

## Karyotypes of nine species of Cicindelini and cytotaxonomic notes on Cicindelinae (Coleoptera, Carabidae)

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### Abstract

The male meioformula of seven species of Cicindelini from the Iberian Peninsula and one species from Canada is 9+XXXY. In addition, female data of *Cylindera paludosa* corroborate previous reports of males. The Palearctic species show a generalized karyotype which presents specific modifications, but it is not possible to establish if it is also present in species of other faunas.

Present data indicate that multiple sex chromosomes is an ancestral condition for the subfamily Cicindelinae. It is postulated that the meioformula of the tribe Cicindelini is 9 or 10 plus XXY and that trends in karyotypic evolution are partially related to the geographic distribution of lineages. Numerical deviations observed in the tribe can be explained by changes occurring independently in autosomes and heterosomes, so that autosome-heterosome fusions do not seem to be a generalized event. A number of criteria may be developed for determining the polarity of change of karyotypic characters, thus making cytotaxonomic studies a valuable tool for understanding the systematics of Cicindelini.

### Introduction

Recent data have increased the number of cicindelid beetles cytologically studied to 46 species (Serrano *et al.*, 1986; Serrano & Collares-Pereira, 1989; Sharma, 1988; Yadav *et al.*, 1985, 1987; Yadav & Burra, 1988; Yadav *et al.*, 1989). These data indicate that the number of X chromosomes varies within the major biogeographical regions. The XXXY type predominates in the Palearctic region and XXY type in the Oriental region. In the Nearctic region the number of species studied is not enough to support sound conclusions (four species have XXY, one species has XXXY). The aim of this paper is to complete the cytotaxonomy of Iberian cicindelids and to test previous conclusions (Serrano, 1986; Serrano *et al.*, 1986) about the karyotypic evolution of the tribe Cicindelini and the subfamily Cicindelinae.

### Material and methods

Adult beetles were collected in Spain, except for *Cicindela oregona* which comes from Canada (localities are listed in Table 1). Karyological analyses were carried out on gonads dissected from anaesthetized beetles (ethyl-acetate), treated hypotonically in either deionized water (10 min) or Ohnuki's modified solution (20–40 min; Weber, 1968) plus colchicine 0.01 to 0.05%, fixed with ethanol-acetic acid (3:1), stained with lactopropionic orcein, and squashed.

### Results

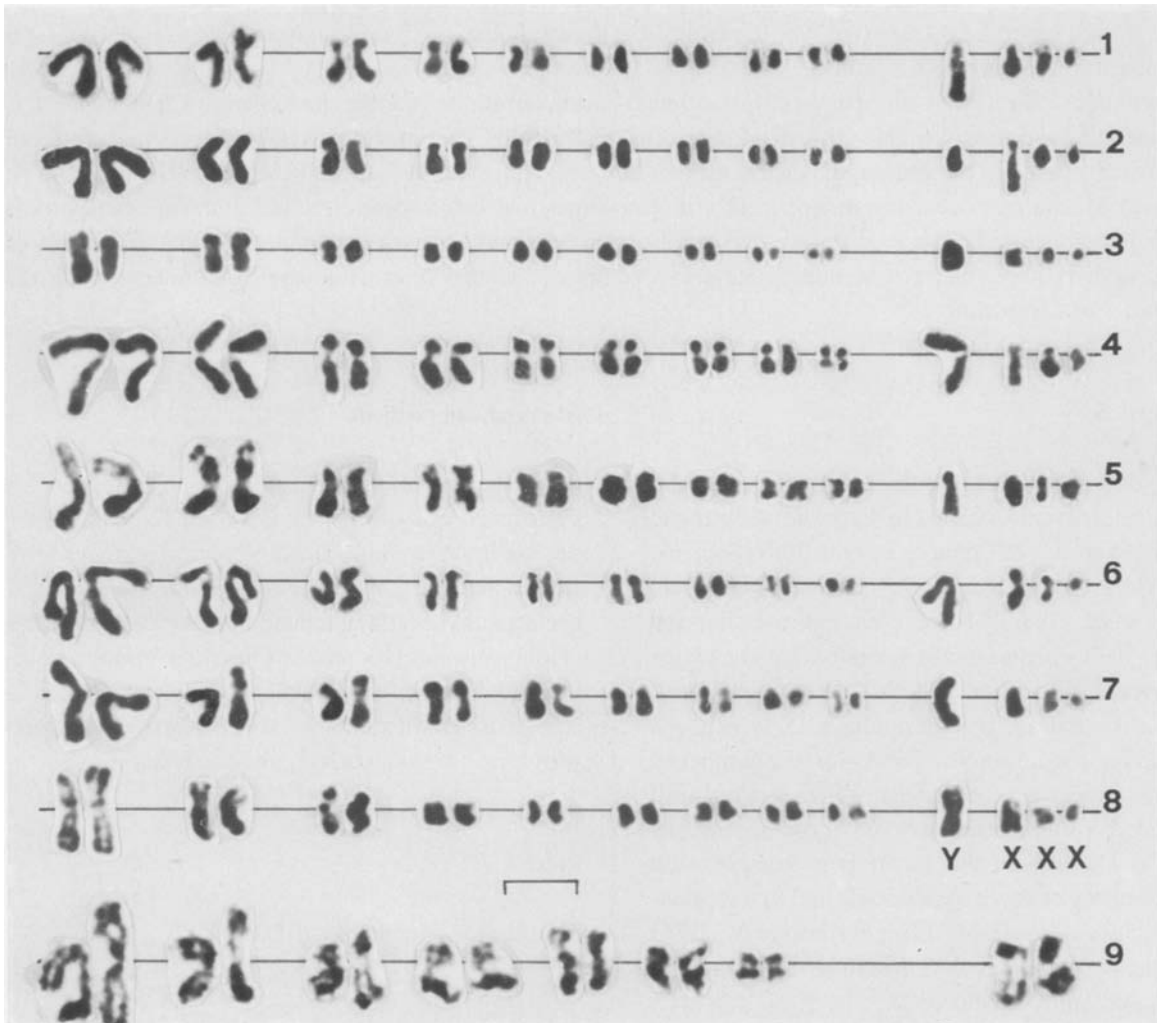
Results are summarized in Table 1.

#### *Mitotic chromosomes*

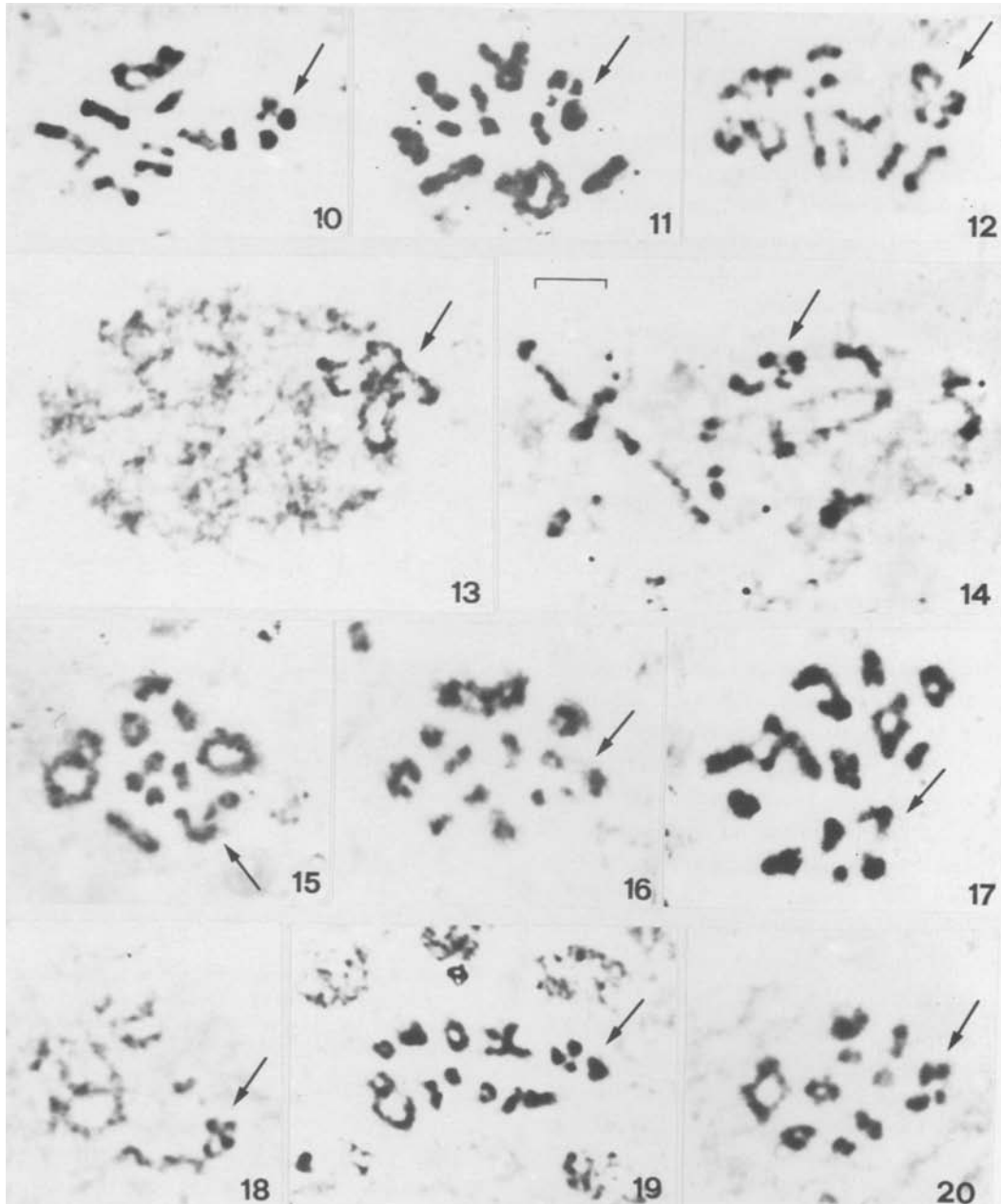
The chromosome number is the same for all species

Table 1. Chromosome number of nine species of Cicindelini.

Species	2n	meioformula	Localities and individuals studied
<i>Cicindela hybrida</i> L. 1758	22	9+XXX $\bar{Y}$	Ordesa, Huesca (1)
<i>Cicindela oregona</i> Lec. 1856	22	9+XXX $\bar{Y}$	Vancouver, BC (2) Nicola River, BC (4)
<i>Spiralia maura</i> (L. 1758)	22	9+XXX $\bar{Y}$	Albatera, Alicante (2) Campos del Rio, Murcia (1)
<i>Taenidia deserticoloides</i> (Codina 1931)	22	9+XXX $\bar{Y}$	Albatera, Alicante (3)
<i>Taenidia circumdata</i> (Latr. et Dej. 1822)	22	9+XXX $\bar{Y}$	Pinilla, Albacete (5)
<i>Lophyridia littoralis</i> (F. 1787)	22	9+XXX $\bar{Y}$	Laguna del Salobrelejo, Albacete (3)
<i>Myriochile melancholica</i> (F. 1798)	22	9+XXX $\bar{Y}$	El Algar, Murcia (6)
<i>Lophyra flexuosa</i> (F. 1787)	22	9+XXX $\bar{Y}$	Sierra de Cazorla, Jaén (1) Laguna Blanca, Ciudad Real (2)
<i>Cylindera paludosa</i> (Duf. 1820)	16(♀)	-	Albatera, Alicante (1)



Figs. 1-9. Male (1-8) ( $2n=22$ ) and female (9) karyograms of: (1) *Cicindela hybrida*; - (2) *C. oregona*; - (3) *Spiralia maura*; - (4) *Taenidia deserticoloides*; - (5) *T. circumdata*; - (6) *Lophyridia littoralis*; - (7) *Myriochile melancholica*; - (8) *Lophyra flexuosa*; - (9) *Cylindera paludosa*. The bar equals 5  $\mu\text{m}$ .



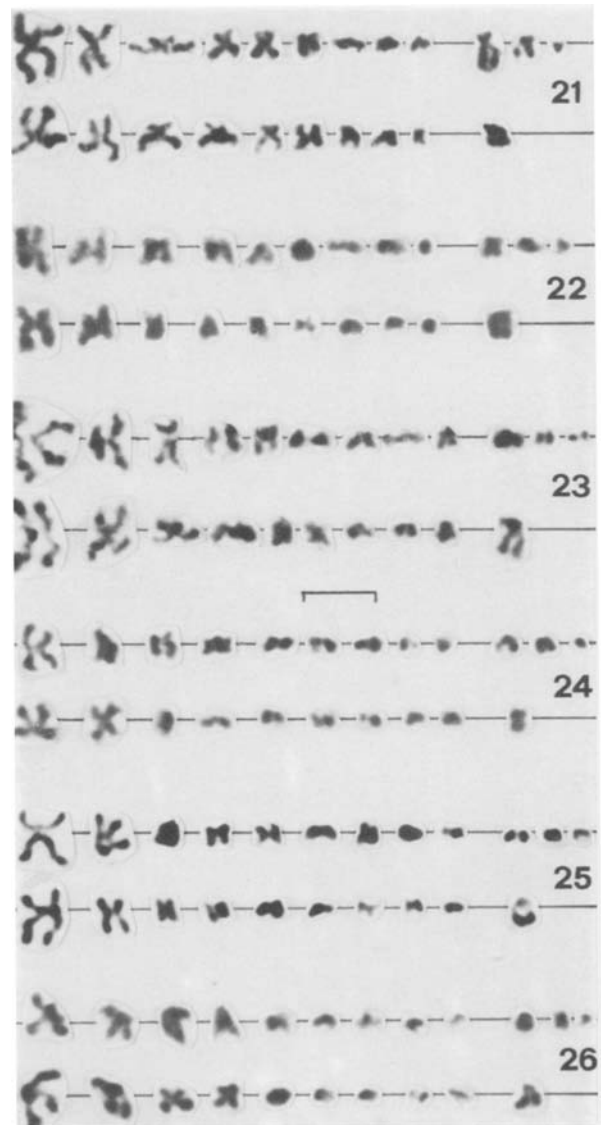
Figs. 10-20. Meiotic stages: (10) *Cicindela hybrida*, metaphase I; - (11) *C. oregona*, diakinesis; - (12) *Spiralia maura*, diakinesis; - (13-15) *Taenidia deserticoloides*; - (13) diffuse diplotene; - (14) diplotene; - (15) diakinesis; - (16) *T. circumdata*, metaphase I; - (17) *Myrioichile melancholica*, metaphase I; - (18-19) *Lophyridia littoralis*; - (18) pachytene; - (19) metaphase I; - (20) *Lophyra flexuosa*, diakinesis. Arrows show sex chromosomes. The bar equals 5  $\mu$ m.

studied,  $2n(\delta)=22$  (Figs. 1-8), except for the female of *Cylindera paludosa* which shows  $2n(\text{♀})=16$  (Fig. 9). Differences between species are found at the morphological level in spite of the existence of many common features for all of them. The two largest pairs are metacentric and clearly differentiated from the following pair. Their size varies between  $8.5 \mu\text{m}$  (*Cylindera paludosa*, *Taenidia deserticoloides*) and  $3.5 \mu\text{m}$  (*Spiralia maura*) for the largest pair, and between  $6 \mu\text{m}$  (*T. deserticoloides*) and  $2.7 \mu\text{m}$  (*S. maura*) for the second pair. The latter in *Taenidia circumdata* shows a marked secondary constriction with satellites; other species, e.g., *Myriochile melancholica* also show signs of these constrictions. The third pair tends to be submetacentric and forms a group of its own as it is usually well differentiated in size from the fourth pair. It shows a secondary constriction in *Lophyra flexuosa*. Pairs 4 to 9 (4-7 in *C. paludosa*) gradually decrease in size and the metacentric morphology predominates. Pair 5 of *C. paludosa* show a marked secondary constriction near the centromeric one; this species also shows marked differences in size between the last pairs.

The multiple heterosomes were identified by combining mitotic and meiotic data, such as size and shape in metaphase I (Figs. 10-20) and metaphase II cells (Figs. 21-26). Nine species have 3 Xs and one Y chromosome whereas the female of *Cylindera paludosa* show 2 Xs which correspond to the single X previously described in males (Serrano *et al.*, 1986). The shape of the Y chromosome varies between species: it is subtelocentric in *Cicindela hybrida*, submetacentric in *Taenidia circumdata* and *Lophyra flexuosa* and metacentric in the others. Its size is usually about that of pairs 2-3, and it is larger than the Xs except in *Cicindela oregona* (Fig. 2), in which the  $X_1$  chromosome is very large as seen in metaphase II plates (Fig. 21). The three Xs show clear differences in size so that the  $X_3$  chromosome is very small and is frequently unnoticed. The two X chromosomes of *Cylindera paludosa* are metacentric (Fig. 9).

#### Meiotic chromosomes

Autosomal bivalents show details of an orthodox meiosis with regard to pairing, changes in pycnosis



Figs. 21-26. Haploid karyograms from metaphase II cells. Above  $n=12$  (3X), below  $n=10$  (Y): (21) *Cicindela oregona*; - (22) *Spiralia maura*; - (23) *Taenidia deserticoloides*; - (24) *Lophyridia littoralis*; - (25) *Myriochile melancholica*; - (26) *Lophyra flexuosa*. The bar equals  $5 \mu\text{m}$ .

during prophase I, chiasma formation, etc. The heterosomes form a typical heteropycnotic vesicle during prophase up to the diplotene stage that follows a diffuse postpachytene stage in which the nuclear volume increases greatly (Fig. 13). At the onset of diplotene the sex chromatin is resolved into individual chromosomes, which are in contact by telomeric connections (Fig. 14), i.e., there are no true chiasmata between them. Finally, the autosomal bivalents ap-

pear showing chiasmata. The male haploid chromosome number is  $n=13$  (3X, Y), meioformula = 9+XXXXY. The number of chiasmata is usually two for the first two pairs which are distal or interstitial. In four species (eg. *Taenidia deserticoloides*, Fig. 15) the largest pair shows three chiasmata, a figure rarely seen in carabid beetles. The following pairs have one distal (rod) or interstitial chiasma (cross) and more rarely form rings. Co-orientation of bivalents and the multivalent is regular (Figs. 11, 12, 20) and normal segregation follows. Metaphase II cells are of two types, with 9+XXX and with 9+Y (Figs. 21-26).

## Discussion

### *Cytogenetic aspects*

The analysis of mitotic chromosomes of the species studied reveals that there is a structural and numerical pattern which is repeated with some specific variations. Thus pairs 1 and 2 form a group of large metacentric chromosomes, pair 3 is submetacentric and frequently distinguished from both pair 2 and 4, pairs 4 to 9 are mediocentric and gradually decrease in size; the Y chromosome is a large chromosome about the size of pairs 2-3; the  $X_1$  is of intermediate size whereas the two smallest Xs are about the size of the smallest autosomes. This generalized karyotype is also found in species of the Palearctic region in which detailed karyotypes have been published (Giers, 1977; Serrano, 1980, Serrano *et al.*, 1986; Serrano & Collares-Pereira, 1989).

Data on species of the Oriental region are unclear as the pattern is recognized in some species but not in others (eg. *Pseudochaetodera vigintiguttata* and *Calochroa sexpunctata*, respectively; Yadav & Karamjeet, 1981). Moreover, corroboration of the pattern is controversial because it depends on the arrangements adopted for ordering the karyotype: the two large chromosomes of *Myriochile undulata* and *M. fastidiosa* might be the typical second pair of Palearctic species (Yadav *et al.*, 1985). However it is noteworthy that the Palearctic species that shows the karyotype more deviating from the generalized karyotype is *Cephalota hispanica*, which has in common with Oriental species the meioformula 9+XXY. A submetacentric pair 2, a

large pair 3 and the small size of the heterosomes, including the Y (Serrano & Collares-Pereira, 1989) are indicative of the singularity of this species.

The occurrence of the pattern in Nearctic species is also undetermined because the data of Smith & Edgar (1954) are not detailed enough. *Cicindela oregona* shows an autosomal morphology fitting this pattern, but the heterosomes are quite different (Fig. 2).

A final aspect of mitotic chromosomes is the marked difference between the chromosome size reported here for *Spiralia maura* and the data of Serrano & Collares-Pereira (1989); e.g., the size of the first pair is 3  $\mu\text{m}$  vs. 9.79  $\mu\text{m}$ . Probably these differences are due either to the age of individuals, as suggested by Rozek & Warchalowska-Sliwa (1987), or to factors such as fixation or the degree of advance of metaphase. Thus it is convenient to compare relative instead of absolute magnitudes.

With regard to the meiotic chromosomes it seems that the figures of bivalents with three chiasmata (Figs. 10, 12, 15, 16) constitute a genuine exception to the statement of Smith & Virkki (1978) concerning the pattern of chiasma formation in the order Coleoptera: 'One chiasma per arm as a maximum is a firm rule as yet unbroken...'. These authors argued that claims of multichiasmate bivalents are due to relational coiling. Exceptions to this rule are expected when considering the large number of species of Coleoptera and the diversity of their cytogenetic mechanisms.

During the study of *Cicindela oregona* the first observations of the sex multivalent suggested the occurrence of only two Xs and the Y chromosome, in agreement with previous reports of other Nearctic species (Smith & Edgar, 1954 and references therein). Only careful observations of different meiotic and mitotic stages led us to conclude that there is a third and minute X which passes frequently unnoticed. The case poses a note of caution about the reported numbers of Xs, especially when only metaphase I cells have been observed.

### *Cytotaxonomic aspects*

The number of species of the subfamily Cicindelinae studied up to date with reliable results is 51 (Table 2). The existence of multiple sex chromosomes in species

of the supertribe Collyritae (Sharma, 1988) favours the hypothesis about the ancestral condition of this type of multiple heterosomes within the subfamily, which had been put in doubt after the finding of *Megacephala euphratica* (tribe Megacephalini) with  $2n=31$  (X) (Serrano *et al.*, 1986).

In the tribe Cicindelini the number of heterosomes varies from one (XO) to five (4Xs, Y) and that of autosomes from 7 to 11 pairs (Table 2). Although a phylogenetic reconstruction of Cicindelini is not yet worked out, it seems likely that it is a Gondwanian group on the basis of its present distribution (the recapitulation of lineages with their distribution of Rivalier, 1971 clearly supports this conclusion). Therefore the search for the plesiomorphic (primitive) karyotypic state of the tribe must be centered in the Oriental fauna instead of the Palearctic or Nearctic ones. There are no data on Ethiopic, Australian or Neotropical faunas.

With these ideas in mind it is assumed that the primitive meioformula of Cicindelini is 9 or 10 + XXY. A formula with nine pairs of autosomes is preferred because it is found in the Palearctic and Nearctic fauna in addition to the Oriental one.

Numerical changes responsible for the diversity of chromosome numbers of the tribe are not well known. However, from the data of Table 2 it is obvious that the number of autosomes may change *without* changes in the number of heterosomes (e.g. *Cylindera*, *Myriochile*, *Cosmodela*), and that the heterosomes may vary without altering the number of autosomes (*Cicindela maroccana*). Thus on parsimonious grounds there is no need of invoking fusions between autosomes and heterosomes (Smith & Edgar, 1954; Yaday *et al.*, 1985), or polyploidy events (Serrano & Collares-Pereira, 1989) for explaining the numerical diversity of the tribe, at least as common mechanisms.

Major trends on karyotypic evolution fitting the above mentioned assumption are: (1) In the Oriental fauna the number of heterosomes is very stable, the autosomes increase in number in many instances (to 10 and 11); alternatively, if the primitive meioformula is 10+XXY, both slight decreases (to 9 pairs of autosomes) and increases (to 11 pairs of autosomes) have occurred. (2) In the Palearctic fauna changes predominantly affect the heterosomes, as most species have 3 Xs and moreover there is one species with 4 Xs.

Table 2. Karyotypic data of the subfamily Cicindelinae, tribes Cicindelini, Megacephalini and Collyrini. Species of Cicindelini are listed according to the systematic criteria of Rivalier (1950, 1954, 1961, 1963), and Acciavatti & Pearson (1989).

Species	Meioformula	Biogeographic region	References
<b>CICINDELINI</b>			
<i>Calochroa sexpunctata</i> F.	10+XXY	Cosmop.	4, 9, 12
<i>Cicindela</i> ( <i>Cicindela</i> ) <i>campestris</i> L.	9+XXXXY	Pal.	3, 6
<i>C. (Cicindela) hybrida</i> L.	9+XXXXY	Pal.	2, 3, 15
<i>C. (Cicindela) maroccana</i> F.	9+XXXXXY	Pal.	6
<i>C. (Cicindela) silvicola</i> Latr.	9+XXXXY	Pal.	3
<i>C. (Cicindela) repanda</i> Dej.	9+XXY	Near.	9
<i>C. (Cicindela) sexguttata</i> F.	9+XXY	Near.	9
<i>C. (Cicindela) oregona</i> Lec.	9+XXXXY	Near.	15
<i>C. (Pachydela) scutellaris</i> Say	9+XXY	Near.	9
<i>C. (Tribonia) tranquebarica</i> Herb.	9+XXY	Near.	9
<i>Lophyridia littoralis</i> F.	9+XXXXY	Pal.	2, 3, 15
<i>L. chloris</i> Hope	10+XXY	Or.	12
<i>L. funerea</i> Macl.	10+XXY	Or.	12
<i>L. sumatrensis</i> Herb.*	10+XXY	Or.	14
<i>L. angulata</i> F.	9+XXY	Or.	14
<i>Cosmodela duponti</i> Dej.	10+XXY	Or.	12
<i>C. intermedia</i> Chaud.	9+XXY	Or.	12, 16
<i>C. virgula</i> Fleut.	10+XXY	Or.	12
<i>Lophyra (Lophyra) flexuosa</i> F.	9+XXXXY	Pal.	15
<i>L. (Lophyra) striatifrons</i> Chaud.	10+XXY	Or.	12
<i>L. (Lophyra) catena</i> F.	10+XXY	Or.	1
<i>L. (Spilodia) multiguttata</i> Dej.	10+XXY	Or.	12
<i>L. (Spilodia) striolata</i> Ill.	10+XXY	Or.	12
<i>L. (Spilodia) vittigera</i> Dej.	10+XXY	Or.	14
<i>Chaetodera albina</i> Wied.	10+XXY	Or.	12, 16
<i>C. vigintiguttata</i> Herb.	10+XXY	Or.	9
<i>Jansenia indica</i> Fleut.	9+XXY	Or.	12
<i>J. chloropleura</i> Chaud.	10+XXY	Or.	14
<i>Cephalota hispanica</i> Gory	9+XXY	Pal.	5
<i>Taenidia deserticoloides</i> Codina	9+XXXXY	Pal.	15
<i>T. circumdata</i> Lat. et Dej.	9+XXXXY	Pal.	15
<i>T. litorea</i> Forsk.	9+XXXXY	Pal.	7
<i>Spiralia maura</i> L.	9+XXXXY	Pal.	5, 15
<i>Cylindera (Cylindera)</i> <i>germanica</i> L.	8+XY	Pal.	2
<i>C. (Cylindera) paludosa</i> Duf.	7+XO/XX	Pal.	7, 15
<i>C. (Cylindera) dromicoides</i> Chaud.	9+XXY	Or.	14
<i>C. (Eugrapha) agnata</i> Fleut.	10+XXY	Or.	13
	9+XXY	Or.	16
<i>C. (Eugrapha) cognata</i> Wied.	9+XXY	Or.	9, 13
<i>C. (Eugrapha) minuta</i> Oliv.	10+XXY	Or.	12, 13
<i>C. (Eugrapha) bigemina</i> Klug.	10+XXY	Or.	12, 13
<i>C. (Ifasina) holosericea**</i> F.	9+XXY	Or.	13
<i>C. (Ifasina) spinolai</i> Gest.	9+XXY	Or.	12, 13
<i>C. (Ifasina) triguttata</i> Herb.***	10+XXY	Or.	12

Table 2. Continued.

Species	Meioformula	Biogeographic region	References
<i>C. (Ifasina) viridilabris</i> Chaud.	9+XXY	Or.	12, 13
<i>Myriochile (Myriochile) undulata</i> Dej.	11+XXY		11
	9+XXY	Or.	14
<i>M. (Myriochile) melancholica</i> F.	9+XXXXY	Pal.	15
<i>M. (Monelica) fastidiosa</i> Dej.	10+XXY	Or.	11
MEGACEPHALINI			
<i>Megacephala euphratica</i> Dej.	15+X	Pal.	7
COLLYRINI			
<i>Neocollyris crassicornis</i> Dej.	12+XXY	Or.	8
<i>N. fuscitarsis</i> Schmidt-Goeb.	12+XXY	Or.	8
<i>N. redtenbacheri</i> Horn	12+XXY	Or.	8

References: (1) Dasgupta, 1967; (2) Giers, 1977; (3) Guénin, 1952; (4) Joneja, 1960; (5) Serrano & Collares-Pereira, 1989; (6) Serrano, 1980; (7) Serrano *et al.*, 1986; (8) Sharma, 1988; (9) Smith & Edgar, 1954; (10) Yadav & Karamjeet, 1981; (11) Yadav *et al.*, 1985; (12) Yadav *et al.*, 1987; (13) Yadav & Burra, 1988; (14) Yadav *et al.*, 1989; (15) present report; (16) Mittal *et al.*, 1989.

\* *L. angulata* F. according to Acciavatti & Pearson (1989).

\*\* Probably *C. cyclobregma* A.& P. according to Acciavatti & Pearson (1989)

\*\*\* *C. viduata* according to Acciavatti & Pearson (1989)

(3) The trend for the Nearctic fauna is unknown because it is not clear whether there are true 9+XXY karyotypes or not.

The model of karyotypic evolution depicted above can explain partially the predominance of a given karyotype in each major region (Serrano, 1986). However it leaves unexplained the findings of species of *Lophyra*, *Lophyridia* and *Myriochile* with 9+XXY in the Oriental region, and with 9+XXXXY in the Palearctic region (Table 2). Assuming that the occurrence of two or three Xs has no direct adaptive value with regard to the environmental conditions of each of these regions, these findings might be caused by the conjunction of at least two kinds of factors: misinterpretation of karyotypic data, and the actual existence of more than one phyletic line in these genera so far considered to be monophyletic.

A particular trend of karyotypic evolution is that of *Cylindera*. Whereas Oriental taxa show an either 9 or 10 plus XXY meioformula (Table 2), the two Palearctic species studied show a lower number of autosomes

and heterosomes. Assuming that *Cylindera* has an Oriental origin on the basis of the number and geographic distribution of lineages (data from Rivalier, 1961), the Palearctic species (*Cylindera germanica*, 8+XY, Western Palearctic; *C. paludosa*, 7+X, Southwestern Europe) fit a model of increasing changes as distance from the Oriental region and primitive taxa increases.

Another case of particular evolution is that of *Cephalota hispanica*. Its karyotypic affinities to Oriental taxa mentioned above suggest that *Cephalota* (*sensu stricto*) is not closely related to *Taenidia*, as had been stated by Rivalier (1950). Further studies on the other two species akin to *C. hispanica* might help in constructing more accurate relationships.

A global evaluation of present data indicates that the tribe Cicindelini is a taxon of moderate karyotypic dynamism, so that the existence of generalized karyotypes does not exclude the identification of species by karyotypic characters. Therefore the cytotaxonomy of Cicindelinae is likely a fruitful field for research.

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