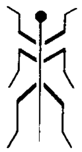

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Chromosomal Variability and Evolution of Chrysomelidae (Coleoptera), Particularly that of Chrysomelinae and Palearctic Alticinae

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ABSTRACT. — Chromosomal variability and evolution within the Chrysomelidae is summarized using information from the studies of 557 bisexual taxa which have been chromosomally surveyed. Some preliminary subfamily conclusions are offered, except in the better sampled Chrysomelinae and Alticinae, where more difinitive conclusions are possible. — [editors]

The number of chromosomes is a trait of the genetic system which is generally not variable for a species but may differ when comparing allied organisms. Since processes of speciation are very often coupled with chromosome changes (White, 1978), the analyses of variation in the number of chromosomes could give insight into speciation and provide better knowledge on evolutionary trends of particular organisms.

In an attempt to check and discuss the presently available data on the chromosomes of chrysomelids, we shall deal with the range of variation and the modal numbers for the whole family and for the relatively well studied subfamilies. We will also try to recognize the potentially most primitive numbers and the sex determining systems which may correspond, in some cases, with archaic morphological or anatomical characters. Furthermore, the resemblances of the modal values and ranges of heterogeneities among groups of chrysomelids should be investigated for clues to establish possible phyletic interrelationships in correlation with other aspects of evolutionary significance. Chrysomelinae and Palearctic Alticinae will be treated here in greater depth because of our concentrated study of them.

MATERIAL AND METHODS

A basic source for the chromosome numbers and male sex determining systems of chrysomelids, as well as for all the other beetles, is given in the appendix of the book by Smith and Virkki (1978). However, a

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large amount of information on the chromosomes of chrysomelids is not mentioned there, that is the period of eight years elapsed from 1977 to the present (Alegre and Petitpierre, 1982, 1984, and unpubl.; Barabas and Bezo, 1978, 1979; Ferreira and Mesa, 1977; Hsiao and Hsiao, 1983; Panzera et al., 1983; Petitpierre, 1977, 1978a, 1978b, 1980, 1981, 1982, 1983, and unpubl.; Segarra and Petitpierre, 1982, in press, and unpubl.; Sharma and Sood, 1978; Vidal et al., 1977; Virkki, 1983a, 1983b). We have compiled the chromosome numbers of all chrysomelid taxa, except the few polyploid parthenotes, as haploid values, including those subspecies or chromosomal races differing in number from others of the same species. The intraspecific numeric variability due to the sex, such as males XO and females XX or males having extra y-chromosomes like Xyy_p, were not considered since they do not affect the haploid value.

CHROMOSOMAL VARIABILITY IN CHRYSOMELIDAE

The Chrysomelidae is one of the beetle families with highest heterogeneity in the chromosome numbers, from 2n=8 in the flea-beetle *Homoschema nigriventre* Blake to 2n(♂)=59 in *Rhaphidopalpa femoralis* Motsch. (Smith and Virkki, 1978). These values are great compared to the extremes for Coleoptera, 2n=4 in the elaterid *Chalcolepidius zonatus* Eschtz. (Ferreira et al., 1984) and 2n(♂)=69 in the carabid *Ditomus capito obscuroides* Oliveira (Serrano, 1981). The histogram depicted in Fig. 1 represents the haploid numbers of the 557 taxa of chrysomelids chromosomally worked out. As it can be seen there is no clear-cut modal value; n=12 is the most frequent value but n=10 and n=11 are also rather common. Any of these three numbers could be considered as the most primitive in our present state of knowledge, but it should be remembered that n=10 is the most frequent and primitive karyotype for polyphagan beetles (Smith and Virkki, 1978). Indeed, since the low chromosome values n=10, 11 or 12 seem to be the primitive ones in chrysomelids it would not be uncommon for the main chromosomal evolution to have occurred by increases in number through the effect of centric fissions. The haploid numbers lower than eight are scarce while those higher than twelve are relatively common, ranging from n=13 to n=20. A better understanding of the possible modal and primitive numbers for chrysomelids is realized from the following study within each subfamily and, as will be seen, the situation can be quite different from one subfamily to another.

INTRASUBFAMILIAL VARIATION

The chrysomelids are divided into nineteen distinct subfamilies according to the recent authors (Gressitt and Kimoto, 1961; Jolivet and Petitpierre, 1981; Seeno and Wilcox, 1982), but there is still not a general agreement about this status (see for instance Crowson, 1981 and Chen, this Symposium). Within the nineteen subfamilies only nine have had at least seven taxa analyzed. Among the morphologically most primitive chrysomelids, the few species checked of Donaciinae are conservative in chromosome number, n=14 or n=15 (Fig. 2). The Criocerinae have n=8 as the modal value (Fig. 3), but the most primitive ones would be those having n=10, a value found in two species of *Lilioceris,* though both of them should be reinvestigated due to some discrepancies (Petitpierre, 1980; Schmitt, 1982). Donaciinae and Criocerinae are related groups based upon both adult and larval morphology (Schmitt, Symposium) and were also included in the old section of Eupodes (Chapuis, 1874). Nevertheless, according to the chromosome numbers there is no apparent interrelationship; the Criocerinae are characterised by low numbers mostly and the Donaciinae by rather high ones. A more intensive search on the chromosomes of Donaciinae, principally of the presumed more archaic species in Africa, would probably throw some light into this problem.

The Cryptocephalinae have two groups of chromosome numbers: that of *Pachybrachis* with n=8 and *Cryptocephalus* with a distinct peak at n=15 (Fig. 4). Both *Pachybrachis* and *Cryptocephalus* are conservative genera in the number of chromosomes and do not deviate from their modal genus value (Alegre and Petitpierre, 1982 and Petitpierre, unpubl.).

The Eumolpinae show n=8 as the mode, but other numbers like n=10 and n=15 are found in several species (Fig. 5). Curiously, there are no representatives with n=7 or n=9, though they will probably be found with increased analysis. If we assume n=8 as the primitive condition, then the chromosomal evolution of Eumolpinae has proceeded by mostly increases but also by some decreases in number explaining the origin of the karyotypes with n=6.

The range of haploid values in Chrysomelinae, from n=10 to n=24 is greater than in any of the previously treated subfamilies, possibly because of the much larger number of species sampled (Fig. 6). All the numbers within the range are represented, and among them n=12 is the distinct modal peak, since it is shared by about 43% of the Chrysomelinae species. In this case the modal value cannot be considered the most primitive as will be seen later when discussing in more detail the karyological evolution within the groupings of Chrysomelinae.

In Galerucinae the range of chromosome numbers is even wider than that of Chrysomelinae, from n=7 to n=30 (Fig. 7). The n=10 is the mode but it can also be tentatively assumed as the most primitive since it is commonly found in the archaic (?) group of Diabroticini. However, it is not rare that species of the same genus display large differences in chromosome numbers, for example two species of the genus *Oides* having 2n(♂)=17 and 2n(♂)=49 (Sharma and Sood, 1979). Again the process of fissions determining the increases in chromosome number seem to be much more frequent than the reverse, fusions producing the decreases.

The Alticinae also display a high diversity in chromosome numbers, from n=4 to n=26 (Fig. 8). The peak is at n=12, but this is probably influenced by the extensive studies carried out by Virkki (see Smith and Virkki, 1978) in the American Oedionychini for more than two decades (Virkki, this Symposium). According to Virkki (1970) the most primitive number is n=12, karyotype formula of 11+Xy_p, found in the Peruvian relict *Forsterita* sp. Starting from the primitive karyotype the chromosomal evolution of the flea-beetles has proceeded in both directions by increases and by decreases in number. An extreme example of repatterning from the presumed ancestral karyotype is that of *Homoschema nigriventre* with 3+XY, which has probably been built up through series of centric fusions of autosomes and incorporation of the sex determining segment into one of the autosomes (Virkki, 1984).

Only seventeen taxa of Hispinae are chromosomally known, n=8 is their clear modal value and possibly the most primitive one (Fig. 9); this subfamily can be considered conservative on cytological grounds. A recent reference about the chromosomal evolution of Hispinae is that by Alegre and Petitpierre (1984).

The chromosomes of Cassidinae are better worked than those of Hispinae. Although they show a great range of variation in haploid number, from n=9 to n=26, more than a half of the species share n=9 chromosomes (Fig. 10); again, this subfamily is conservative in chromosome number. In dealing with both Hispinae and Cassidinae, it is interesting to point out the lack of correspondence between morphological and chromosomal divergence since the two subfamilies are highly evolved chrysomelids according to their unusual morphologies; however, their karyotypes remain close to the ancestral type of n=10, and are much less variable than in most chrysomelid subfamilies. The hispine/cassidine male sex chromosomes are associated mostly in the "parachute" way Xy_p, which can also be considered a primitive type of association as seen in the following section.

MALE SEX DETERMINING SYSTEMS

We have compiled 544 data on the sex chromosomes of chrysomelids, classified into eight types (Table 1), which cover almost all kinds of male sex systems so far encountered in beetles. About half of the species show the most characteristic system of Coleoptera, the "parachute" type Xy_p, an achiasmatic association of a large and generally metacentric X and a minute and mostly metacentric y-chromosome. They hold together from mid prophase to the end of metaphase in the first meiotic division by the nucleolus, but at least in some cases also by telomeric heterochromatin (Smith and Virkki, 1978; Virkki, 1984). The

Table 1. Male sex-chromosome systems in the subfamilies of Chrysomelidae.

	Xy_p	Xy_r	Xy	XY	neo-XY	X+y/ X+Y	XO	multiple sex-systems	TOTALS
Sagrinae	-	-	-	-	1	-	-	-	1
Donaciinae	7	-	-	-	-	-	-	-	7
Aulacoscelinae	-	-	-	-	-	-	1	-	1
Megalopodinae	-	-	-	-	-	3	-	-	3
Criocerinae	14	1	-	-	-	-	-	-	15
Clytrinae	1	-	-	1	-	2	-	1	5
Cryptocephalinae	9	10	-	1	-	-	-	-	20
Chlamysinae	-	-	-	-	1	-	-	-	1
Eumolpinae	24	2	2	2	2	-	1	1	34
Chrysomelinae	121	-	-	-	-	-	41	1	163
Galerucinae	21	1	4	-	3	-	57	5	91
Alticinae	25	1	32	5	5	70	3	15	156
Hispinae	15	-	1	-	-	-	-	-	16
Cassidinae	26	-	1	-	-	-	-	4	31
	263 (48.3%)	15 (2.8%)	40 (7.4%)	9 (1.7%)	12 (2.2%)	75 (13.8%)	103 (18.9%)	27 (5.0%)	544

Xy_p has been recorded in almost all subfamiies of chrysomelids, with more than one checked species, except in Megalopodinae and possibly in Clytrinae, because our finding of Xy_p in *Clytra quadripunctata* (Linn.) (Petitpierre *in* Smith and Virkki, 1978) should be reinvestigated. In addition, the Xy_p seems to be the prevalent system in primitive chrysomelids like Donaciinae and Criocerinae, in fairly evolved ones such as Eumolpinae and Chrysomelinae, and in the most morphologically evolved subfamilies, Hispinae and Cassidinae.

The XO system is found in nearly 20% of chrysomelid species and is common in Chrysomelinae and even more so in Galerucinae. This system could arise either by loss of the y-chromosome or more often by its transfer to autosomes (Smith and Virkki, 1978). Also, in all Coleoptera the XO system is the second most common, after the Xy_p.

The distance pairing of sex chromosomes, X+y or X+Y, occurs in about 15% of the species, especially Megalopodinae, Clytrinae, and the flea-beetles of the genus *Altica* and the tribe Oedionychini (Smith and Virkki, 1978). The behavior of these sex chromosomes in first meiosis seems to be prereductional in flea beetles but postreductional in Megalopodinae and Clytrinae (Virkki, 1984b).

All the remaining classes of sex systems in chrysomelids appear in amounts less than 10% and none seem to be exclusive of any subfamily, although the multiple sex systems are more abundant in Alticinae and the "rod" type, Xy_r, is frequent in Cryptocephalinae (Alegre and Petitpierre, 1982 and Petitpierre, unpubl.). The multiple systems are heterogeneous kinds of sex mechanisms, including true chiasmatic, nucleolar, and distance pairing among other types of associations, and the Xy system is also a mixed assemblage of undetected Xy_p and true chiasmatic types.

The only proved cases of parthenogenetic species or races in leaf beetles are the triploid populations of *Adoxus obscurus* (Linn.) (Eumolpinae) and the triploid or tetraploid taxa of *Calligrapha* (Chrysomelinae). The parthenogenesis has not played a crucial role in the evolution of chrysomelids or for beetles and other animals in general.

A brief summary of the present state of knowledge concerning the modal and most primitive chromosome numbers and their sex system counterparts is reported in Table 2. The modal and presumed most primitive numbers do not normally deviate far from the beetle ancestral value of n=10, but the exceptions of Donaciinae and Cryptocephalinae should be kept in mind. Some identities in the peak number such as that of Criocerinae, Eumolpinae and Hispinae at n=8, could probably be ascribed to simple examples of convergence, since the interrelationships among the three subfamilies are not close in any of the proposed phyletic and taxonomic systems (review in Seeno and Wilcox, 1982; Stienhausen, in this Symposium). Moreover, John (1981) has pointed out that "there is no necessary, and certainly no consistent, relationship between chromosome change and morphological change." The superficial similarity among these karyotypes with eight haploid metacentric chromosomes of Criocerinae, Eumolpinae and Hispinae should be assessed by banding techniques, which we presume would reveal clear-cut differences.

Table 2. Main chromosomal data on subfamilies of Chrysomelidae.

	Modal haploid no. and ♂ sex system	Probable most primitive haploid no./♂ sex system
DONACIINAE	15,Xy_p	??
CRIOCERINAE	8,Xy_p	10,Xy_p ?
MEGALOPODINAE	10,X+y	10,x+y ?
CRYPTOCEPHALINAE	15,Xy	8,Xy ?
EUMOLPINAE	8,Xy_p	8,Xy_p ?
CHRYSOMELINAE	12,Xy_p	10,Xy_p
GALERUCINAE	10,XO	10,XO ?
ALTICINAE	11,X+y	12,Xy_p
HISPINAE	8,Xy_p	8,Xy_p ?
CASSIDINAE	9,Xy_p	9,Xy_p

CHROMOSOMAL EVOLUTION OF CHRYSOMELINAE

The Chrysomelinae together with the Alticinae are the two best known groups of chrysomelids from a cytogenetic viewpoint. In a recent classification of the subfamily Chrysomelinae, Seeno and Wilcox (1982) divide it into two tribes, Timarchini and Chrysomelini, the latter constituted by twelve subtribes. Of these 13 groupings of Chrysomelinae, nine have been chromosomally studied at least for one species.

We have reported succinctly elsewhere (Petitpierre, 1982, 1984) the main steps of the cytological evolution of Chrysomelinae. Basically, this evolution can be explained by a gradual series of increases in the number of chromosomes, with three principal peaks corresponding to each evolutionary stage of rough karyological divergence. The most primitive group of Chrysomelinae is the tribe Timarchini, whose species are clearly characterized by the archaic ring-shaped tegmen of male genitalia among other primitive traits. The modal chromosome number of *Timarcha*, the only genus in the tribe, is n=10 with Xy_p sex system, which is the ancestral formula of Coleoptera Polyphaga as stated above (Fig. 11). All the other Chrysomelinae share a derived type of tegmen in male genitalia having a V-shape, and accordingly none of the species so far studied share the primitive karyotypic formula, 9+Xy_p. The Chrysolinina (Fig. 12), Doryphorina (Fig. 13), Gonioctenina (Fig. 14), and Paropsina, plus the only checked species of the closely related Dicranosternina (Fig. 15) all display n=12 as the modal or only haploid value. There are great ranges of haploid numbers in the first three subtribes and even some species in the same genus, like *Chrysolina* (Petitpierre, 1981) and *Gonioctena* (Petitpierre, 1978; Smith and Virkki, 1978), can exhibit striking differences in the number of chromosomes. Furthermore, it is worth noting the bimodal distribution of Doryphorina (Fig. 13), mostly due to the fact that all bisexual species of *Calligrapha* have n=12 while most species of *Leptinotarsa* have n=18. Among these last two genera are a few species that seem to have derived by decreases in chromosome number (Hsiao and Hsiao, 1983), an unusual kind of shift in Chrysomelinae leaf beetles but relevant explanation compared to the simplistic view of only unidirectional changes in number of chromosomes. The third and last stage of the cytogenetic evolution of Chrysomelinae is represented by the subtribes Chrysomelina and Phratorina, having n=17 chromosomes as the peak value (Fig. 16). This modal number is found in species of several genera such as *Chrysomela, Linaeidea, Hydrothassa, Phaedon* and *Phratora,* though a few species of Chrysomelina have kept the modal subfamilial value of n=12 chromosomes.

An interesting correspondence between the three steps of chromosomal evolution of Chrysomelinae and the three most evident larval types is a relevant aspect of interrelationship in aspects of evolutionary significance. The ancestral type of larvae is found in the species of *Timarcha,* because they lack any kind of setiferous tubercles. The second step is represented by those larvae with setiferous tubercles but having no glands, like Chrysolinina and Doryphorina, except for one pair as in some examples of Gonioctenina and Paropsina ("non-glanduliferous" group of larvae). The third step is constituted by the larvae with eversible defensive glands ("glanduliferous" group of larvae), typical of Chrysomelina and Phratorina (see Kimoto, 1962 and Takizawa, 1976 for an extensive study on this subject). These three kinds of larvae fit well with the three previous karyotypic stages with modal chromosome numbers of n=10, n=12 and n=17.

A phylogenetic tree of the Chrysomelinae groupings from the chromosomal shifts is depicted in Fig. 17. Although the fissions are the predominant shifts in the chromosomes of Chrysomelinae, other classes of rearrangements (inversions and translocations) have played an important role in this evolution and are common structural changes in the adaptive radiations within each stage of main karyotypic divergence. Thus, changes in centromere position, probably by pericentric inversions, were detected in *Timarcha* (Petitpierre, 1970) and *Chrysolina* (Petitpierre, 1983) through karyometric analyses and also within populations of *Leptinotarsa decemlineata* (Say) (Hsiao and Hsiao, 1982), but unequal reciprocal translocations would possibly cause differences among karyotypes of species of *Timarcha* (Petitpierre, 1970, 1976). Also, because the range of total complement length (TCL) in species of *Timarcha* goes from about 55 μm (taxa belonging to the *T. goettingensis* "complex") to about 100 μm (*T. calceata* Perez (Petitpierre, unpubl.)) and that of nine species of *Chrysolina* from near 65 μm to about 107 μm (Petitpierre, 1983), the additions or deletions of chromatin (constitutive heterochromatin?) should be responsible for these differences. All of these assumed structural changes should be checked by banding chromosome techniques to insure these preliminary interpretations. In spite of the substantial morphological separation between the Chrysolinina and Doryphorina, the labiophagous *Chrysolina,* (those with n=12 chromosomes) and the species of *Leptinotarsa* share a satellited first autosome pair (Petitpierre, 1983; Hsiao and Hsiao, 1983 respectively), as a probable proof of their common origin.

A distinctive aspect of any karyotype is its symmetry, which gives an an account of the similarities in length and shape among the chromosomes of a particular set (Levintzky, 1981; Stebbins, 1958, 1971). In order to explain the karyotypic changes in evolution of Chrysomelinae, we have measured a reversed parameter asymmetry, as the standard deviation (S.D.) of each chromosome to the average chromosome size per karyotype. This method dispenses with the sometimes difficult discrimination between uniramous and biramous chromosomes by studying size only. There is a good correspondence between the decrease in the asymmetry of karyotypes and the progressive rise in the number of chromosomes (Fig. 18 and Table 3). The remodelling of karyotypes in Chrysomelinae has taken place towards an equalization of sizes among chromosomes, that is by increasing the symmetry of the chromosomal sets. However, since the species with low chromosome numbers (n=10 or 11) have almost always biramous chromosomes, the numeric increases by centric fissions would turn a biramous into a uniramous chromosome, and so, it is not unusual to find more uniramous chromosomes in high numbered species than in those with low numbers. But the arm number does not remain constant during the cytological evolution of Chrysomelinae, due to the subsequent change of many uniramous chromosomes into biramous ones, presumably by pericentric inversion. Therefore, the observed number of uniramous chromosomes is in fact much lower than the expected by centric fissions alone, with the remarkable exception of *Chrysolina carnifex* Fab. whose karyotype is composed of only telocentric chromosomes (Fig. 18m).

Finally, we should point out parallelism between chromosomal evolution and trophic selection in the genus *Chrysolina* (Petitpierre, 1975, 1981; Jolivet and Petitpierre, 1976). The species with low chromosome numbers (2n=22 to 30) are almost always feeding on Labiatae plants, while those with high nubmers (2n>30) feed on different plants, such as Hypericaceae, Compositae, Umbelliferae and Plantaginaceae mostly (Fig. 19). The adaptation to these latter plant families from the labiatophagous species stock appears to be indirectly correlated to the karyo-

Table 3. Relationship between haploid number and asymmetry of karyotype (S.D.) in several Chrysomelinae species. S.D.= standard deviation.

	haploid no.	S.D.
Timarcha sicelidis	10	5.65
Timarcha perezi	10	4.35
Chrysolina kuesteri	11	5.54
Timarcha lugens	10	4.41
Timarcha balearica	11	4.17
Chrysolina affinis	12	2.32
Timarcha rugosa	13	3.68
Cyrtonus plumbeus	14	2.54
Timarcha laevigata	14	3.01
Timarcha strangulata	14	1.88
Phratora tibialis	17	1.83
Chrysolina haemoptera	20	1.80
Chrysolina carnifex	20	1.04

type remodelling implied in the origin of species with high chromosome numbers. In addition, an interesting species, *C. aurichalcea* Mannerheim, has at least two well established chromosomal races or sibling species; the European one with 2n=40 chromosomes feeds on Asclepiadaceae while the Japanese one has 2n(♂)=45 or 2n=46 chromosomes and feeds on *Artemisia* spp. (Compositae) (Barabas and Bezo, 1978; Jolivet and Petitpierre, 1976, 1981; Petitpierre, 1981). The case of *Chrysolina* is the only known example of this type of beetle-plant coevolution in chrysomelids since other well examined genera such as *Timarcha* (Petitpierre, 1973) and *Leptinotarsa* (Hsiao and Hsiao, 1983) do not evidence any such correlation.

CHROMOSOMAL STUDIES ON EUROPEAN ALTICINAE

While the American flea beetles have been subjected to several chromosome surveys and even some groups like the Oedionychini are reasonably well known (see Virkki *in:* Smith and Virkki, 1978), the European flea beetles remained completely neglected until the end of the last decade when we started our analyses.

Unfortunately, the chromosomal results have been obtained on male first meiotic metaphases mostly, and since good spermatogonial mitosis were rarely found, we can only detect shifts in number and rough variations in size of bivalents. On this basis, our aim is to undertake a comparative chromosome research on the Spanish Alticinae from cytogenetic, cytotaxonomic and evolutionary viewpoints.

The preliminary findings were based on 26 species (Segarra and Petitpierre, 1982, and in press), but currently 50 species are chromosomally known and, thus, we can discuss all data in an attempt to reveal trends of intrageneric variation and possible interrelationships among the genera.

The presumed most ancestral karyotype of flea beetles is $11+Xy_p$ (Virkki, 1970) found in a South American species. None of our sampled European species has the primitive formula, though the diploid number of 24 chromosomes is shared by five species, but having another sex-system than Xy_p. Among the 24-chromosome species are the four checked representatives of the genus *Altica,* all of them with 11+X+y formula, in agreement with those of the American species (Smith and Virkki, 1978). The morphological features of many species of *Altica* are extremely close (sibling species?) so that they can only be separated by careful observations of their male genitalia. This great morphological resemblance is consistent with the karyological conservatism, and presumably, the process of speciation in *Altica* has occurred generally by genic mutations only.

The only species examined of *Hermaeophaga, H. cictrix* (Illiger), can be easily differentiated from those of *Altica* because of its formula of $7+X_1X_2Y$ (Segarra and Petitpierre, in press). The similarities in morphology between both genera are not reflected in their chromosome formulae. *H. cicatrix* is the only species of our sampled Palearctic flea beetles having multiple sex chromosomes, which is not rare among the American species. The only checked American species, *H. cubana* Bryant, has the same formula as most species of *Altica* (11+X+y) and so it is clearly distinguishable with regard to *H. cicatrix.* Additional studies on other species of *Hermaeophaga* would be valuable in searching for the modal number and possible further multiple sex systems or asynaptic ones.

Arrhenocoela lineata (Rossi) and *Crepidodera (=Chalcoides) plutus* (Latr.) are two species with fairly allied morphologies and both share 26 diploid chromosomes, the former with XY and the latter with Xy_p sex system. Furthermore, two American species of a related genus, *Epitrix,* show also 26 chromosomes and Xy_p sex system (Smith and Virkki, 1978).

Four species of *Chaetocnema* have chromosome numbers close to the primitive formula, three of them having 22 chromosomes and the fourth with 20 chromosomes. The genus is rather uniform on cytological grounds but there are at least two types of sex chromosomes. The chromosomal origin of these species of *Chaetocnema* has probably taken place by two steps of centric fusions which would explain the decrease from 24 to 22 and to 20 chromosomes (Segarra and Petitpierre, 1982, and in press).

The species of *Phyllotreta* are difficult for chromosomal studies because, besides the minute size of their bodies, they have very small chromosomes. Only two European species have until now provided chromosome results, one with 30 and another with 32 chromosomes, both having the primitive type of sex chromosomes, Xy_p. One American species, *P. fallax* Suffr., has 32 chromosomes and a Xy_p system too (Virkki, 1970), which is in agreement with one of the European species.

The range of chromosome numbers in the eight analysed species of the genus *Aphthona* is quite large, from 24 to 32 diploid chromosomes, with 28 chromosomes as possible modal value since it is found in half of the species. All the species of *Aphthona* have shown a synaptic sex bivalent which may be constituted by a medium X and a small y-chromosome, the Xy system (Segarra and Petitpierre, in press).

Longitarsus is our best surveyed genus because 17 European species are cytologically known. They display a range of chromosome numbers from 2n=26 to 2n=32 with 2n=30 as the peak value. Also, their sex bivalents look like those of the species of *Aphthona,* Xy sex system. A peculiar feature of metaphases I in *Longitarsus* species is the regular presence of an autosomal bivalent of large size. Spermatogonial metaphases and metaphases II have been obtained in *L. ochroleucus* (Marsham) (Segarra and Petitpierre, in perss) and *L. tabidus* (Segarra and Petitpierre, 1982) respectively, showing only metacentric chromosomes, which is the rule for coleopterans and in particular most chrysomelids. One American species of *Longitarsus, L. oakleyi* Blake, has been examined by Virkki having a 13+X formula (Smith and Virkki, 1978). So far this is the only example of XO system in *Longitarsus,* and further analyses on other American species would be useful.

There is a substantial heterogeneity of the diploid numbers among the species of *Psylliodes,* from 20 to 36 chromosomes. Each of the five studied species is characterized by a different number, but the Xy_p sex system is maintained in three of them. At present it is not possible to assume a primitive karyotype, though, for example, that of *P. affinis* (Paykull) with 9+XY formula should be derived from higher chromosome number owing to the large size of its bivalents and the chiasmatic XY (neo-XY?) system. A possible relationship in species of *Psylliodes* between low chromosome numbers and feeding preferences on the Solanaceous plants and high numbers feeding on the Cruciferous plants as suggested by Furth (pers. comm.) should be checked with caution.

Three other European genera of flea beetles, *Dibolia, Podagrica* and *Sphaeroderma,* have been subjected to chromosomal analyses. One species of *Dibolia, D. timida* (Ill.), has a high number but with the primitive sex system, $19+Xy_p$. Another species of *Dibolia,* the North American *D. penstemonis* Parry, has also a rather high number but a different sex system, 15+neoXY (Smith and Virkki, 1978). Of course we would need more analyses to get a preliminary perspective on the chromosomes and their evolution in comparing species of *Dibolia.*

The four European species of *Podagrica* have evidenced an identity in the chromosome formula ($19+Xy_p$) in good correspondence with their close morphological interrelationships. Due to this high number, the genus *Podagrica* should be placed in an advanced evolutionary position within the phyletic tree of Alticinae (Segarra and Petitpierre, 1982, and in press).

From the karyological data the species of *Sphaeroderma* are probably an offshoot of the cytological evolution of flea beetles, because our two examined species show the highest number so far encountered in Alticinae, $25+Xy_p$ (Segarra and Petitpierre, 1982, and in press). In addition, since most bivalents have a large size, this fact should correspond with a great DNA content.

In conclusion, the present chromosome findings on the European flea beetles provide a similar array of chromosome numbers to that found in American ones but of higher modal value and much less diversity in the sex systems than in the New World species. The genus *Altica* would be near to the basis of the cytological evolution. *Chaetocnema* on one hand and the flea beetles with an impressed pronotum on the other, like *Crepidodera* and *Arrhenocoela,* would not be far from *Altica* on these grounds. In a further advanced stage are *Aphthona, Longitarsus* and a bit farther *Phyllotreta,* a group with modal 28-30 diploid chromosomes. The chromosomal situation of *Psylliodes* is not clarified yet due to a greater diversity of chromosome numbers than in the remaining genera, but it could also be in an intermediate stage of chromosomal evolution. Finally, *Podagrica, Sphaeroderma* and probably *Dibolia* are strikingly derived genera, a fact which is consistent in the two last genera with their specialized morphological features.

SUMMARY

The chrysomelids display a great diversity of chromosome numbers, from n=4 to n=30, and sex determining systems too. Among the 557 bisexual taxa that have been chromosomally surveyed, n=10, n=11 and mainly n=12 are the most frequently found haploid values. Within the wide heterogeneity of sex systems, the "parachute" type (Xy_p) is found in almost a half of the species, but the XO system and the distance pairing sex chromosomes, X+y and X+Y, also appear in substantial percentages. Each subfamily seems to share a characteristic peak value of chromosomes: Donaciinae n=15, Criocerinae n=8, Megalopodinae n=10, Cryptocephalinae n=15, Eumolpinae n=8, Chrysomelinae n=12, Galerucinae n=10, Alticinae n=11, Hispinae n=8, and Cassidinae n=9. However, the most primitive number for each of them can only be tentatively proposed, except for the best sampled subfamilies of Chrysomelinae and Alticinae. The chromosomal heterogeneity within the Chrysomelinae is analysed in greater detail. Their karyological evolution seems to have happened by three stages of increases in the chromosome number according to the modal values of n=10 in Timarchini, n=12 in most other groups, and n=17 in Chrysomelina and Phratorina subtribes, which is consistent with the three basic kinds of larval mor-

phology. The chromosomal evolution of Chrysomelinae by the principle effect of increases in number, is coupled with a regular rise in the symmetry of the karyotypes. Furthermore, there is an indirect correlation between chromosome number and trophic selection in the particular case of the genus *Chrysolina,* since the species of low numbers (n=11 or 12) are almost always Labiatae feeders, while those with high numbers (more than n=15) are feeders on other plants, mostly Compositae, Hypericaceae, Umbelliferae and Plantaginaceae.

Among the 50 European flea beetles chromosomally surveyed, there is an extensive array of numbers, from n=8 to n=26, as in the American species checked by Virkki (see Smith and Virkki, 1978), but with a lesser heterogeneity in the sex chromosome systems. Good data have been obtained in some genera such as *Altica, Chaetocnema, Aphthona, Longitarsus, Podagrica* and *Psylliodes,* which show characteristic chromosome patterns. *Altica* is chromosomally invariant in the four analysed species with 11+X+y formula, *Chaetocnema* has a mode of n=11, *Aphthona* n=14, *Longitarsus* n=15, and all the species of *Podagrica* have n=20, while *Psylliodes* display a huge variation in number from n=10 to n=18 chromosomes. One species of *Hermaeophaga, H. cicatrix,* possesses 7+X_1X_2Y male formula, which clearly differs from that found in the allied species of *Altica.* Finally, *Dibolia* and *Sphaeroderma* are greatly derived genera and have high chromosome numbers.

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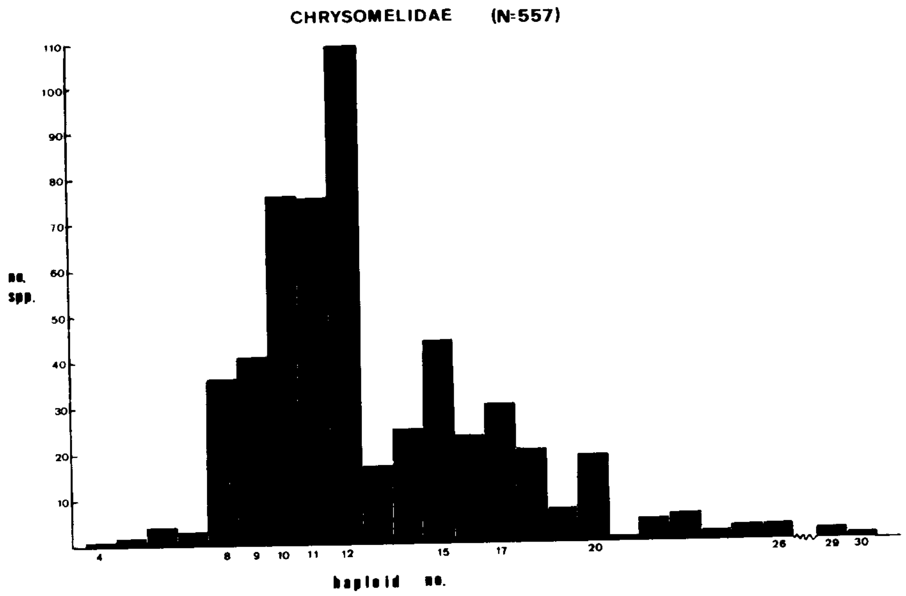


Fig. 1. Histogram of haploid chromosome numbers of Chrysomelidae.

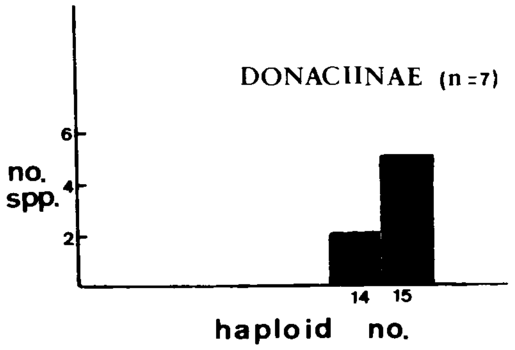


Fig. 2. Histogram of haploid chromosome numbers of Donaciinae.

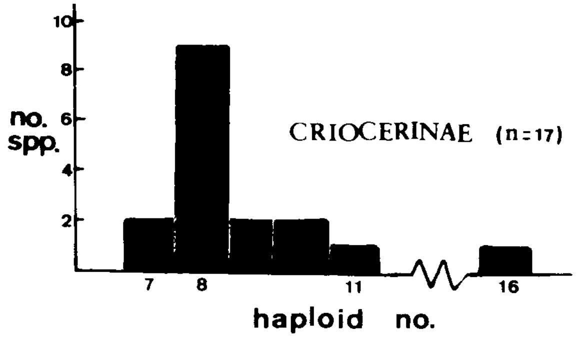


Fig. 3. Histogram of haploid chromosome numbers of Criocerinae.

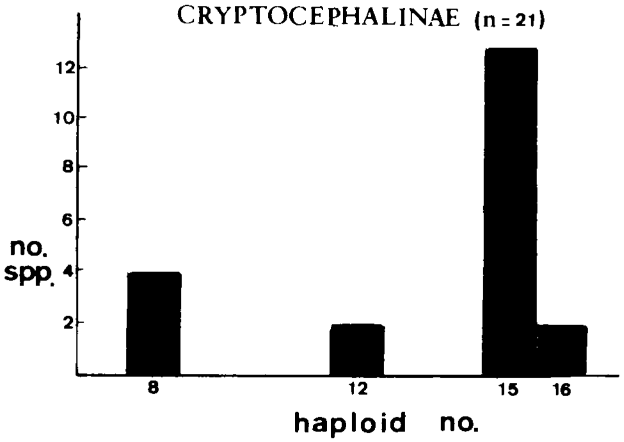


Fig. 4. Histogram of haploid chromosome numbers of Cryptocephalinae.

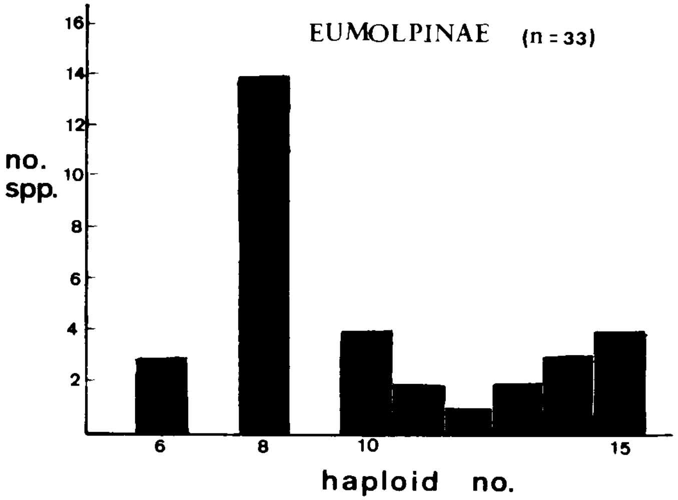


Fig. 5. Histogram of haploid chromosome numbers of Eumolpinae.

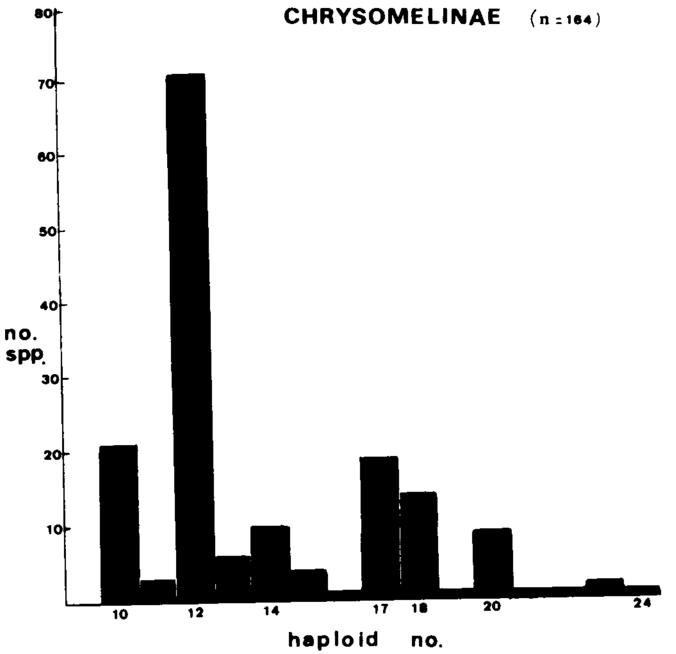


Fig. 6. Histogram of haploid chromosome numbers of Chrysomelinae.

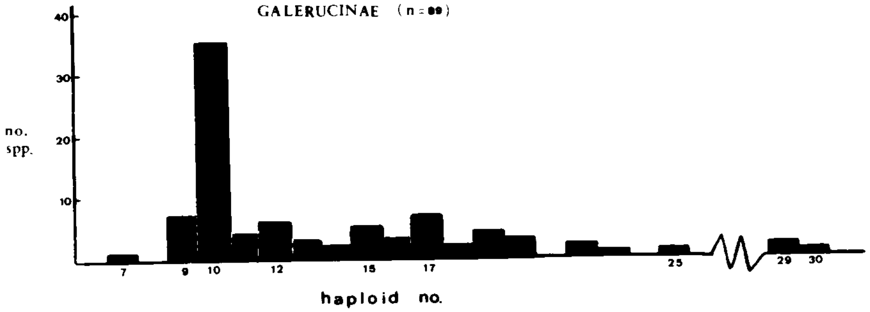


Fig. 7. Histogram of haploid chromosome numbers of Galerucinae.

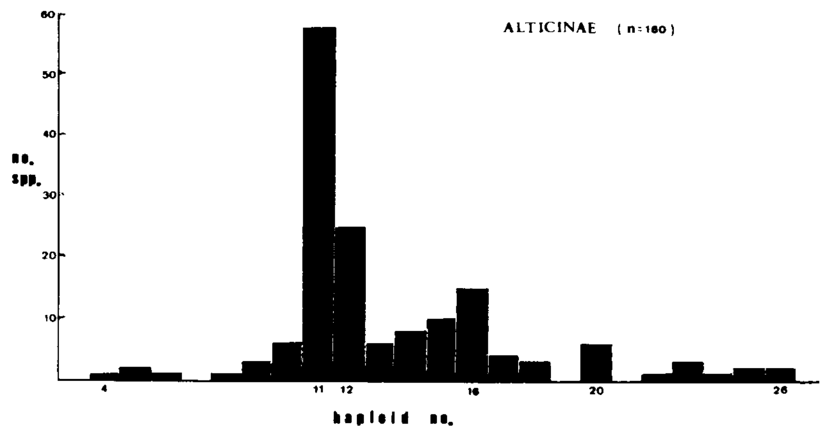


Fig. 8. Histogram of haploid chromosome numbers of Alticinae.

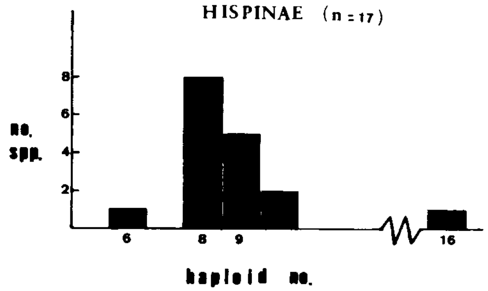


Fig. 9. Histogram of haploid chromosome numbers of Hispinae.

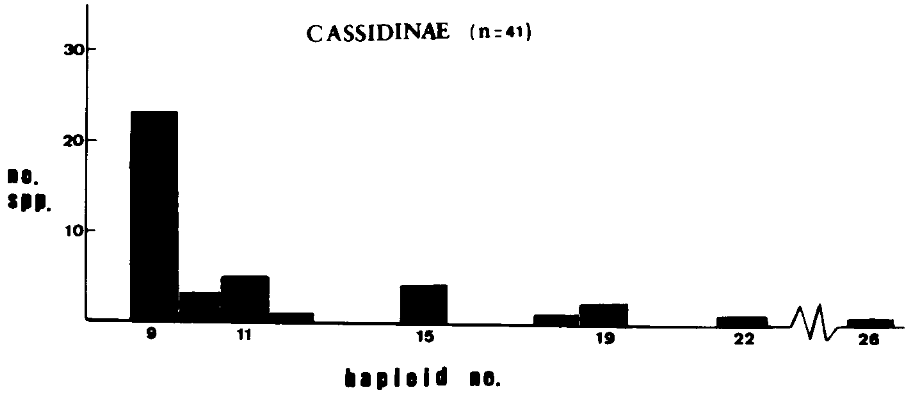
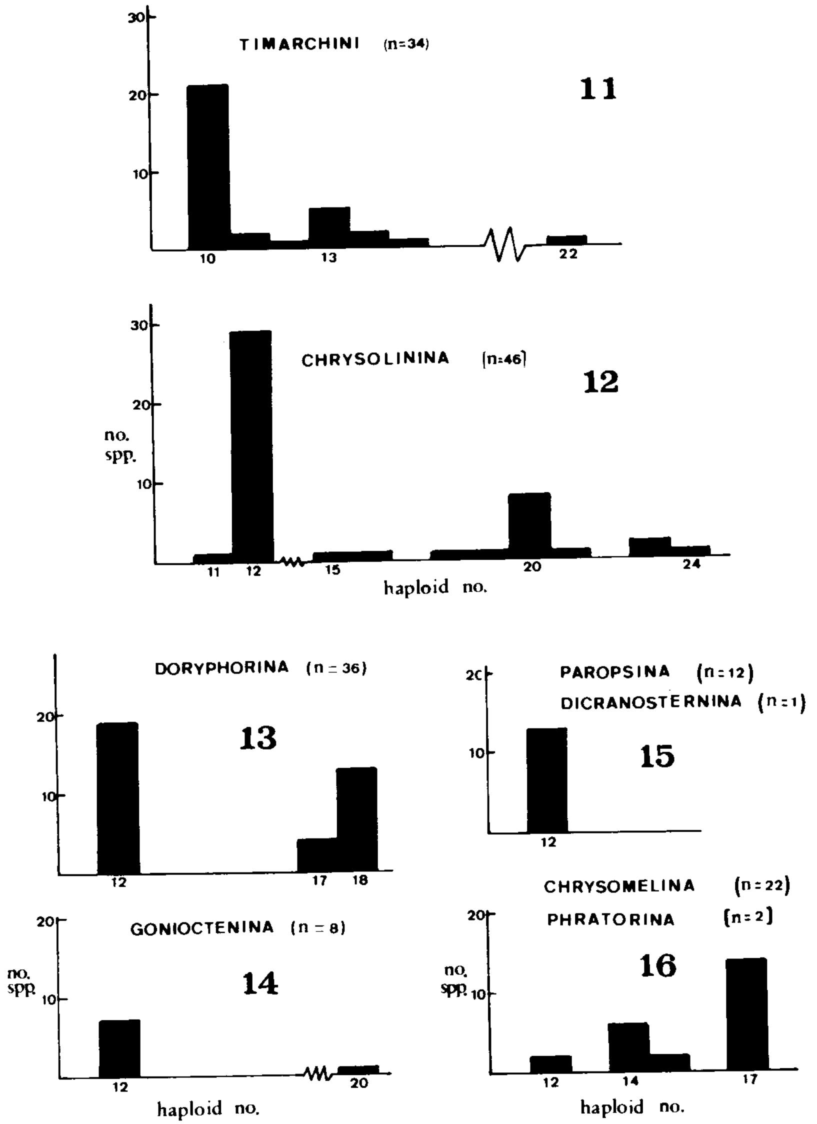


Fig. 10. Histogram of haploid chromosome numbers of Cassidinae.



Figs. 11-16. Histograms of haploid numbers in groupings of Chrysomelinae leaf beetles.

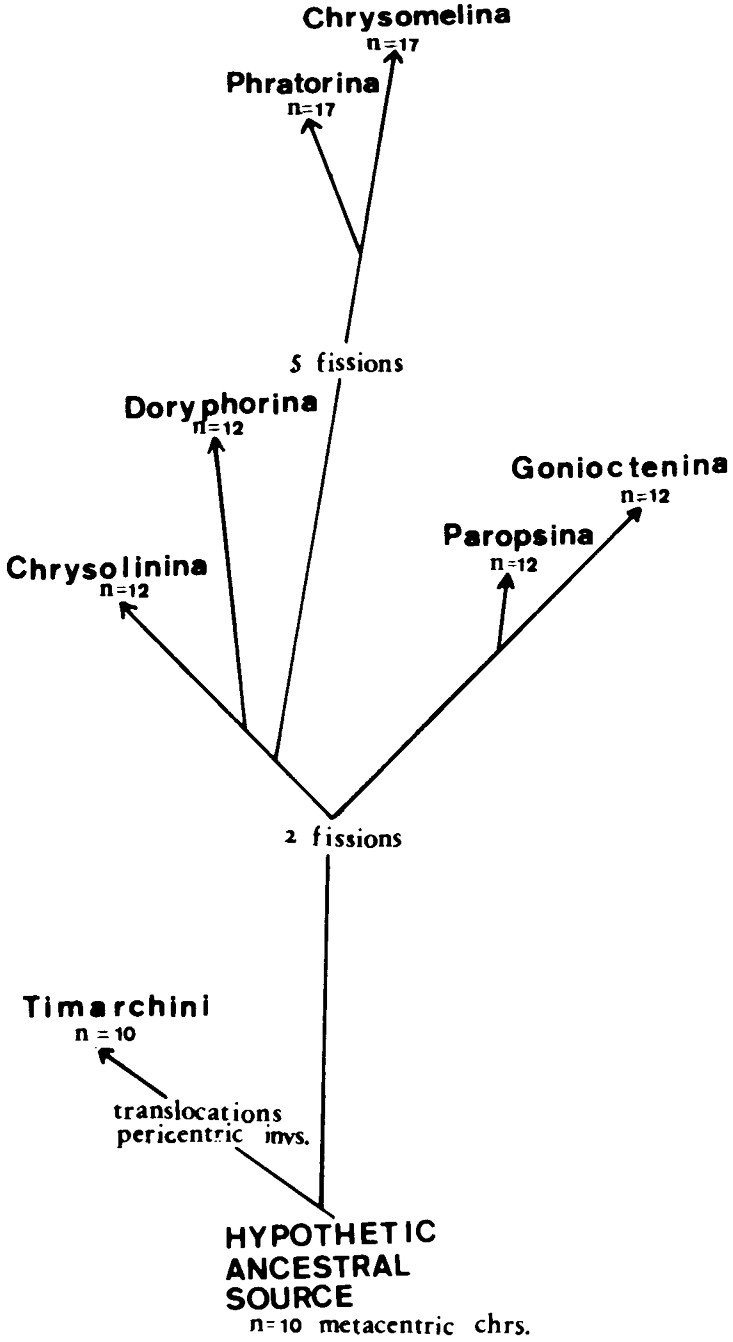


Fig. 17. Main chromosomal changes involved in the origin of the Chrysomelinae groupings.

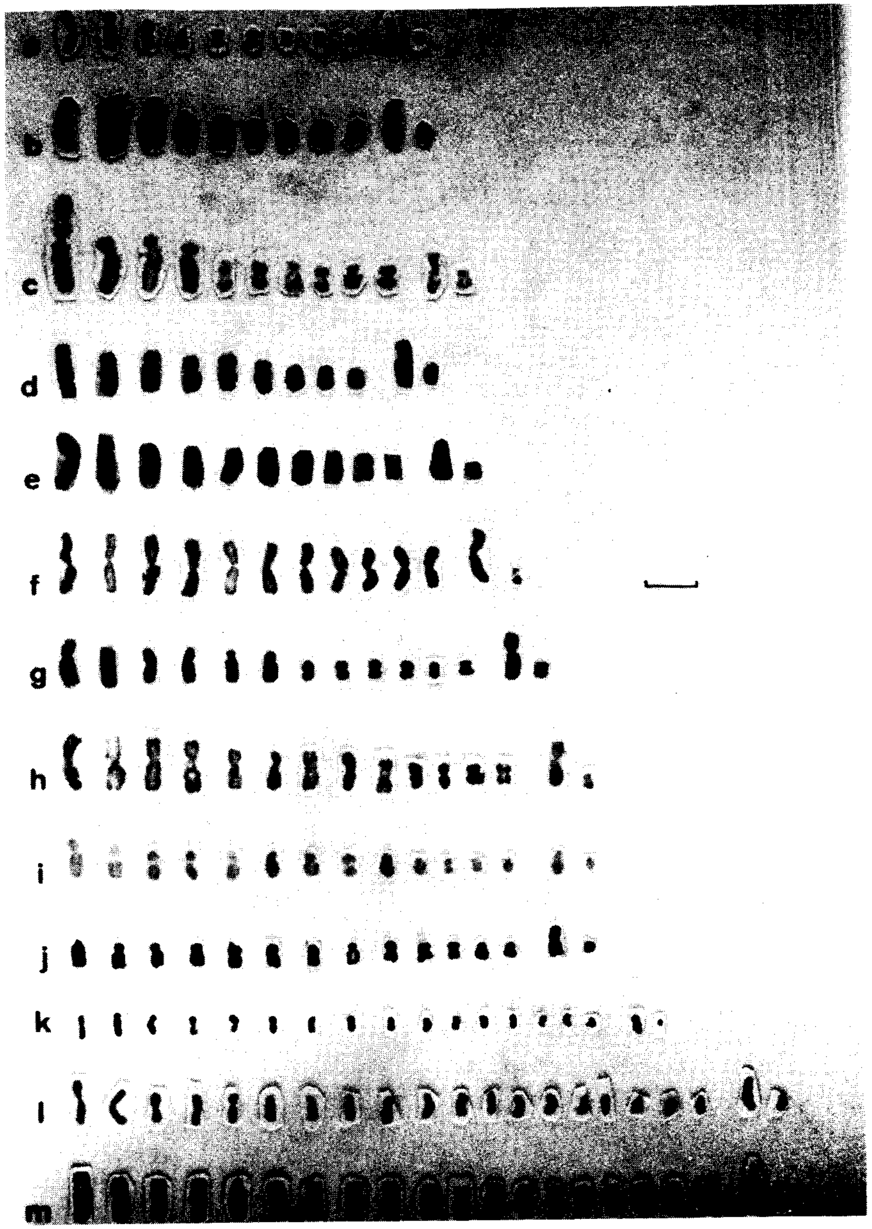


Fig. 18. Haploid sets of several species of Chrysomelinae leaf beetles. The male sex chromosomes are in the right of each set. The bars are 5 μm. **a**, *Timarcha sicelidis*; **b**, *T. perezi*; **c**, *Chrysolina kuesteri*; **d**, *Timarcha lugens*; **e**, *T. balearica*; **f**, *Chrysolina affinis*; **g**, *Timarcha rugosa*; **h**, *Cyrtonus plumbeus*; **i**, *Timarcha laevigata*; **j**, *T. strangulata*; **k**, *Phratora tibialis*; **l**, *Chrysolina haemoptera*; **m**, *C. carnifex*. Note the direct interrelationship between the increases in number and symmetry of karyotypes.

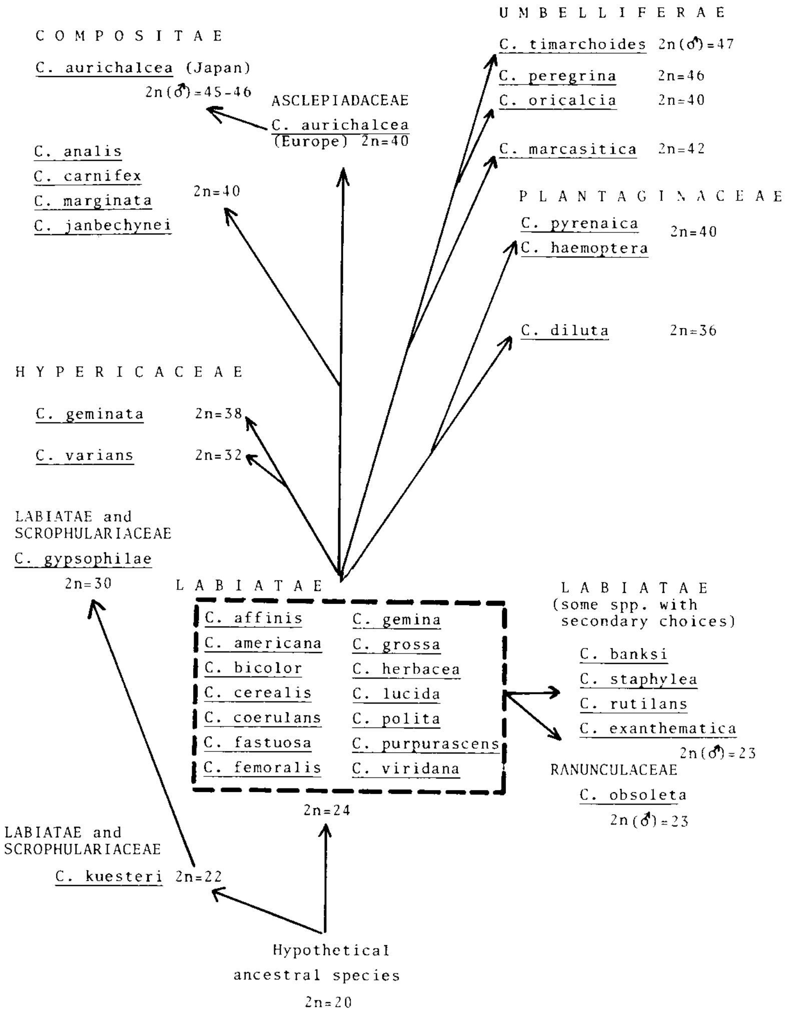


Fig. 19. Chromosomal evolution and trophic selection in the genus *Chrysolina*.

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Systematics and Ecology — an attempt at correlation in Leaf Beetles
(Coleoptera: Chrysomelidae)

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ABSTRACT. — An attempt is made to correlate the systematics and ecology of some groups of Leaf Beetles. The determination keys of adults and larvae are compared with the arrangement of plant families. Only groups with many species are suitable for this comparison in which a certain number of larvae are also known. The subfamily Chrysomelinae, and the genera *Cryptocephalus* Geoffroy, *Chrysolina* Motschulsky, and *Cassida* Linnaeus are used for this purpose. There are differential confirmations between the keys of adults and larvae and the groups of plant families, respectively. For species arrangement within one genus, too few larvae are known to obtain a definite statement.

The ecology of phytophagous insects is an interesting problem for a scientist, but there has been little progress besides recording some of the plants used for their food and development. The question of the cause of such phytophagous specialization seems to be unresolvable, but it is possible to make an attempt at a probable correlation between systematics and ecological groups. It is the intention of this paper to compare ecologically related groups with determination tables (keys) for adults and larvae. It is postulated that such a correlation is more likely between the ecology and the larval systematics than with the systematics of adults. However, this has not been proven to date, and hopefully this paper will provide an inspiration to start or continue such investigations.

In the following comparisons, the tables of Mohr (1966) for adults and the author's data for larvae are used. The latter will be published soon with the aid of the tables of Ogloblin et al. (1971) and Medvedev et al. (1978). Four taxa have been selected, namely the genera: *Cryptocephalus, Chrysolina, Cassida,* and the subfamily Chrysomelinae.

The first part of Table 1 shows the grouping in the genus *Cryptocephalus* according to the food plants (= ecology) and the key to the adults. There are differences between the Fagales/Salicales ecological group and the adults, because the latter is divided into two groups; this is also found to be the case among the larvae. The remaining species are distributed differently, and there is a discrepancy of eight species