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The cytogenetics and cytotaxonomy of *Chrysolina* Mots. and *Oreina* Chevr. (Coleoptera, Chrysomelidae, Chrysomelinae)

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Thirteen species of *Chrysolina* and four of *Oreina* have been chromosomally analyzed. *C. (Euchrysolina) graminis* and three species of *Oreina, O. (s.str.) basilea, O. (Chrysochloa) speciosissima* and *O. (Protorina) ludovicae* have shown a diploid number of 24 chromosomes and a $11 + Xy_p$ male meioformula. *Oreina (s.str.) viridis* has an asymmetrical karyotype of $9 + Xy_p$ meioformula, probably derived from the former $11 + Xy_p$ by two centric fusions. The *Chrysolina* of subgenus *Stichoptera* are chromosomally heterogeneous but all of them share asymmetrical karyotypes a fact which probably supports their common ancestry, *C. latecincta* and *C. ripoceanensis* have $11 + Xy_p$, *C. gypsophilae* $15 + Xy_p$, and *C. sanguinolenta* $16 + Xy_p$. *C. (Hypericia) hyperici* and *C. (Hypericia) quadrigemina* display 38 chromosomes in agreement with another species of that subgenus. The recent proposal of joining *C. fuliginosa* and *C. lepida* within the subgenus *Allochrysolina* is reinforced by their common diploid number of 42 and $20 + Xy_p$ meioformula. *C. (Heliostola) montana* shares the same $19 + Xy_p$ meioformula with the species of the somewhat related subgenus *Chalcoidea* which also lives on Asteraceae. *C. (Craspeda) limbata* shows a $20 + Xy_p$ meiformula, quite similar to the $19 + Xy_p$ previously found in species of the subgenera *Colaphodes* and *Ovosoma* which also feed on Plantaginaceae *C. (Threnosoma) helopioides* presents the highest chromosome number, $2n = 47$ and $23 + X$ male meioformula, in agreement with that found in another species of *Threnosoma*. The proposed chromosomal evolution of *Chrysolina*, mainly due to centric fissions and coupled to their host-plant shifts, is not contradicted by the molecular phylogeny even though the latter provides a better resolution. The possible joining of *Chrysolina* and *Oreina* within a same genus might be supported by the cytogenetic data but should await enlarged analyses of molecular phylogenies.

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The genus *Chrysolina* is one of the largest genera of Chrysomelidae with roughly 400 species in almost seventy subgenera (DACCORDI 1994; KIPPENBERG 1994; BOURDONNÉ 1996). Their relationships with the allied genus *Oreina (= Chrysochloa)*, a taxon having twenty-seven species (PETITPIERRE et al. 1993), are a matter of debate since some recent authors suggest placing both in a single genus (BOURDONNÉ and DOGUET 1991; DACCORDI 1994), while others keep them as different genera (KÜHNELT 1984; WARCHALOWSKI 1993; KIPPENBERG 1994; DOBLER et al. 1996). Previous chromosomal analyses on the *Chrysolina* have covered 44 species and those on the *Oreina* eight (PETITPIERRE et al. 1988; PETITPIERRE and JUAN 1994). The former have shown a wide range of chromosome numbers from $2n = 22$ (Xy_p) to $2n = 47$(XO), which have been used along with their host-plant families to set up a possible chromosomal phylogeny (PETITPIERRE and SEGARRA 1985), whereas the latter are much more conservative being all but one of $2n = 24$ (Xy_p). However, both genera share $n = 12$ chromosomes and particularly the Xy_p "parachute" sex chromosome system so common in beetles, as the prevalent cytogenetic states.

In the present paper we report the chromosomal findings on thirteen species of *Chrysolina* and four of *Oreina* with some of their subgenera being investigated for the first time. The whole of karyological results obtained on both genera are discussed in the light of current subgeneric taxonomy, host plant affiliations and the recently established molecular phylogenies (DOBLER et al. 1996; GARIN et al. 1999; HSIAO and PASTEELS 1999).

MATERIAL AND METHODS

The species and subgenera studied and their geographical sources are given in Table 1. These species were caught and checked within the period between the years 1988 and 1998. The chromosome analyses were conducted mostly from living individuals by using the simple technique of fixation and Giemsa staining reported elsewhere (PETITPIERRE et al. 1998) but a few of them were obtained from testes previously treated for 20–30 minutes with 0.05% colchicine just before fixation in order to increase the number of suitable metaphase cells.

RESULTS

1. *Species of Oreina*

Four taxa of *Oreina* have been surveyed. *O. (s.str.) viridis* provided metaphases II of $9 + Xy_p$ meioformula and metaphases II of $n = 10$ chromosomes where two large autosomes or autosomal bivalents stand out clearly from the rest (Fig. 1). *O. (Protorina) ludovicae* has spermatogonial metaphases composed of metacentric chromosomes whose sizes gradually decrease, with the y chromosome the smallest element of the set (Figs. 2 and 17). *O. (s.str.) basilea* (Fig. 3) and *O. (Chrysochloa) speciosissima* (not shown) displayed metaphases I with a $11 + Xy_p$ meioformula, of fairly similar medium size bivalents.

2. *Species of Chrysolina*

2.1. *Chrysolina (Euchrysolina)*

One of the two species of the subgenus *Euchrysolina* was cytogenetically examined. *C. (Euchrysolina) graminis* displayed metaphases I of a $11 + Xy_p$ meioformula, composed of medium and small size bivalents (Fig. 3).

2.2. *Chrysolina (Stichoptera)*

Four species of this subgenus have been studied. *C. latecincta* and *C. ripoceanensis* had metaphases I of $11 + Xy_p$ with four and five large autosomal bivalents respectively (Figs. 5 and 6), *C. gypsophilae* had a meioformula of $15 + Xy_p$ with only two large autosomal bivalents (Fig. 7) and *C. sanguinolenta* one of $16 + Xy_p$ with a single large autosomal bivalent (Fig. 8). Thus all four species have asymmetrical karyotypes of two modal size classes unlike to any of the remaining species of *Chrysolina*.

2.3. *Chrysolina (Sphaeromela)*

C. varians from the Central Pyrenees is characterized by metaphases I of $15 + Xy_p$ composed of small size bivalents mostly (Fig. 9). This result is in agreement with previous data by Barabás and Bezo (1979) who analyzed specimens of *C. varians* from Central Europe and reported $2n = 32$ chromosomes and the same meioformula.

2.4. *Chrysolina (Allochrysolina)*

Two species of this subgenus have been checked in the present analysis. *C. fuliginosa* ssp. *galii* from the French Pyrenees had a $20 + Xy_p$ meioformula made of rather small and similar bivalents (Fig. 10), and this finding agrees with that obtained in *C. fuliginosa* ssp. *coriacea* from South Spain which displayed $2n = 42$ chromosomes, medium or small metacentrics (Fig. 15). Another species, *C. lepida*, yielded the same meioformula of $20 + Xy_p$ but its karyotype of $2n = 42$ chromosomes differs from that of *C. fuliginosa coriacea* by having at least six acrocentric autosome pairs (Fig. 14), indicating pericentric inversions.

Table 1. *Chromosomal data on seventeen species of Oreina and Chrysolina from France (FR), Spain (SP) and Russia (RU).*

Species	Geographical source	No. ind.	2n	Meioformula
O. (s.str.) basilea (Gebler)	Altai-Sayan Mts. (SW Siberia, RU)	2	24	$11+Xy_p$
O. (s.str.) viridis (Duft.)	Massif des Vosges (Haut-Rhin, FR)	1	20	$9+Xy_p$
O. (Chrysochloa) speciosissima (Scop.)	Les Bordes (Pyren. of Lleida, SP)	2	24	$11+Xy_p$
O. (Protorina) ludovicae (Muls.)	Gourette (Hautes Pyrénées, FR)	1	24	$11+Xy_p$
C. (Euchrysolina) graminis (L.)	Bidache (Pyrén. Atlantiques, FR)	1	24	$11+Xy_p$
C. (Stichoptera) gypsophilae (Küst.)	Bènac (Ariège, FR)	1	–	$15+Xy_p$
"	Aniane (Herault, FR)	1	32	$15+Xy_p$
C. (Stichoptera) latecincta (Dem.)	Alès: fôret de Rouvergue (Gard, FR)	3	24	$11+Xy_p$
C. (Stichoptera) ripoceanensis Bourdonné & Doguet	Bains d'Uchet (Landes, FR)	2	24	$11+Xy_p$
C. (Stichoptera) sanguinolenta (L.)	Le Breuil (Sâone-et-Loire, FR)	1	34	$16+Xy_p$
C. (Sphaeromela) varians (Schall.)	Eth Portilho (Pyren. of Lleida, SP)	1	32	$15+Xy_p$
C. (Allochrysolina) fuliginosa (Ol.)				
ssp. *Galii* (Weise)	Lesparrou (Ariège, FR)	1	–	$20+Xy_p$
ssp. *Coriacea* (Suffr.)	Lagos (Málaga, SP)	2	42	$20+Xy_p$
C. (Allochrysolina) lepida (Ol.)	Marseille: Château de Gormont (Bouches-du-Rhone, FR)	2	42	$20+Xy_p$
C. (Hypericia) hyperici (Forst.)	Prèbois (Isère, FR)	1	38	–
C. (Hypericia) quadrigemina (Suffr.)	Son Serra de Marina (Mallorca, SP)	1	38	–
C. (Heliostola) montana (Gebler)	Altai-Sayan Mts. (SW Siberia, RU)	2	–	$19+Xy_p$
C. (Craspeda) limbata (F.)	Quériguet (Ariège, FR)	1	42	$20+Xy_p$
C. (Threnosoma) helopioides (Suffr.)	Ardalejos (Málaga, SP)	2	47	$23+X$

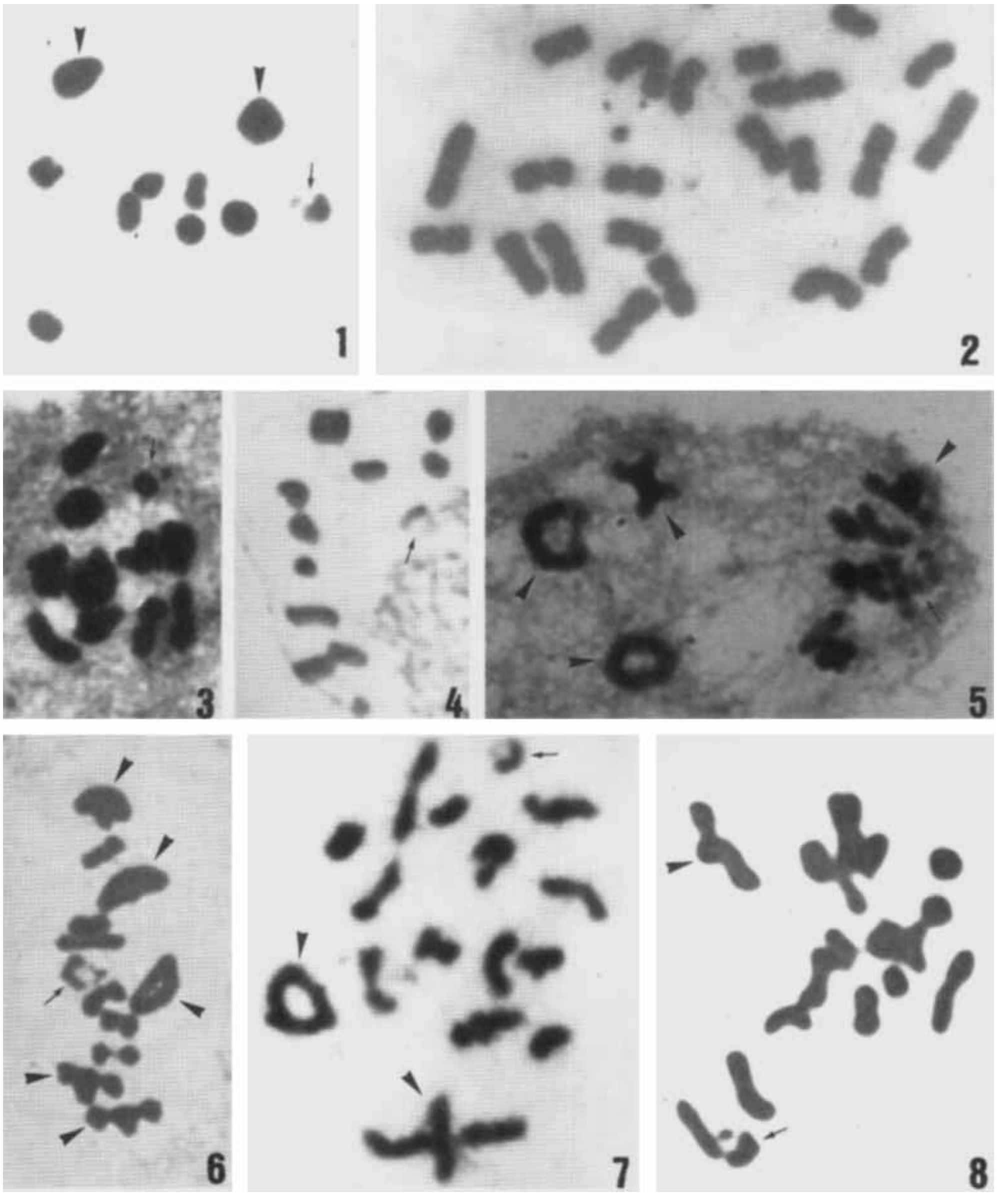

Fig. 1–8. Metaphase I of *Oreina (s.str.) viridis* with 9 + Xy_p **(1)**. Spermatogonial metaphase of *O. (Protorina) ludovicae* with 2n = 24 chromosomes **(2)**. Metaphases I of *Oreina (s.str.) basilea* **(3)**, *Chrysolina (Euchrysolina) graminis* **(4)**, *C. (Stichoptera) latecincta* **(5)** and *C. (Stichoptera) ripoceanensis* **(6)** all with 11 + Xy_p. Metaphases I of *C. (Stichoptera) gypsophilae* with 15 + Xy_p **(7)** and *C. (Stichoptera) sanguinolenta* with 16 + Xy_p **(8)**. The large autosomal bivalents of the asymmetrical karyotypes are indicated by arrowheads and the Xy_p by an arrow. All figures at × 2000.

2.5. *Chrysolina (Heliostola)*

The only species chromosomally studied in this subgenus, *C. montana* from SW Siberia, showed metaphases I of a 19 + Xy_p meioformula, whose bivalents were mostly of medium size with a few smaller ones (Fig. 11).

2.6. *Chrysolina (Craspeda)*

Again only one species in this subgenus has been available for the present analysis. *C. limbata* is defined by a meioformula of 20 + Xy_p, composed of rather large and medium sized metaphase bivalents, of rod or cross shapes which points out their unichiasmatic condition (Fig. 12). The chromosomes of *C. limbata* are metacentrics as could be observed in a few metaphases II (not shown).

2.7. *Chrysolina (Hypericia)*

C. hyperici gave spermatogonial metaphases made of 2n = 38 chromosomes, all but two pairs of which are metacentrics, of gradually decreasing sizes from medium to small. The X chromosome seems to be the largest element and the y chromosome the smallest (Figs. 15 and 18). A similar karyotype of $2n = 38$ chromosomes was also found in the closely related species *C. quadrigemina* (not shown).

2.8. *Chrysolina (Threnosoma)*

The only currently examined species of this subgenus, *C. helopioides*, showed the highest male diploid number, $2n = 47$, we have recorded among the sampled species of *Chrysolina*, being all the spermatogonial metaphase chromosomes of metacentric shapes and of medium or small sizes (Fig. 16).

DISCUSSION AND CONCLUSIONS

Our present chromosomal analysis on seventeen species of *Chrysolina* and *Oreina* enlarges the list of the sampled leaf beetles to 54 taxa of the former and 11 of the latter. The range of diploid numbers of *Chrysolina* from 22 to 47 in males and of *Oreina* from 20 to 24, is keeping unchanged from to our last report (PETITPIERRE et al. 1993). However, the addition of new species of *Chrysolina* and *Oreina* with $2n = 24$ and $11 + Xy_p$ meioformula strengthens their presumed ancestral condition in both genera, since this formula is the most widespread, being found in twelve of the twenty-eight checked subgenera of *Chrysolina* and in the five checked ones of *Oreina*.

The finding of one species of *Oreina*, *O. viridis*, with 20 chromosomes and Xy_p sex-chromosome system might be tentatively interpreted as the basic condition for *Oreina*, because this is the presumed ancestral number for Coleoptera suborder Polyphaga (SMITH and VIRKKI 1978) and is the most common karyotype in the plesiomorphous chrysomeline genus *Timarcha* (PETITPIERRE and SEGARRA 1985), but this would not be the most likely explanation taking into account the clear prevalence of the 24 diploid number in *Oreina* and *Chrysolina*. Thus both the 20 chromosome karyotype of *O. viridis* and the 22 of *C. (Stichoptera) kuesteri* (PETITPIERRE 1981, 1983), should be considered as apomorphous states derived by centric fusions from the ancestral 24 chromosome karyotype. Interestingly, these karyotypes of *O. viridis* and *O. kuesteri* are remarkably asymmetrical and bimodal, with two conspicuous classes of chromosome sizes. Thus the two large autosome pairs of *O. viridis* and the largest one of *C. kuesteri* would have arisen by these presumed fusions.

The seven species of *Chrysolina* subgenus *Stichoptera* so far analyzed constitute a well defined group on morphological, male genitalia and ecologi-

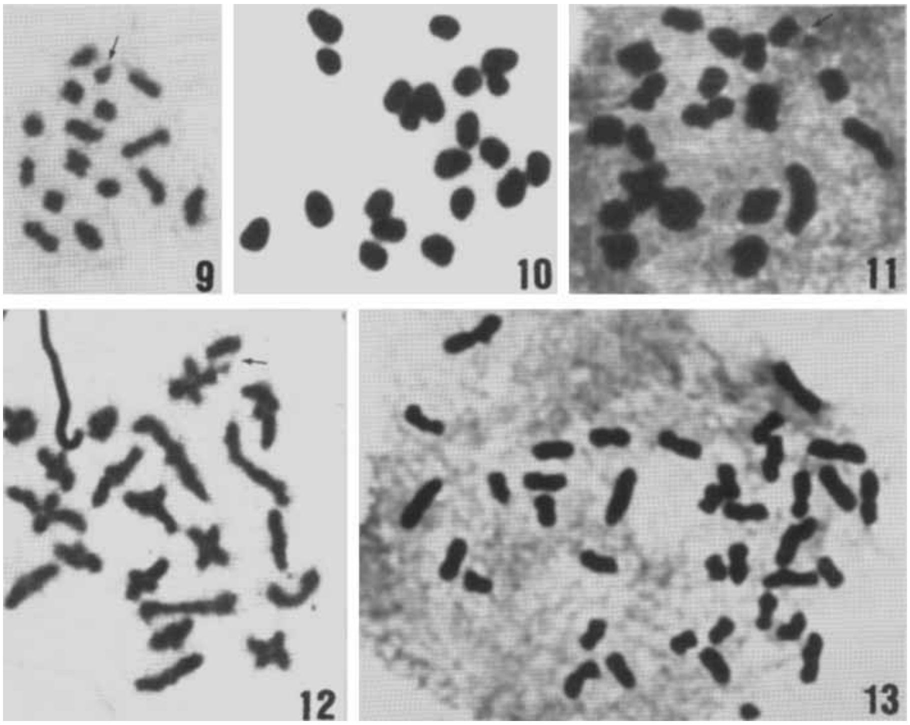

Fig. 9–13. Metaphases I of *Chrysolina (Sphaeromela) varians* with $15 + Xy_p$ **(9)**, *C. (Allochrysolina) fuliginosa galii* with $20 + Xy_p$ **(10)**, *C. (Heliostola) montana* with $19 + Xy_p$ **(11)** and *C. (Craspeda) limbata* with $20 + Xy_p$ **(12)**. The Xy_p is indicated by an arrow. Spermatogonial metaphase of *C. (Hypericia) hyperici* with $2n = 38$ chromosomes **(13)**. All figures at × 2000.

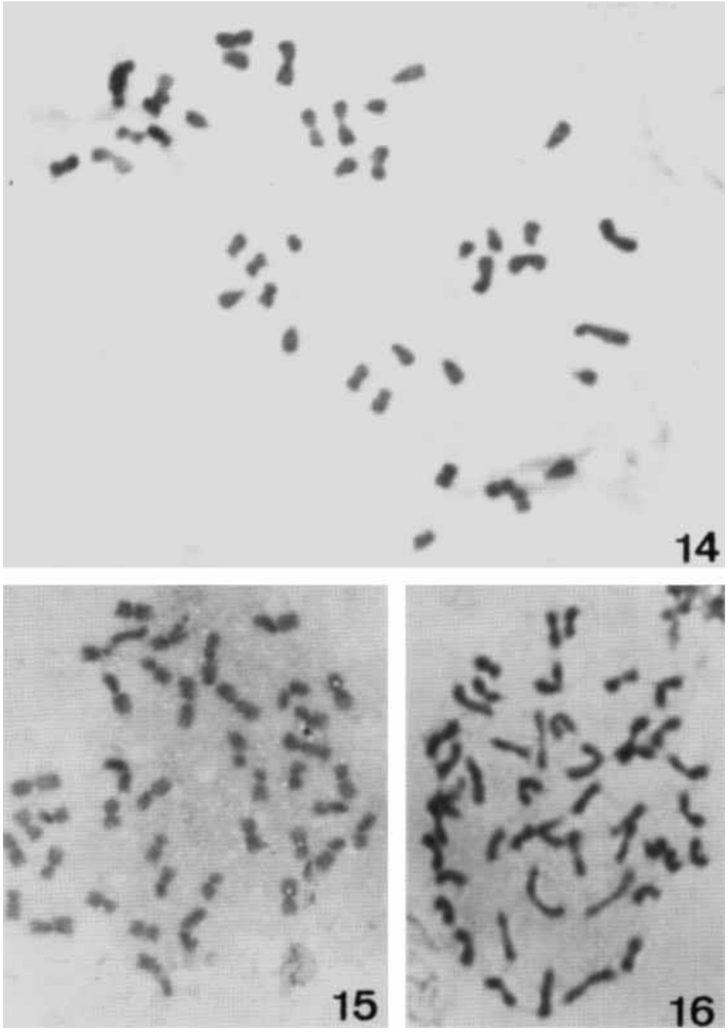

Fig. 14–16. Spermatogonial metaphases of *Chrysolina (Allochrysolina) lepida* with 2n = 42 chromosomes of which six autosomal pairs at least are acrocentrics **(14)**, *C. (Allochrysolina) fuliginosa coriacea* with 2n = 42 chromosomes all metacentrics **(15)** and *C.* (*Threnosoma*) *helopioides* with 2n = 47 chromosomes also metacentrics **(16)**. All figures at × 2000.

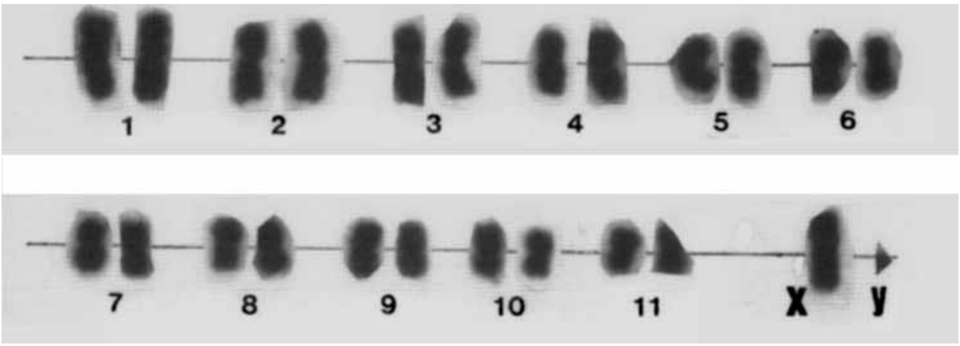

Fig. 17. Karyogram of *Oreina (Protorina) ludovicae* at × 2000.

cal grounds, being mostly associated with plants of Scrophulariaceae (Bourdonné and Doguet 1991), but amazingly they are highly heterogeneous in chromosome numbers, ranging from $2n = 22$ in *C. kuesteri* to $2n = 34$ in *C. sanguinolenta*. In spite of these differences in chromosome number all the species of *Stichoptera* display asymmetrical karyotypes whose numbers of large autosome pairs are inversely correlated with the diploid number. Namely, *C. ripoceanensis* and *C. latecincta* with $2n = 24$ and $11 + Xy_p$ meioformula, have five and four large autosome pairs respectively. Also, two previously studied species in this subgenus, *C. kuesteri* with $2n = 22$ and *C. colasi* with $2n = 24$, show four large autosome pairs each (Petitpierre 1981, 1983). The current species *C. gypsophilae* with $2n = 32$ and $15 + Xy_p$ meioformula has two large autosome pairs and *C. sanguinolenta* with $2n = 34$ and $16 + Xy_p$ meioformula has only one. It seems that the possible origin of these two latter species was in part due to centric fissions of two or three large autosome pairs giving rise to four and six small autosome pairs respectively, which might have occurred in a hypothetic ancestral species of $2n = 24$ chromosomes and $11 + Xy_p$ meioformula allied to *C. ripoceanensis*, *C. latecincta* or *C. colasi*.

Our finding of a $15 + Xy_p$ meioformula in *C. (Sphaeromela) varians* from the Pyrenees corroborates the precedent results on other specimens of this species coming from Central Europe (Barabás and Bezo 1979), and proves the karyological conservatism of this taxon. *C. varians* is related to the species of subgenus *Hypericia* by several morphological characters and their common feeding on *Hypericum* plants (Clusiaceae) (Jolivet and Petitpierre 1976; Bourdonné and Doguet 1991). In addition, the recently obtained mtDNA phylogenies prove the genetic similarity of *C. varians* with the species of *C. (Hypericia)* as members of the same clade (Garin et al. 1999; Hsiao and Pasteels 1999), although they are differing in their chromosome numbers.

Two investigated species of *Chrysolina* subgenus *Allochrysolina*, *C. fuliginosa* checked from two distinct subspecies and *C. lepida*, have demonstrated an identical chromosome number of $2n = 42$ and $20 + Xy_p$ meioformula, which is concordant with their inclusion in the same subgenus, as recently claimed by Bourdonné and Doguet (1991) on several common characters and contrary to the view of Bechyné (1950), who placed *C. lepida* within the subgenus *Hypericia* on the basis of its regular pairwise elytral punctures. However both species can be chromosomally distinguished by the number of acrocentric autosome pairs, six in *C. lepida* and none in *C. fuliginosa*. These two species of *Allochrysolina* are Asteraceae feeders (Jolivet and Petitpierre 1976; Bourdonné and Doguet 1991) as well as it is *C. (Heliostola) montana* (Jolivet et al. 1986), a Siberian species with a similar $19 + Xy_p$ meioformula. Since no other species of *Heliostola* have been cytogenetically analyzed the intrasubgeneric comparisons are precluded, but in another Asteraceae feeding subgenus the four examined species of *Chrysolina (Chalcoidea)*, *C. analis*, *C. carnifex*, *C. curvilinea (= C. janbechynei)* and *C. marginata* also have $19 + Xy_p$ (Petitpierre 1981; Petitpierre and Segarra 1985; Petitpierre et al. 1988), which may hint at some relationship between the two subgenera.

C. (Craspeda) limbata, a Eurosiberian species feeding on Plantaginaceae, is characterized by $2n = 42$ chromosomes and a $20 + Xy_p$ meioformula. Other species feeding also on Plantaginaceae such as *C. (Colaphodes) haemoptera* and *C. (Ovosoma) vernalis*

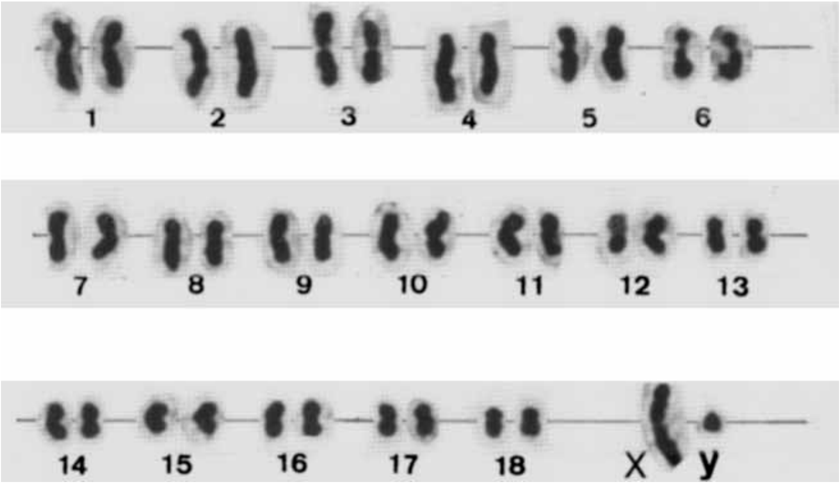

Fig. 18. Karyogram of *Chrysolina (Hypericia) hyperici* at × 2000.

pyrenaica display a similar number $2n = 40$ and $19 + Xy_p$ meioformula (PETITPIERRE 1981; PETITPIERRE and SEGARRA 1985; PETITPIERRE et al. 1988). Furthermore, BOURDONNÉ and DOGUET (1991) joined in their group 3 *C. limbata* and *C. (Palaeosticta) diluta*, another species feeding on Plantago with $2n = 36$ and $17 + Xy_p$ meioformula (PETITPIERRE 1981). But according to the karyology *C. limbata* seems to be much closer to *C. haemoptera* and *C. vernalis pyrenaica* than to *C. diluta*. Nevertheless, we should come to a more convincing conclusion only by building up their molecular phylogenies.

C. (Hypericia) hyperici and *C. (Hypericia) quadrigemina* have $2n = 38$ chromosomes, the same number found in *C. geminata* (PETITPIERRE and SEGARRA 1985; PETITPIERRE et al. 1988), a species belonging also to the subgenus *Hypericia* and feeding on Clusiaceae (JOLIVET and PETITPIERRE 1976; BOURDONNÉ and DOGUET 1991). Their identity of chromosome number and probably of meioformula, a number which has not been recorded to date in any other species of *Chrysolina*, provides a substantial support to their close interrelationship. Besides that these species of *Hypericia* are clearly differentiated by their chromosome number with regard to *C. (Allochrysolina) lepida* ($2n = 42$) with which the latter was erroneously associated by BECHYNÉ (1950) as mentioned before.

Finally, the karyotype of *C. (Threnosoma) helopioides* comprising $2n = 47$ chromosomes and a $23 + X$ meioformula in males, is coincident with that reported in the Pyrenean endemic *C. (Threnosoma) timarchoides* (PETITPIERRE 1981), and constitutes the highest value so far obtained in *Chrysolina*. Despite of its high chromosome number, *C. helopioides* does not show acrocentric chromosomes, so the presumed centric fissions responsible for the increase of diploid number were very likely followed by pericentric inversions or chromatin accretions to reconstitute the metacentric shape of their chromosomes, as the most common structural rule found in coleopterans (VIRKKI 1984). The matching cytogenetic results obtained from *C. helopioides* and *C. timarchoides* seems to reinforce the phylogenetic congruence of the subgenus *Threnosoma*.

Once again, as was claimed before (PETITPIERRE 1981; PETITPIERRE and SEGARRA 1985), the karyology of *Chrysolina* is in good agreement with the plant-choices and with the current systematics. The species belonging to a same subgenus of *Chrysolina* do not differ, apart from those of *Stichoptera*, in their diploid number and sex-chromosome system. Although the species of the several subgenera of *Chrysolina* feeding only on Lamiaceae share always $2n = 24$ (Xy_p), this karyotypic character also occurs in most species of *Oreina* including three presently studied, which do not live on Lamiaceae but on Apiaceae or Asteraceae (BOURDONNÉ and DOGUET 1991). Does this karyological resemblance of *Oreina* and the Lamiaceae feeding *Chrysolina* imply a close common evolutionary origin?. It would be doubtful because this number and formula is the modal one for all the subfamily Chrysomelinae and it is found in many different genera of distinct subtribes such as Chrysolinina, Gonioctenina and Paropsina (PETITPIERRE and SEGARRA 1985; PETITPIERRE et al. 1988). The molecular phylogenies based on the sequences of mitochondrial gene fragments of cytochrome oxidase I (COI) and 16S ribosomal DNA allows discrimination by using a maximum likelihood tree among at least three Lamiaceae feeding clades in *Chrysolina*, and neither of the two studied species of *Oreina* appeared closely related to any of these previous clades of *Chrysolina* (GARIN et al. 1999). Consequently they should be considered paraphyletic despite of their rough karyological resemblance. Furthermore, since these two species of *Oreina* were not related to each other in a single clade, the separation of *Oreina* and *Chrysolina* in independent genera could not be substantiated contrary to that stated by DOBLER et al. (1996) based on allozyme analyses, plant-choices and defensive substances of twelve species of *Oreina* but only two of *Chrysolina*. Nevertheless, until a much larger and sufficiently representative joint screening of these two taxa *Chrysolina* and *Oreina* were available for a molecular phylogenetic analysis, caution should be exercised before accepting either of the two alternative taxonomic decisions

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