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BIOLOGY OF CHRYSOMELIDAE (COLEOPTERA)

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RESUM

Biologia dels Crisomèlids (Coleoptera)

Es fa una revisió general fins l'any 1976 dels aspectes més importants relatius a la biologia del coleòpters Crisomèlids. En primer lloc es posa un èmfasi especial en l'estudi dels hàbits alimentaris dels Crisomèlids considerant la seva selecció tròfica, la fisiologia de la selecció de l'aliment i la importància econòmica. La majoria de les espècies tenen unes preferències alimentàries bastant estrictes, encara que hi ha molts casos d'al·lotrofisme. Els factors responsables d'aquests hàbits semblen ésser principalment olfactius i gustatius. S'han citat un gran nombre d'espècies com a perjudicials per a bastants cultius. Per a les diferents subfamílies de Crisomèlids es considera la seva distribució geogràfica, s'examina particularment la d'alguns gèneres com **Megamerus, Timarcha, Chrysolina** i **Gastrophysa,** i es descriu la colonització de certes espècies introduïdes com **Leptinotarsa decemlineata** a Europa i **Oulema melanopus** als Estats Units. L'heterogeneïtat cromosòmica dels Crisomèlids és molt marcada ja que presenten els nombres més extrems trobats fins ara en els Coleòpteres, i també una ampla variació en els sistemes de la determinació del sexe. Cada subfamília sembla mostrar un valor cromosòmic modal característic, però és actualment impossible de reconèixer només un cariotip primitiu a l'origen dels Crisomèlids. L'evolució cromosòmica és relativament estudiada tan sols als **Chrysomelinae, Galerucinae** i **Alticinae,** dels quals s'han analitzat més de cent espècies de cada grup. En els diversos estadis del seu cicle, el Crisomèlids utilitzen diferents sistemes de defensa davant els enemics reals o potencials. Algunes larves usen sistemes mecànics com estoigs o excrecències; diverses espècies, tant en fase de larva com d'adult, tenen glàndules repugnatòries, altres utilitzen l'autohemorràgia d'una hemolimfa tòxica, com els adults de **Timarcha,** o la immobilització reflexa, com passa a un gran nombre d'espècies. Molts crisomèlids quan es troben en perill escapen per mitjà del vol **(Donaciinae, Clytrinae, Galerucinae** i **Alticinae),** o bé saltant **(Alticinae),** mentre d'altres són protegits per homocromia **(Cassidinae),** el mimetisme respecte a certs escarabats depredadors **(Disonycha, Altica** i **Mesoplatys),** o el color aposemàtic **(Timarcha).** El dimorfisme sexual dels Crisomèlids no és aparent excepte en alguns **Clytrinae,** que tenen mascles amb potes anteriors molt llargues. Els ous, els dipositen quasi sempre sobre o sota les fulles i el seu nombre varia segons l'espècie des de 10-15 fins a 500; també es coneixen alguns casos de viviparisme o ovoviviparisme, particularment entre les espècies que viuen a climes freds. Quasi totes les espècies son bisexuals, els exemples de partenogènesi són restringits a uns pocs gèneres **(Calligrapha** i **Adoxus,** per exemple). Els ous

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o els adults poden sofrir una diapausa depenent de la temperatura baixa, la longitud del fotoperíode i factors interns. Les larves dels Crisomèlids es poden classificar segons els seus hàbits vitals en: aquàtiques, portadores d'estoigs, portadores d'excretes, d'alimentació externa, menjadores d'arrels, menjadores de tiges i minadores de fulles. La nimfosi té lloc a terra, dins del sòl, o sobre la mateixa planta. Es coneix una llista nombrosa d'espècies simbionts, paràsites, parasitoides o depredadores sobre crisomèlids, i algunes d'elles poden tenir interès pel control biològic de les plagues. Alguns crisomèlids han desenvolupat adaptacions curioses, com per exemple viure a la vora o dins dels nius de formigues o termites (**Clytrinae** i alguns **Cryptocephalinae** i **Eumolpinae**). Altres espècies tenen larves aquàtiques (**Donacia**) o fins i tot adults (**Haemonia** i **Donaciasta**). L'aptèria com a adaptació a la vida muntanyenca és també bastant freqüent, mentre que les adaptacions a la vida desèrtica o subdesèrtica són rares, i els crisomèlids cavernícoles falten quasi completament.

INTRODUCTION

The Chrysomelidae, commonly referred to as leaf-beetles, are normally included into the Phytophaga and the latter suborder contains also the Cerambycidae and the Bruchidae. The Bruchidae resemble closely the Chrysomelidae and some transition genera such as *Eubaptus* and *Rhaebus* show morphology and (for the second) color close to the Sagrinae.

The Chrysomelidae comprise a group of 35,000 species that have been described. New taxa, and even new genera remain to be described chiefly among the tropical Alticinae, which is the most important, widely distributed and adaptable subfamily. The Chrysomelidae are actually divided into 19 subfamilies of unequal importance and distribution, and even if the taxonomic opinion about the status of the tribes varies, there is generally an agreement about the subfamilies.

Various authors have raised the subfamilies to family rank in the past (Bechyne, Jolivet, Monros) and even recently CHEN (1964) has divided the Phytophaga or Chrysomelidae into six families regrouping the old subfamilies. Later CHEN (1973) split again the Phytophaga into the Cassidoidea and the Chrysomeloidea.

It seems, however, that the previous division into 19 subfamilies (fig. 1) is actually the most reasonable treatment of

TABLE I. Classification of the Chrysomelidae (after JOLIVET, 1959: modified).
Classificació dels Crisomèlids (modificat de JOLIVET, 1959).

Section 1.	EUPODA	1. Sagrinae 2. Aulacoscelinae 3. Orsodacninae 4. Zeugophorinae	5. Donaciinae 6. Megalopodinae 7. Criocerinae 8. Synetinae
Section 2.	CAMPTOSOMA	9. Clytrinae 10. Cryptocephalinae	11. Chlamisinae
Section 3.	CYCLICA	12. Lamprosominae 13. Megascelinae	14. Eumolpinae
Section 4.	TRICHOSTOMA	15. Chrysomelinae	16. Galerucinae 17. Alticinae
Section 5.	CRYPTOSTOMA	18. Hispinae	19. Cassidinae

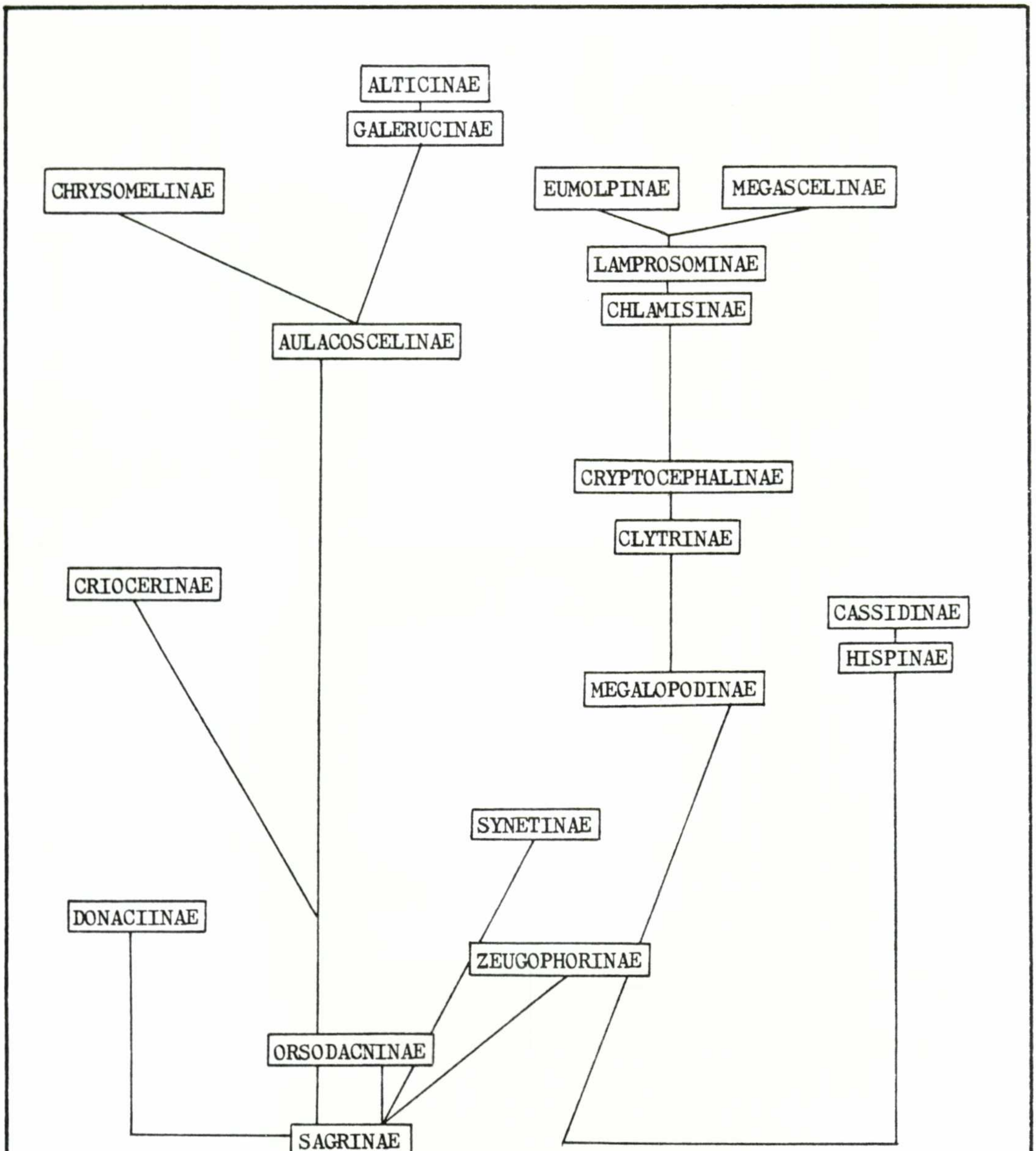

FIG. 1. Relationships among the 19 subfamilies of Chrysomelidae (after JOLIVET, 1959; modified).
Relacions entre les 19 subfamílies de crisomèlids (modificat de JOLIVET, 1959).

the Chrysomelidae, leaving apart the Bruchidae. The families are grouped however into 5 huge sections: Eupoda, Camptosoma, Cyclica, Trichostoma and Cryptostoma (table I). The relative value of the sections is variable according to the authors and rearrangements made.

Some of the Chrysomelidae, like various *Lema, Leptinotarsa, Chrysolina, Timarcha, Calligrapha, Paropsis, Aulacophora, Dia-*

brotica. Coelaenomenodera, etc., are among the best known of the Coleoptera, some for their pest status, others for their ecological interest.

Size of the Chrysomelids varies enormously from very small Alticinae (less than 1 mm) to the huge Sagrinae (25 mm) and Hispinae (27 mm).

CROWSON (1960) has studied the evolution of the Chrysomelidae and supposed that the ancestral Chrysomeloid larva was internal stem feeder and that the adult was frequenting the Jurassic precursors of flowers. Sagrinae, Megalopodinae, Auloscoscelinae have all primitive cerambycid characters in adult and larval stages and can be regarded as the most primitive of the Chrysomelids.

General ecology and biology of the Chrysomelidae are reviewed below, but not physiology or biochemistry. Only a few of the thousands of articles are quoted in the bibliography. A choice of articles has been made chiefly from recent publications. Review covers only up to the end of 1975, except for some reports on cytogenetics.

FOOD HABITS

1. Trophic selection

With the possible exception of some myrmecophilous larvae among the Clytrinae and related subfamilies, all the Chrysomelidae are phytophagous during the adult and larval stage. It is not even proved that Clytrinae larvae are not really phytophagous, but in that case they must feed on dry stems and seeds. Cannibalism is known among *Leptinotarsa* and *Calligrapha* but they eat only the eggs and larvae. *Clytra* larvae have been observed preying on ant eggs in addition to their vegetable diet. Mono- and oligophagy seem to be the rule and relative polyphagy the rare exception. The economic importance of the group as pests of cultivated and wild plants is well known.

There is a great difference in choice and specificity between the various subfamilies and the choice of primitive food-plants does not seem always to be linked with the primitiveness of the beetles (JOLIVET & PETITPIERRE, 1976).

The Sagrinae feed mainly on Dicotyledoneae (Malvaceae, Papillionaceae, etc.), in the same manner the Cerambycidae do, and their larvae are gallicolous and stem-miners. Some feed on Monocotyledoneae and Gymnospermae (Cycadaceae). *Carpophagus,* an Australian Sagrinae, morphologically very close to the Bruchidae, feeds on the seeds of Cycadaceae. There is no Chrysomelid beetle adapted to *Ginkgo biloba L.,* the only remnant of the Ginkgoaceae, still wild in East China and related to Cycadaceae.

The Orsodacninae are flower and pollen feeders on Rosaceae, Umbelliferae, or Oleaceae, when adults. Their larvae, like those of the Zeugophorinae, are leaf-miners. Adults and larvae of Zeugophorinae are found on various Dicotyladoneae (Salicaceae, Celastraceae), and Synetinae on Betulaceae and others. The Donaciinae are partly (or totally: *Haemonia*) aquatic and less selective on various aquatic plants, especially the Nymphaeaceae. They feed underwater (*Haemonia* larvae) or above it (*Donacia* at the adult stage).

The Criocerinae are found on various Monocotyledoneae, especially Gramineae, Liliaceae, Orchidaceae, Commelinaceae, Dioscoreaceae and few species are feeding on Solanaceae. Adult neotropical Aulacoscelinae feed only on pollen of Cycadaceae (Gymnospermae) and Bromeliaceae. They are very primitive in their morphology and anatomy. The Megalopodinae are pan-tropical and their larvae are stem-borers. Although the food-preferences of their group are little known they seem to feed on Solanaceae (South America) and on Leguminosae (Asia). The Clytrinae are the only true polyphagous subfamily. They feed on detritus and possibly ant eggs at the larval stage and on various Dicotyledoneae during the adult stage. The Cryptocephalinae are a little more selective and feed, as imagos, mainly on Dicotyledoneae but also on Gymnospermae and Monocotyledoneae in some species. The Chlamisinae are as a group rather polyphagous on Dicotyledoneae, but often specific (Rosaceae, Betulaceae, Salicaceae, Corylaceae, etc.) as species.

The Lamprosominae feed on Araliaceae in the holartic and subtropics, but on various Dicotyledoneae in the tropics. The Megascelinae, related to Eumolpinae, seem to feed on Papillionaceae but their biology is little known. The important group of the Eumolpinae live on about 50 families of Mono and Dicotyledoneae, on few

Gymnospermae, but are very specific as a genus or a group of genus (for instance: *Chrysochus* and allies on Asclepiadaceae and Apocynaceae).

The large group of the Chrysomelinae feed only on Dicotyledoneae (40 families, 200 genera of plants), but are rather specific in their food choice. Among 135 genera, 48 (36 %) have their food-plant known. Some have a very complex feeding spectrum, like *Timarcha* and *Chrysolina* (Jolivet & Petitpierre 1973, 1976, figs. 2 and 3), and relationships between the plant families are not always absolutely evident. Generally, there is some evolutive link, either chemical or botanical or even statistical (Paropsini). *Leptinotarsa,* normally a *Solanum* feeder, seems to show also a tendency towards Asclepiadaceae and Compositae, a general tendency of few other allied genera. *Gonioctena, Phratora, Plagiodera* and many others have a simple feeding pattern as well as the Australian Paropsini, which are mainly *Acacia* and *Eucalyptus* feeders. *Calligrapha* feeds on 12 plant families, more or less related, but on shrubs, trees and herbs. *Chrysolina* and *Timarcha* never feed on trees or shrubs but on herbaceous plants only. This can be linked with the loss of flight ability or any other reason. Very often genera like *Chrysomela* or *Paropsis* feed on young tender leaves of trees and never on old leaves.

The Galerucinae are generally (not always: *Galeruca*) very selective in their foodplants: Mono- or Dicotyledoneae, 60 or 70 families in all. The Alticinae are generally very specific in their choice, more than 100 plant families, from Gymnospermae to Mono- or Dicotyledoneae. They show very often biological races, morphologically similar but feeding in the same area on very different host-plant. Seasonal races have also been quoted among the Alticinae. Some complexes or related forms, like the *Podagrica/Nisotra* feed on a plant group rather closely related (Jolivet, 1972): the Malvales. The same is true in the holartic and in the tropics. Hispinae are more eclectic in their choice of host plant and their main choice is the Gramineae (spiny species) and the Palmae (smooth species). Other plant families (30) are also a possible choice for certain species. The Cassidinae feed mainly on Convulvulaceae, Compositae, Labiatae, Chenopodiaceae and various other Dicotyledoneae.

From the above review of the feeding

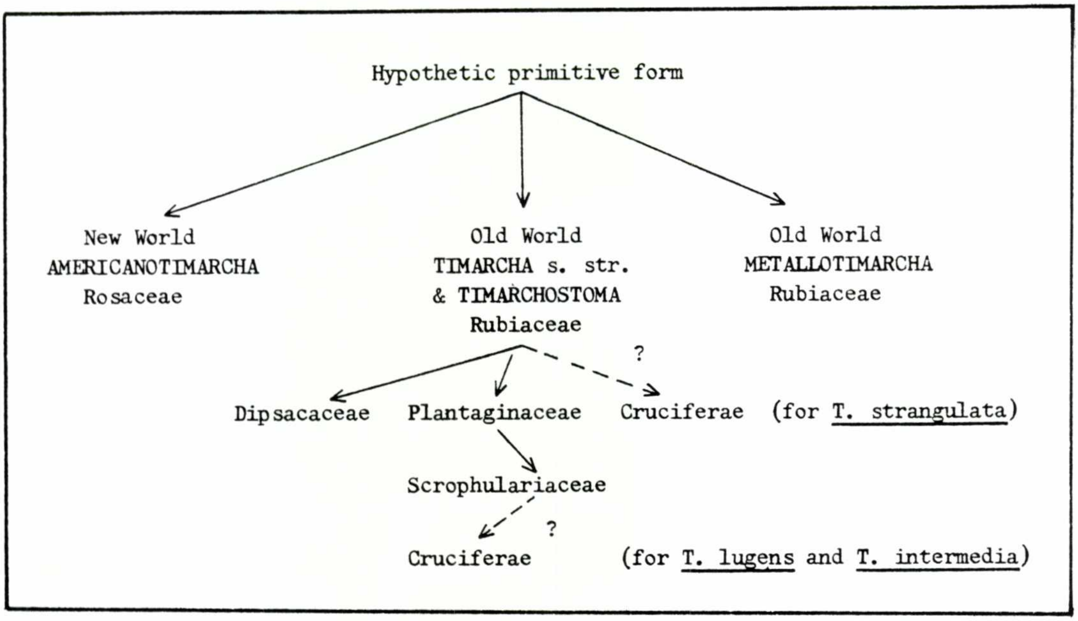

Fig. 2. Trophic selection among the *Timarcha* spp. (after Jolivet & Petitpierre, 1973).
Selecció tròfica en les espècies de *Timarcha* (de Jolivet & Petitpierre, 1973).

preferences of the Chrysomelidae, it can be said that the rare species which feed on Pteriodophytes are specialized forms which are linked with the ferns only by secondary adaptation. Only few authentically primitive forms, like some Australian Sagrinae and the Aulacoscelinae are linked with primitive plants like the Cycadaceae. Whilst on the contrary, a very specialized group, the Hispinae, feed on Monocotyledoneae, like the primitive Criocerinae.

There are many cases of allotrophy known among the Chrysomelidae, but very often there is below some kind of hidden botanical relationships or the choice is due to lack of suitable host plant or due to the succulence of the cultivated plants.

Food is normally taken in temperate areas and in the tropics, during day time. Only in subdesertic or mountainous areas, the feeding habits become crepuscular or nocturnal. This is also the case for some North American *Timarcha* feeding on *Rubus* in Oregon, but generally speaking the larvae eats almost day and night (JOLIVET, 1976). In the Turkmenistan, both adults and larvae of *Nyctiphantus hirtus* feed on *Calligonum* (Polygonaceae) only at night (KOPLIN, 1975).

Most of the Chrysomlidae feed on leaves, roots or dead stems or bark (Clytrinae). They generally eat the epidermis in the open air, but larvae also can feed on the collar of the root (Alticinae, Galerucinae) or under water (Donaciinae). Larvae of Hispinae and some Alticinae and Galerucinae are miners (roots, leaves) or gallicolous (Sagrinae). One species *(Haemonia mutica)* feeds on *Potamogeton* and *Zostera* in the brackish water of the North Sea. Adult Megalopodinae cut plant shoots

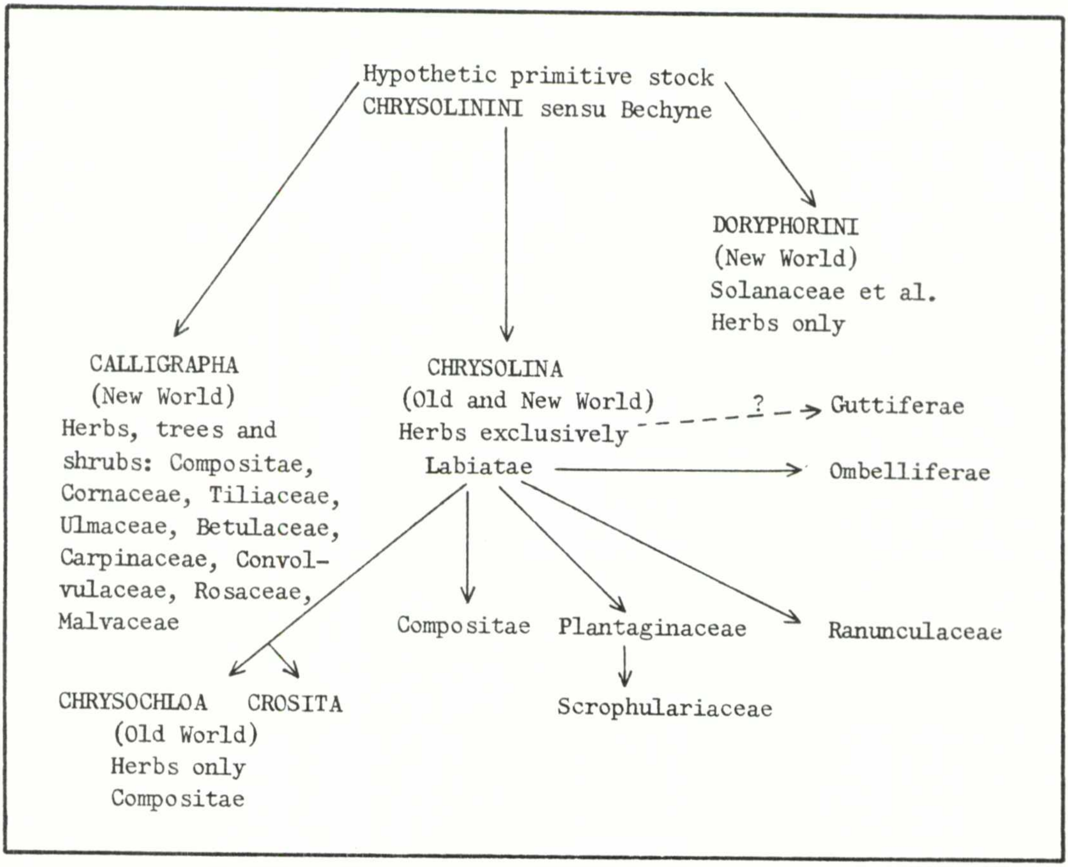

FIG. 3. Probable trophic selection among *Chrysolina* (after JOLIVET & PETITPIERRE, 1976).
Probable selecció tròfica a *Chrysolina* (de JOLIVET & PETITPIERRE, 1976).

to feed on sap (MONRÓS, 1954). They behave very much like the Cerambycidae in the way they make a circular or spiral incision round the stem, one centimeter below the former cutting. They use their mandibules to do it and they lay their eggs at 2-3 mm below the first cutting into the stem.

Many larvae of Chrysomelidae stay at the inferior side of the leaves (Cassidinae, Galerucinae), but that can be linked with microclimate or with the difference between both epidermis of the density of stomata. Other interpretations seem rather doubtful (RABAUD, 1921).

Among *Calligrapha*, a North American genus of Chrysomelinae, of which the species restrict their feeding to one or to a few species of plants, sibling species are very common (BROWN, 1945). *Altica, Galerucella, Arthrochlamys, Chrysomela* species have been segregated in the same way «by testing the ability of populations from one food-plant to utilize food-plants of other populations» (WOODS, 1918, 1924; BROWN, 1945).

There are few troglobionts among the phytophagous insects. Among the Chrysomelidae, only some Galerucinae have been mentioned in Indian caves (ABDULALI, 1948), but they are only trogloxenes, i.e. accidental guests without any morphological regression or special adaptation.

The adaptation of aquatic (*Haemonia*, some *Donacia* and *Donaciasta*) and semiaquatic *(Donacia)* phytophagous insects to underwater life has not modified their food habits. Underwater larvae, pupae or larvae respire through the aerifeous lacunae of the plants or the adults get the oxygen from bubbles liberated by chlorophyllian assimilation. Hairy antennae and water-proof sternite hairs help in keeping the air. Feeding is done underwater by sucking the sap of aquatic plants, such as *Phragmites, Typha* and *Nymphaea*.

According to HODSON (1929), *Oulema melanopus* consume around 6 cm^2 of leaves, i.e. 5 leaves, during its larval life. Quantity of food eaten varies enormously according to such factors as the life-habits, the size and the length of larval stages, etc.

2. Physiology of food selection

It has been proved that color vision exists in Chrysomelid beetles *(Chrysolina, Agelastica)* (SCHLEGTENDAL, 1934 in WIGGLESWORTH, 1961; DE WILDE & PET, 1957) and they are able to distinguish green tints from one another, as well as yellow and orange from blue-violet and green. Food selection is also olfactive, gustative and mechanical. MITCHELL & SCHOONHAVEN (1974) have shown on *Leptinotarsa decemlineata* that sensillae on various mouthparts of the larva contain chemosensory cells in direct relation to feeding habits.

On cotton (BRADER, 1967), *Podagrica* spp. are lead by an attractive, probably olfactory factor perceived at some distance. Once settled on the host-plant gossypol exerts a repulsive or inhibitory action on the feeding process of *P. uniformis* and *P. dilecta,* but not on *P. pallida.*

The cucurbitacins, tetracyclic triterpenes, are the well known bitter principles present in Cucurbitaceae. There is a quantative relation between the concentration of the chemical in the plant and the degree of the *Diabrotica* feeding (CHAMBLISS & JONES, 1966).

Mustard oil glucosides, principal constituants of ·the Cruciferae, stimulated a feeding rsponse on bean leaves of *Phyllotreta cruciferae* (HICKS, 1974) which is normally an unacceptable host. Similar results have been obtained previously with leaf beetles like *Gastrophysa viridula* (KOZANCHIKOV, 1941) and others.

Researches of HSIAO (1967, 1968, 1969, 1974) have shown that chemical stimuli in plant selection include attractants, repellents, sign stimulants, feeding stimulants and deterrents. *Leptinotarsa decemlineata* can be reared on some selected *Solanum*, but also on *Asclepias* (Asclepiadaceae), *Capsella* (Cruciferae), *Lactuca* (Compositae). The attractiveness to Solanaceae, Asclepiadaceae and Compositae is shared by many species of Zygogrammini and Doryphorini. Among the *Leptinotarsa* species tested by HSIAO (1974), *L. decemlineata* because of its adaptability in feeding habits, is the only species that has reached pest status.

According to CHIN (1950), in *Leptinotarsa* larval antennae and palpi carry the olfactory organs and the internal surface of the labre and labium has a gustatory function. According to MITCHELL & SCHOONHOVEN (1974), the sensillae which contains chemosensory cells are found on the galea, maxillary palps, and labial palps. REES (1969) has shown that tarsal receptors of *Chrysolina brunsvicencis* are stimulated by hypericin from its host-plant *Hypericum*. Beetles of the subgenus *Hypericia* are all strictly monophagous.

Specificity is often very strict on few species of a given plant genus (some *Chrysolina*) but is often linked with many species of the same genus. *Plagiodera erythroptera* feeds only on *Salix* and all other plants are rejected (ZAPATA, 1970). It seems that if some insects feed only on young and more succulent leaves (*Chrysomela, Paropsis*), there is also sometimes a correlation between abundance and weather which is believed to stress the plants making them more nutritious for the insects *(Paropsis)* (WHITE, 1973).

The repellent effect of nicotine on the potato beetle is shown by certain grafting experiments (in FRANKEL, 1959). In tobacco, nicotine is synthetised by the root. A tobacco plant grafted onto root is free of nicotine and eaten by *Leptinotarsa*. The contrary, when a potato plant is grafted onto a tobacco root, is also true: the potato becomes resistant to *Leptinotarsa*. Highly toxic Solanaceous plants like *Petunia* and *Salpiglossis* are nevertheless attractive to *Leptinotarsa*.

There is some kind of relationship between the carotenoids found in the *Lilioceris* and their host-plant, but some are partly converted by the beetle from its food (MUMMERY & VALADON, 1974).

When two species of *Oulema* (*O. cyanella* and *O. melanopus*) cohabit on the same plant (wheat) at low competition level, there is no competition for food (FILLAUX, 1968). Survival depends more on the aptitude to reach and exploit food than on its abundance. Similarily, CROMARTIE (1975) has studied the colonization of collard plants by various insects, including *Phyllotreta striolata* and *P. cruciferae* and concluded that each species has a different pattern of colonization behavior. Average size of *Oulema melanopus* seems to be inversely related to population density, probably to availability of larval food (JACKMAN & HAYNES, 1975).

When two species of *Diabrotica* (LUDWIG & HILL, 1975) feed on the same food-plant (corn), there are some differences in the gut contents (corn leaf, corn pollen, corn silks, weed pollen, fungal spores and gregarines) between species and sexes. Structure of the leaf can be an important resistant factor in species and variaties of plants. *Timarcha* refuses hairy *Galium (G.aparine)* and the effect of density and length of trichomes determines the oviposition and larval survival of *Oulema melanopus* (HOXIE, WELLSO, WEBSTER, 1975). It is well known that resistance to the cereal leaf beetle, *Oulema melanopus*, in wheat is a function of pubescence of the leaves (SCHILLINGER & GALLUN, 1968; RINGLUND, 1968, in HORBER, 1972).

Under selection pressure, it has been possible to force *Gastrophysa viridula* to accept various host plants slightly different from the ones accepted in the field (KOZHANCHIKOV, 1941). The species remains anyhow feeding on Polygonaceae. Among some Chrysomelidae, cases of allotrophy or accidental choice of a different food plant remain a rather rare case (JOLIVET, 1952b). However, some selections remain potential as for *Agelastica*, normally an *Alnus* feeder, the selection of Rosaceae. Among Alticinae, biological races feeding on a different host plant are rather frequent. They belong to the same species, can exist in the same area (sympatric), but can be slightly different in aspect or in wing status.

3. Economic importance of the phytophagous Insects

A large number of studies have been made on the Chrysomelidae of economic importance. Many species, belonging to many genera, are in some or other way attacking the roots, stems, leaves, flowers or fruits of flowering plants. It would take too long to quote the Chrysomelid pests from the Sagrinae to the Hispinae. Damages caused by imported pests (*Leptinotarsa* in Europe, *Oulema, Microtheca* in the USA) or local ones (*Diabrotica*, Alticinae and Galerucinae) are well known and it is impossible to quote even the most recent literature on the subject.

For information containing these useful Chrysomelidae used against imported weeds reference should be made to HUFFAKER (1959), DEBACH (1965) and more recent papers. Here also it would be fastidious to quote all sources.

The following Chrysomelids have been imported overseas from their place of origin: *Physonota alutacea* and *Schematiza cordiae* against *Cordia macrostachya, Altica carduorum* against *Cirsium arvense,* *Chrysolina brunsvicensis, C.varians, C.hyperici, C.quadrigemina* against *Hypericum perforatum,* etc.

Many species of Chrysomelidae become involved directly and indirectly in the transmission of some important fungal, bacterial and viral diseases of plants, like *Diabrotica, Chaetocnema,* and various other Alticinae and Galerucinae.

In the USA, various species of Chrysomelidae *(Cerotoma, Diabrotica, Acalymma, Colaspis;* TURNISPEED & KOGAN, 1976) have shifted from wild leguminous hosts to soybean after the crop was introduced. The same is true in Indonesia with *Phaedonia inclusa* (ANKERSMIT, 1952). In Africa, where soybean is still rarely cultivated, only very few Chrysomelidae feed occasionally on the plant (*Ootheca mutabilis* Sahlberg) and some leguminous feeders, like *Phaedonia* and *Mesoplatys* have not yet shown any interest in soybean. In Asia, the native land of soybean, some *Luperodes* feed on soybean leaves.

GEOGRAPHICAL DISTRIBUTION

The Chrysomelidae are present almost everywhere but the density of species is greater in the tropics than in the holartic zone. The Alticinae are the most abundant and widely distributed group and they exist on some Pacific islands where all other representatives of the Chrysomelidae have disappeared or never existed. Normally, the number of species and genera diminish towards the east of the Pacific and they are absent in the most eastern archipelagoes. There are no endemic Chrysomelid in Hawaii and Tahiti and only imported species. GRESSITT (1967) has studied the distribution of the Chrysomelidae in the Papuan region.

There are very few species of Clytrinae in the Papuan and Australian region, and that does not seem to be linked with the lack of host plants. Clytrinae are mostly abundant in tropical Africa (31.1 %), in Tropical America they represent, 24.3 %, in the Palaearctic region 21 %, in South East Asia, 20.2 %, in North America 3.6 % and only 0.1 % in the Australian region (MONRÓS, 1953).

Certain islands, like Juan Fernández, St. Helena, etc., have their own endemic Alticinae. There are few species in the Galápagos and the fauna of New Caledonia is extremely original in itself. Many Chrysomelids are endemic there and a big Eumolpinae *(Bohumiljania)* is very close to the Chilean genus *Stenomela* (JOLIVET, 1957, 1959; MONRÓS, 1958). *Stenomela pallida* feeds in Chile on *Gunnera chilensis* (Gunneraceae). There are other cases of links between New Caledonia and South America. New Caledonian and New Guinean faunas are somewhat dysharmonic in composition.

The Chlamisinae have a worldwide distribution, but not in Europe. The only Palaearctic species are found in Eastern Asia and are of tropical stock. 9.39 % are found in the Palaearctic region, 6.68 % in the Nearctic, 8.14 % in the Oriental region, 1.87 % in the Ethiopian region and 79.94 % in the Neotropical region. The Chlamisinae are essentially a tropical subfamily as are the Megalopodinae and certain subfamilies like the Aulacoscelinae and the Megascelinae which are only found in South America. There are no Chrysomelidae in the subantarctic islands, but few species live in Iceland; including probably an introduced *Timarcha* (JOLIVET, 1972a). *Timarcha* has also been introduced into one of the Canary Islands (JOLIVET, 1954b). There are no records of Chrysomelidae in Greenland, Spitzberg and Nova Zembliae, but they reach *(Chrysolina)* as far as Kamchatka, Okhotsk in Siberia and the Kuriles.

Survival of alpine communities of the species *Chrysomela collaris* in Southern Norway is due to a combination of several factors•(HAGVAR, 1975): the beetle utilizes only those parts where the snow melts very early. It feeds on *Salix herbacea* and has only one year cycle. Adults become active as soon as the snow has melted, feed on unopened shoots, achieve copulation and lay eggs after a short time and eggs hatch soon after the leaves are developed. The larvae grow quickly and both larvae and imagos are active at low temperature. Other species are either ovoviviparous or extend their life cycle over 2 or more years. It seems that such a mechanism for survival has been used by many alpine or boreoalpine species of *Chrysolina* and even by a more thermophilic genus like *Timarcha* along the southern extension of the quaternary glaciers. Two year cycle and egg diapausis of *T.tenebricosa* seem as protective as the viviparity of many northern species of *Chrysolina.*

A good example of a cold boreal species is given by *Chrysolina staphylea* which is found in North-eastern Canada, including Newfoundland, northern Europe and Siberia and in an isolted area in the Alpine zone of Mount Halla in Cheju-do island, Korea (Jolivet, 1975). However the island is actually subtropical and the beetle is a relict from a cold pleistocene bridge with the continent.

The distribution of the archaic Sagrinae like *Megamerus* and allies (Monrós, 1956) shows evidently some kind of Gondwanian distribution. *Megamerus* survives in Australia, Madagascar and Brazil, hardly modified and is probably a pre-cretaceous genus which has spread through Gondwanaland before the isolation of Australia. Some other Sagrinae from the Southern hemisphere evidently belong also to archaic and Gondwanian stock.

The Paropsini are linked with the *Eucalyptus* distribution in Australia and New Guinea, but outside that area they are feeding on Rosaceous trees. The *Donacia* are represented in the holartic and the subtropics (Cuba, Central America, Taiwan) by brightly colored species, but they are replaced in the tropics (Africa, New Guinea, Indonesia, Northern Australia) by dull species (*Donacia, Donaciasta* and *Donaciocrioceris*), probably totally aquatic like the *Haemonia.* The Donaciinae seem to be missing in the neotropics (Jolivet, 1972a); *Haemonia* (with the subgenus *Neohaemonia*) is distributed through the holarctic, and as far as we know, has not yet been found in the tropics and the Southern hemisphere.

Among the Chrysomelidae, the archaic genus *Timarcha* seems to be unique in its structure, anatomy, physiology, behavior and distribution. *Timarcha* is limited to the warm part of Europe and North America, the northern limits corresponding exactly with the maximum extension of the quaternary glaciations. With its subelytral cavity and its wingless status, *Timarcha* is also preadapted to desert life and it prospers in oases and the steppic areas in North Africa (Jolivet, 1968b). The apterism of the genus *Timarcha* must be extremely old, since the pupae are themselves apterous, a rather rare thing among the beetles but shared with *Meloe* and some Tenebrionids.

The distribution of the species of the genus *Timarcha* belongs to the discontinous holarctic type: Mediterranean and Western Pacific and it is a typical case of a thermophilic genus which probably disappeared from Siberia, its possible birth place, and from Northern Europe and Canada (except southern British Columbia and Vancouver Island) during the ice ages.

Gastrophysa is another example of an holarctic genus with distribution through North America, Europe, Siberia and China-Japan with a short incursion in the northern subtropics (Mexico, Taiwan, Tonkin). *Gastrophysa* has shown a rather erratic distribution on its host plants (Polygonaceae) (Jolivet, 1974b).

Balearic Chrysomelidae (Jolivet, 1953a) show some pliocene connection with Spain, and Canarian Chrysomelidae (Jolivet, 1954b) are an example of dysharmonic palearctic fauna, formerly connected with Morocco.

Eumolpinae are chiefly abundant in the tropics and well represented in Madagascar (260 species), the Mascareignes, and South America. Hispinae are mostly tropical or subtropical, with and endemic tribe in Madagascar.

There exists apterous, micropterous and brachypterous forms in species among certain families of Chrysomelidae and chiefly among the most evolved forms (Chrysomelidae, Galerucinae and Alticinae). The brachypterism starts only from Lamprosominae and above in the general classification. The Chrysomelidae only show insular apterism in a few cases (*Minotula,* Alticinae from Juan Fernández island). However, many mountainous species are apterous or brachypterous. Biological forms among the Alticinae are sometimes connected with the different host plants and different wing status (Jolivet, 1956).

An excellent study of the variation of Chrysomelid species in an archipelago (Ryukyu Islands) has been made by Kimoto (1964, 1966, 1967).

Some *Chrysolina (C. aurichalcea)* produce different color forms according to the area concerned. In the Yellow Sea islands, only the blue form is met (Jolivet, 1973, 1974b); Brown (1959), has mentioned a complex of sibling species among the genera *Lema, Chrysomela, Calligrapha* and *Chlamisus.* The species vary geographically in feeding habits and can be easily confused morphologically. More research remains to be done in species distribution and feeding preferences. Brown (1959), quoting Benson, noted that apparent polyphagy often hides a subdivision of the species into highly specialized foodplant races, species of subspecies.

The distribution of some highly monophagous species can be linked only with the distribution of one species of host-plant. For instance, *Altica brittoni* can be met only where *Empetrum nigrum* grows in Eastern Europe (Mohr, 1975).

There have been several Chrysomelidae introduced accidentally in Europe, the USA and some tropical or subtropical lands. Generally, the insects devoid of their natural parasites adapt and multiply rapidly. In the case of the South American *Microtheca,* introduced accidentally from Argentina to Florida on local Cruciferae, the beetle reversed its cycle. The example of the spread of *Leptinotarsa decemlineata* from its focus of introduction in South Western France towards Europe during the last forty years is striking. Siberia has not yet been reached and due to climatic conditions it was not established in Finland (Markkula, 1974) and the North of the Baltic states. It must be outlined that the northern limit of the distribution of *Leptinotarsa* in that area corresponds approximately to the area occupied by *Timarcha.* Cold seems to be the limiting factor. *Oulema melanopus,* which is a pest in the USA, rarely occur in number on the cereals in Europe, its native place.

L.decemlineata, which invades actively (migratory flight) or passively England every year (Seymour, 1974), has not yet established itself thanks to strict control measures. The active spread of the Colorado beetle through Europe gives an idea of the mechanism of the distribution of winged insects and the time needed (Jolivet & Petitpierre, 1976). In case of flightless insects, the time necessary to colonize the Paleaearctic can be measured by millions of years.

The paleaearctic species *Oulema melanopus* was first found in Michigan in 1962. Since then, it is expanding in the USA and Canada. Its ability to adapt to diverse climatic conditions suggests that someday it may inhabit most of the cereal-growing regions of North America. It is an example of quick expansion of a winged species (Wellso *et al.,* 1970a).

Lopatin (1969) has speculated about the possible origin of the alpine fauna of the Chysomelidae of Central Asia. For the Russian author, the pretertiary autochtonous fauna of leaf beetles has adapted to high altitude during or after the orogenesis of the Alpine mountains (*Oreomela, Xenomela, Entomoscelis,* the three genera being apparented). From the high mountains of Central Asia, there were migrations towards the Karakorum and Himalaya. *Crosita* is also partially a mountain genus of Central Asia but seems also differenciated from low altitude species.

CHROMOSOMIC EVOLUTION AND HEREDITY

Smith (1953, 1960) compilated chromosome numbers and karyotypic formulae of the Coleoptera species checked till 1959; since then a large number of papers concerning the chromosomes of Chrysomelids and many other beetles have been published. Most papers present records on chromosome numbers and sex-determining systems but a few of them have analyzed other more important cytogenetic characteristics which are valuable for a better understanding of chromosomic evolution and meiotic systems, such as karyometric analyses in closely related species, presumed chromosomal rearrangements involving autosomes and heterochromosomes, chromosome behavior in both divisions of meiosis, frequency of chiasmata per bivalent, etc.

As far as we know the total number of chromosomally analyzed Chrysomelids amounts about 400 species. From the whole cytological data obtained in Chrysomelidae it becomes evident that this family exhibits the maximum of heterogeneity in chromosome numbers among Coleoptera. Thus *Homoschema nigriventre* (Alticinae) shows the lowest number, $2n=8$ (Virkki & Purcell, 1965) shared with the carabid *Graphipterus serrator* (Wahrman, 1966), while the male of *Rhaphidopalpa femoralis* (Galerucinae) shows the highest, $2n=59$ (Yosida, 1953). Smith (1950, 1953, 1960), in his wide screening on chromosome numbers of Coleoptera, found $2n=20$ and $9^{II}+Xy_p$ karyotypic formula (Xy_p=parachute system of sex-chromosomes), as the most frequent and primitive formula for the order, excluding Coleoptera Adephaga which modal number seems to be

$2n(♂)=37$ (Wahrman, 1966; Dasgupta & Chakravarti, 1972).

It is difficult to assume what is the ancestral chromosome number for Chrysomelids because besides $2n=20$ other numbers as $2n=22$ and $2n=24$ are largely represented too. Dasgupta (1973) has considered $2n=24$, $11^{II}+Xy_p$ formula, as the possible ancestral number for Chrysomelidae, but the evidence does not seem conclusive before a larger sample of species and particularly those more primitive will be subjected to chromosomic analyses.

At the present knowledge only a few subfamilies of Chrysomelidae have been worked with to permit preliminary conclusions. Among the section of Eupodes, a group including the less evolved Chrysomelids, the Donaciinae are known by five species (Smith, 1953, 1960; Petitpierre, unpublished), two with $2n=28$ and three with $2n=30$, all five species with Xy_p sex-chromosome system. In the same section, the Criocerinae are known by twelve species, most of them quoted in the recent paper by Yadav & Pillai (1974a) and the remaining from our unpublished results, having $2n=16$, $7^{II}+Xy_p$ formula, as the most frequent number though there are two 20-chromosome species. The striking difference between the chromosome numbers of Donaciinae and Criocerinae seems to indicate a clearly divergent chromosomal evolution but does not contribute to solve the problem of the hypothetic primitive karyotype. Other subfamilies of the Eupoda, such as Orsodacninae and Zeugophorinae, are completely unworked and the Sagrinae are only known by one species, *Sagra femorata,* a rather evolved species within the group (Monrós, 1959), which could probably explain its derivative karyotypic formula, 7^{II}+neo XY (Yadav & Pillai, 1974a).

The sections of Camptosoma and Cyclica are poorly analyzed. In the Camptosoma some Clytrinae seems to be very different in chromosome number, for example two species of *Clytra, C. quadripunctata* and *C. succinata,* have $2n=24$ (Petitpierre, unpublished) and $2n=40$ chromosomes (Yadav, 1971), respectively. On the other hand a few species of Iberian *Lachnaea* evidence $2n(♂)=25$ as the most frequent number (Petitpierre, unpublished). The Cryptocephalinae are cytologically known by seven species of *Cryptocephalus* (Smith, 1960; Alegre & Petitpierre, unpublished), the majority of them having $2n=30$ while the only three analyzed *Pachybrachis* have $2n=16$ chromosomes (Smith, 1960).

In the section of Cyclica the Eumolpinae are checked in for twenty-one species (Smith, 1953, 1960; Virkki, 1964; Yadav, 1970; Dasgupta, 1973). Here again the range of variation in chromosome number is clearly wide from $2n=12$ to $2n=30$; the species of some genera like *Brachypnoea* and *Colasposoma* show low chromosome numbers, $2n=12$ and $2n=16$, whereas two *Corynodes* show $2n=30$. Dasgupta (1973) has pointed out the difficulty of assuming any primitive condition for karyotypes of Eumolpinae, however according to Virkki (1964) a possible initial condition of 9-11 pairs of metacentric autosomes gave rise to one line characterized by a decrease and to another line characterized by an increase in the number of chromosomes. There is also a tendency in Eumolpinae towards a neo-XY formation which could possibly be coupled to the decrease of number by centric fusion between autosomes and sex-chomosomes (Virkki, 1964). Finally, with regard to the sex-chromosomes both sections, Camptosoma and Cyclica, have the y_p parachute-type systems as the prevalent one.

The sections of Trichostoma and Cryptostoma are the best cytologically worked within Chrysomelidae and therefore, they will be more extensively dealt with. Among the first section, the Chrysomelinae have been studied by more than one hundred species, and some genera like *Timarcha, Chrysolina* and *Calligrapha* have been subjected to rather deep chromosomic investigations. The cytological evolution or Chrysomelinae seems to have developed by increasing chromosome number. The genus *Timarcha* has as its more frequent number, $2n=20$, and Xy_p sex-system, that is the primitive formula of Coleoptera Polyphaga, in agreement with its primitive morphological traits, but there are also species with 22, 24, 26, 28 and 44 chromosomes (Petitpierre, 1970, 1976; Petitpierre & Jolivet, 1976). The most common number of *Chrysolina, Calligrapha, Gonioctena* and the Australian Paropsini seems to be $2n=24$, $11^{II}+Xy_p$ chromosome formula. More than 60 % species of *Chrysolina* are characterized by this last number and formula with the extreme ranges of 2n=22 and 2n(♂)=47 (PETITPIERRE, 1975, 1981). The *Timarcha* and *Chrysolina* have followed a similar chromosomal evolution by increases in the number of chromosomes though other structural rearrangements such as pericentric inversions and translocations seem to have played a certain role in their evolution. The *Calligrapha,* at least the North American species, are very conservative in chromosome number because all of them except six parthenogenetic tetraploids, have 2n(♂)=23 (ROBERTSON, 1966). Nevertheless, the recent finding of a 2n=24 male karyotype in *C. polyspila,* a South American species (VAIO & POSTIGLIONI, 1974a), could probably be taken as an indication of the most primitive complement of *Calligrapha,* being the North American species derived after losing the *y*-chomosome. Other *y*-chromosome losses have been detected in the cytological evolution of *Chrysolina* determining a change from the y_p sex-chromosome system to XO (PETITPIERRE, 1975).

JOLIVET & PETITPIERRE (1976b) have studied the possible indirect relationships between chromosome numbers and feeding preferences in Chrysomelinae, having encountered only in *Chrysolina* an apparent correspondence between both aspects.

The Galerucinae are inequally worked out since most species chromosomally checked belong to Diabroticites (ENNIS, 1972; SMITH, 1972). VIRKKI (1964) distinguishes two different groups in Galerucinae based upon chromosomes. A «conservative» line having low chromosome numbers which includes most Diabroticites, and a «derivative» line with high chromosome numbers including very different species. As far as we know all species of *Diabrotica* show a karyotype of 2n(♂)=19 metacentric chromosomes closely related to the hypothetical most primitive karyotype of Chrysomelidae (SMITH, 1972). Again in this subfamily the majority of chromosomic evolution seems to have occurred by increases in the number of chromosomes from the primitive formula of *Diabrotica* species, $9^{II}+X$, or an allied one of 20-chromosomes in male, though all Diabroticites possess an XO sex-determining system with only one exception. It is interesting to mention that several Diabroticites exhibit B-chromosomes whose possible adaptive significance would be worth to investigate. Furthermore, one of the few papers devoted to the chiasmata frequency in Coleoptera took some species of *Diabrotica* as object (ENNIS, 1972). Out of Diabroticites the remaining Galerucinae are to disparate and bad chromosomally known that trying to recognize evolutive trends and phylogenies would be pure speculation.

The Alticinae are perhaps the best chromosomally studied chrysomelids. The chromosomic evolution in Alticinae is assumed to have proceeded in various lineages from the primitive karyotype of 24 chromosomes ($11^{II}+Xy_p$ formula) by increases and decreases from this number (VIRKKI, 1970). VIRKKI (1969) has reported a relationship between this chromosomic evolution and the decrease in the number of spermatozoa per bundle from 256 to 16, which is a rather common trend in Insects. Some of the oddest sex-chromosomes of animals have been reported in this subfamily where the subtribe Oedionychina is characterized by their giant, but not polytenic X and Y chromosomes, showing asynaptic orientation and segregation (VIRKKI, 1961, 1963, 1967, 1971, 1972). These giant sex-chromosomes are presumably derived from those of normal size of an *Altica*-like karyotype, $11^{II}+X+y$, by translocations of autosome-formed heterochromatin and by duplications. In addition, these chromosomal rearrangements in Oedionychina are coupled with the acquisition of a new spindle system for these sex-chromosomes different from that specific for autosomes, and with the change from amphitelic type of orientation of their centromeres in metaphase I plate to the syntelic type (VIRKKI, 1970). Whereas most Chrysomelidae have the Xy_p system as the prevalent mechanism of sex-chromosomes, only a few species of Alticinae have retained it. Thus it is not rare that many Alticinae exhibit asynaptic pairing of these last chromosomes, and systems of multiple sex-chromosomes have also been reported (VIRKKI, 1968a, 1968b, 1970).

In the section of Cryptostoma, the Hispinae are chromosomally analyzed by eight species which are distinguished by their low chromosome numbers, mostly 2=18 and 2n=20, and Xy_p as the unique sex-chromosome system (YADAV & PILLAI, 1974b). The case of *Hispa armigera* is very peculiar since it has two chromosomal races in India, a diploid with 2n=12 and a triploid one with 3n=18 chromosomes (Saha, 1973). A possible tendency towards a decrease in number has also been hypothesized in the chromosomal evolution of Hispinae (Yadav & Pillai, 1974). The other subfamily of this section, the Cassidinae, is better known than the previous one since the present record amounts to twenty-eight analyzed species (Smith, 1953, 1960; Manna & Lahiri, 1972; Takenouchi, & Shiitsu, 1972; Dasgupta, 1973; Vaio & Postiglioni, 1974b; Yadav & Pillai, 1975; Petitpierre, 1977, unpublished). About 60% analyzed species have $2n=18$ chromosomes and $8^{II}+Xy_{p}$ formula, being this number and formula tentatively considered as the modal and most primitive one for Cassidinae. This subfamily has also a wide range of variation in chromosome number from $2n=18$ to 2n(♂)=51 though the Cassidinae are more conservative in this aspect than other chrysomelid subfamilies (Vaio & Postiglioni, 1974b; Petitpierre, 1977). A small number of Cassidinae species have been karyotyped showing complements constituted by large metacentric chromosomes in species of 18 and 20 diploid numbers, while there are metacentric or acrocentric small elements in species with high numbers (Vaio & Postiglioni, 1974b; Yadav & Pillai, 1975; Petitpierre, 1977). This difference in the size of chromosomes between both groups could probably indicate the origin of the latter group from the former one by chromosomal dissociations or centric fissions, but other chromosomal rearrangements have possibly taken place in evolution of Cassidinae as it has been pointed out by the previous group of authors.

We can conclude that chromosomic rearrangements that have occurred in the evolution of Chrysomelidae need a more careful research to get an exact picture. It is probable that after an extensive application of the new banding techniques many of the assumed chromosomic rearrangements will be accurately demonstrated. On the present data besides the Robertsonian changes already mentioned, translocations and duplications have been claimed in the cytological evolution of Alticinae (Virkki, 1970), pericentric inversions in the evolution of some Cassidinae (Yadav & Pillai, 1975), and pericentric inversions, translocations and duplications in the evolution of *Timarcha* (Petitpierre, 1970, 1976). The most primitive karyotypes of Chrysomelidae are clearly distinguished by their low numbers and similar sizes of metacentric chromosomes. Karyotypes of these characteristics have been found in almost all largely surveyed subfamilies of Chrysomelids. Thus the main cytological diversification in Chrysomelidae has seemingly occurred by increases in the number of chromosomes.

The papers on the heredity of Chrysomelidae are very scanty. The four colour forms of *Chrysolina varians*, green, red-brown, blue-violet and black, seems to be based on genetic differences and are therefore inherited (Johansson, 1962; Pulliainen & Nederstrom, 1966). On the other hand, there are no differences in the humidity and light behavior of these colour forms.

Elytral patterns and color, sometimes under external factors, are often under genetic control. Some old papers (Tower, 1906, 1918; MacCracken, 1905, 1906, 1907; Kuntze, 1923, 1928; Zulueta, 1925, 1929) and a few recent ones, which will be shortly commented below, have studied the inheritance of those characters. For *Gonioctena variabilis,* the colour types are governed by five alleles which regulate the general basic colour and the black spot distribution. In the same study it has been reported the first case in beetles of a *y*-chromosome linked character (Zulueta, 1925). However, in *Leptinotarsa* and *Chrysomela* some of the colour variations are not genetic and only phenocopies.

The dark mutant of *Oulema melanopus* has been detected in a natural population of USA with a frequency of 0.47 %. This trait was found to be controlled by a single autosomal recessive allele (Wellso *et al.*, 1972).

The genetic studies on colour variations in Chrysomelidae may sometimes provide useful taxonomic information. Two chromatic forms of the South American Cassidinae, *Chelymorpha variabilis,* which were previously classified as different species, by intercrossing proved to pertain to the same species (Zolessi, 1968). A double epistasis of two dominant genes determines one color phenotype being the double recessive combination responsible for the other (Vaio *et al.*, 1975).

The individual variations in color characteristics of several Chrysomelidae, for instance *Gonioctena, Oreina, Plagiodera* and *Timarcha balearica,* offer without doubt a wide way for genetic researches in spite of the difficulties derived from the long generation span common to almost all Chrysomelidae.

A very recent study on population genetics of the Eumolpinae *Adoxus obscurus*, has allowed to compare by gel electrophoresis the level of allozyme polymorphism between a Canadian diploid bisexual population and various Scandinavian triploid parthenogenetic populations (LOKKI *et al.*, 1976). In contrast to several polyploid parthenogenetic species of Curculionidae, the parthenogenetic populations of *Adoxus obscurus* show very little genic variation, probably because the highly efficient migration manifested by this Chrysomelid with regard to those of the Curculionids being apterous species almost always restricted to small biotypes. The allozyme patterns of the parthenogenetic populations of *Adoxus obscurus* closely resemble that of the bisexual population, a fact which probably indicate their monophyletic origin.

DEFENSE MECHANISMS

A rather wide system of protection against their enemies has been devised by the Chrysomelidae and it varies sligthly according to the subfamilies.

Larvae of the Camptosoma (Clytrinae, Cryptocephalinae, Chlamisinae) and those of the Lamprosominae hide themselves in self-made sheaths made of excreta. In some cases, it is a special protection against ants in ant-hills, but free Chlamisinae show the same protecting device. When disturbed by the ants, the larvae retract themselves into the shell and the sclerified vertex closes the opening. The eggs capsule is at the beginning of the case making. The adults protect themselves when escaping from the ant nest after emergence from the pupa, by using reflex immobilisation and autohaemorrhage.

The larvae are soft, round or flattened or sclerified like the mining Hispinae. The larvae of some Criocerinae *(Lilioceris)* are camouflaged with excreta produced by themselves, and continuously rejected towards the front. Similar protection is produced by the larvae of Cassidinae and the excreta are sometimes supported by the abdominal fork. For instance, the packet of cast skins and faeces carried on the fork of *Cassida rubiginosa* larva is a manoeuverable one used to protect itself against attack. It seems highly effective against ants (EISNER *et al.*, 1967).

Generally, the larvae which are not miners are not protected, except by some kind of regurgitation, toxic secretions produced by hypodermic glands and dorsal tubercules (*Chrysomela,* Paropsini, *Microtheca*) and immobilisation reflex. Paropsini larvae secrete hydrogencyanide (MOORE, 1967). It is probably salicylaldehyde which is secreted by dorsal glands of the larvae of *Chrysomela* and *Phyllodecta,* which both feed on poplar and willow. This defense mechanism seems to be very eficcient against birds, lizards and other predators.

Certain larvae (Galerucinae, Cassidinae) are constantly on the inferior side of the leaves. The choice seems conditioned by the structure of tissues, the search for humidity but it can be also an advantage against the predators.

Pupae are free, often brigthly colored, sometimes protected by a shell made by the larvae (*Crioceris,* Donaciinae) or even by a cocoon *(Microtheca)*. The Camptosoma have special individual protection for their eggs, which look like seeds and are sometimes even pedunculated. A special depression at the end of the female sternite makes the egg rotating with the help of the hind tarsi and the excreta cover it. Cassidinae protects their eggs into an ootheca.

In case of danger adult Chrysomelidae shows generally the rellex immobilisation and drop to the ground where they are often difficult to detect. Others show the autohaemorrhage or reflex-bleeding, localized in the articulations of the legs and tarsi or in a prebuccal opening (*Timarcha,* etc.), or a regurgitation of stomach contents *(Timarcha, Chrysolina)*.

Autohaemorrhage in *Timarcha* has been formerly studied by HOLLANDE (1911) in various publications and by CUÉNOT (1896). Toxicity of the blood of *Timarcha* to Vertebrates seems high but not so high in the case of *Leptinotarsa decemlineata* and *L.juncta.* The haemolymph of *Leptinotarsa* has been injected to albino rats (GESINSKY *et al.*, 1974) with a state of shock resulting for the animals.

Sometimes, the insect jumps (Alticinae and few Galerucinae). To that end the Alticinae have specially enlarged hind femora, special muscles, and endosclerites (Maulik or Lever organs). Leaping is effected by the sudden extension of the tibiae of the hind legs.

Sagrinae do not jump, despite their big femora and the presence of the same organites inside them (PAULIAN, 1942).

Other Chrysomelidae, like Alticinae, Galerucinae, Donaciinae, fly away to escape their predators. In the case of the Alticinae, they combine reflex immobilisation, flight and leaping. Many Chrysomelidae have lost their flight ability, either by loss or reduction of wings, or by reduction of flight muscles *(Chrysolina, Timarcha)*. The word «timarchisation» has been coined by Jolivet for the complete apterism which is typical among *Timarcha* and other Chrysomelids. Timarchisation brings together many correlations such as hardening, fixin gland knitting of the elytra, enlargement of epipleura, atrophy of elytra and wing nerves, atrophy of wing muscles and apodemes, bigger fecundity, shortening of metasternum, atrophy of metasternum, adherence of pleurae, reduction of metathoracic stigmata, etc. (JOLIVET, 1959). Correlations between apterism and morphology are also valuable for some Galerucinae but not for all and generally for the Alticinae. Hidden life of brachypterous or subbrachypterous *Chrysolina* is certainly also a means of protection.

Another protection for the adult of certain Chrysomelidae is given by the repugnatory glands of the elytra (*Chrysomela*, etc.; JOLIVET, 1959) which cover partly the surface. Similar glands are sometimes met on the pronotum, the legs, the head. Sometimes, the glands are completely missing (*Cryptocephalus, Cassida, Clytra, Luperus*).

Many Chrysomelidae (Cassidinae, etc.) are perfectly homochromic with their substratum and the homocromy can be structural or nutritional (Cassidinae) (MEQUIGNON, 1941). Some exotic Cassidinae seem to be able to change their color under factors still to be analysed (GRANT, 1946; JOLIVET, 1950).

Chlamisinae have some kind of mesh sutural attachment. The wrinkled aspect of the elytra make them sometimes to look like seeds, which can be a means of protection.

In Brazil, among the Lamprosominae, there are some larvae enclosed into a sheath which look like the spines of their host-tree, *Terminalia catappa.*, a Combretaceae (COSTA LIMA, 1953). There are also mimetic series between Chrysomelids in the tropics, like the mimetic resemblance between the genera *Lema* and *Diabrotica* (GAHAN, 1891). Both genera being unpalatable, it could be useful to the species. However, they have sometimes different host-plants and that can diminish the so-called utility of the phenomenon. Both fly easily and can be confused even by the specialist.

Some very toxic species which autohaemorrhage, like *Timarcha*, live at ground level. The black color of the body against a light green background can be considered as a warning (aposematic) device. All species of *Timarcha* remain black, but some species can have green or purple metallic reflects, like some Spanish southern species *(T. balearica)*.

Red blood secretion of the *Timarcha* contains highly toxic anthraquinones. The hardness of the elytra of *Timarcha, Elytrosphaera, Iscadida,* etc., can be also a secondary means of protection. *Elytrosphaera,* a tropical rain forest species, is either dull black or reddish yellow, metallic green, etc. Possible ecological reasons for that difference are not known.

Some Cassidinae have a very hard cuticle, practically unbreakable by potential predators *(Desmonota variolosa)*. Others adhere to the substratum with the sticky moistened pads of the sole of their broad tarsi *(Hemisphaerota cyanea)*. It is extremely hard to detach them and the oily secretion is produced by special glands. Normally, the Cassids rest or walk with a loose hold. They clamp down when disturbed like sea shells on the rocks (EISNER, 1972). It seems defensive against ants and other predators. *Paropsis* (Chrysomelinae) is an Australian genus which clings also tenaciously on leaves or stems, but not so well as *Hemisphaerota.*

The Clytrinae are not highly toxic, but they are distasteful enough to predators as are the majority of leafbeetles (*Chrysolina, Chrysomela,* etc.).

The highly toxic blood of certain big and brightly colored Alticinae *(Diamphidia, Polyclada, Blepharida)* is used by the Bushmen as a powerful arrow poison (JOLIVET, 1968). The beetles are highly distasteful and feed on poisonous shrubs (*Commiphora,* Burseraceae, and *Sclerocarya,* Anacardiaceae).

LINDROTH (1971) has interpreted the mimetism between some species of Alticinae *(Disonycha, Altica)* and certain species of *Lebia* (which are ectoparasites of the Chrysomelid pupae) as a case of Batesian mimicry. The protection would come from the jumping habits of the flea-beetles. In the case of the poisonous flea-beetles of South Africa, the *Diamphidia,* already mentioned, and the *Lebistina,* the protection would be of a chemical nature.

BALSBAUGH (1967) already interpreted similitude between *Lebia* and flea-beetles as a case of aggressive mimicry. A new case of aggressive mimicry between a Callistinae (Carabidae) and a Chrysomelinae *(Mesoplatys)* has been recently described (JOLIVET & VAN PARYS, 1976) from West Africa.

Chrysomelid pupae are also toxic, due to their haemolymph, and the toxicity of the *Chrysomela, Paropsis, Timarcha* nymphs is well known. They are well protected even if not surrounded by a shell or a cocoon.

Pupae of *Chrysomela,* like some other pupae without cocoons, are able when disturbed to expel drops of a poisonous fluid from cuticular reservoirs in the attached larval skin. *Plagiodera* pupa has a similar habit in a less developed form (HINTON, 1951). Chrysomelid pupae which contain a poisonous fluid have generally an aposematic pattern.

MATING HABITS. REPRODUCTION. SEXUALITY

Generally males (exception in some Hispinae) are smaller than the females and in many genera the anterior tarsi of the males are enlarged to help grasping the female. The underneath of the male tarsi is covered with dense hairs and their adherence on the female elytra is rendered more efficient. Statistically, the females of *Chrysolina* are bigger than the males (SACCHI & BUSARDO, 1935), but the difference is not striking as it is for *Timarcha.* Among certain genera of Clytrinae, like *Labidostomis* and *Macrolenes,* the greatly enlarged anterior legs of the male seize the female like forceps and permits an almost vertical position during copulation.

Male of *Oulema melanopus* has a narrower head capsule and shorter elytra than the female (HOXIE & WELLSO, 1974).

Copulation among the Chrysomelinae can last hours, with or without interruption *(Timarcha, Chrysolina)* and is generally diurnal, but it can be crepuscular or nocturnal among some orophilic (*Metallotimarcha, Cyrtonus)* or subdesertic species *(Timarcha).* Copulation is rather frequent between related species living on the same plant (JOLIVET, 1949, 1951b, 1954a, 1966b) like *Chrysolina menthastri* and *C.polita, C.graminis,* etc. Females *Diabrotica* generally copulate only once, but males will mate with several females (HILL, 1975). Generally females live longer than the males, but this is not always the case *(Diabrotica).*

Hydridization occurs in the field but is rather rare and hybrids are generally non viable. *Gastrophysa viridula* from Belgium has been hybridised experimentally with *G.cyanea* from California. F_1 seems dysplasic (elytra) and sterile (JOLIVET, *in litt.*)

In the laboratory, in different species of *Timarcha* even larvae and adults can mate (JOLIVET, 1966b), but matings between different species of *Timarcha* have never been observed in nature. There are size and morphological barriers in sympatric species like *T. goettingensis* and *T. tenebricosa.*

Generally speaking, sexual dimorphism is not very apparent among the Chrysomelidae, but outside the differences in size and width of the tarsi there are variations affecting the last abdominal sternite and the elytra. In some oriental *Chrysolina (C.aurichalcea)* sexual dimorphism is practically non existent, except for the size (YU, 1936), but in the case of another oriental species, the female of *C. (Caudatochrysa) angusticollis* shows a long pygidium and a kind of ovipositor (CHEN, 1934b; BECHYNE, 1950). Other species, like the female of Cryptocephalinae, Clytrinae, Chlamisinae, possess an abdominal depression used during the making of the ootheca. Such depression is missing or small among the males.

There is among the female of certain species, like *Timarcha, Chrysolina, Galeruca, Agelastica,* a relationship between the loss of flight muscles, apterism and the fecundity or size of the eggs, the males often retaining normal muscles *(Chrysolina, Oreina)* (JOLIVET, 1957).

Egg morphology of the Central European Chrysomelidae has been reviewed by KLAUSNITZER & FORSTER (1971). Most Chrysomelidae lay their eggs on or under the leaves *(Chrysolina)* or on the stems *(Paropsis)*, sometimes in lines *(Lema, Leptinotarsa)*, or they thrust them into the soil *(Timarcha)*. They protect them by a whitish mucous secretion *(Donacia)* or they insert them into the plant tissues *(Phaedon, Prasocuris, Hydrothassa, Donacia, Megalopus, Hispinae)*. *Gonioctena* insert their eggs into bark crevices and they cover them with a mixture made of wooden debris, intestinal secretion and excreta. So do *Pyrrhalta viburni* into twigs of *Viburnum*. The holes are made first with the mandibles of the female; then she introduces some eggs.

The Cassidinae produce some kind of ootheca, often elaborate for exotic species, and the Camptosomata protect their eggs with excreta, individually or in groups. The number of eggs laid by the female varies enormously according to the subfamilies or the species. It can be from a few *(Timarcha)* to 150 *(Lema)* or even more (200 to 500 for some *Galerucella*). *Rhagiosoma*, a Gondwanian genus, makes an ootheca around a stem in Madagascar (PAULIAN, 1961).

In *Timarcha*, a definitive approach is made to an ootheca (PATERSON, 1931). The eggs are laid in or on the ground according to the species in batches of five to six, and are covered with a thick layer of excrement. The ootheca of *Galeruca* contains around 70 eggs.

WELLSO *et al.* (1975) showed that mating exerted a stimulus which induced greater efficiency and egg production for the cereal leaf beetle.

Generally, the new born larva changes its light color and darkens rapidly. The larva begins to feed on the eggshells, then eats voraciously green food. It is generally easier to detect the host plant of one given species when dealing with the larva than with the adult. First instar larvae are often gregarious (Paropsini), pupation taking place in the ground, or in the soil, under dead leaves or plant debris, or on a plant itself attached by the exuvia. The last group includes a few Chrysomelinae *(Chrysomela)*, some Galerucinae and the Cassidinae. During prepupal stage, the larva attachs itself to the leaf by means of a secretion and the larval skin is retained as support for the pupae.

It has been shown that in nature, *C. varians* is photonegative at 10° C (PULLIAINEN & NEDERSTROM, 1966), a fact which may be of ecological importance to the species when it finds its way to hibernation, in the ground.

Among the Paropsini, the pupal cell is formed at a depth of 20 to 50 cm and consists of earth particles cemented together by an exudation from the anus. Some aquatic (Donaciinae) and terrestrial forms (Criocerinae, some Chrysomelinae and others) pupate into cocoons secreted probably by Malpighian tubes *(Donacia)* or produced by mesenteron and stomach regurgitation (Criocerinae). The cocoons are either made on the leaves (some Criocerinae), in the soil (Criocerinae, *Microtheca*) or on the roots of aquatic plants *(Donacia, Haemonia)*. Pupation does not take generally more than one week. Adult hibernates in the soil or under bark. Estivation in warm countries is also generally done under bark of native trees or imported ones like *Eucalyptus*. Estivation is sometimes very short in temperate countries (*Longitarsus linnaei*, BECCARI, 1952), longer in tropical places with a long dry season.

Many mountainous or artic species (*Oreina, Chrysolina, Gonioctena,* etc.) are viviparous or ovoviviparous. The young larvae can be easily detected inside the female oviduct of such species (BROWN, 1962). Viviparity for *Chrysolina* is the rule in Siberia, Hokkaido in Northern Japan, Sakhalin, Europe or Canada, but there are cases also in temperate climates (*Chrysolina varians, Gonioctena viminalis, G. rufipes,* etc.). According to certain authors, viviparity in temperate areas would be a relic of glacial ages, an adaptation to short summers. Sometimes, if the species is not really viviparous, the eggs hatch immediately after laying (*Oreina tristis*). According to RETHFELDT (1924), the eggs of viviparous *Chrysolina* are fertilized directly in the egg follicles by sperm travelling up the oviducts. There have been some cases of parthenogenesis among some species like *Adoxus* (Eumolpinae), *Poecilapsis* (Cassidinae) and chiefly among the *Calligrapha* (Chrysomelinae). In the last genus, males are rare or scarce in several species (BROWN, 1945). Thelytoky is compulsory for certain species of *Calligrapha*, like *C. vicina, C. virginea, C. alnicola, C. apicalis, C. ostryae,* and *C. scalaris*. Parthenogenesis is accompanied by tetraploidy as generally 48 chromosomes are present. According to ROBERTSON (1964, 1966), parthenogenetic evolution has been diploid bisexual, diploid facultative thelytoky, and finally tetraploid obligatory parthenogenesis. *Gastrophysa viridula* shows exceptionally a rudimentary parthenogenesis, but produce unviable larvae. There have been some cases of parental care recorded among the Chrysomelidae (Von Lengerken, 1954, Goidanich, 1956). The fact is known among some *Gonioctena* where females hatch their eggs and their first stage larvae on the stems of the food plant. Also some neotropical female Cassids cover with their enlarged body the eggs and the newly hatched larvae. In all the cases, the larvae are left free after the first molt.

The male genitalia varies strongly in shape between the subfamilies, but is really characteristic of genera and species chiefly in evolved groups like some Chrysomelinae, Galerucinae and Alticinae. For Chrysomelinae, constant specific differences are visible among the *Chrysolina* and allied genera, but not much in *Timarcha*. Genitalia of primitive subfamilies from Sagrinae to Chlamisinae do not show very stable differences between the species. A very sophisticated study of the phallus structure of the male *Timarcha* has been done by Stockman (1966) and a general study of the structure of the female genitalia by Spett & Lewitt (1926) and of the male one by Zia (1936), Powell (1941) and Metcalfé (1932). The reproductive system of *Oulema melanopus* has been described in detail by Wellso (1972).

Various authors have studied the embryology (Lecaillon, 1898; Wheeler, 1889; Hager, 1953) and the larval development of various Chrysomelidae (Paterson, 1930, 1931, 1941; Cumpston, 1939). Postembryonic development of *Leptinotarsa* has been studied by Patay (1939) and others. Bourdon (1937) has specially studied the development of *Timarcha* and Abeloos (1938) their growth. It is almost impossible to quote most of the recent papers on embryology, experimental embryology and cytology of *Leptinotarsa*. Among them we can mention Bergerard & Maisonhaute (1967), Bruzat (1971, 1972, 1974), Maisonhaute (1971, 1973, 1975, 1976), Richard-Mercier (1974), Schetter (1974), Labour (1974), Schooneveldt (1974), etc.

When Chrysomelid eggs hatch, the young larvae use oviruptors of which the disposition varies. They are made of deciduous thoracic sclerites (Bertrand, 1924; Bruneteau, 1924; Abeloos, 1937; Cumpston, 1939; Dobson, 1960). Many Chrysomelids show three larval stages and two molts, plus a pupal molt. However, the number of stages can be more: four for *Chrysolina* and *Leptinotarsa*. Length of development varies according to the temperature and the species. A good average is three weeks for the Chrysomelidae from newly born larvae to pupae. Under the tropics, the complete cycle of the Hispinae, *Coelaenomenodera elaeidis*, lasts, with four larval stages, more than three months and there are four annual cycles (Morin & Mariau, 1970).

Paropsis species overwinters in Australia in the adult stage sheltering in crevices of bark or under stones. Flea beetles of the species *Disonycha glabrata* overwinter in Arkansas as adults in leaf trash (Hemenway & Whitcmob, 1968). There are three generations a year and the beetle feeds on *Amaranthus*.

Gonnin & Hoopingarner (1971) have shown that only the female of *Oulema melanopus* requires a period of diapause to reach sexual maturity. Diapause can be prevented or terminated in the female with hormonal treatments. The males are able to differentiate between active receptive females and inactive unreceptive females.

Gonioctena olivacea survives three years in England thanks to adult diapause. The cycle is rather complex (Richards & Woloff, 1961). *Timarcha* (Abeloos, 1928, 1935, 1941; Jolivet, 1948) shows in cold climates, obligatory *(T. tenebricosa)* or facultative *(T. goettingensis)* embryonic diapause. The development is halted very late in embryogenesis when the larva is fully formed but it can be more complex and three types of cycle have been found among the *Timarcha* (Jolivet, 1966, 1967): type *T. tenebricosa*, type *T. goettingensis* and type *T. balearica*. The last one is characterized by a normal activity in winter and an adult pseudo-diapause in summer, corresponding to the dry season.

In *Leptinotarsa decemlineata*, the proportional increase of diapause from generation to generation seems to be induced by the diminution of day length from June to fall at least under European climate. Internal factors such as endocrine secretions, changes in metabolism are involved in the diapauses and the hibernation. Estivation also exists in certain parts of the range of the species.

In the case of an egg diapause, as for *Atrachya menetriesi* (ANDO, 1974), oxygen is indispensable for the termination of diapause and the onset of diapause seems related to O_2 deficiency in the egg.

Agelastica alni shows compulsory adult diapause (BEAUMONT, 1944) which terminates dormancy at rather low temperature. In the case of *Chrysolina haemoptera* in Western Europe (CHEVIN, 1970) there is no interruption in the cycle in winter and eggs and larvae evolve normally. Adult development is very similar to the one shown by *Galeruca tanaceti* (SIEW, 1966): prediapause in spring, summer diapause induced by long photoperiod (June), sexual maturation induced by short photoperiod (end of August). *Galeruca tanaceti* undergoes two periods of diapause, in the egg and in the adult stage (SIEW, 1966). The adult one is under the influence of photoperiod and temperature during summer.

Some *Chrysolina (C. fastuosa)* and Donaciinae seem to have a two-year life history. *Donacia* probably hibernate as larvae. Duration of life in the case of the female of *T.tenebricosa* is one year or more. It can be 25 months for *Lema* with 2 winter diapauses. It is generally shorter for the Chrysomelids and many generations occur the same year in the tropics and the subtropics. Two or three are a maximum under temperate climates for some species, like *Gastrophysa.*

According to KOSIER (1975), the maximum length of life in Poland for Cassids was not one year, but two, three or four years according to the species of *Cassida,* the female living longer than the males. The complete development may take as little as 30 days.

CHEN (1940) has divided artificially the larvae of Chrysomelids owing to their life habits into: 1) aquatic (Donaciinae); 2) case-bearers (Clytrinae, Cryptocephalinae, Chlamisinae, Lamprosominae); 3) excreta-bearers (Criocerinae, Cassidinae); 4) externally feeding [Chrysomelinae, Alticinae (pars), Galerucinae (pars)]; 5) root-feeders [Galerucinae (pars), Alticinae (pars), Eumolpinae, Synetinae]; 6) stem-feeders (Sagrinae, Galerucinae and Alticinae occasionally); 7) leaf-miners [Orsodacninae, Zeugophorinae, Alticina (pars), Hispinae (major parts)].

Nothing is known of the larvae of Aulacoscelinae and Megascelinae. Probably both are stem feeders. Larvae of Megalopodinae are stem-feeders (MONRÓS, 1954) and those of Synetinae root-feeders (KURCHEV, 1967). The Camptosomatic section plus the Lamprosominae constitutes a natural grouping of larvae as well as the Cryptostomatic section. Among the Eumolpinae larvae, KURCHEVA & DURDYKLYCHEV (1975) have distinguished three morphological groups: a) Adoxini and Typophorini, b) Eumolpini, Nodini and Leprotini, c) Corydonini and Myochroini. Such divisions are somewhat linked with life and food habits.

SYMBIOSIS, PHORESY, NATURAL ENEMIES

Symbiontes localized into a mycetome are known in certain Chrysomelidae (Donaciinae, Eumolpinae, Cassidinae, etc.) and they are missing in others. This can be linked with the food and the way of life. Transmission of the bacteroides is done when smeared on the egg. The newly hatched larva becomes infested when chewing the chorion.

There are special organs in adults (modified median Malpighian tubula, filled evagination of the midgut, etc.) which contain the symbionts and that varies according to the families, the genera or even the species and also the stage (larva or adult). The bacteroides are eliminated with the gut and sometimes the mycetome is sterile (males, some species).

Predators of Chrysomelidae are numerous and belong to Vertebrates (frogs, Reptiles, Fishes, Birds, bats) and Invertebrates (Acari, Coleoptera, Hemiptera). Commensals are also quite common and five species of Gregarines have been found to parasitize the Chrysomelidae of the New and Old Worlds. Only Australia and South America have not yet been prospected for Gregarines. Only Trichostoma have Gregarines. They have never been found in any other families of bettles (JOLIVET, 1959).

Phoretics among Chrysomelidae belong mainly to Acari and, outside some Uropoda, these are mainly among the Sarcoptiformes, the Canestriniidae. The Canestriniidae are quite common among the Chrysomelidae of the world (also on Cetoniinae and Carabidae), under the elytra and often on the sternites (JOLIVET, 1948; COOREMAN, 1950; THEODORIDES, 1955). Subelytral cavity of some apterous genera like *Timarcha* are well preadapted for harboring the mites which feed mainly on desquamations of the cuticle and dry blood. Larvae are contaminated on the soil but mites are rare on larval stages. *Chrysomelobia labidomerae,* a Tarsonemia, is parasite of the milkweed leaf-beetle (*Labidomera clivicollis*) (BAKER & EICKWORT, 1975). Adult parasites feed on the host's abdominal terga and occur sometimes on the sternites. Dispersion is done during copulation. As for Canestriniidae, the mite does not affect longevity or fecundity of the host.

Parasitoids (Diptera and Hymenoptera) are numerous among the Chrysomelidae; so are the real parasites like worms (Cestoda, Nematoda, Trematoda, Nematomorpha) (THEODORIDES & JOLIVET, 1950) and pathogens like fungi, Protozoa and others. Up to now, *Howardula,* a genus of Anguillulidae, has been found to parasitize only Galerucinae and Alticinae, which is another proof of the narrow relationships of the two subfamilies.

Many studies of the Chrysomelids and their parasitoids have been published in the literature. Let us quote the studies of the parasitic complex of some Alticinae in France (JOURDHEUIL, 1960), in England (DOBSON, 1955), of the Hispinae in Fiji (TAYLOR, 1937), of the *Coelaenomenodera* in Ivory Coast (MORIN & MARIAU, 1970, 1974; MARIAU & MORIN, 1971, 1972, 1974; MARIAU & BESOMBES, 1972, etc.). For the *Coelaenomenodera,* the population dynamics of host and parasites have been rather well studied and natural mortality of above 99 % maintains normally a stable population (MARIAU & MORIN, 1974). MARIAU (1975) has studied the parasite spectrum of the *Coelaenomenodera* in Madagascar. KUWAYAMA (1932) has studied the biology of *Lema oryzae* in Japan and recently TOGASHI (1974) has reviewed the hymenopterous complex parasitizing the beetle. Biology of *Oulema melanopus* in the USA with a review of its parasites in the ecosystem has been studied by HAYNES *et al.* (1974).

Ancient and recent studies on *Leptinotarsa* are also of special interest (WEISER & HOSTOUNSKY, 1967; HOSTOUNSKY & WEISER, 1973, 1975). *Leptinotarsa undecemlineata* has been found parasitized with two Tachinids in Cuba with a rather high infection rate, and *Gastrophysa polygoni* showed an outbreak of a microsporidian infection in Czechoslovakia with *Nosema gastroideae.* The microsporidian is experimentally transmissible to *Leptinotarsa decemlineata.*

Two Microsporidia have also been found in Cuba infecting the gut epithelium of *L. undecemlineata* (a *Nosema* and a *Plistophora*) with a 80 % mortality. The pathogens are also infectious for *L. decemlineata.*

ECOLOGY - ETHOLOGY

Some available information on the environmental relationships of Chrysomelidae has been brought together here.

1. Myrmecophily and Termitophily

There are very few tropical Galerucinae larvae in association with termites in India and Sri Lanka *(Ceratia)* as synoekoetes.

Almost all Clytrinae larvae, some larvae and adults of Cryptocephalinae (GRANDI, 1951), some Eumolpinae (SELMAN, 1962) are myrmecophilous, either as synoekoetes or symphiles. Practically all larvae of Clytrinae (species from temperate, neotropical and palaeotropical areas) live in or around ant-nests. Some genera like *Labidostomis* live close to ant-nests, but not inside, a little like some Cetoniidae or Tenebrionidae do, but their larvae are also protected by a sheath.

The species of Eumolpinae, Clytrinae and Cryptocephalinae, quoted by SELMAN (1962), live in aerial ant-nests in Kenya and are real symphiles with trichomes on the thorax.

Biology of Clytrinae has been reported by various authors (DONISTHORPE, 1902; FIEBRIG, 1910; SKAWARRA, 1927; JOLIVET, 1952; MONRÓS, 1953; MEDVEDEV, 1962a; MOLDENKE, 1971, etc.). It seems that everywhere the behavior of the subfamily is the same, at least for the synoekoetes. It can be resumed as follows; taking *Clytra quadripunctata* as an example:

The adults feed on foliage of trees, vines, etc. and are rather polyphagous. The eggs are laid down by the female on the ground, generally from a small bush near an ant-hill. The eggs is protected by excrement deposited with help of the hind tarsi, the egg being retained into the abdominal depression on last sternite. Egg capsule varies from genera to genera, but very often it gives the appearance of a seed with bractae *(Clytra)*. Sometimes, the egg is pedunculated *(Labidostomis)* or fixed to a leaf *(Ischiopachys)*. When the egg is free, it is carried into the nest by the ants themselves. When it is attached or pedunculated, the ants cut off the peduncule. If the egg is naked, it is eaten by the ant. The larva hatchs after twenty days, feed on plant detritus and eventually on ant eggs and build its sheath with excreta, starting from the egg shell. Only the sclerified head protrudes and closes the sheath in case of ant attack. Normally, head, legs and part of pronotum are out of the sheath. Molt and pupation take place into the sheath. Shape and ornamentation of the larval sheath varies much according to the species. After pupation, the adult escapes from the cocoon by a circular opening into the sheath and gets out of the nest without being much disturbed by the ants. Reflex bleeding and reflex immobilisation are the only means of defense of the adult. Then the adult is positively phototropic and feeds on leaves for a short time, before copulation takes place. When the ants are nomadic as is the case for *Dorylus*, the Clytrinae larvae follow the migrations of their hosts outside the nest during day or night when they occur (JOLIVET, 1952c).

2. Aquatic species

Essentially only the Donaciinae are really aquatic either as larvae *(Donacia)* or as larvae and adults (*Haemonia*, some *Donacia*, *Donaciasta*). Other subaquatic genera like *Phaedon* are only adapted to short submersion.

The almost apodous larvae of *Haemonia* and *Donacia* live on the roots or stems of various aquatic plants, especially Nymphaeaceae and *Phragmites, Typha, Juncus*. Their physiology has been well studied (BOVING, 1906, 1910; DEIBEL, 1910; BERTRAND, 1924). Beside some respiration through the skin, the larvae respire through two hind modified spiracles which are inserted into the plant tissues and effect a connection with the intercellular airspaces. The adults have a special waterproof pubescence under the sternites and on the antennae, and get their oxygen through the cuticle. Before pupating, the larvae secrete a transparent brownish cocoon which contains a part of the partly eaten root of the food-plant. Oxygen is provided by that way. The oxygen uptake of the larvae of *Donacia* occurs by diffusion and does not hinder the metabolism of the plant. During winter, the oxygen pressure may fall to 1 % if the plants are covered by water, but adults and larvae are adapted to that reduced metabolism (HOOLIHAN, 1969, 1970).

Adult *Donacia* are diurnal and terrestrial insects. They lay eggs into the water on the stems of plants. Adult *Haemonia* are flying occasionally during the night and copulation possibly takes place outside the water. Normally, they stay inside the water even as adults.

Haemonia mutica is found in very protected stations of the Baltic Sea in association with *Zostera* and *Potamogeton.*

3. Abnormal habitats

As seen previously, there have been few records of cavernicolous Galerucinae in India and Sri Lanka. The fact is rather unusual for phytophagous insects and the beetles *(Ceratia)* are only accidental hosts (trogloxenes). Among the real cave dwelling phytophagous insects (troglobionts), there are only some rare records of Homoptera in tropical caves and they feed on roots of aerial plants growing into the caves.

Root-feeder larvae among Chrysomelids are either miners or soil-dwelling. There are few adult leaf beetles really adapted to endogeous life in the tropics, but they have been rarely searched for. SCHERER (1974) has recently mentioned the Alticinae genus *Clavicornaltica*, endogeous in Sri Lanka and specially adapted to its habitat. Similar species must exist elsewhere in the tropics and not be so rare.

4. Desert adaptation

Chrysomelidae are not, like Tenebrionidae, a kind of beetles living normally in deserts. There are however some cases of adaptation to steppic and subdesertic life and, for instance, *Timarcha,* due to its subelytral cavity, seems perfectly preadapted to steppic and oases surrounding, in North Africa and Libya (Jolivet, 1968b). Normally *Timarcha* are living in humid areas. In dry surroundings, life becomes crepuscular and nocturnal. In completely dry tropical deserts there are no Chrysomelids, but they do exist in cold deserts, like the Gobi, for instance.

Chen & Wang (1961) have mentioned desert adaptation in the deserts of Dzungaria and Taria (Sinkiang). Adaptive of garia and Taria (Sinkiang). Adaptive features of desert Chrysomelids met in Sinkiang consists in coloration, structure and behavior, the most significant of which lies, according to Chen in their adaptation to subterranean concealment with reduction of the tarsal brush, apterism, flattening of the body (under stones) or fusiform shape (on sand).

5. Mountain adaptation

As seen before, most of the purely orophilic Chrysomelids, like *Metallotimarcha, Oreomela, Xenomela,* numerous Chrysomelinae, Galerucinae and Alticinae are apterous.

There are also terrestrial species which are apterous but statistically there are less than for the mountain species.

6. Flight ability

Flight ability is not uniformly distributed among the Chrysomelidae. Some groups are good flyers (Donaciinae, Criocerinae, Alticinae, Galerucinae, etc.), some bad (Cassidinae) or non-flyers, such as most of the *Chrysolina* and the genera with reduced or absent wings *(Timarcha).* Flight is generally done during the heat of the day, under the sun, or even in the shade in the tropical forest. Sometimes, flight is migratory *(Leptinotarsa, Paropsis, Diabrotica)* and linked with physiological changes and external stimuli (Jolivet, 1959).

Generally, flight is diurnal, but can be nocturnal *(Haemonia, Donacia).* Flea-beetles were supposed to be day-flyers, but it has been shown by Taylor (1970) that two species of Nigerian *Podagrica* from Malvaceae had their peak flight activities at dawn and dusk and flew intermittently during the day and night. For *Diabrotica virgifera* in corn fields, flight activity is bimodal, with peaks occurring after sunrise and before sunset. Activity peaks happened at a temperature range of 22 to 27°C for the two sexes (Witkowsky, Owens & Tollefson, 1975).

The age of the adult Chrysomelid beetle can be detected by the degree of coloration of the membranous wing, mainly when the color of the haemocel is red, as in *Chrysolina, Leptinotarsa,* etc. (Dunn, 1948, 1951; Jolivet, 1957). In case of green, yellow, pale haemocel the wing is slightly colored. Sometimes male and female have a different colored haemocel (*Phytodecta, Galerucella,* some spp.).

7. Stridulation

Some Chysomelidae produce some kind of stridulation (Criocerinae, Clytrinae, Megalopodinae, etc.). Stridulation varies in intensity according to the species. Stridulation is sometimes produced by rubbing the rear lobe of the pronotum against a file on the mesothorax (American Clytrinae). Many groups do not stridulate at all (Aulacoscelinae, Galerucinae, Alticinae, etc.).

Criocerinae stridulate (600 abdominal movements per minute; Dingler, 1932) by rubbing a striated plate on the 7th abdominal tergite against hooks on the elytra. The Megalopodinae have the mesonotal file characteristic of the Cerambycids (Crowson, 1966).

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