

PHYLOGENY AND CLASSIFICATION

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1.1 POSITION OF THE FAMILY

1.1.1 The Cerylonid complex

The family Coccinellidae includes approximately 6000 described species in some 360 genera and 42 tribes. Coccinellids belong to the superfamily **Cucujoidea** of the Coleoptera suborder Polyphaga, and the family is a member of the phylogenetic branch frequently referred to as the **Cerylonid complex** or series of families, which is composed of Alexiidae, Cerylonidae, Coccinellidae, Corylophidae, Discolomatidae, Endomychidae (s. lat. including Mychotheninae, Eidoreinae and Mero-physiinae) and Latridiidae (Crowson 1955, Lawrence & Newton 1995). Bothrideridae were added later (Pal & Lawrence 1986). Monophyly of the Cerylonid series was based on morphological characters (Slipinski & Pakaluk 1992) and confirmed by parsimony analysis of molecular data (Hunt et al. 2007, Robertson et al. 2008).

Phylogenetic relations between the families and subfamilies included in the Cerylonid complex are rather complicated and not fully resolved (Slipinski & Pakaluk 1992). Early morphological studies supported a clade Endomychidae plus Corylophidae as the sister group of Coccinellidae (Crowson 1955, Sasaji 1971a). Affinities have been proposed between Endomychidae and Coccinellidae (Pakaluk & Slipinski 1990; Burakowski & Slipinski 2000) due to the presence of a characteristic basal (= median) lobe of male genitalia, pseudotrimerous tarsi and absence of coronal suture on the head of larvae (except in Epilachninae); Eupsylobiinae (Endomychidae) and Coccinellidae (Pakaluk & Slipinski 1990) due to the long penis and coccinellid-like tegmen; Mycetaeinae (Endomychidae) and Coccinellidae (number of abdominal spiracles, open middle coxal cavity, Kovář 1996; distinct pronotum with sublateral carina, hidden mesotrochantin, Tomaszewska 2000); Alexiidae (= Sphaerosomatidae) and Coccinellidae (Slipinski & Pakaluk 1992); Endomychidae plus Alexiidae and Coccinellidae (Pakaluk and Slipinski 1990); or between Corylophidae and Coccinellidae (Sasaji 1971a; anterior tentoria separated, frontoclypeal suture absent, common type of antenna and tarsus, Tomaszewska 2005).

1.1.2 Sister families

Tomaszewska (2000) argued monophyly of the Endomychidae plus Coccinellidae from the common characters of procoxal cavity externally open, tarsal formula 4-4-4, abdomen with five pairs of functional spiracles and median lobe without additional struts. However, the polyphyletic nature of the family Endomychidae has been known for a long time (Slipinski & Pakaluk 1992) and was confirmed with molecular analyses by Robertson et al. (2008) that grouped the subfamily Anamorphinae with the Corylophidae, and the rest with the Coccinellidae. Later analysis by Tomaszewska (2005), based on adult and larval characters, failed to confirm a sister relationship of the Endomychidae and Coccinellidae.

The comprehensive **molecular study** of beetles by Hunt et al. (2007) placed the family Alexiidae or the pair of Alexiidae plus Anamorphinae (Endomychidae) as the sister group of the Coccinellidae. Molecular analysis of the Cerylonid complex by Robertson et al. (2008) proposed the subfamily Leiestinae (Endomychidae) or the complex of Endomychidae (part) plus (Corylophidae plus Anamorphinae (Endomychidae)) as sister groups of the Coccinellidae.

1.1.3 Feeding habits

In either case, the sister group of Coccinellidae, and their common ancestor, were probably **fungivorous** (Giorgi et al. 2009). Feeding on hemipterans (mainly Sternorrhyncha) has evolved predominantly in coleopteran lineages that contain fungus feeders (Derodontidae, Silvanidae, Laemophloeidae, Nitidulidae, Endomychidae, Anthribidae) and whose ancestors were fungus feeders (Coccinellidae) or sap feeders (Scarabaeidae: Cetoniinae) (Leschen 2000).

1.1.4 Monophyly of Coccinellidae

The **monophyly** of the family Coccinellidae was based on morphological synapomorphies, and has repeatedly been supported by molecular phylogenetic analyses (Hunt et al. 2007, Robertson et al. 2008, Giorgi et al. 2009), even early ones (Howland & Hewitt 1995) that did not place the family in the Cucujiformia. The first to recognize the morphological synapomorphy (although the term did not exist at that time) of

the family, the **siphonal structure of penis**, was Verhoeff (1895).

1.2 CHARACTERISTICS OF THE FAMILY

The family Coccinellidae may be distinguished from the rest of the cerylonid complex by the combination of the following **adult characters**: (i) five pairs of abdominal spiracles, (ii) tentorial bridge absent, (iii) anterior tentorial branches separated, (iv) frontoclypeal suture absent, (v) apical segment of maxillary palps never needle-like, (vi) galea and lacinia separated, (vii) mandible with reduced mola, (viii) procoxal cavities open posteriorly, (ix) middle coxal cavities open outwardly, (x) meta-epimeron parallel sided, (xi) femoral lines present on abdominal sternite 2, (xii) tarsal formula 4-4-4 or 3-3-3, tarsal segment 2 usually strongly dilated below, (xiii) male genitalia with tubular curved siphon, distally embraced by the tegmen. **Larvae** are armed with setae and setose processes (three pairs on each abdominal segment), antennae of one to three segments, not over three times as long as wide, frontoclypeal suture absent (except some Epilachnini). Pupae of coccinellids are of the type **pupa adectica oblecta** – all appendages are glued to the body by exuvial fluid. The pupa is attached to the substrate by the tip of the abdomen. Coccidophagy is a synapomorphy for the family, other feeding habits, including mycophagy, are secondary (Giorgi et al. 2009).

Liere and Perfecto (2008) suggested that the evolution of coccinellid morphology was influenced by relationships with ants. The result of a parallel evolution in several subfamilies is a mosaic of various grades of characters and/or apparent similarities, which mosaic may considerably obscure the true phylogenetic relationships within the family. One of these characters may be the enlarged eye canthus, formerly considered an apomorphy of the Chilocorinae, but which probably evolved independently in the Platynaspidini (Slipinski 2007). Mouthpart morphology was used in determining diet and host specificity in Coccinellidae (Klausnitzer 1993, Klausnitzer & Klausnitzer 1997), but it is also constrained phylogenetically (Samways et al. 1997). Major larval types were defined by LeSage (1991). Pupal morphology was used for phylogenetic purposes separately from other characters (Phuoc & Stehr 1974).

1.3 CHANGES IN THE CLASSIFICATION OF SUBFAMILIES

1.3.1 Morphologically based classifications

Six subfamilies of Coccinellidae were recognized by Sasaji (1968, 1971b): Sticholotidinae, Coccidulinae, Scymninae + Chilocorinae, Coccinellinae + Epilachninae. However, his knowledge of non-Japanese taxa was limited. Korscheffsky (1931) classified the genus *Lithophilus* in a separate subfamily on account of the tetramerous structure of tarsus. Klausnitzer (1969, 1970, 1971) distinguished this subfamily (as Tetrabrachinae) from its sister group Coccidulinae based mainly on six sclerites on the pronotum of larvae as apomorphy, while he considered adult tetrameric tarsi as a plesiomorphy. Kovář (1973) added this seventh subfamily (as Lithophilinae) to Sasaji's phylogenetic tree, but later reassigned it to tribal level within the Coccidulinae and proposed another subfamily, the Ortaliinae (Kovář 1996). Chazeau et al. (1990) retained Sasaji's six subfamilies with slightly rearranged tribes.

The **monophyly** of several of the six subfamilies proposed by Sasaji has been disputed. The higher classification of Coccinellidae appears to suffer from the presence of para- and polyphyletic taxa (Vandenberg 2002). This problem is most conspicuous in the formerly basal subfamilies Sticholotidinae and Coccidulinae, and in the fauna of poorly studied regions.

1.3.2 Split of Sticholotidinae

In morphology based studies, Duverger (2003), Slipinski and Tomaszewska (2005) and Vandenberg and Perez-Gelabert (2007) proposed dividing up the highly diverse subfamily **Sticholotidinae**. In *Sticholotis* and allies, the terminal segment of the maxillary palp has a long obliquely oriented distal sensory surface on one side of the tapered apex, similar to the large sensory surface of the securiform (axe-shaped) palps of derived 'true' ladybirds; while in *Sukunahikona* and allies the sensory surface is small, oval and positioned distally, suggesting a basal position for this group. The subfamily Sticholotidinae also formed an unresolved polytomy in cladistic analysis by Yu (1994).

The subfamily Sticholotidinae was established by Sasaji (1968) with four tribes, whilst Sticholotidinae

sensu Kovář (1996) contained 10 tribes. However, the phylogenetic relations among the constituent tribes remained obscure for a long time, in spite of an attempt at clarification by Gordon (1977). These Sticholotidinae *s. lat.* were characterized (Kovář 1996), among other traits, by the shape of the apical maxillary palp segment which differs from the rest of Coccinellidae (narrowed apically, conical or barrel shaped). However, this applies to the recently re-established **Microweiseinae** (*sensu* Slipinski 2007), while in the Sticholotidinae *s. str.* the last segment is more or less enlarged, approaching the typical securiform shape found in the other Coccinellidae.

These two lineages differ substantially, such as in the shape of the metendosternite, presence or absence of anterolateral carinae of the pronotum, and also in characters of both male and female genitalia. Microweiseinae retained their basal position, while Sticholotidinae *s. str.* appeared among more derived subfamilies. Slipinski (2007) was even stricter, dividing the entire family into only two subfamilies, Microweiseinae and Coccinellinae that contained, in his approach, all other usually separate subfamilies as tribes.

1.3.3 Monophyly of other subfamilies

The traditional **Coccidulinae** constitutes another polyphyletic group which suffers from a paucity of serious global study (Pope 1988, Vandenberg 2002). Coccidulinae was a paraphyletic group in respect to the Scymninae + Chilocorinae in cladistic analysis by Yu (1994) based on adult characters. The genera *Bucolus* and *Cryptolaemus* were variously classified in the past as either Coccidulinae or Scymninae. Pope (1988) proposed combining the tribes of Coccidulinae and Scymninae into a single subfamily. On the other side, Chinese specialists (Pang et al. 2004, Ren et al. 2009) distinguished a higher number of subfamilies: Sticholotinae (*s. lat.*), Scymninae, Ortaliinae, Hyperaspinae, Aspidimerinae, Chilocorinae, Coccidulinae, Lithophilinae, Coccinellinae and Epilachninae.

1.3.3.1 Contribution of immature stages

Savoiskaya and Klausnitzer (1973) regarded the **larval** armature of the **thorax and abdomen** as of considerable taxonomical significance. Savoiskaya (1969) proposed the two tribes Tythaspidini and Bulaeini as

independent, based mainly on morphology of larvae, while the tribe Coccinellini was considered polyphyletic (Savoiskaya & Klausnitzer 1973) only because different genera of this tribe have variable abdominal structures. Cladistic analysis based solely on larval characters would indicate not only paraphyletic and polyphyletic Chilocorinae, Coccidulinae and Scymninae, but also a generally unacceptable topology of the tree (Yu 1994).

1.3.4 Molecular analyses

In their molecular cladistic study, based on cytochrome oxidase I (COI) and internal transcribed spacers (ITS1), Cihakova and Nedvěd (unpublished) found that the subfamily Coccinellinae is monophyletic with the Halyziini at the base. The three subfamilies Chilocorinae, Scymninae and Coccidulinae formed a second closely related group, with the Chilocorini and Platynaspidini not grouped together. COI discriminated well at the intergeneric, interspecific and intraspecific levels (Palenko et al. 2004). On the other hand, Schulenburg et al. (2001) found the extremely long and variable ITS1 sequence to be unsuitable for phylogenetic reconstruction at the subfamily level. A small total **genome size** (0.19–0.99 pg DNA) is typical for many coccinellids, excluding *Exochomus* (Chilocorinae; 1.71 pg) (Gregory et al. 2003).

Although molecular studies usually prove stable for studying higher taxa (e.g. families of Coleoptera, Hunt et al. 2007), the relationships they suggest for lower levels (subfamilies and tribes) are sometimes dubious because of low sample sizes and the gene used. When only four coccinellid genera (*Adalia*, *Coccinella*, *Calvia* and *Exochomus*) were analysed, different outgroups and different tree-searching algorithms yielded strikingly different topologies (Mawdsley 2001). A cladogram based on combining 16S and 12S mitochondrial rDNA, used for determining genetic distances of 8 coccinellid species (Tinsley & Majerus 2007), gave ambiguous results. Even in larger studies, unexpected clades are reported, with only Coccinellinae remaining monophyletic (Hunt et al. 2007). The subfamily Chilocorinae is polyphyletic in the study by Robertson et al. (2008), because the Platynaspidini were grouped with the Hyperaspidini (Scymninae). In the same study, the Scymninae is polyphyletic, the tribe Ortaliini were grouped with the Epilachninae and the Stethorini with the Coccinellinae.

1.3.4.1 Alternative molecular methods

Zhang et al. (1999) used isoenzyme analysis to reveal the relationship between five species of Coccinellidae and Zhang and Zheng (2002) used RAPD analysis to reveal the relationship between six species of Coccinellinae, both with reliable results. Phylogenetic distance was also measured indirectly through the transmission efficiency of male-killing bacteria, which has been found to be perfect within the genus from which the bacterium was isolated, but was lower in less related species of coccinellids (Tinsley & Majerus 2007).

1.3.5 Rejection of the monophyly of subfamilies

A comprehensive molecular phylogenetic analysis of the family is still in progress, but the preliminary results (Giorgi et al. 2009) rejected the monophyly of four of the six subfamilies proposed by Sasaji. The **Sticholotidinae** were split into two unrelated groups, where the Sukunahikonini, Microweiseini and Serangiini formed a basal clade, while the Sticholotidini grouped together with the Exoplectrini and lay higher up the tree. The subfamily **Chilocorinae** might be limited to the Chilocorini + Telsimiini, while the Platynaspini tend to group with the Scymninae. The **Scymninae** may also include the **Ortaliinae** and parts of the Coccidulinae; however, the genera *Bucolus* and *Cryptolaemus* should fall into the Coccidulinae s. str. The **Coccidulinae**, besides being added near or to the Scymninae, lose the Exoplectrini, which group either with the Sticholotidinae s. str. or the Chilocorinae s. str. The monophyly of **Epilachninae** was not rejected, but the sample was too small to support it. The **Coccinellinae** appeared as the only stable monophyletic subfamily. Both Coccinellinae and Epilachninae were monophyletic in a smaller study with 16 species and one gene (COI) (Fu & Zhang 2006). Genera *Epilachna* and *Henosepilachna* were mixed together; tribe Halyziini was embedded deeply in Coccinellini.

Similarly, in another recent molecular phylogenetic reconstruction (Magro et al. 2010) of the family, Coccinellinae remained the single subfamily supported as monophyletic. Although there was a relatively good sample of genes (six, both mitochondrial and nuclear, both ribosomal and protein), this study suffers from low taxon sampling, except for the subfamily Coccinel-

linae. Monophyly of other subfamilies cannot be either rejected or supported. However, a noteworthy finding was the placement of the tribes Tyttaspidini and Halyziini well inside the tribe Coccinellini. The concept of these three tribes should be re-examined.

1.4 CHARACTERISTICS OF THE SUBFAMILIES AND TRIBES

1.4.1 Proposed classification

Based on the above suggestions for reclassifying the higher taxonomy of the family and on molecular evidence, we propose a preliminary classification (see Fig. 1.1) of Coccinellidae with nine subfamilies: (Microweiseinae, (Coccinellinae, (Epilachninae, (Sticholotidinae, Exoplectrinae, Chilocorinae, (Scymninae, Coccidulinae), Ortaliinae))))).

1.4.2 Microweiseinae

The basal subfamily – **Microweiseinae** – is composed of the tribes **Carinodulini**, **Sukunahikonini**, **Microweiseini** and **Serangiini** which, except for an apomorphic much simplified mandible (with single apical tooth and no mola), share many ancestral characters as are seen on the metendosternite with a broad and very short furcate stalk bearing slender anterolateral arms. Male tegmen asymmetrical with no or only slightly differentiated basal lobe. Maxillary palps with long slender apical segment with small sensoric area. Larvae densely granulate bearing single minute seta on each granule, without defence gland openings.

1.4.3 Sticholotidinae

Narrowly defined **Sticholotidinae** s. str. is composed of the tribes Shirozuellini (syn. Ghanini), Cephaloscyminini, **Plotinini**, **Limnichopharini**, **Sticholotidini** and **Argentipilosini**. It is rather heterogeneous and displays both primitive and derived characters. Compactly articulated antenna with well-developed spindle-shaped 1–4 segmented club bearing concentration of short sensory setae on mesal surface of last antennomere. Maxillary palps geniculate, terminally pointed. Larvae broadly fusiform with lateral setose processes, finely granulate and densely pubescent,

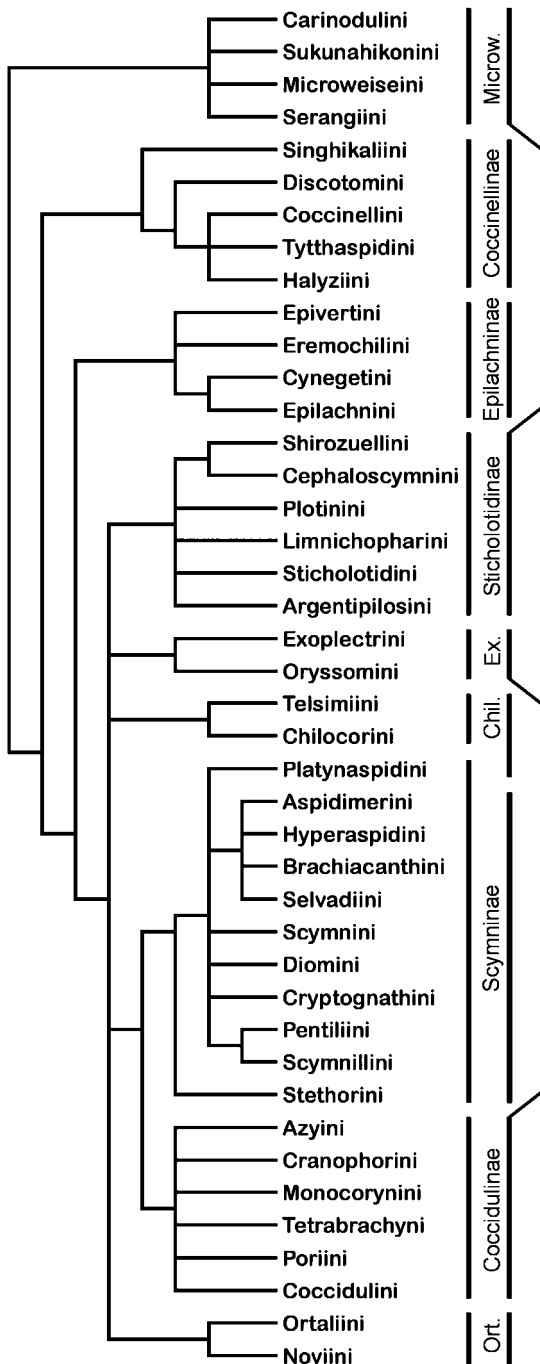


Figure 1.1 Proposed phylogenetic relationships between subfamilies and tribes compared with the classification by Kovář (1996) in right bars. Ort., Ortaliinae; Chil., Chilacorinae; Ex., Exoplectrinae; Microw., Microweiseinae. Tree drawn by Phy.fi online utility (Fredslund 2006).

abdominal segments 1–8 with defence gland openings. Pupa with urogomphi.

Among the tribes included in the Sticholotidinae s. str. an oriental tribe, the **Shirozuellini**, and the **Cephaloscymnini** from the New World are close to each other and more primitive than the rest in having an only slightly derived prosternum and a six-segmented abdomen (although in the Cephaloscymnini the last segment is reduced). However, the head capsule is largely derived in both, somewhat resembling that of the Chilacorinae. The remaining four tribes share a derived five-segmented abdomen.

1.4.4 Coccinellinae

A great number of characters are more or less universal and shared by particular tribes of the subfamily **Coccinellinae**. However, it seems that the **female genital plate** of the 'handle and blade' type is the only true **synapomorphy** of the Coccinellinae. Other characters may be shared with diverse tribes of other subfamilies. Mandible with double apical tooth and molar tooth. Maxillary palp is securiform. Abdomen with six ventrites. Colour pattern may be very striking and aposematic. Eggs are spindle shaped, laid in clusters in upright position, similarly to Epilachninae, while they are laid singly on their side in other subfamilies. Larvae are elongate fusiform with variable setose processes, often with conspicuous colour pattern.

The Neotropical tribe **Discotomini** combines the normal carnivorous type of mouthparts, dorsally shifted antennal insertions as usual in the Epilachninae, and the serrate type of antennae. The oriental **Singhikaliini** is a single tribe within the Coccinellinae represented by pubescent species. The peculiar colour pattern of *Singhikalia* resembles that of the tribe Noviini (Ortaliinae). Fuersch (1990) moved the Singhikaliini into the Coccidulinae. Jadwiszczak (1990) supported their original position in the Coccinellinae as proposed by Miyatake (1972).

The tribes **Coccinellini**, **Tytthaspidini** (syn. Bulaeini) and **Halyziini** (syn. Psylloborini) form a major, species-rich part of the subfamily Coccinellinae, containing the species referred to as 'ladybirds' or 'ladybugs' in the narrow sense.

Although only the tribes Coccinellini and Halyziini are usually considered distinct, the third (Tytthaspidini) should also be treated as a distinct tribe because of the parallel development of certain important characters, especially the **frons** and **pronotum**. Both

plesiomorphic and apomorphic types of frons occur here in parallel. Thus, the apomorphic frons type is homoplastic between the Tytthaspidini and the other tribes.

The plesiomorphic type of pronotum is quadrate with anterior corners which are never pointed, and anterior margin slightly emarginate, not or partly concealing the head; this character state is shared by certain, usually elongate members of all three tribes. However, the apomorphic state of a trapezoidal pronotum which is strongly emarginate anteriorly is predominant in the Halyziini and less frequently observed in the Coccinellini and Tytthaspidini.

In tribe **Halyziini** the eye canthus does not divide the eye (plesiomorphy), with the eye facets sometimes coarse, and a simple flagellum on the median lobe of the male genitalia. The mandible, with several small teeth arranged in a row, is an adaptation to mycetophagy. A similar mandible and a non-typical feeding habit occur also in some genera of the **Tytthaspidini** (*Tytthaspis*, *Bulaea*, *Isora*). The peculiar **simple type of male genitalia** in the above genera and the common type of **colour pattern** are striking. Due to the position of Tytthaspidini and Halyziini well inside the tribe Coccinellini in some molecular analyses (Magro et al. 2010) and similarity of some genera of tribe Coccinellini in their morphology and life history, the concept of these tribes must be widened (see Appendix: List of Genera). Differentiation of several parallel lineages within the numerous genera of the tribe **Coccinellini** may be expected to be identified in the future.

1.4.5 Epilachninae

The subfamily **Epilachninae** is characterized by synapomorphic features in the organization of the **mouthparts** in both adults and larvae, adapted to their phytophagous habit. The mandible possesses multidentate terebra but lacks a basal tooth (mola). The galea of the maxilla is large, round to transversely oval, and the mentum converges anteriorly. Maxillary palp of adults strongly securiform. Antennae are inserted in a depression on inner side of eye. Eggs are laid in clusters in upright position, similarly to Coccinellinae, while they are laid singly on their side in other subfamilies. **Larvae** are oval, armed with dense, **spinose senti** but without gland openings. Head with epicranial stem and frontal arms V-shaped.

The Epilachninae include four tribes, i.e. Epivertini, Epilachnini, Cynegetini and Eremochilini. The main

part of the subfamily is formed by two tribes (Epilachnini and Cynegetini), both rich in species although the latter tribe is limited mostly to the Neotropical and Afrotropical regions. The two tribes differ mainly in the presence (in **Cynegetini**, syn. Madaini) or absence (in **Epilachnini**) of the anterior fovea of the elytral epipleura. They both have apomorphic positioning of the antennal insertions, which are dorsal and placed at or behind the level of the anterior margins of the eyes.

The tribe **Epivertini**, represented by the single Chinese species *Epiverta chelonina*, displays the plesiomorphic position of the antennal insertions, although the Cassidinae-like shape of the adult body is highly derived. The Neotropical tribe **Eremochilini** is characterized by cylindrical body form and quite hypognathous head with opistognathous mandibles and without labrum.

1.4.6 Exoplectrinae

For a long time the tribe Exoplectrini was considered a true member of the subfamily Coccidulinae. However, Gordon (1994) grouped it with the tribe Oryssomini and established the subfamily **Exoplectrinae**. Molecular analyses place the tribe Exoplectrini either near the Sticholotidinae *s. str.* or near the Chilocorinae *s. str.*, but never near any part of Coccidulinae. This leads us to treat this taxon on the subfamily level. However, morphological characterization of the subfamily is difficult. The adults share a finely expanded, anteriorly emarginate clypeus with the Azyini (Coccidulinae). Although the structures associated with the insertions of various movable parts of the body in the Exoplectrinae are poorly developed, they are very striking in the Azyini. Apomorphic states in the **Exoplectrini** opposite to Azyini are also evident in the antenna (with large lobate scape) and wide apical segment of the maxillary palp. All steps in the development of coccinellid eyes may be seen within genera of the Exoplectrinae. Some genera possess a compact and asymmetrical antennal club. Abdomen has five ventrites. The Exoplectrinae tribe has a Gondwanan origin. They are suspected to be not only predators but also plant feeders (Gordon 1985).

1.4.7 Chilocorinae

In the phylogeny of the three tribes until now placed in the subfamily **Chilocorinae**, Sasaji (1968)

proposed the sequence from primitive to advanced forms from **Telsimiini** through **Platynaspidini** to **Chilocorini**. They all show a complete fusion of the clypeus with the eye canthus, together with distinctly ventral insertions of the antennae. The two former tribes do not occur in the New World. Chilocorini occur in the Old World, and one homogeneous line of Chilocorini genera has developed independently in the New World, the monophyly of which is suggested by the synapomorphic absence of a basal marginal line on the pronotum, a character shared by all the American species. Larvae of the **Telsimiini** are covered with waxy exudations like those of the Scymnini. Adults are pubescent. Adult **Chilocorini** are often smooth, and the **larvae** possess **very long setose processes** for mechanical defence. They are mostly coccidophagous, and the mandibles have a single apex.

The **Platynaspidini** share with the Chilocorinae s. str. (i.e. Telsimiini and Chilocorini) the **enlarged eye canthus**, dividing the eye and covering the antennal insertion. Molecular analysis, however, groups them with the Scymninae. Adult Platynaspidini are covered by long hairs; the **larvae** are very wide, have **short pubescence** and lack long setose projections. They are aphidophagous and myrmecophilous.

1.4.8 Ortaliinae

Two tribes (Noviini and Ortaliini), that combine some characters of the Coccidulinae and Scymninae and some Coccinellinae and even Epilachninae, have been placed in the separate subfamily **Ortaliinae** (Kovář 1996). Their body is robust, oval to rounded, discontinuous, of medium to large size. Pubescence is simple and short. The eyes are large to strikingly enlarged, prominent anteroventrally at the sides, with the eye facets small to minute. The antennal insertions are placed between the eyes. The apex of the mandible is bifid; a basal tooth is present. The pronotum is trapezoidal, emarginate anteriorly with the anterior corners widely rounded and the posterior corners not pointed. The elytral epipleura are not foveolate for reception of legs, and rather broad. The colour pattern, if present, is simple, not strongly aposematic, resembling that of certain Epilachninae.

In the tribes **Noviini** and **Ortaliini** there are some noteworthy common trends: enlarged eyes, shortened antenna and shortened elytral epipleuron, broadened

genital plate and spermatheca in the female, along with a certain peculiarity in larval organization: the lateral setose projections are nipple-shaped, and there are abundant clavate setae at the apex of the tibiotarsus. **Larvae** are covered by **poor waxy secretions**. The **Noviini** differ from the **Ortaliini** in the derived state of the antenna (7–8 segments, enlarged scape), the vertical basisternal lobes of the prosternum, and in the externally angulate legs and trimerous tarsi. *Ortalia* feeds on Psylloidea, larvae of some species are myrmecophagous.

1.4.9 Coccidulinae

The subfamily **Coccidulinae** has been considered to have the most primitive body organization of the Coccinellidae without the basal Microweiseinae. Six tribes were placed in the Coccidulinae by Chazeau et al. (1989) in their systematic survey: Tetrabrachyni, Coccidulini, Sumniini, Exoplectrini, Noviini, and Azyini. Fuersch (1990) added the Monocorynini and Singhikaliini (now Coccinellinae) to the Coccidulinae. Gordon (1974, 1994) excluded the Oryssomini from the Cranophorini and placed near the Exoplectrini, while Fuersch (1990) transferred the Oryssomini directly from the Sticholotidinae to the Coccinellinae. The tribe **Noviini** has been a **permanent member** of the **Coccidulinae** in many authoritative works since Sasaji (1968). To make Coccidulinae a natural group, some taxonomic changes in the position of several tribes are necessary. A combination of morphological and molecular studies suggests the following tribes as probably true members of the subfamily Coccidulinae: Tetrabrachini, Monocorynini, Coccidulini, Cranophorini, Poriini and Azyini. All tribes are of Gondwanan origin.

The body organization of Coccidulinae is rather simple and contains a set of plesiomorphic character states: the **antennae** are **long**, 10–11 segmented, with the basal flagellomeres slender and the club more or less striking, always with a well-developed apical segment (distinction from Scymninae); the pronotum is commonly quadrate with the anterior corners broadly rounded and the anterior margin slightly emarginate, so that in several tribes the head is partly covered by it; the posterior corners are more or less pointed. The subfamily may be characterized by a slightly convex, more or less elongate, moderately discontinuous body shape, well developed and sometimes

double pubescence and elytral punctation. Eye facets are coarse. **Larvae** are fusiform, dorsal and lateral surfaces with diverse **setose processes**, many covered by at least sparse **waxy secretions**.

In the **Cranophorini** the pronotum is corylophid-like, where the head is completely hidden under the anterior lobe of the pronotum. Basal depressions on the pronotum are present only in the **Monocorynini** and they have also a large, quite compact antennal club with some resemblance to that of ants. The epipleuron is usually broad and entire without distinct foveae, but in the Azyini the epipleuron is modified, with the anterior fovea strikingly margined on the outer side even if the fovea is shallow.

The hypothesis that the **Tetrabrachini** is a distinct tribe rests solely on their unusual adaptations, such as tetramerous tarsi facilitating soil dwelling and six sclerites on pronotum of larvae. The characters of the **Azyini** are derived; the structures associated with the insertion of various movable parts of the body are very striking. The clypeus is derived, and the antenna (especially the small scape) and the apical segment of the maxillary palp (also small) remain plesiomorphic in the Azyini.

Some genera, endemic in the Australian region, i.e. *Cryptolaemus*, *Bucolus*, *Bucolinus* (but not *Scymnodes*) were considered to fall in the Scymnini, perhaps due their scymnoid or platynaspoid appearance. However, they are not true Scymnini having a plesiomorphic long antenna with club of the Coccidulinae type (well-developed terminal segment). The elytral pubescence of *Cryptolaemus* does not have vortices and the size is larger than in most Scymnini. However, **larvae** of *Cryptolaemus* and *Bucolus* are covered by an **extensive waxy secretion** like Scymnini. *Bucolus* (and included *Bucolinus*) has bilobate tibiae like *Azya*. These genera may be included in the Azyini. The tribe **Poriini** possesses fine faceted eyes, reduced prosternum, and metallic colouration. The nominal tribe **Coccidulini** seems to be a likely candidate for further splitting into several lineages.

1.4.10 Scymninae

Sasaji (1968) defined the subfamily **Scymninae** as composed of the tribes Scymnini, Stethorini, Hyperaspini (correctly Hyperaspidini), Aspidimerini and Ortaliini. Later, Sasaji (1971a, b) further added the

Scymnillini and Cranophorini (now considered Coccidulinae). The tribes **Cryptognathini** and **Selvadiini** were established by Gordon (1971, 1985) as members of the Scymninae, the separation of Brachiacanthini (syn. Brachiacanthadini) from Hyperaspidini has been proposed by Duverger (1989), and finally Gordon (1999) separated **Diomini**.

Scymninae have a rather compact, minute to small-sized body. The subfamily is distinguished from the **Coccidulinae** by **short antennae** and a weakly securiform to parallel-sided apical segment of the **maxillary palps**. The shape of the antenna is very important in the study of the phylogeny of Coccinellidae, but not always strictly applied though it is decisive. The reduced apical segment of the antennal club, often combined with distal flagellomeres being gradually broadened, provides a clear synapomorphy for the Scymninae. The **head** has an arched frons, rather large eyes with inner orbits usually parallel and facets that are usually fine. The **pronotum** is apomorphic, of the trapezoidal type, emarginate anteriorly, and never conceals the head, with anterior angles that are narrowly rounded to pointed and sides that frequently descend ventrally. The **larvae** have simple setose processes and are typically covered in **waxy exudations**.

The above listed characters made it possible to exclude the tribe **Cranophorini** and genera ***Cryptolaemus*** and ***Bucolus*** (now considered Coccidulinae) and tribe **Ortaliini** (Ortaliinae) from the Scymninae.

The narrowing and shortening of the **elytral epipleuron** and the broadening of the **mesocoxal distance** distinguish the subfamily Scymninae from the **Chilocorinae**. Complete fusion of the **clypeus with the eye canthus** together with distinctly ventral insertions of the antennae clearly distinguished Chilocorinae from typical Scymninae, but is no longer applicable after including **Platynaspidini** into Scymninae. The long and narrow eye canthus in front of the eyes is present in all groups of Scymninae, while the derived shortened type occurs in some genera of Scymnini and Hyperaspidini.

Probably the most primitive tribe of Scymninae is the **Stethorini** in having somewhat coarsely faceted eyes, a primitive abdomen (six ventrites), plesiomorphic male and female genitalia and (apart from the anteriorly lobate prosternum, partly concealing the mouthparts) no special structure for reception of moveable parts of the body. Stethorini is separated from other tribes of Scymninae because the **clypeus**

is not emarginate around the antennal bases. The Stethorini have a peculiar feeding specialization (acarophagy), and worldwide distribution.

Plesiomorphic states of the prosternal carina and spermatheca are present in two Neotropical tribes, the Scymnillini and Pentiliini. These tribes have an apparently five-segmented abdomen and an autapomorphic development of the prosternum, which in its most apomorphic state forms an entire anterior lobe partially concealing the mouthparts. The elytral epipleuron is strongly foveolate in the **Pentiliini** and there is an unusual reduction of the apophysis of the ninth sternite in the **Scymnillini**.

A group of tribes Aspidimerini, Brachiacanthini, Selvadiini and Hyperaspidini possesses many derived characters including the particular states of the insertion of movable body parts, and the characters of genitalia of both sexes. The penultimate antennal segment is strikingly elongate. The exclusively Oriental tribe **Aspidimerini** remains relatively primitive in the degree of development of the eyes, male genitalia and also the spermatheca, as well as being completely pubescent. They have extremely short antenna and maxillary palpus. The **Hyperaspidini** have derived states in the above-mentioned characters, like loss of pubescence and usually bare genitalia. The body is not perfectly limuloid. The larvae have a wide body. The **Brachiacanthini** and **Selvadiini** have a combination of plesiomorphic and apomorphic states; both are restricted to the New World. The **Platynaspidini** (formerly Chilacorinae) may be related to these tribes.

The **Scymnini** have rather large, finely faceted, laterally not prominent pubescent eyes with parallel inner orbits, the pronotum is truly trapezoidal with very narrow anterior angles and a deeply emarginate anterior margin. The epipleuron is very narrow with its inner edge not reaching the epipleural apex. The body is **pubescent**. **Larvae** are covered by extensive **waxy secretions**.

1.5 FUTURE PERSPECTIVES

While coccinellid subfamilies are more or less worldwide in distribution, many tribes are restricted to particular biogeographical regions, and this has resulted in alternative classifications (Vandenberg 2002). Some derived groups of species are often classified under a separate name, leaving the rest of related

species as a paraphyletic assemblage. Vandenberg (2002) proposes these sets of genera to be reunited or paraphyletic genera to be split to achieve a balanced classification.

Knowledge of the relationships of subfamilies and tribes within the family will allow us better to discriminate general patterns and specific cases, as recommended by Sloggett (2005). It will enable us to name precisely some compared groups – e.g. contrast is often incorrectly emphasized between **aphidophagous** (in fact almost exclusively Coccinellini) and **coccidophagous** coccinellids (in fact a heterogeneous assemblage from the Chilacorinae, Scymninae plus Coccidulinae clade).

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