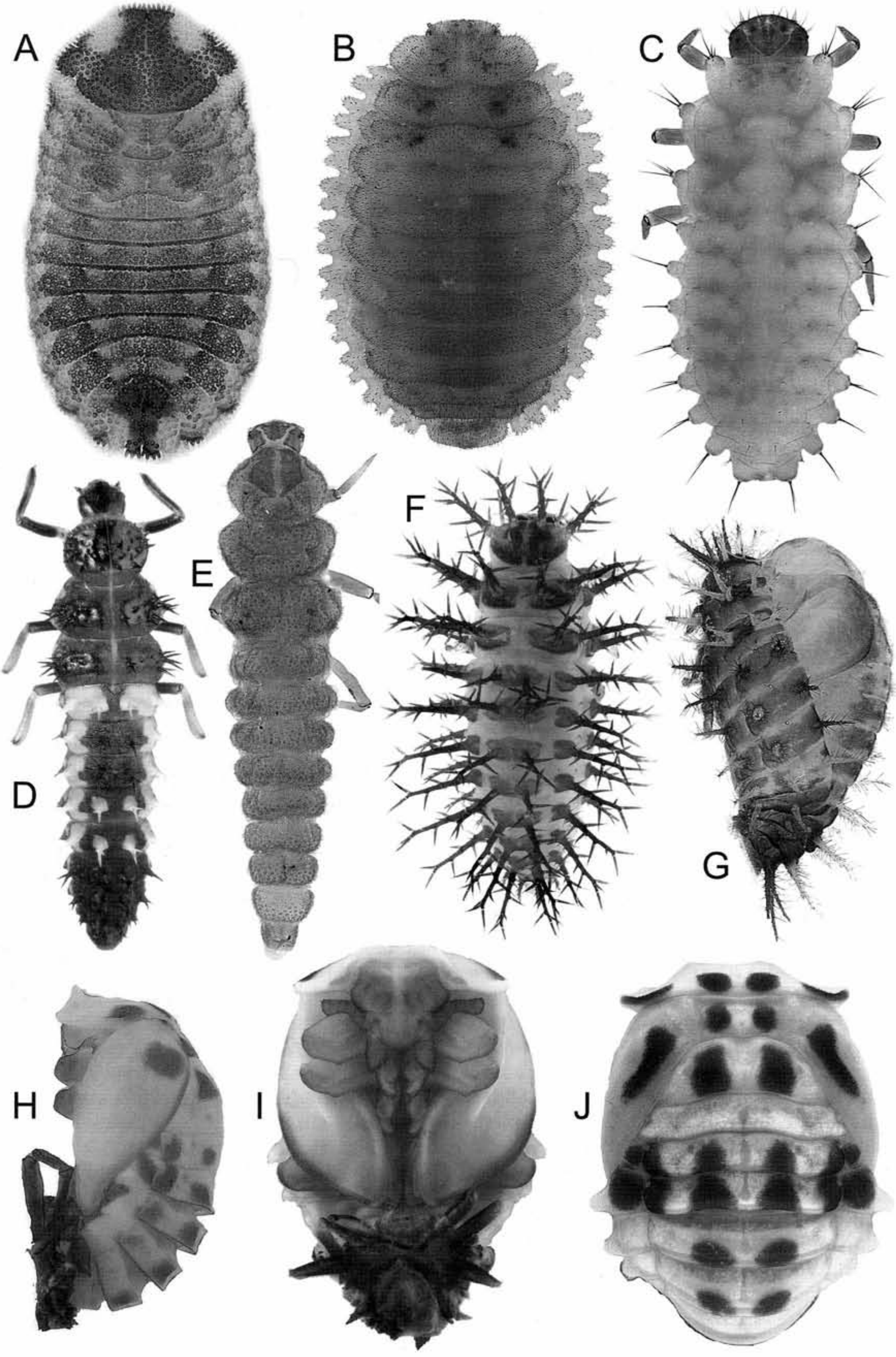

Fig. 10.33.7. Coccinellidae larvae and pupae: A, *Scymnodes bellus* Pope & Lawrence, larva, dorsal, length = 6 mm; B, *Diomus* sp., Australia, dorsal, length = 4 mm; C, *Telsimia* sp., Australia, dorsal, length = 2.5 mm; D, *Harmonia* sp., Russia, length = 5 mm; E, *Serangium* sp., Australia, length = 2.5 mm; F, *Epilachna* sp., Australia, length = 8 mm; G, *Orcus lafertei* Mulsant, pupa, lateral, length = 5 mm; H, *Archegleis kingi* (MacLeay), pupa, lateral, length = 5 mm; I, *Antineda princeps* (Mulsant), pupa, ventral, length = 6 mm; J, *Archegleis edwardsi* (Mulsant), pupa, dorsal, length = 4.5 mm. (All, except D from Ślipiński 2007 © Commonwealth of Australia; D, © Artem Zaitsev.)

Morphology egg. 0.2–2.0 mm long. White or yellow to red (white or creamy-yellow when freshly laid, darkening during embryogenesis); oval or spindle-shaped, laid singly or in batches of various sizes, always with the long axis perpendicular to the substrate. Chorion smooth, distinct microsculpture visible only in Epilachninae. [Clausen 1940; Klausnitzer 1969; Hodek 1973; Ahmad 1970; Richards 1981; Booth *et al.* 1995.]

Phylogeny and Taxonomy. The genus *Coccinella* was established by C. Linnaeus in 1758 for 36 species with a rounded and convex body, short, clubbed antennae and expanded terminal maxillary palpomere. The first major work on beetle classification by Latreille (1804) recognizes Coccinellidae as a distinct family under the name 'Tridigités' (referring to apparently 3-segmented tarsi) with the three genera *Coccinella* (including *Scymnus* Kugellan as species group), *Eumorphus* Weber and *Endomychus* Panzer. Latreille (1807) used the name Coccinellidae for a similar grouping of genera, and in one of his late publications (Latreille 1825) he split endomychids and coccinellids into separate families. Latreille's beetle classification, based on the number of tarsal segments, was generally accepted with little change for almost a century until major classifications were developed by Lameere (1900), Kolbe (1901) and Ganglbauer (1899, 1903), who recognized Coccinellidae as a part of Clavicornia (or Diversicornia). Verhoeff (1895) recognized Coccineliidae as a separate beetle suborder (Siphohophora) based on the structure of the male genitalia, but this has been ignored. Crowson (1955, 1960, 1981) classified Coccinellidae in the superfamily Cucujoidea among families related to Cerylonidae (Cerylonid Series) that included presumed closely related and relatively advanced Cerylonidae, Coccinellidae, Corylophidae, Alexiidae, Endomychidae and Latridiidae. The Cerylonid Series has been discussed and analysed by Sen Gupta & Crowson (1973), Pal & Lawrence (1986), Ślipiński (1990), and Ślipiński & Pakaluk (1992). While subsequent workers perceived Endomychidae as the most obvious candidate for the sister group of Coccinellidae, Ślipiński & Pakaluk (1992) voiced serious reservations on the monophyly of the Cerylonid Series as well as the monophyly of Endomychidae and other members of the group.

Sasaji (1971 a) hypothesized that Endomychidae and Corylophidae may be the closest relatives of Coccinellidae and this was confirmed in the cladistic studies of Endomychidae based on adult morphology by Tomaszewska (2000, 2005). Recent molecular studies by Hunt *et al.* (2007) and Robertson *et al.* (2008) showed strong support for the monophyly of the Cerylonid Series and Coccinellidae with inconsistent support for Leiestinae (Endomychidae), Anamorphinae (Endomychidae) + Alexiidae) or Endomychidae + Alexiidae + Corylophidae as sister groups to Coccinellidae. These results are in sharp disagreement with results published by Marvaldi *et al.* (2009) based mostly on the same loci (18S and 28S rDNA) that place Endomychidae + Coccinellidae outside of the remaining Cucujoidea and as a sister taxon to some Cleroids. The last study agrees with the suggestions by Wanat (2007) in his paper on male genitalia.

The internal classification of Coccinellidae was heavily influenced by Mulsant (1846, 1850), who monographed the family and proposed the first suprageneric categories (tribes) in Coccinellidae, provided keys to genera, and descriptions of all the known world species. Mulsant's monograph was significantly revised by Crotch (1874) who provided a critical synopsis of the world taxa and proposed a slightly altered classification that departed from the division of Coccinellidae into the hairy Trichoisomides and glabrous Gymnosomides of Mulsant, and classified setose Epilachnides as a subgroup of the subfamily Coccinellidae. Subsequently Chapuis (1876) recognized a major division of Coccinellidae into phytophagous and aphidophagous ladybirds (apparently after Redtenbacher 1844), replacing the hairy versus glabrous classes as recognized by Mulsant. Subsequent studies by Ganglbauer (1899) and Casey (1899) introduced additional higher categories to ladybird classification. Casey's contribution included many new generic and tribal divisions of Coccinellidae based on careful morphological observations with vital relevance for the global family classification. Korschefsky (1931, 1932) in his world catalogue followed Ganglbauer and Casey to a large extent and divided Coccinellidae into three subfamilies, Epilachninae, Lithophilinae and the Coccinellinae containing 20 tribes.

The first modern attempt to reconstruct the phylogeny of Coccinellidae was done by Sasaji (1968 a). In this landmark study, Sasaji examined and analysed critically both adult and larval characters of Coccinellidae and constructed a hand-worked phylogenetic tree of the major groups and proposed a revised classification. In a later contribution, Sasaji (1971 a) attempted to use numerical taxonomic methods to elucidate the phylogeny of the Coccinellidae. Based on these studies he (1971 b) proposed the division of Coccinellidae into six subfamilies and several tribes: Coccidulinae (Noviini, Lithophilini, Coccidulini, Exoplectrini); Sticholotidinae (Shirozuellini, Sticholotidini, Serangiini, Sukunahikonini); Scymninae (Scymnillini, Stethorini, Cranophorini, Syperaspini, Scymnini, Aspidimerini, Ortalini); Chilocorinae (Telsimini, Platynaspini, Chilocorini); Coccinellinae (Discotomini, Coccinellini, Psylloborini) and Epilachninae (Epilachnini). Yu (1994) attempted a cladistic analysis of Coccinellidae based on 36 adult and 18 larval characters (taken mostly from Sasaji 1968 a) and exemplar taxa representing 21 terminals corresponding to recognized tribes. The analyses of adult and larval data run separately are highly incongruent but the adult data are in partial agreement with Sasaji's (1968 a) results, supporting Sticholotidinae, Epilachninae, Coccinellinae, Coccidulinae and Scymninae + Chilocorinae. This system was followed by Chazeau *et al.* (1989). Kovář (1996 b) presented hand-made phylogenetic tree of Coccinellidae and briefly discussed the major groupings, their potential synapomorphies, and recognising seven subfamilies and 38 tribes. The tree of Kovář (1996 b) was formalized into a revised classification of Coccinellidae by Duverger (2003).

Vandenberg (2002) and Vandenberg & Perez-Gelabert (2007) discussed many problems regarding the classification of former Sticholotidinae and Scymninae-Coccidulinae highlighting misclassified taxa, important characters, and evolutionary trends. In his treatment of the Australian fauna, Ślipiński (2007) recognized two subfamilies, Microweiseinae and Coccinellinae based on adult and larval morphology. Microweiseinae includes three tribes (Microweiseini, Serangiini and Sukunahikonini) that share the unique asymmetrical tegmen with reduced and fused parameres, multi-cameral and sclerotized spermatheca, antennal insertions positioned close together in front of the eyes, and the antenna short, clubbed and comprising a maximum of 10 segments. Their larvae have a granulate integument, a simple mandible simple without a molar lobe, and a tibiotarsal apex with two spatulate setae; the pupa does not have urogomphi. Potential apomorphies for Coccinellinae (including most of the remaining tribes) are unclear at the moment, as the characters common to these groups appear to be plesiomorphies (symmetrical tegminal phallobase and well-developed and articulated parameres in the adults, and the mandible with a distinct molar lobe and usually numerous tibiotarsal setae in the larva). Further subdivision of Coccinellinae is very problematic and based more on guess work than on real data, even though some groups appear distinctive (e. g., Coccinellini, Epilachnini, Chilocorini, Aspidimerini, Platynaspidini, Telsimini). Other subgroups of coccinellines (mostly Scymnini + Coccidulini) are only defined by plesiomorphic characters.

The division of Coccinellidae into two major clades is well supported by molecular data (Giorgi *et al.* 2009) based on two loci (18S and 28S rDNA). Molecular data also support a monophyletic Coccinellini (including Discotomini, Bullaeini, Halyziini), Chilocorini + Telsimini, Hyperaspidini + Brachiacanthidini, Aspidimerini and Diomini. However, internal groupings of the Coccinellinae (sensu Ślipiński 2007) has not been resolved by these molecular characters.

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10.34. Corylophidae LeConte, 1852

Adam Ślipiński, John F. Lawrence and
Andrew R. Cline

Distribution. The corylophid subfamily Periptyctinae, containing the genera *Periptyctus* Blackburn, *Pakalukodes* Ślipiński *et al.* and *Weirus* Ślipiński *et al.* is restricted to the eastern part of Australia, while