Eumolpinae – a widely distributed and much diversified subfamily of leaf beetles (Coleoptera, Chrysomelidae)

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Summary

This communication is a general review of Eumolpinae, a subfamily of Chrysomelidae. The subfamily includes more than 7000 species. It is specially numerous and much diversified in the tropics, with both the attributes declining northward. It has several distinctive features, and is clearly related to Clytrinae, Cryptocephalinae, Chlamisinae, Lamprosomatinae, Hispinae, and Cassidinae. Megascelidines, though generally treated as a subfamily, they should be taken as a part of Eumolpinae. Through some larval features, Eumolpinae seem related also to Galerucinae-Chrysomelinae. Separation from Eumolpinae of the primitive eumolpines, the Tribe Spilopyrini, and inclusion of *Syneta* among Eumolpinae have been contradicted.

1. Introduction

Eumolpinae is a large subfamily of Chrysomelidae. It includes more than 500 genera and 7000 species. More eumolpine species are being discovered and described every year. Chaboo (2007), in her recent monograph on Cassidinae, shows Eumolpinae as third in species diversity after Galerucinae (= Galerucinae Jacoby 1886 + Alticinae/Halticinae Harold 1875) and Cassidinae (= Cassidinae Stephens 1831 + Hispinae Peringuey 1898).

Eumolpinae are widely distributed. They are numerous in the tropics and subtropics. Many Eumolpinae remain to be described and recorded, particularly in tropical Africa, tropical America, and the Pacific Basin including Sunda Islands, New Guinea, and New Caledonia.

In this review paper we aim at summarizing the present knowledge about the subfamily Eumolpinae.

2. Distinctive features and taxonomy

Eumolpinae are characterized by oblong, convex, and globose form, but some are quite elongated. Head not strongly hypognathous, partially retracted into the prothorax, with frons perpendicular to the body axis, antennal insertions not closely approximated. Antennae are usually filiform, but sometimes with the terminal antennomeres a little swollen. Mandibles two to three toothed, maxillary palpi three segmented. Eyes not prominent. Prothorax margined, sometimes without margins. Metendosternite not at all hylecoetoid (Crowson, 1955). Tarsi with the first three tarsal joints dilated and almost triangular, the third joint extending as lobes on sides of the last part of the tarsus (Figure 1); tarsal claws mostly appendiculate or bifid (Figure 2, D), but in some cases simple. Wings with two cubital cells (1 Cuc and 2 Cuc), and with a subcubital fleck. Ninth abdominal segment terminal. Elytra with well defined shoulders. Pygidium not exposed, and aedeagus with clear differentiation of flexible basal hood and the rigid and ventrally curved aedeagus proper.
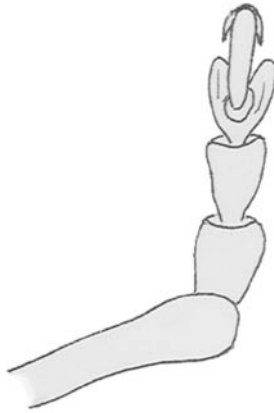

Figure 1. *Colasposoma crenulatum*, foretarsus (from Zoia, 2007b).

Eumolpinae are generally smooth, and often shiny with metallic colours. But some are dull coloured, some rugose, and some have elytra and body densely hairy, e.g. *Colasposoma fairmairei* Lefevre, *Aoria nigripes* Baly, all *Aoria*, and species of *Trichochrysea* from S. E. Asia, *Nerissus tuberculatus* Jacoby from Congo etc. The hairs may be short or long, and irregularly distributed, or seriate. In some genera, e.g. *Glyptoscelis*, the body is covered with white scales.

Eumolpines, in the first sight, look like Chrysomelinae; the main adult differences between the two: (i) Eumolpine wings have two cubital cells (1Cuc and 2 Cuc), while Chrysomelinae have only one cubital cell, 1Cuc (see Figure 3 i in Suzuki, 1994),
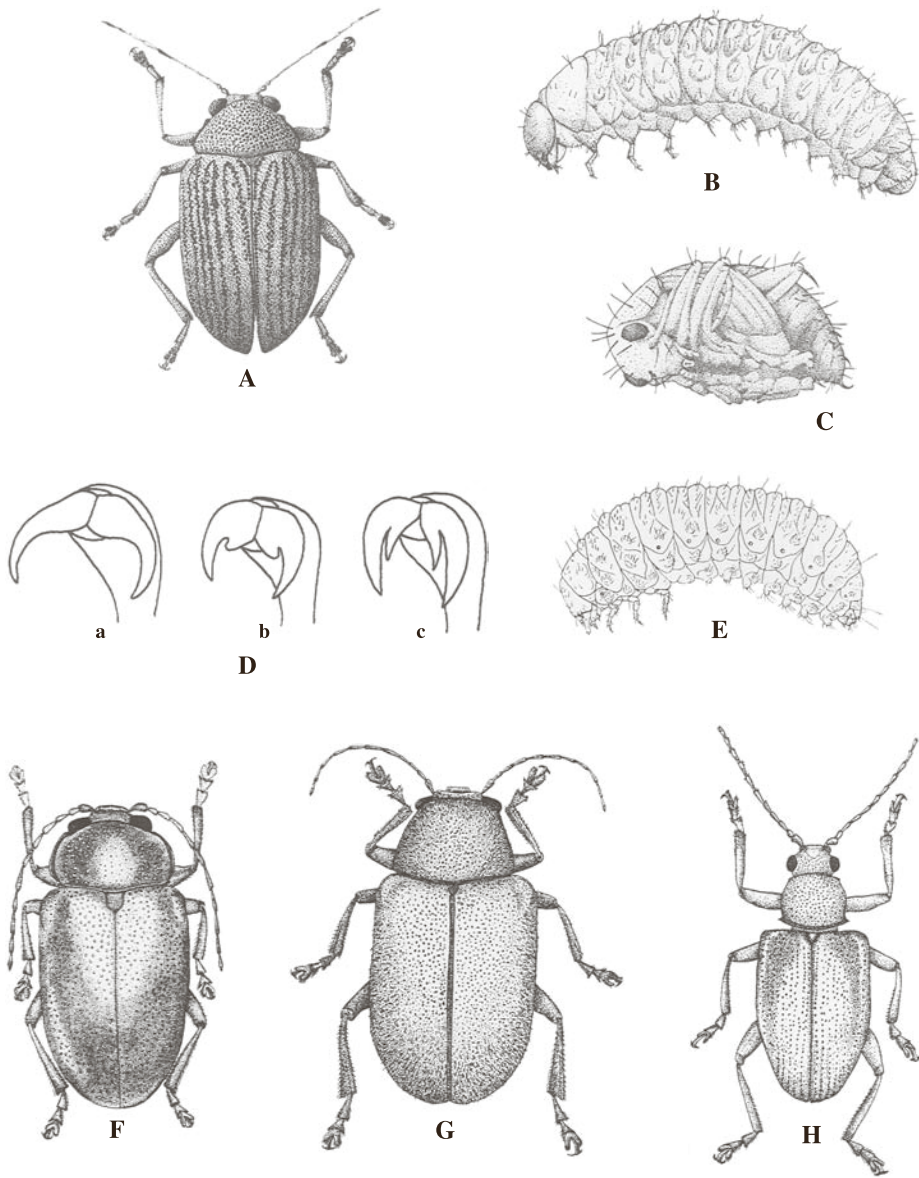
Figure 2.

A: *Colaspis hypochlora* Lefèvre. Adult habitus. Colombia.

B: *Colaspis hypochlora*. Larva, 3rd instar.

C: *Colaspis hypochlora*. Pupa.

D: Claw types among Eumolpinae. a) simple. b) appendiculate. c) bifid.

E: Larva of *Chrysochus auratus* F. USA. Lateral view.

F: *Dematochroma helleri* Jolivet, Verma and Mille. New Caledonia.

G: *Dematochroma doiana* Jolivet, Verma and Mille. New Caledonia.

H: *Taophila mantilleri* Jolivet, Verma and Mille. New Caledonia. A, B, and C from Salt, 1928; D, from Yu et al., 1996; E, from Böving and Craighead, 1930; F, G, and H from Jolivet et al., 2008.

(ii) the tarsal structure in eumolpines is characteristic, as described above, but in Chrysomelinae the third tarsal segment, as seen from beneath, is "entire apically or with a slight median notch" (Borror et al., 1976), and (iii) Aedeagus in eumolpines presents a clear differentiation into the aedeagus proper and the basal hood. (In Chrysomelinae the basal muscular bulb formation in the aedeagus is at an incipient stage. The basal orifice has only a limited anteroposterior extent, and the median portion of the 1st spiculum or the tegminal apodeme does not take the form of a prominent vertical keel nor of a horizontal shield like plate, Verma, 1996), and (iv) on average Eumolpinae are much smaller than Chrysomelinae.

Authors differ as to the number of tribes in the subfamily. While Jacoby (1908) divided the subfamily into 17 tribes, Seeno and Wilcox (1982) mention only 14 tribes. Flowers (1999), in his paper on male genitalia of Eumolpinae, covers nine tribes, including the Synetini. Placing *Syneta* among Eumolpinae is controversial (*vide infra*). Flowers points out that Neotropical eumolpine fauna is mostly constituted by the tribe Eumolpini, but in the Old World two tribes are dominant, the Typophorini and the Adoxini.

3. Biology and life-history

3.1. *Life-history*

All larvae of higher or typical Eumolpinae develop entirely in soil, and are root feeders. They don't have ocelli (Figure 2, B, E). Reid (2000) (as cited in Australian Biological Resources Study, 2006) says that in some cases there are two ocelli on each side of the larval head. They are elongated or C-shaped grubs. All the eumolpine larvae look very similar (Boving and Craighead, 1930; Peterson, 1960; Stehr, 1991; Reid & Storey, 1993).

Eggs are inserted into soil. Pupation is also subterranean. Pupal features in Eumolpinae have been described by Cox (1996).

The above account holds for higher Eumolpinae. Biology and life-history of primitive Eumolpinae will be later discussed in this review.

3.2. *Biology of Chrysochus*

Several workers (*vide infra*) have recently studied extensively the biology of the eumolpine *Chrysochus*. These studies have led to some significant inferences. These inferences about *Chrysochus* biology, in view of a number of previous studies and studies to come, should prove to be of a much wider application.

Two species of *Chrysochus*, *C. auratus* Fab. and *C. cobaltinus* LeConte feed in North America on species of the genus *Apocynum* (Apocynaceae). *Chrysochus auratus* is strictly monophagous, feeding exclusively on *Apocynum cannabinum*. But *C. cobaltinus* populations feed on three different species, *Apocynum cannabinum*, *Asclepias speciosa*, and *Asclepias eriocarpa*, the latter two species belonging to Asclepiadaceae. Different populations of *Chrysochus cobaltinus* differ considerably in their food preference.

Plants of some species of Apocynaceae and of Asclepiadaceae contain toxic compounds, the cardenolides. *Chrysochus auratus* and *C. cobaltinus* feed on the plant species

with cardenolides. All other species of the genus feed on plants of Apocynaceae and Asclepiadaceae without cardenolides. On comparing DNA profiles of *C. auratus* and *C. cobaltinus* with other species of the genus, which do not feed on plants with cardenolides, Labeyrie & Dobler (2004) have noted only a small difference between the two. The latter species have the code for the amino acid asparagine at the position 122, whereas in the two cardenolides feeding species the code at this position is for another amino acid, histidine. Thus it seems that a small mutation at this point has helped the two species of *Chrysochus* to invade a new niche, namely plant species with cardenolides.

The above mentioned point mutation has been of help to the two species of *Chrysochus* not only in invading a new niche but also in another way. Beetles of the genus *Chrysochus* release a secretion from their pronotal and elytral glands on being disturbed. Dobler et al. (1998) have analyzed this secretion in three species of *Chrysochus, C. auratus*, *C. cobaltinus*, and *C. asclepiadeus* Pallas, the last named species, a European species, feeding on a species of Asclepiadaceae lacking in cardenolides. They have noted that the secretion in *C. auratus* and *C. cobaltinus* contains cardenolides, whereas in *C. asclepiadeus* the secretion has phenylalanine, tryptophane, leucine, and diacetyl putrescine, and is devoid of cardenolides. The contents of the secretion of *C. asclepiadeus* are not toxic, but, as they are bitter in taste, may have a repellent effect on the predator. Cardenolides are both toxic and also with a repellent effect due to a bitter taste. The volume of the secretion by *C. asclepiadeus* is much more than in the two cardenolides feeding species. Thus the development of insensitivity to cardenolides is also of a defensive value.

It has been noted above that, while *C. auratus* is strictly monophagous, *C. cobaltinus* feeds on three different species of the host plants, preference for the host varying in different populations of the beetle. Agreeing with this is the observation of Dobler and Farrell (1999) that mt-DNA sequence shows almost uniformity among populations of *C. auratus*, but there is considerable genetic divergence among populations of *C cobaltinus*, indicating lack of gene flow among the populations.

Dobler and Farrell (1999) have made sequence based phylogeny estimates, and have tried to reconstruct the historical diet evolution of *Chrysochus*. They have inferred, "Starting from an original association with Asclepiadaceae, the common ancestor of *C. auratus* and *C. cobaltinus* included Apocynaceae in its diet. The strict specialization on *Apocynum* and loss of acceptance of Asclepiadaceae observed in *C. auratus* could have resulted from a process similar to that displayed by *C. cobaltinus* populations."

Chrysochus auratus and *C. cobaltinus* have generally been considered as allopatric in distribution in N. America. But Peterson et al. (2001) have found two narrow areas, in which they are sympatric. One of these areas is about 25 km wide, and is located in South-central Washington. In this area they have identified hybrids between the two species through morphological features as well as by comparison of allozymes, the latter by study of three species specific loci. At one site in the zone of sympatry they have found that 22.9% of all matings were heterospecific, and 20.8% of all mating involved at least one hybrid individual. In spite of these frequencies of all matings only 10 to 15% of the analyzed individuals were F_1 hybrids. These observations suggest that the hybridization was not being favoured by selection.

Peterson et al. (2005a) have tried to measure fitness level of the hybrids between the two species, *C. auratus* and *C. cobaltinus*, using both direct and indirect methods. For the direct approach they have recorded mating frequency, longevity, fecundity and fertility of the hybrid females. In the indirect approach they made a prediction about frequency of multilocus hybrid genotype in a chosen area on basis of heterospecific matings in the previous generation. In the direct approach they noted that hybrid females produced fewer eggs than their parents, and their eggs failed to hatch in the lab. They had expected that in the chosen site 15.8% should have multilocus genotypes other than expected in the parentals or F$_1$ hybrids. But they found no such genotype in the chosen area. These observations clearly point to loss of fitness in the hybrids.

Peterson et al. (2005b) have shown that reproductive isolation between *C. auratus* and *C. cobaltinus*, which is due to extremely low fitness of hybrids, is reinforced by male choice. Males prefer to mate with conspecific females, because a heterospecific mating reduces the opportunity to mate with females of the same species. The authors say, "…there is evidence for male choice in these beetles and that male mating mistakes may be costly, due to reduced opportunities to mate with conspecific females."

Peterson et al. (2007) have found that in the two species, *C. auratus* and *C. cobaltinus* the mate choice is also influenced by cuticular hydrocarbons profile, which is both sex and species specific.

These studies suggest how, through a small mutation, a polyphagous species may succeed in invading a new niche and evolve into a new species, how, through dietary evolution oligophagy may lead to monophagy, how related species are kept apart, even in sympatry, through reproductive isolation, and how different factors contribute to such a reproductive isolation. Such inferences are obviously of a much wider application in the Animal World.

Wilson (1934) has studied general external and internal anatomy of *C. auratus* (Figure 2, E), and information on gross morphology of this eumolpine may be had from this paper.

3.3. *Trophic selection*

For the beautiful neotropical *Platyphora* (Chrysomelinae), plant selection is often among Solanaceae or Apocynaceae, and the tendencies are similar among many Eumolpinae: *Colaspis* and related forms on Solanaceae, *Eumolpus*, *Corynodes*, *Platycorinus*, *Chrysochus* on the Asclepiadaceae-Apocynaceae complex (Jolivet, 1971, 1982, 1988; Jolivet & Hawkeswood, 1995; Jolivet & Verma, 2002). It seems quite certain that this choice is in relation with alkaloid sequestration and latex protection to the insect feeder. According to Sennblad and Bremer (1996), the cladistic analysis shows that the Asclepiadaceae are nested within the Apocynaceae. The Apocynaceae and Asclepiadaceae total approximately 5000 species within the order of Gentianales (Asteridae). The plants contain indole alkaloids and cardenolides, and self defense is probably one of the reasons of the food choice among many Chrysomelinae and Eumolpinae. Species of one genus (*Platycorinus*) feed on Asclepiadaceae in Asia and other species of the same genus choose Euphorbiaceae in Africa, both latex producing

plants. There seems to be a tendency in eumolpines to choose tall plants, for instance, low growing plants, such as *Vinca* and *Catharanthus* (Apocynaceae) do not harbour any eumolpines, while others, also low growing, like *Asclepias* (Asclepiadaceae) do. Generally bushes (*Calotropis*) and trees in the tropics are the hosts of many species, but we cannot generalize as *Leptadenia*, host-plant of *Euryope* in Africa, is a small climber or creeper.

It seems that, in Europe, the palaearctic *Chrysochus asclepiadeus* Pallas is becoming rarer. This species of *Chrysochus* feeds on *Vincetoxicum officinale* Moench., and various other Asclepiadaceae. Its biology has not been studied, and on the contrary, the American species were the object of many studies (see subsection 3.2). It is evident that winged species can survive, while apterous or brachypterous ones are disappearing with spread of urbanisation. In the Palearctic, *Chrysochus* species feeds on *Cynanchum* and *Vincetoxicum* (Asclepiadaceae), and in the Nearctic, they feed on *Asclepias* (Asclepiadaceae) and *Apocynum* (Apocynaceae) (Dobler, 2004). The various species of the Asian *Chrysochares* feed on *Cynanchum*, *Vincetoxicum* and *Antitoxicum* (Asclepiadaceae) as well as on *Apocynum*, *Poacynum* and *Trachomitum* (Apocynaceae), but some have been found on *Calystegia* (Convolvulaceae). In Vietnam, it has not been rare to find eumolpines on the Asclepiadaceae and on related plant family Convolvulaceae. Asian species of *Platycorinus* feed on *Calotropis*, *Cynanchum*, *Tylophora*, *Atherandra* (Asclepiadaceae) as well as on *Trachelospermum* (Apocynaceae). The phylogenetic relationships of those genera are still to be reconsidered. In Africa, *Platycorinus* species have been found on *Mallotus* (Euphorbiaceae) and *Asclepias* (Asclepiadaceae). The host plant choice has led to the evolution in *Chrysochus* milkweed beetles in America (Dobler & Farrell, 1999). The big *Eumolpus*, in the New World feed also on Asclepiadaceae and also on Apocynaceae. Many Spilopyrini, including *Bohumiljania*, feed on various Myrtaceae, but host plant choice varies among some genera of the tribe Spilopyrini.

Among the Eumolpinae we come across many other plant families as normal hosts. For instance, one species of *Rhembastus* has been found as feeding on *Bryophyllum delagoense* Schinz, a Crassulaceae in Madagascar (Witt et al., 2006), but other species of the genus *Rhembastus* have been collected from a wide range of plants (Jolivet and Hawkeswood, 1995). *Cleorina modiglianii* Jacoby feeds exclusively on *Rubus* spp. (Rosaceae) in Sumatra, but other species of this Indonesian genus feed on various plants belonging to other plant families. Generally species of Eumolpinae are mono- or oligophagous, but the choice, if we consider a genus, is much wider. Several genera seem to be polyphagous on various flowering plants, mostly the small brownish Asian species, but no absolute rule can be given. It seems also that often the larvae feed on the roots of the normal host plant of their adults, but, for instance, for some cocoa pests in Brazil, roots of Poaceae can also be eaten by the larvae, as well as cocoa roots (Ferronato, 1988). Those cocoa Eumolpinae are generally polyphagous as adults and larvae. Associated with the genital tract, there are a pair of vesicles containing bacterial endosymbionts, transmitted externally by the egg shell eaten by the larvae (Becker and Ferronatto, 1990; Becker, 1994). Angiosperms and several Gymnosperms are hosts of Eumolpinae, but so far there is no real record from ferns, which are common hosts for

Alticinae. Several Eumolpinae are attracted by *Vitis*, but, like *Bromius obscurus* L., many feed normally on *Epilobium angustifolium* L., and still others, e.g. *Syagrus* spp. in Africa, are specially attracted by Malvaceae. Many other eumolpines are really polyphagous.

Several species of *Colaspis* (*C. hypochlora* Lefèvre, (Figure 2, A,B,C) *C. blakeae* Ostmark, *C. gemellata* Lefèvre, *C. ostmarki* Blake and *C. submetallica* Jacoby) may infest fruits, e.g. bananas, in South America (Gowdey, 1926; Salt, 1928; Ostmark, 1975). The adult removes the outer layers and the underlying parenchyma of the fruit skin. Eggs are laid in the soil and the larva is root-feeding as usual, and are quite polyphagous. The potentialities of *Colaspis* adults are quite large and they can feed also on *Ipomoea*, *Solanum* spp.*,* grapes and many other plants.

3.4. *Toxicity and defense secretions*

That some toxic compounds, present in the host plant, may be used by an eumolpine for its own defense, is well illustrated by the case of *Chrysochus* species, as discussed above under the subsection 3.2. There are many more eumolpines feeding on toxic plants, for example *Platycornus peregrinus* Herbst. feeding on the very toxic *Calotropis procera* Aiton in s. e. Asia. But these cases have not been studied in detail.

3.5. *Vein cutting habit*

Latex-producing angiosperms are recorded in 40 families and in more than 20 000 species (Lewinsohn, 1991). According to Becerra et al. (2001), *Chrysochus auratus*, in the US, feeding on *Apocynum cannabinum* (Apocynaceae), chews a channel that transects major veins adjacent to the leaf margin. The rupture of the laticifers stops the flow of latex and the beetle can consume the leaf (Williams, 1991). Dussourd & Eisner (1987), however, wrote that *Chrysochus auratus* feeds, without prior vein cutting, apparently undeterred by the copious latex emission, elicited by its bites. Dussourd and Denno (1991) explain this behavior this way: dogbane beetles (*Chrysochus auratus*) feed from the edge of *Apocynum* leaves, often accumulating sizable drops of latex under their mandibles. The beetles remove the latex simply by dragging their mouthparts while backing across the leaf. The authors infer that observations on this beetle, in multiple populations in three states, show that it really lacks vein-cutting behavior. But observations by Williams (1991) as well as Dussourd & Denno (1991) seem contradictory, and it is likely that different populations have become adapted to different behaviour. No data exist on any other eumolpine and very probably the techniques used may differ with the species and with the plants. However, *Eumolpus* in America, *Euryope* in Africa, *Platycorinus* in South East Asia, and related genera, must show some way of avoidance of overconsumption of latex from their food plant, but they remain to be studied from this standpoint.

3.6. *Biogeography*

Eumolpinae are distributed world-wide, but are basically a tropical group, diminishing progressively towards the north. They could have been abundant in the Antarctic forests in the Mesozoic and middle Tertiary, but none have survived even in the

subantarctic islands. Moving northward they are first met with in the Eastern Pacific archipelagos. They have spread passively over the Indonesian and Western Pacific archipelagos, and are well differentiated in New Zealand and New Caledonia, probably from the very few introduced pioneers. Spilopyrini were very probably largely distributed over Gondwana in the Jurassic, and very likely eumolpines, like rest of the Chrysomelidae, evolved during the Triassic, early Jurassic, from which periods they have left very few traces. Spilopyrins, after origin in the Gondwana supercontinent, have survived in South America, Australia, New Caledonia and New Guinea, but probably never reached New Zealand, where all eumolpines belong to more advanced tribes. Madagascar, which was isolated very early, does not possess any spilopyrine, while archaic sagrines (*Megamerus*) are still present there and are shared with South America and Australia. We know several fossil eumolpines, including one well preserved from the Oligocene of Chiapas (Gressitt, 1963), the diversification of the group occurred during the Cretaceous and early Coenozoic, together with the flowering plants.

Numbers of genera and species of Eumolpinae vary considerably even in the southern tropics and in the lands of the Gondwanan origin. While there are many genera and species of Eumolpinae in Argentina, Chile and Brazil, there are 30 genera and 500 species in Australia (Lawrence & Britton, 1994; Reid, 2006). There are 38 genera and 175 species of Eumolpinae described from South Africa (Scholtz & Holm, 1985) and approximately 17 genera and 36 species in Mozambica (Ferreira, 1963), but, beyond this, the inventory is quite incomplete. In Madagascar Paulian (1961) mentions 39 genera of Eumolpinae, including 27 endemic, with 256 species. Among the non-endemic, most are African or Indo-Malaysian in origin. There are four genera and 18 species in New Zealand (Leschen et al., 2003; Leschen & Reid, 2004), and nine genera and 45 species in New Caledonia (Jolivet & Mille, 2008). There are many Eumolpinae in New Guinea and many more remain to be described. In Malaysia, Mohamedsaid (2004) recorded 31 genera of Eumolpinae and 170 species.

There are also two genera and three species of Spilopyrini in South America, four genera and 18 species in Australia, two genera and some species have survived in New Guinea, and one genus and two species in New Caledonia. There are no Spilopyrini in Southern Africa, Madagascar, India and in New Zealand, probably due to early disconnections with the rest of Gondwana. A complete flooding of New Caledonia and New Zealand, in the Oligocene, as proposed by some geologists and biologists, does not seem very plausible. Gondwanan relics in both places survived the alleged flood. However, when New Zealand remained quite isolated from foreign invasions, except from Australia, New Caledonia received after the Oligocene many arrivals from Indonesia and New Guinea through the Solomon and Vanuatu archipelagos. In New Guinea, Gressitt (1966, 1967a,b, 1969) recorded in all 29 genera and 137 species.

In Micronesia, north to New Guinea, there are four genera and 12 species (Gressitt, 1955). In the Pacific islands, Eumolpinae, along with Alticinae, are the last to survive, extending the range to East (Samoa). They are missing in Easter island and Hawaii, volcanic islands, which are too isolated to be colonized by wind. There are alticines in Juan Fernandez, but probably no eumolpines. There is only one *Metachroma* in the Galapagos.

As in New Caledonia, Eumolpinae are the largest subfamily of chrysomelids in New Guinea (Gressitt, 1982) and in Fiji (Bryant & Gressitt, 1957). A few genera in New Guinea are endemic, and most are derived from South East Asia and Wallacea. Others have their origin from the Australian fauna, but the *Stethotes*, present in New Caledonia, Samoa, Fiji and New Guinea, are missing in Australia. There are also relationships with Sulawesi. The New Zealand fauna seems to Gressitt unrelated to the neighbouring land masses, but he insists on the relationships of Papuasia with New Caledonia. Of course, Solomon and Vanuatu faunas must be transitional, but we don't have any recent data from the two archipelagos. Gressitt, however, has not mentioned the few spilopyrins present in New Guinea. In Fiji, there are thirteen genera and 56 species of Eumolpinae and in Samoa, to the East, three genera and eight species only are on record. In Samoa, only a few Cryptocephalinae, Eumolpinae, Galerucinae, Alticinae, Hispinae and only one cassidine have survived. There are no Eumolpinae in Tahiti. Four chrysomelids have been found there, and all are imported.

Going north, Eumolpinae become rarer and rarer and that is true for all the Holarctic zone. In France, for instance, there are five genera and 13 species. In Fennoscandinavia, there are three genera and four species (Silfversberg, 2004), but most of them in the Baltic States. One, *Pachnephorus* (*P. pilosus* Duftschmidt) survives also in Karelia and in Finland. It seems that *Bromius obscurus* is rather common, even if its grape variety seems to have been eliminated almost everywhere in the South by insecticides. In fact (Silfverberg, pers. comm.) *B. obscurus* reaches the very North of Fennoscandia and *Pachnephorus villosus* is also in Finland. In the Northern points of Siberia the Eumolpinae are, according to Silfverberg:

> *Bromius obscurus*: West Siberia, Satiga and Leushi; C. Siberia: Jeniseisk; E. Siberia: Ust-Aldan.
> *Pachnephorus pilosus*: W. Siberia, Tobolsk; E. Siberia, Ust-Kut.
> *Pachnephorus tesselatus* Duftschmidt: Central Siberia, Jeniseisk.
> *Chrysochus goniostoma* Weise: Central Siberia, Minusinsk.

This progression towards the north in Siberia is rather surprising, but not more than the records for Canada, or for Japan. Kurcheva (1967) estimated roughly the genera of Eumolpinae in the European part of Russia to be 23 and the species to be 50. Since then, several new species have been described. Three eumolpines have been found in Sakkalin (Mikhailov & Hayashi, 2002) one *Basilepta*, one *Colasposoma* and one *Bromius*. They seem to live far away north. However, no eumolpines survived in Wrangel island in Siberia when several *Chrysolina* thrived there, even if their life-cycle has been extended to three years (Khruleva, 1996).

In Spain and Italy there are more species, and only one lamprosomatine. In Bulgaria, in the South, there are seven genera and 11 species. In Hungary, where *Eupales* is present, there are four genera and only six species (Kaszab, 1962). In Macedonia (Gruev, 1998), there are only three genera and three species recorded, but we have no clear record for Turkey. In Greece, Gruev (1990) records only five genera, including *Eupales*, and 11 species. There must be more. There are Lamprosomatinae in England, but no Eumolpinae are there, nor in Ireland. No Eumolpinae have been recorded from

Iceland. In Latvia (Lettonia), in the middle of the Baltic states, there are still some Eumolpinae (Telnov, 2004): three genera and four species.

In North Africa, there are approximately five genera and 17 species in Morocco (Kocher, 1958), 4 genera and 12 species in Tunisia, and five genera and eight species in Egypt (Alfieri, 1976). In Saudi Arabia, at the cross-roads in the Middle East, there are (Daccordi, 1979; Lopatin, 1983; Medvedev, 1996) 12 genera and 25 species recorded. A few Eumolpinae were recorded from Israel, one *Macrocoma* and one *Pachnephorus*, a few also from Syria and Lebanon. In Iran, divided between palaearctic and asian faunas, there are only four eumolpine genera and 10 species (Borumand, 2000). Socotra at the east of Somalian coast has many tenebrionids, but very few chrysomelids have been collected there. However, one *Eryxia* (*E. socotrana* Gahan and a variety) has been described from there and one *Colasposoma* (*C. densatum* Fairmaire), common in Somaliland, was also found. Interestingly, also only one *Lema* and a cassidine, *Oxylepis deflexicollis* Boheman, were recorded from there (Wranik, 2003). There must be more chrysomelids, especially on Cucurbitaceae in Socotra, and all depends on the season of the collection. The genus *Eryxia* is essentially African and is known from Morocco, East Africa, and also from Arabia. *Eryxia* seems polyphagous, but somewhat floricolous and petalophagous. It is interesting that we find one *Euryope*, a tropical African genus, in Arabia, essentially linked with Asclepiadaceae. Zoia (2001) described a new genus, *Endroedymolpus*, with two new species from South Africa. The same author (Zoia, 2007a), in his monographic study of the eumolpine genus *Pachnephorus* of the Afrotropical region has revised the taxonomy of the genus and has described biogeography of its species.

In Asia, the fauna is richer, 21 genera in Japan with 66 species, in Taiwan 21 genera with 58 species, in China there are 50 genera and 366 species, but part of those countries are subtropical or tropical (Kimoto & Takizawa, 1994, 1997; Tan et al., 1980, 2005). In Mongolia proper, Medvedev (1982) has recorded nine genera and 11 species. In Central Asia, Lopatin (1984) has put on record 18 genera and 39 species. In Eastern Europe and Northern continental Asia, we have on record 25 genera and 66 species.

In North America, 13 genera and 43 species have been reported for Canada (LeSage, 1991). In the USA, there are 21 genera and an unrecorded number of species, probably around 70. In America, as in Europe, the number of Eumolpinae decreases when going north. For instance in Ohio (Wilcox, 1954) there are 15 genera and 41 species, and the number does not vary much between the states. In New York 13 genera and 26 species have been recorded, In the Pacific Northwest (British Columbia, Washington, Idaho and Oregon) only 10 genera and 19 species are on record (Hatch, 1971). In Florida, subtropical, but quite isolated, there are 10 genera and 56 species (Peck & Thomas, 1998), in Alabama 14 genera and 48 species have been recorded (Balsbaugh & Hays (1972); in South Carolina, Ciegler (2007) has mentioned 16 genera and 71 species of Eumolpinae, but this number wrongly includes *Syneta* (Synetinae) as a member of the group. For Mexico, we don't have any reliable number, but the country is subtropical and has migrants from both north and south. In the province of Baja California, there are only seven genera and 10 species (Andrews & Gilbert, 2005). Wilcox (1975)

estimates the total number of Eumolpinae in North and Central America to be 692 species under 57 genera. The number increases towards the tropical south. In the small Nicaragua only, Maes & Staines (1991) estimate the total number of Eumolpinae to be 21 genera and 53 species. These figures do not seem to be much different for Costa Rica or Panama. Fossil Eumolpinae are known from the Mesozoic, and early migrations of Spilopyrini may have occurred during the Jurassic.

In conclusion, we can consider all the figures given above as only approximate. In temperate holarctic countries, the figures are relatively exact. In the tropics probably they have to be doubled or more with further taxonomic studies. Eumolpines are tropical or subtropical beetles but their limits in Scandinavia, for instance, does not fully coincide with the northern limit of *Timarcha* (Latvia), where they were probably eradicated in the north by the quaternary glaciations. Surprisingly, some rare species of Eumolpinae have survived in Finland and Karelia, or have been probably reintroduced later. New Guinea is the richest tropical subregion, but tropical Africa, Brazil and the rest of the neotropical realm should be much richer in species numbers than on record.

4. Anatomy

4.1. *Hind-wing venation*

Hind-wing venation in Eumolpinae is characterised by presence of two cubital cells (1Cuc and 2 Cuc) (Jolivet, 1954, 1957-1959; Suzuki, 1994) (Figures 3 and 4). There
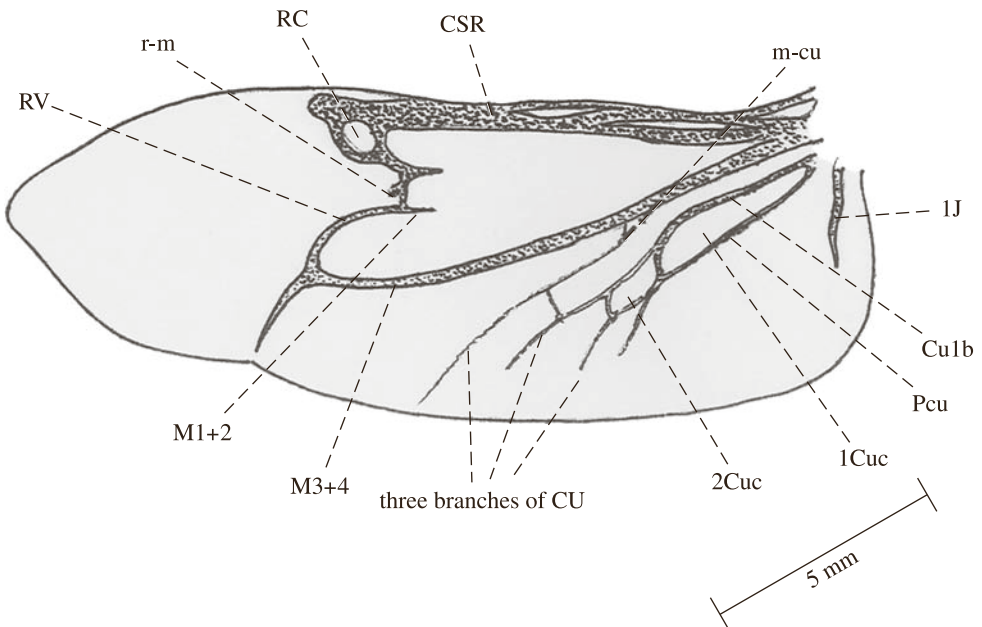

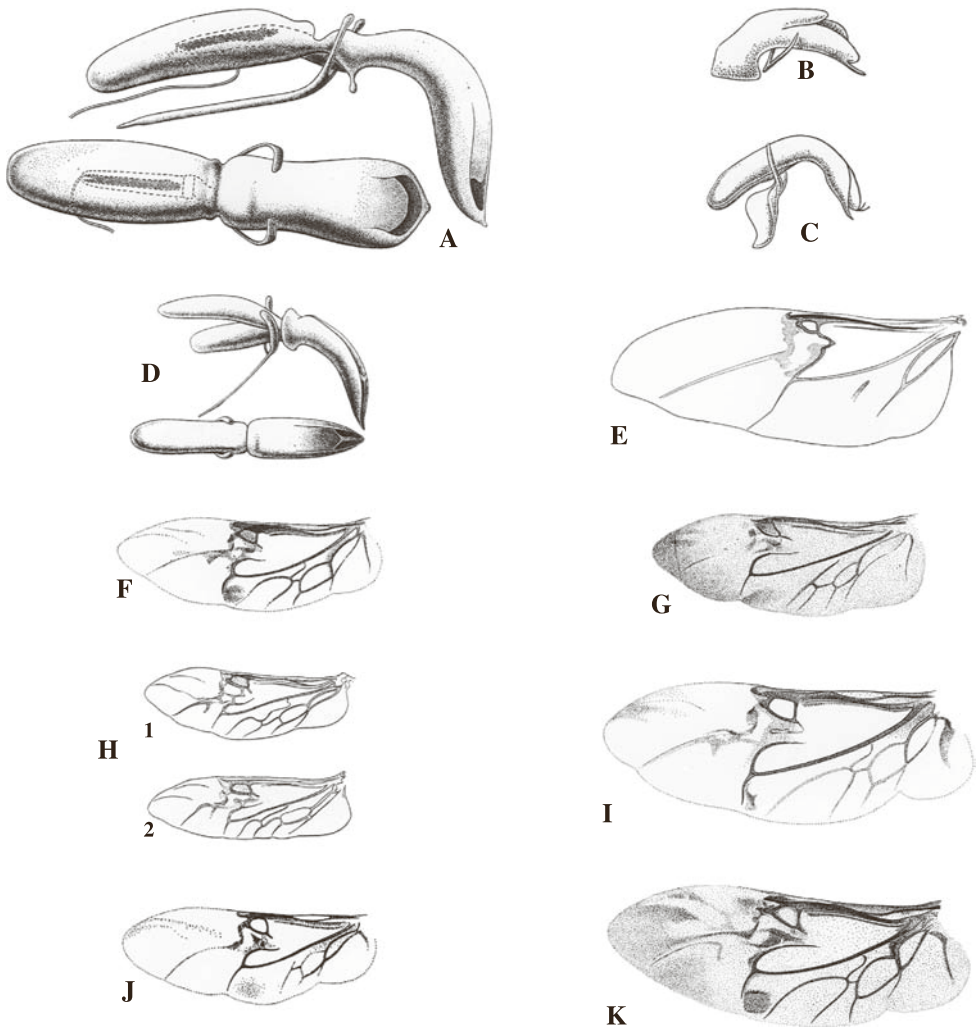**Figure 3.** *Bohumiljania*, hindwing. (Terminology for veins as per Suzuki, 1994), (from Jolivet et al., 2003).

Figure 4.

A: Aedeagus of *Eumolpus surinamensis* Fabricius (Eumolpinae). Lateral and front view.

B: Aedeagus of *Syneta betulae* Fabricius (Synetinae). Lateral view.

C: Aedeagus of *Cheiloxena westwoodi* Baly (Spilopyrini). Lateral view.

D: Aedeagus of *Megascelis flavipes* Lacordaire (Eumolpinae). Lateral and front view.

E: Wing of *Syneta adamsi* Baly (Synetinae). The anal and cubital system is regressed, but it can be more developed among other species.

F: Wing of *Chrysolampra curvipes* Jacoby (Eumolpinae). To be noted the subcubital fleck, slightly split.

G: Wing of *Bohumiljania caledonica* (Jolivet) (Eumolpinae). The subcubital fleck becomes only a small darkening.

H: Hind wings of 1) *Megascelis unicolor* Lacordaire, 2) *Megascelis flavipes* Lacordaire. The subcubital fleck is absent.

I: Wing of *Eumolpus surinamensis* Fabricius (Eumolpinae). The subcubital fleck is almost absent.

J: Wing of *Eupales ulema* Germar (Eumolpinae). The subcubital fleck is reduced to a shadow.

K: Wings of *Colasposoma pradieri* Lefèvre (Eumolpinae). A clear subcubital fleck, not split (from Jolivet, 1957-59).

are exceptional cases, in which the second cell has disappeared partially through regression, but is faintly indicated, as in *Pachnephorus cylindricus* Lucas. Such a regression is seen among brachypterous and micropterous forms, e.g. in *Dictyneis pulvinosus* Blanchard. Reid (in a personal communication) has referred to the senior author's book (Jolivet, 1959) for apparent absence of 2Cuc in *Pachnephorus*, and Suzuki (1994) has mentioned absence of 2Cuc in some Eumolpinae. Such cases are due to degeneration of the cell, which may be faintly indicated in a lateral view, when the wing is held almost horizontally. Other Chrysomelidae showing two cubital cells: Megascelinae (which in fact are Eumolpinae; this aspect has been discussed under Section 5), Lamprosomatinae, Clytrinae, Hispinae, and Cassidinae. In the last three subfamilies the nature of the connection of the cells with M is different from what is seen in typical Eumolpinae. The eumolpine like connection may be seen also in Megascelinae and Lamprosomatinae. The absence of 2Cuc, and of such a connection with M in *Syneta* is one of the points of contradiction of the view that this chrysomelid be amalgamated with Eumolpinae. (For this taxonomic controversy see the discussion under the Section 5). *Plastonothus aureus* Blanchard, a Chilean species, is also very primitive, and has lost, or more probably not yet evolved, the eumolpine connection with M.

What author P.J. used to name as the medio-cubital patch in the wing (Jolivet, 1957-59), or binding patch (Hammond, 1979), is used by the beetle for folding its wing. It is another characteristic feature of the wings in typical or higher Eumolpinae. Lamprosomatinae and spilopyrins do not have this patch.

4.2. *Aedeagus*

A typical eumolpine aedeagus is a specialized organ. It includes two parts, the aedeagus proper and the basal hood. The latter is formed by the dorsal and lateral wall of the aedeagal tube extended and grown in the anterior direction, so that the basal orifice becomes ventrally placed and quite extensive anteroposteriorly. The basal hood, which is a part of the aedeagal tube, looks quite different from the rest, as it is in most cases thinly sclerotized and flexible. In addition to its texture, the basal hood is differentiated from the rest by a constriction, usually more marked on the dorsal side. Typically the aedeagus proper presents a transverse ring-like enlargement in its basal part, the basal ring. The ring has a pair swellings ventrally, the basal spurs, which may be hook like. In some cases, in place of the paired basal spurs there may be a median swelling. The aedeagus proper presents a deep ventral curvature (Figure 5).

The first spiculum or the tegmen is triangular or quadrangular, dorsoventrally flattened and plate like. Its paired arms extend upward behind or across the basal ring of the aedeagus proper. It is important to note that the body or the median part of the tegmen is almost entirely confined to the anteroposterior extent of the basal orifice.

This typical aedeagal organization presents a number of variations. The ventral curvature of the aedeagus proper may be distributed evenly throughout the length, or it may be specially pronounced in its basal part or in its distal part (Figure 6 a, b, c). The aedeagus in Typophorini (e.g. *Typophorus* sp. and *Metachroma pallucidum* Crotch) there is no differentiation of the basal ring, though the remaining specialized features
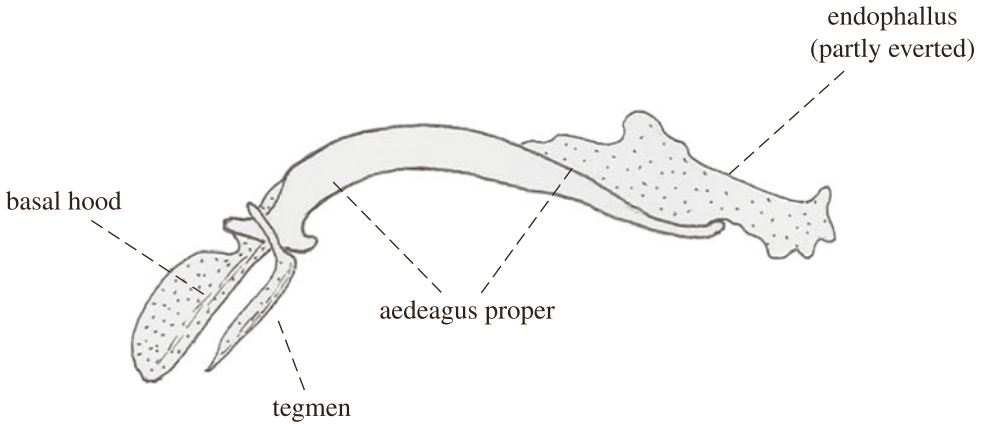
Figure 5. *Adorea chontalensis*, aedeagus, in lateral view. Sclerites of the endophallus not shown (based on Flowers, 1999).

are present (Flowers, 1999). It is so also in *Colasposoma auripenne* Motsch. (Kumar & Verma, 1980). Besides in this species there is no constriction between the basal hood and the aedeagus proper. Similar unspecialized features may be seen in the figures of the aedeagi of *Colasposoma crenulatum* Gerstaecker (Figure 7) and *Mecistes flavipes* Gerstaecker in Zoia (2007b). In most Eumolpinae the body of the tegmen is like a horizontal plate. But in *Rhabdopterus picipes* Oliv. (Powell, 1941) and in *Eumolpus surinamensis* Fabricius (Sharp & Muir, 1912) (Figure 4, A) this part of the tegmen is like a low vertical keel. The primitive Eumolpinae (Spilopyrini and *Eupales*) present a number of primitive aedeagal features, which are to be described under the Section 5.

Kumar and Verma (1980) have described the aedeagal musculature of *Colasposoma* auripenne Motsch., and, in view of asymmetry of the protractor of the first spiculum or the tegmen and of the twisted nature of the tracheal and nervous supply reaching the aedeagal base, as observed by Kumar & Verma (1971) in this species, a developmental change in the orientation of the aedeagus or its 'retournement' has been inferred. It may be noted here that 'retournement' of the aedeagus has been detected in all the Chrysomelidae/Phytophaga, examined from this standpoint, but it remains to be shown that it is universal in Phytophaga (Verma, 1994).

The aedeagal apparatus in Eumolpinae often show species specific features (Figure 6 a, b, c).

Flowers & Eberhard (2006) have studied fitting together of male and female genitalia in copula in several chrysomelids, including five eumolpines, and have described remarkable coadaptation of the male and female organs for achieving successful sperm transfer. In the eumolpines the female has a telescoping ovipositor, the inner tube of which is penetrated by the everted endophallus, with the long flagellum reaching the mouth of the spermathecal duct or penetrating the duct. For holding the endophallus in position there are a number of interesting adaptations. In *Colaspis sanjaseana* Bechyne, *Brachypnoea irazuensis* Jacoby, and *Metaxyonycha amasia* Marshall (Figure 8) there are two pairs of digitiform appendages on the everted endophallus, an apical pair and a lateral pair. In addition there is a swollen part or "supporting block" in the basal
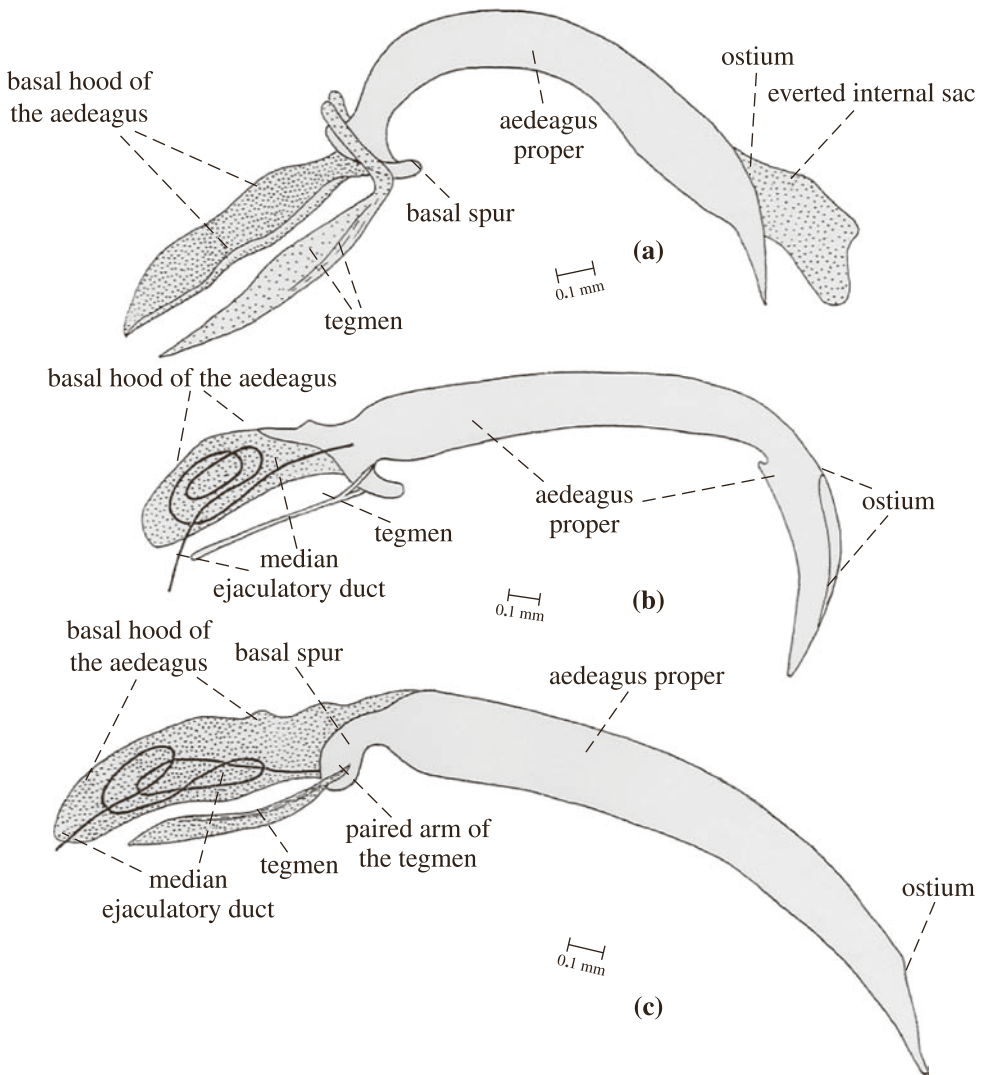
Figure 6. Aedeagi, in lateral view, of three species of *Dematochroma* from New Caledonia; a) *D. terastiomerus*; b) *D. pilosa*; c) *D. antipodum*; (from Jolivet et al., 2007).

part of the everted internal sac. While the female gonapophyses hold the "supporting block", the appendages help holding the endophallus in place within the female. In *Xanthonia* the surface of the endophallus is beset with microspicules for this purpose (Figure 9). In all the cases the various bulgings and swellings on the everted endophallus also help in holding it in a suitable position in the female genital tract.

4.3. *Internal organs of reproduction in male*

The testis on each side includes two multilocular or septate testis follicles (Verma, 1996). The two follicles of the same side may be quite separate, as in *Corynodes* (Pajni
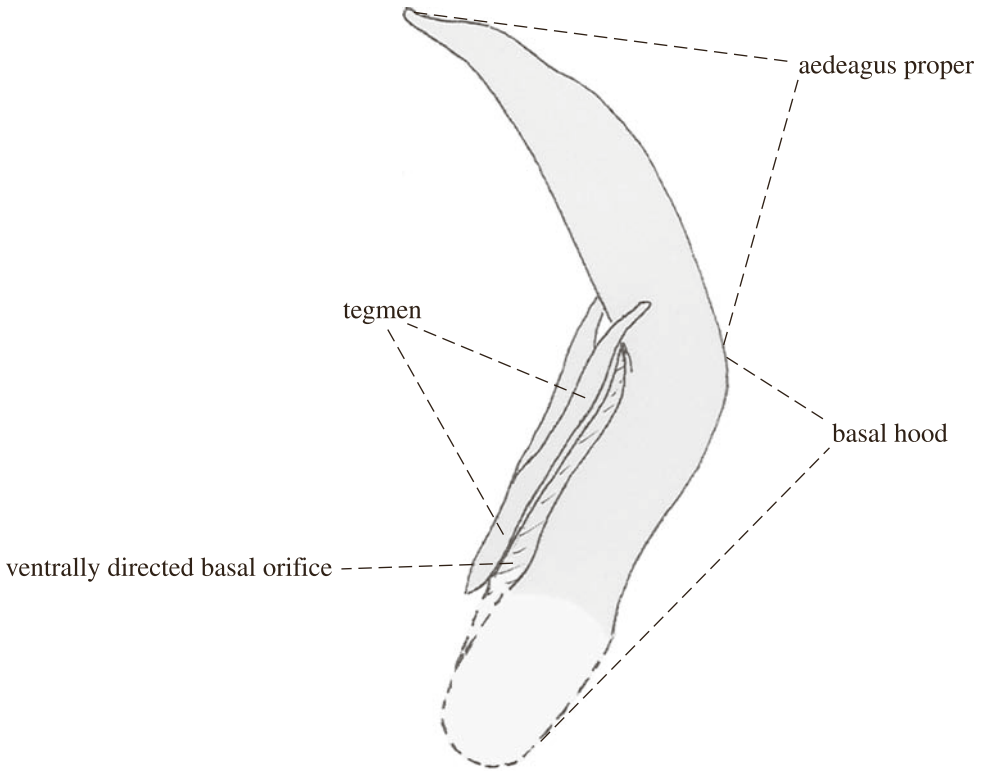
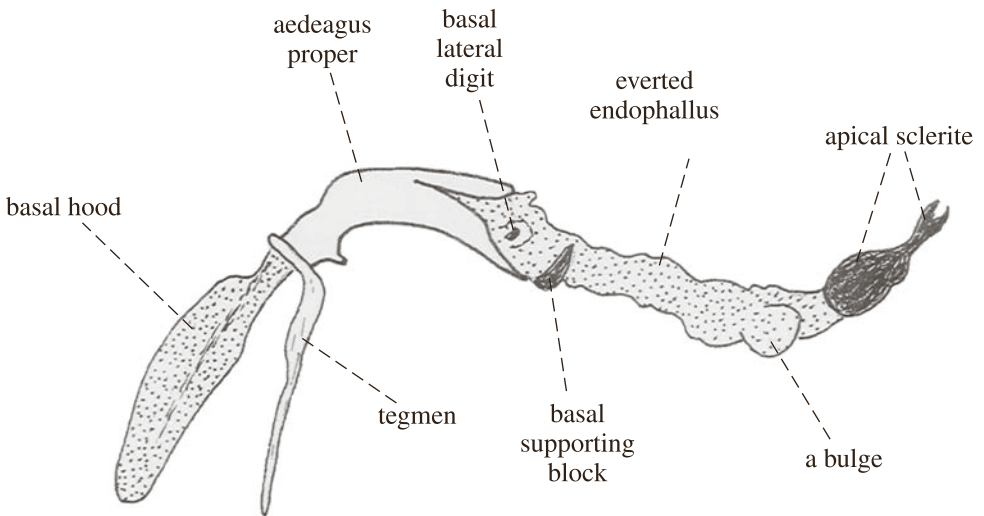**Figure 7.** *Colasposoma crenulatum*, aedeagus, in lateral view (from Zoia, 2007b).

Figure 8. *Metaxyonycha amasia*, aedeagus with everted endophallus, lateral view (based on Flowers and Eberhard, 2006).
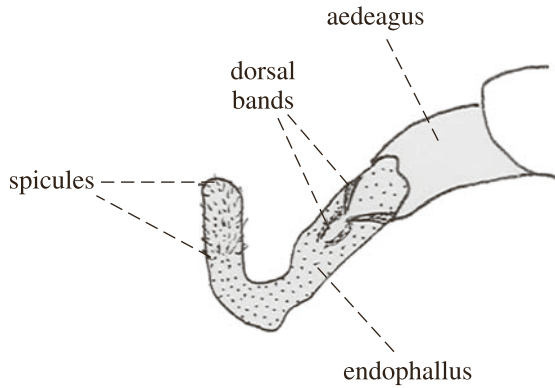
Figure 9. *Xanthonia* sp., aedeagus, protruded, with everted endophallus (based on Flowers & Eberhard, 2006).
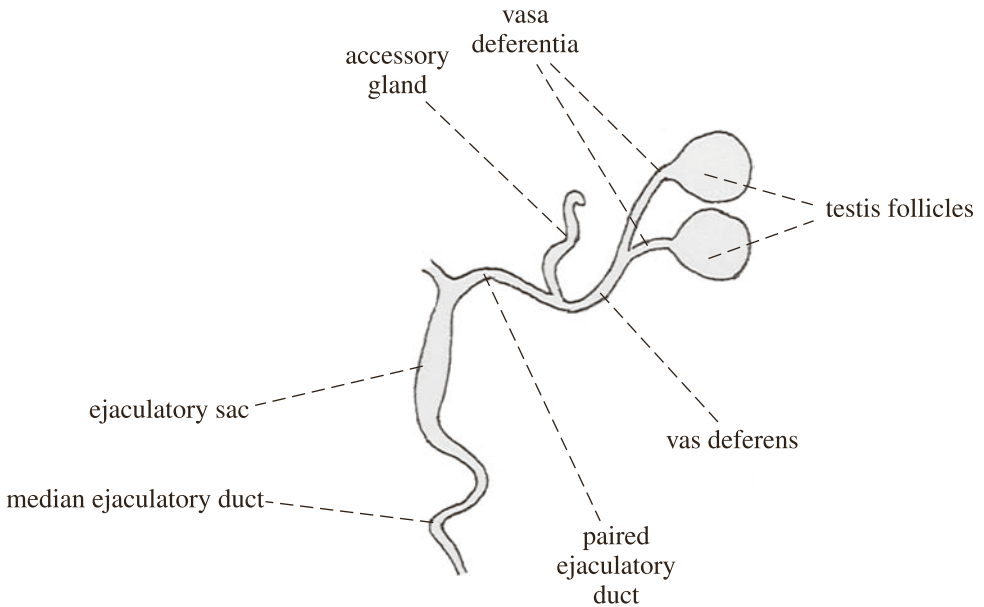

Figure 10. *Corynodes* sp., male internal reproductive system. Testis shown only on one side. (After Pajni et al., 1987).

et al., 1987) (Figure 10), *Tricliona* (Kasap & Crowson, 1979), or they may be closely pressed together, as in *Cleoporus* (Suzuki, 1988) (Figure 11), *Colasposoma* (Pajni et al., 1987), *Nodina* (Mann and Crowson, 1883b), and *Geloptera* (Kasap & Crowson, 1979). The male genital set also includes vasa deferentia, which are long and well exposed, when the two testis follicles of the same side are quite separate, and short and more or less concealed, when the two follicles are pressed together, a 'prostata', often well marked, the median ejaculatory duct, which may be moderately long,
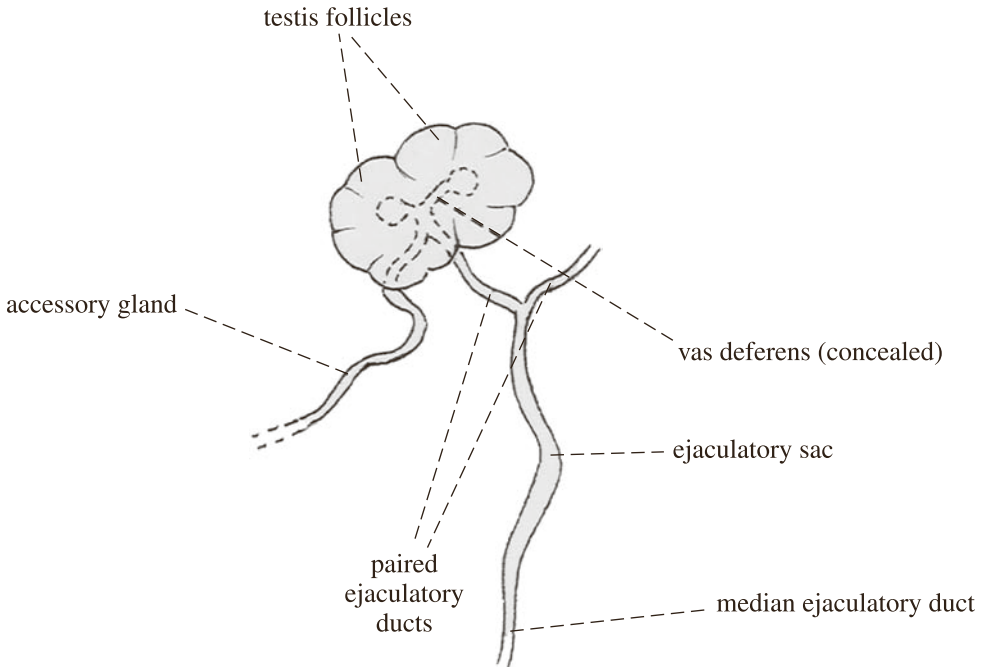
Figure 11. *Cleoporus variabilis*, male internal reproductive organs. Testis shown only on one side. (After Suzuki, 1988).

or very long, thin and winding, and with or without an ejaculatory sac, and a pair of long and tubular accessory glands.

4.4. *Spermatheca*

The spermathecal capsule is bent on itself, like a horseshoe, or like a flask with a bent or a curved neck. The spermathecal lining is fairly well sclerotised, yellowish or brownish in colour, and smooth. A special feature of the spermathecal capsule in Eumolpinae, as pointed out by Suzuki (1988), is that a proximal most part of the capsule is constricted or differentiated from the rest, giving out the spermathecal duct and receiving the duct of the spermathecal gland (Figure 12). This last mentioned feature is present even in the primitive Eumolpinae (Verma & Jolivet, 2004). The feature, however, is not confined to Eumolpinae; it may be seen, among the spermatheca figures included in Suzuki (1988), in Synetinae, Chrysomelinae, Clytrinae, and Cassidinae.

4.5. *Ovariole number*

Ovariole number varies much among Eumolpinae. It is known to vary from seven per ovary to 28, with a small range of intraspecific variation in some species. As per an inference by Suzuki (1974), the number of ovarioles is primarily determined by the
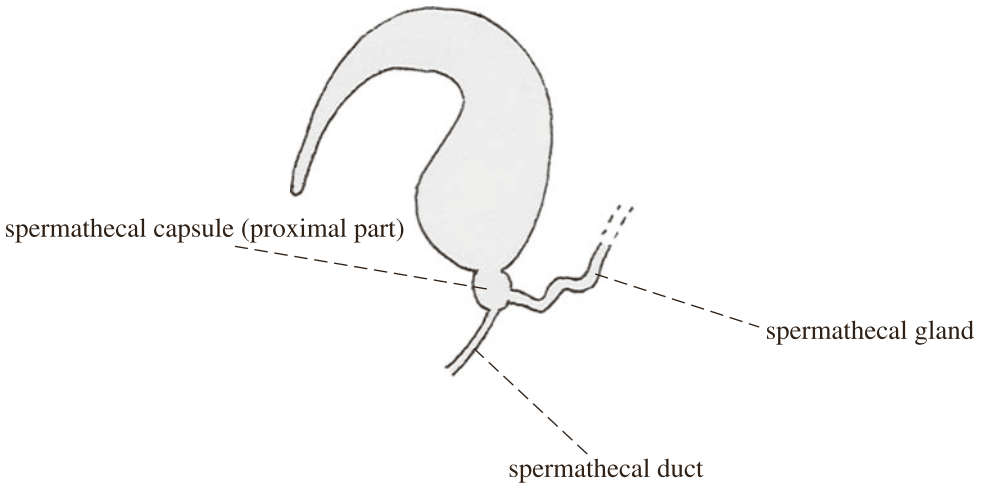
spermathecal capsule (proximal part)

spermathecal gland

spermathecal duct

Figure 12. *Lypesthes ater*, spermatheca (after Suzuki, 1988).
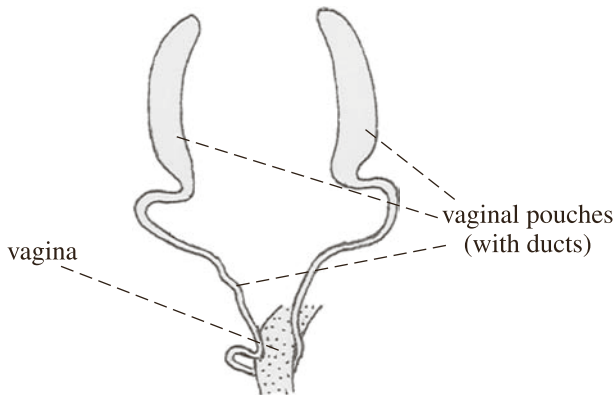

vaginal pouches
(with ducts)

vagina

Figure 13. *Nodina crassipes*, vaginal pouches (from Mann and Crowson, 1983a).

genetic mechanism, and secondarily by ontogenetic factors, chiefly nutrition. The author also finds a correlation between the ovariole number and the body size.

4.6. *Vaginal pouches*

A pair of simple unbranched and tubular pouches are present both in adult and larval Eumolpinae, opening into the last part of the female genital tract (Figure 13). They are referred to as the genital pouches. They contain symbiotic bacteria along with a secretion (Mann & Crowson, 1983a). When eggs are being laid, their surface gets coated with the secretion containing the bacteria. After hatching the larva eats up the egg shell, and thus the bacteria are passed on to the next generation (Stammer, 1936).

From their comparative study of the vaginal pouches and their association with the symbiotic bacteria in Chrysomelidae, Mann and Crowson (1983a) have inferred that the features were present in ancestral Chrysomelidae or they are plesiomorphic.
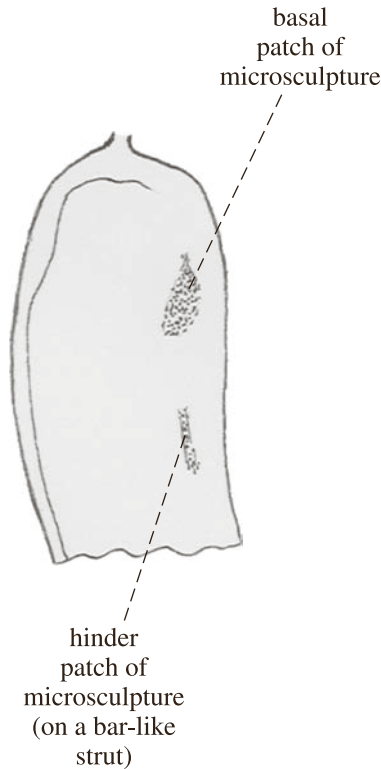
Figure 14. *Rhyparda fasciata*, undersurface of an elytron with two binding sites covered with microsculpture. The hinder patch is carried on a bar-like strut. (Based on an electron micrograph in Samuelson, 1996).

4.7. *Elytral binding sites*

As has been recorded in all the superfamilies of Adephaga and Polyphaga, in the Eumolpinae too there are a pair of patches of microsculpture on the undersurface of each elytron to mesh with the microrough areas on the body to hold the elytra in repose in place (Samuelson, 1996). In eumolpines there is a nearly rounded basal patch in the region covering the metathorax, and a second patch on a bar like strut, running along the elytral axis some distance behind the basal patch (Figure 14). This bar like nature of the second patch is also found in some Chrysomelinae, many Cassidinae, and in rare cases in Hispinae.

5. **Primitive Eumolpinae**

Under this subheading are being covered the tribe Spilopyrini and *Eupales*, for which Verma et al. (2005) have suggested formation of a new tribe, a monogeneric and monospecific one, Eupalini. Besides *Syneta* and Megascelinae have also been briefly discussed, as their inclusion under Eumolpinae has been suggested sometimes.

Eumolpinae, with not a well marked differentiation of the aedeagal basal hood, with tegminal arms extending considerably beyond the ventroposterior edge of the basal

orifice, and with larvae, which are exposed and external feeders on plants and not sub-terranean root feeders, are being taken as primitive Eumolpinae.

5.1. *Spilopyrini*

Spilopyrini are Gondwanan in distribution, and include seven genera, *Spilopyra* Baly 1860, (Australia and New Guinea), *Macrolema* Baly 1861 (Australia and New Guinea), *Richmondia* Jacoby 1898 (Australia), *Cheiloxena* Baly 1860 (Australia), *Stenomela* Erichson 1847 (Chile), *Hornius* Fairmaire 1848 (Chile and Argentina), and *Bohumiljania* Monros 1958 (New Caledonia) (Reid, 2000).

The aedeagal structure in spilopyrins presents some obvious primitive features:

(1) The aedeagus in most genera shows only a moderate ventral curvature. But in *Cheiloxena* the curvature is considerably greater, almost as in higher eumolpines (Figure 4, C).

(2) There is only a poor differentiation of the aedeagus proper and the basal hood, due to lack of a distinct constriction between the two regions, because of lack of the basal ring at the base of the aedeagus proper, and also lack of basal spurs or of a median thickening in place of the basal spurs. Some of these primitive features of the aedeagal architecture may be seen also in some higher Eumolpinae, e.g. in Typophorini and in *Colasposoma* (see above).

(3) The paired arms of the first spiculum or tegmen extend posteriorly considerably beyond the posterior lip of the ventrally directed basal orifice of the aedeagus (Figure 15), whereas in higher Eumolpinae the tegmen is almost confined to the anteroposterior extent of the basal orifice.

(4) Zoia (personal communication to Jolivet) noted that in *Cheiloxena* and *Macrolema*, in dissection, the tegmen may be made to move freely along the length of the aedeagus proper. Such movements could be effected also in *Bohumiljania* by one of the present authors (KKV), who, however, found that in *Eupales* and *Colasposoma* the tegmen was not free to move this way. If there is a limited and narrow area of arthrodial membrane between the forked posterior end of the tegmen and the ventroposterior edge of the basal orifice, such movements would not be possible. On the other hand, that the tegmen can be readily made to move along the aedeagus, is indicative of ample arthrodial membrane in this location. In the cassidine type of aedeagus the arthrodial membrane is limited and narrow (Verma & Kumar, 1972; Verma, 1996). Presence of limited area of arthrodial membrane between the arms of the tegmen and the basal orifice of the aedeagus is associated with formation of a basal muscular bulb, which may be seen in Cassidinae, Hispinae, Clytrinae, Chamisinae, and higher Eumolpinae (Verma, 1996). Free movements of the aedeagus against the tegmen is obviously a less specialized feature than restricted anteroposterior length of the tegmen, its little movement against the aedeagus,
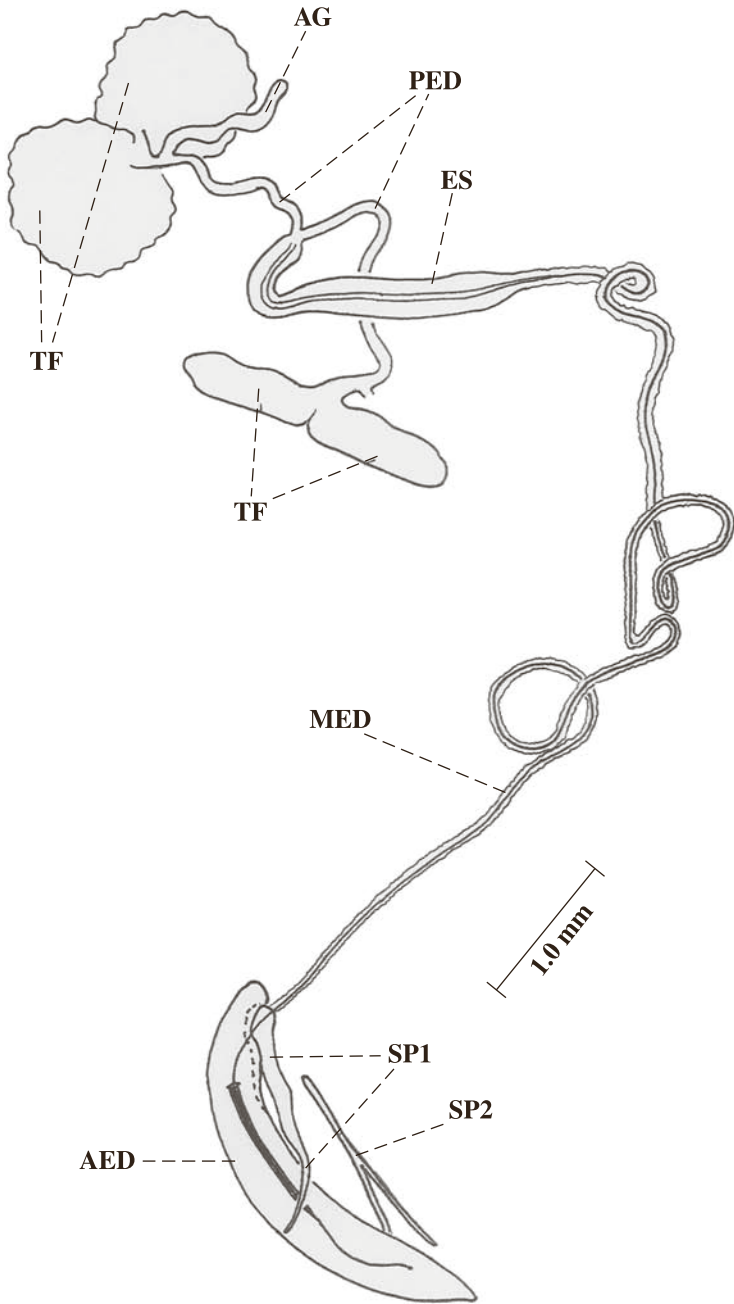
Figure 15. *Bohumiljania caledonica*, male genital system. AED = aedeagus, ES = ejaculatory sac, PED = paired ejaculatory duct, SP1 = first spiculum or tegmen, SP2 = second spiculum, TF = testis follicles. (from Jolivet et al., 2003).

and formation of a basal muscular bulb (Verma, 1996). (For relations among the basal hood differentiation, restricted length of the tegmen and formation of a basal muscular bulb, see Verma & Kumar, 1972, and Verma, 1996).

Spilopyrine larvae have five pairs of ocelli, and are exposed feeders on leaves and buds. In contrast the larvae of higher or typical Eumolpinae are without ocelli, lead a subterranean life, and are root feeders. All spilopyrin larvae, studied so far, have a dorsal and terminal abdominal shield, in the region of the 8th and 9th abdominal segments. Such a shield is not present in the larvae of typical or higher eumolpines. It may be noted here that a larval terminal abdominal shield is known also in Aulacoscelinae, Orsodacninae, Synetinae, and some Galerucinae-Alticinae. In Galerucinae larvae, the shield is used to repel predators. Such an abdominal shield in the larva may be a plesiomorphic feature.

Though the spilopyrins have such primitive features, their natural position is in the subfamily Eumolpinae. This assertion is supported by the following eumolpine features in spilopyrins.

(1) As in higher Eumolpinae, there is a basal hood differentiation in the aedeagus of spilopyrins, though less well marked (Figure 15).

(2) The median ventral part of the tegmen is shaped as a flattened horizontal plate in most higher Eumolpinae and also in most spilopyrins.

(3) The testis follicles in *Bohumiljania* among spilopyrins is septate and multilocular (Jolivet et al., 2003) as in higher Eumolpinae.

(4) In *Bohumiljania* the vasa deferentia are greatly reduced in length, and the two testis follicles of the same side are drawn close together (Jolivet et al., 2003) (Figure 15), as in *Cleoporus*, *Colasposoma*, *Nodina*, and *Geloptera* among higher Eumolpinae.

(5) In spilopyrins, as in higher eumolpines, the proximal most part of the spermatheca is differentiated from the rest, and is connected both with the spermathecal duct and the spermathecal gland. In *Bohumiljania* the proximal part of the spermatheca, connected with the ducts, is elongated and presents some spiral coiling (Jolivet et al., 2003), in which feature it resembles Megascelinae (Suzuki, 1988). It is notable that Megascelinae are Gondwanan in distribution, being mostly in South and Central America. Hence presence of this special spermathecal feature further attests the view that *Bohumiljania* is a primitive member of Eumolpinae, under which subfamily we are including now megacelines too (vide infra), and is suggestive of a gondwanan origin of the two eumolpines.

(6) Hind wing venation is typically eumolpine, with the cubital cells 1Cuc and 2Cuc (Figure 3 and Figure 4, H).

(7) In the first larval instar there are egg bursters on meso- and metathorax (Reid, 2000; Jolivet et al., 2003), as is usual among higher Eumolpinae.

A more detailed comparison of spilopyrins with higher Eumolpinae is in Verma & Jolivet (2002). Reid (2000) suggested separation of spilopyrins from Eumolpinae to form a new subfamily, Spilopyrinae. Retention spilopyrins among Eumolpinae has been defended by Verma & Jolivet (2000). In addition to the arguments, presented in that paper, it may be pointed out that even among typical Eumolpinae there are different grades of specialization in the aedeagal apparatus, even almost as low

specialization as in spilopyrins; hence the primitive aedeagal features in spilopyrins do not warrant their separation from Eumolpinae. It is notable in this context that Hunt et al. (2007), in their phylogenetic study of beetles, do not give place to 'Spilopyrinae' among the subfamilies of Chrysomeloidea.

5.2. *Eupales*

Another primitive eumolpine is the enigmatic *Eupales,* which is monospecific. *Eupales ulema* (Germar, 1813) is non-Gondwanan in distribution, and occurs mostly in Hungary, Greece, Bulgaria, Romania, former Yugoslavia, and Turkey. Crowson (1955) recognized it as a primitive member of Eumolpinae, and mentioned several points of resemblance with spilopyrins.

While *Eupales* aedeagus shows some primitive features, such as not a very well demarkated basal hood, and only moderate ventral curvature in the aedeagus proper, it also presents features of resemblance with higher Eumolpinae (Verma et al., 2005), such as:

 (i) the median part of the tegmen is confined to the anteroposterior extent of the basal orifice.
(ii) Unlike the aedeagal apparatus of spilopyrins, the tegmen is not able to move freely along the length of the aedeagus, indicating presence of a narrow and limited area of arthrodial membrane between the forked posterior end of the tegmen and the ventroposterior edge of the basal orifice.

The larva of *Eupales* does not have lateral ocelli, and is not an exposed feeder. It burrows into soil soon after hatching, and is a root feeder, as in higher Eumolpinae. It lacks in a dorsal caudal abdominal plate.

In a phylogenetic tree, based on morphology and rDNA sequences, included in Verma et al. (2005), *Eupales* appears standing in a different clade from spilopyrins, and as an early branch off from the stem leading to higher Eumolpinae (Figure 16).

5.3. *Syneta*

Another enigmatic form is *Syneta.* Following Edwards (1953), it has been generally placed under its own subfamily, Synetinae. But Reid (1995) has chosen to place *Syneta* under the Eumolpinae as the tribe Synetini, on basis of results of his cladistic analyses. Flowers (1999) has supported Reid's placement in view of some similarity with spilopyrines.

But a number of morphological differences and molecular studies do not support the placement of *Syneta* with Eumolpinae. These differences have been discussed at length in Verma & Jolivet (2000, 2002, 2005). The main reasons for denying inclusion of *Syneta* under Eumolpinae are:

  (i)   The aedeagal morphology in *Syneta* is almost galerucine or chrysomeline.
 (ii)   Testis follicles in *Syneta* are with only a small number of loculi, which are loosely held.
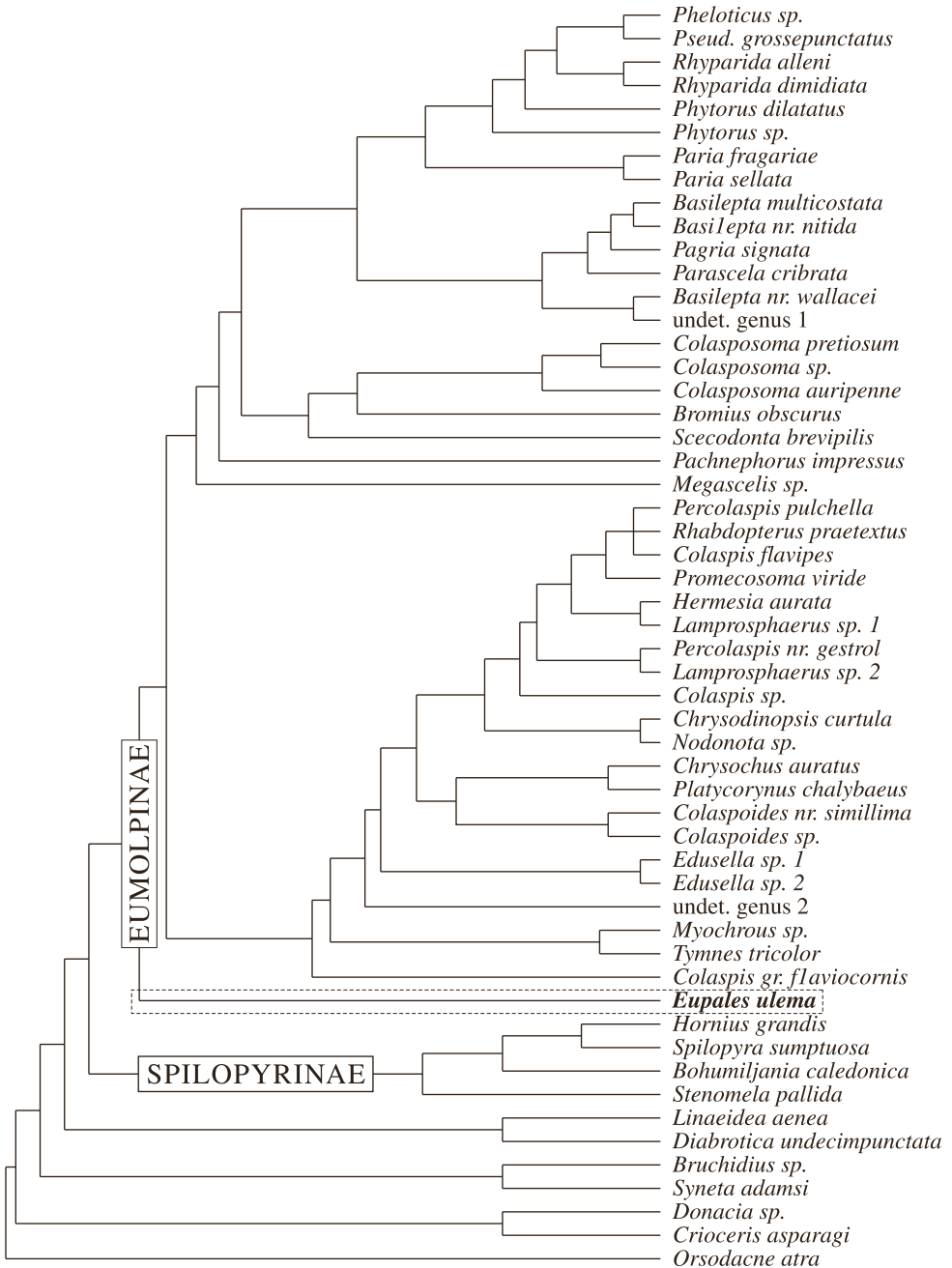(iii)   In the hind wing venation there is only one cubital cell, 1Cuc, and not two cubital cells, as in Eumolpinae.

Figure 16. Phylogenetic tree for Eumolpinae, based on morphological and ribosomal DNA sequence data (from Verma et al., 2005). N.B.: The following non-eumolpine chrysomelids have been included in the tree for comparison: *Linaeidea aenae* (Chrysomelinae), *Diabrotica undecimpunctata* (Galerucinae), *Bruchidius* sp. (Bruchidae), *Syneta adamsi* (Synetinae), *Donacia* sp. (Donaciine), *Crioceris asparagi* (Criocerinae), and *Orsodacne atra* (Orsodacninae).

(iv) Eumolpine head is without an anteclypeus, whereas an anteclypeus is present in Synetinae, Chrysomelinae, Galerucinae, and Alticinae.

In the phylogenetic tree, based on morphology and rDNA sequence data, included in Verma et al. (2005) (Figure 16), *Syneta* stands quite apart from typical Eumolpinae as well as Spilopyrini. Studies by Farrell & Sequeira (2004) provide only a weak support for the view of Reid (1995).

5.4. *Megascelinae (alternative name Megascelidinae)*

Generally Megascelinae are taken as a subfamily, close to Eumolpinae. But Reid (1995) included Megascelini as a tribe under Eumolpinae.

Megascelis undoubtedly shows some close resemblance with Eumolpinae, e.g.:

 (i) The hindwing venation of *Megascelis* is fully eumolpine (Jolivet, 1957-1959) (Figure 4, H). The wings lack the binding patch as in spilopyrines and primitive eumolpines.
 (ii) The aedeagus is also as in Eumolpinae (Figure 4, D).
(iii) The internal sac or endophallus of the aedeagus is mostly a simple dilated tube, with or without a flagellum, in Eumolpinae. This simple tubular nature of the aedeagal inner tube is seen also in *Megascelis*.
(iv) The spermatheca in *Megascelis* shows a proximal part of the capsule differentiated from the rest, and connected with the spermathecal duct and receiving the duct of the spermathecal gland, as in Eumolpinae. In this context it is important to note that the proximal part of the spermatheca presents some spiral coiling both in the spilopyrin *Bohumiljania* and in *Megascelis* (Figure 17). Further it is remarkable that both spilopyrins and *Megascelis* are Gondwanan in distribution. While *Bohumiljania* occurs in New Caledonia, 85% species of megascelines are in South America. Only about 15% species of the latter are in the southern part of North America, including Mexico, up to Panama. There is an interesting parallel between the distribution of megascelines and of Metatheria in the New World. The above pointed peculiar form of the spermatheca seems to be a plesiomorphic feature.
 (v) There is a notable similarity between eumolpines and megascelines in the presence of egg bursters Ms, Mt, and A1 in the first instar larva (Cox, 1998).
(vi) Cox (1998) has pointed out. "According to Crowson (personal communication) the *Megascelis* larva is eumolpine-like in lacking ocelli and endocarina…..".
(vii) In a phylogenetic tree, based on morphology and rDNA sequences, included in Verma et al. (2005), *Megascelis* clades with Eumolpinae (Figure 16).

But there are some differences too between *Megascelis* and Eumolpinae, viz.:

 (i) Metaendosternite shows a different basic morphology in the two.
 (ii) The elytral binding sites differ in the two. In *Megascelis* there is a single oval patch of microsculpture, but in Eumolpinae this patch is divided into two parts, a
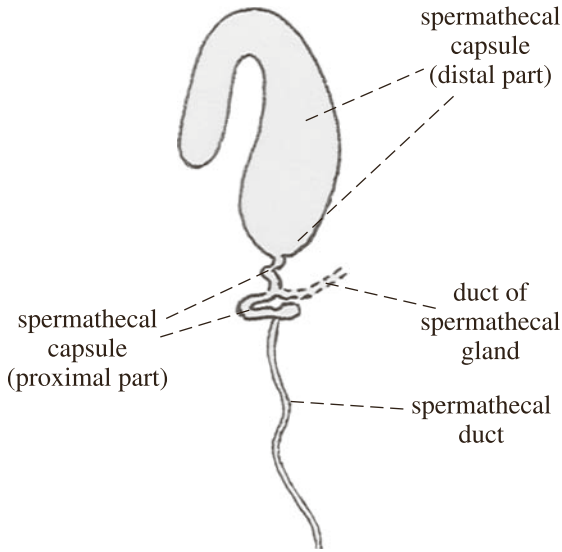
Figure 17. *Megascelis* sp., spermatheca (after Suzuki, 1988).

proximal part, which is suboval, and a distal part, which is carried on a longitu-
dinal bar like strut (Samuelson, 1996).

(iii) The abdominal egg bursters in the 1st instar larva in Eumolpinae are A1; A1+2,
but in *Megascelis* A1-A6/7 (Cox, 1998).

As similarities with Eumolpinae out-weigh differences, it would be reasonable to
include *Megascelis* Sturm and the related genus *Mariamela* Monros under Eumolpinae
as a tribe, Megascelini. Jolivet (1954) was first to regard *Megascelis* as an eumolpine.
This would be in agreement with the views of Bechyne & Springlova de Bechyne
(1969), who took eumolpines as a family, Eumolpidae, and suggested inclusion of
Megascelis as a subfamily under this family. Similar taxonomic placement has been
taken to by Suzuki & Windsor (1999). Flowers has pointed out, "The inclusion of
Megascelidini within Eumolpinae by Reid (1995) is confirmed by the structure of the
median lobe, tegmen and basal hood."

However, in view of a well marked differentiation of a long basal hood in the aedea-
gus in *Megascelis*, and *Megascelis* clading with higher Eumolpinae like *Pachnephorus*
(Figure 16), this member should not be treated as a primitive eumolpine, though it has
been found convenient to place it in this section.

6. Phylogeny

Suzuki (1988, 1992, 1994), mainly on basis of internal organs of reproduction,
has inferred that the Clytrinae, Cryptocephalinae, Chlamisinae, Lamprosomatinae,
Hispinae, Cassidinae, Megascelinae, and Eumolpinae are monophyletic. He has,
however, referred to these taxa as tribes.

Verma (1996), in his comparative study of the male genital system in Chrysomelidae, has regarded Bruchidae, Sagrinae, Donaciinae, Criocerinae, Cassidinae, Hispinae, Clytrinae, Cryptocephalinae, Chlamisinae, Lamprosomatinae, and Eumolpinae a monophyletic assemblage.

After an extensive discussion on phylogeny of Chrysomelidae subfamilies, Schmitt (1996) inferred, "…a Kotpresse (Clytrinae, Cryptocephalinae, Chlamisinae, Eumolpinae, Synetinae and Lamprosomatinae) form one monophyletic taxon to which probably also Megascelinae belong. The phylogenetic relations between these taxa and the remaining subfamilies are not very well substantiated."

Both Suzuki and Verma, cited above, have shown Eumolpinae branching off early from the stem leading to other subfamilies in the monophyletic assemblage.

Recently Gomez-Zurita et al. (2007) have constructed phylogenetic trees for Chrysomelidae based on sequence data of three partial ribosomal gene markers. They have inferred a monophyletic origin for Eumolpinae, Spilopyrinae (taking spilopyrins as a subfamily following Reid, 2000), Cryptocephalinae, Chlamisinae, Clytrinae, Cassidinae, and Hispinae, with Eumolpinae and spilopyrines separating from the common stem earlier than others.

Some notable similarities between Eumolpinae with some other subfamilies:

(i) Septate organization of testis follicles; this feature Eumolpinae share with Sag-rinae, Donaciinae, Chrysomelinae, Lamprosomatinae, Cassidinae, Hispinae etc.
(ii) Chen (1985) points to similarity in head features between Eumolpinae and Chrysomelinae.
(iii) From their comparative study of the aedeagal internal sac in Chrysomelidae, Mann & Crowson (1996) have suggested the following evolutionary series: Orsodacninae > Eumolpinae> Synetinae> Galerucinae> Alticinae.
(iv) All spilopyrin larvae, studied so far, have a terminal abdominal dorsal shield. Such a sclerotisation is also seen in larvae of Aulacoscelinae, Orsodacninae, Synetinae, and some Galerucinae-Alticinae.

Chapuis (1874) gave the first acceptable classification within the subfamily Eumolpinae. In this pioneer work there were many sensible remarks about *Eupales*, *Spilopyra*, *Stenomela*, and *Megascelis*. Since then, with increasing number of genera and species coming to record, all attempted classifications of Eumolpinae seem to be with some artificial features.

Within the limits of this subfamily there are forms, seemingly at different stages of evolution. This is suggested by varying organization of the aedeagal apparatus and the male internal genital system, as noted earlier in the subsections 4.2 and 4.3 of this review. In the phylogenetic tree, based on morphology and ribosomal DNA sequence data, included in Verma et al. (2005), and also in the phylogenetic cladograms in Gomez-Zurita et al. (2007), based on sequences in three partial ribosomal gene markers, within the clade of Eumolpinae two clearly separate subclades may be seen. Powell (1941) has noted. "While there is a general similarity in the character of the aedeagus (in the subfamily Eumolpinae), as well as in the tegmen, there are certain interesting differences noted which probably indicate two smaller groups within this subfamily."

Kasap & Crowson (1979) have said, " in Eumolpinae the general structure of the male reproductive organs are very variable and the structural differences are of systematic importance at the generic level….".

Now it is time to develop a more natural classification of the Eumolpinae, taking into account carefully studied and interpreted morphological features together with data from molecular sequence studies. A first notable effort in this direction has been that of Gomez-Zurita et al. (2005), who have made a molecular systematic study, reorganizing tribes and excluding 'Synetini' from the subfamily Eumolpinae.

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