

CHROMOSOMES OF SOME PUERTO RICAN  
DISONYCHINA AND OEDIONYCHINA  
(COLEOPTERA: CHRYSOMELIDAE: ALTICINAE:  
OEDIONYCHINI):  
EVOLUTIONARY IMPLICATIONS

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INTRODUCTION

Bechyné and Springlová de Bechyné (1966) divided the tribe Oedionychini into the subtribes Disonychina and Oedionychina based, mainly, on thoracic and hind tarsal structures. This classification is supported also on cytological grounds (Virkki 1988b, 1989b). The Oedionychini, a lineage that shows some of the most interesting chromosomal relationships within the Coleoptera (Smith and Virkki 1978, Virkki 1985, 1988a, 1989a), is cytologically characterized by asynaptic sex chromosomes in male meiosis, increased spermatocyte size, and, in correlation with it, fewer spermatozoa per bundle (spz/b) (Virkki 1988a). The inferred polarity of the last character points to Oedionychina (spz/b=16) as relatively derived (Disonychina, spz/b=32). The Oedionychini is considered the most derived tribe of the Alticinae (J. Bechyné 1968 *pers. comm.*). A correlation of characters on the internal reproductive system of the Chrysomelidae has recently been discussed by Suzuki (1989).

Meiograms and chromosomal illustrations of four Puerto Rican Disonychina and three Oedionychina are presented. Phylogenetic implications of these finds are discussed.

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*Manuscript received 8 March 1991.*

## METHODS

Species, host plants (author and family), sample size, and collecting data are as in Table 1. Nomenclature and protocols follow Virkki, *et al.* (1992).

## RESULTS

**Disonychina.** This Neotropical subtribe (Bechyné and Springlová de Bechyné 1966) comprises seven genera of which, only two, *Disonycha* Blake and *Phenrica* Bechyné, have been partially studied cytologically (Virkki 1989b). Autosomes (13–30 pairs) have been found to combine with a sex chromosome system consisting of one Xy bivalent and one or two additional, univalent, X chromosome(s) ( $Xy+nX$ ,  $n=1$  or  $2$ ).

*Disonycha spilotrachelata* Blake

This is perhaps the most polyphagous Puerto Rican *Disonycha* (Table 1). A dense and persisting population feeds on *Turnera ulmifolia* (Turneraceae) on the south coast of Laguna Tortuguero. This species has been reported for Cuba, Haiti, and Puerto Rico (Wolcott 1948; Blake 1933, 1955; Wilcox 1983).

Meiogram (Fig. 1A) and MI (Fig. 2B):  $13+X_1y+X_2$ . The segregation results in  $15(2X)$  and in  $14(y)$  chromosomes at M II plates (Figs. 3E, F, respectively).

Karyogram (Virkki 1988b):  $2n=30(4X)$  on females,  $2n=29(2X,y)$  on males. All chromosomes are metacentric. Nucleolar organizing regions (NOR's) are located on a homologous pair of medium-sized autosomes.

*Disonycha comma* White

This species also lives on Hispaniola, and perhaps has invaded Puerto Rico recently. Possibly, *D. comma* is synonymous with *D. peruana* Jacoby that inhabits mainland areas of tropical America. The first Puerto Rican specimens were collected in 1988 and now it is becoming common in the south coast of Laguna Tortuguero where it thrives on *Croton lobatus* (Euphorbiaceae), a common weed. In captivity, it has accepted only *Passiflora murucuja* (Passifloraceae) among the various *Passiflora* spp. offered (J. Escudero 1989 *pers. comm.*, see also Jolivet 1991).

Table 1. Species, plant association, and collection data for specimens examined.

Taxon	Plant Association	# Examined for each locality	Collection Data
<b>Disonychina</b>			
<i>Disonycha spilotrachel</i> Blake	<i>Ipomoea imperati</i> (Vahl) Griseb. (Convolvulaceae)	20	Isabela, Playa de Jobos, 1 Feb. 86
	<i>Turnera ulmifolia</i> L. (Turneraceae)	>50	Vega Baja, Laguna Tortuguero, Jan. 87–June 88
	<i>Passiflora foetida</i> L. (Passifloraceae)	10	Guánica, Laguna de Guánica, 8 Oct. 87
<i>Disonycha comma</i> White	<i>Croton lobatus</i> L. (Euphorbiaceae)	10	Vega Baja, Laguna Tortuguero, Aug.–Oct. 89
<i>Disonycha leptolineata</i> Blatchley	Unidentified low herbs	1	Ponce, Playa de Ponce, 2 Mar. 87
<i>Disonycha eximia</i> Harold	<i>Amaranthus</i> sp. (Amaranthaceae)	20	Dorado, rd. 165, Nov.–Dec. 84
<b>Oedionychina</b>			
<i>Omophoita cyanipennis</i> F.	<i>Clerodendrum aculeatum</i> (L.) Schlecht (Verbenaceae)	>50; >50	Salinas, Playa de Salinas, 1962–85; Carolina, Vacía Talega, 1962–85
	<i>Phyla nodiflora</i> (L.) Greene (Verbenaceae)	>50	Salinas, Playa de Salinas, 1962–85
<i>Omophoita albicollis</i> F.	<i>Heliotropium indicum</i> L. (Boraginaceae)	>20	Salinas, Playa de Salinas, Jul.–Dec. 69
	<i>Stachytarpheta jamaicensis</i> (L.) Vahl (Verbenaceae)	>10; >10	Mona Is., airstrip, 8 Mar. 84; Vega Baja, Tortuguero airport, 5 July 87
<i>Alagoasa bicolor</i> (L.)	<i>Clerodendrum aculeatum</i> (L.) Schlecht (Verbenaceae)	>100	Salinas, Playa de Salinas, 1962–85
	<i>Aegiphila martinicensis</i> Jacq. (Verbenaceae)	>50	Vega Alta, rd. 675, 1973–85

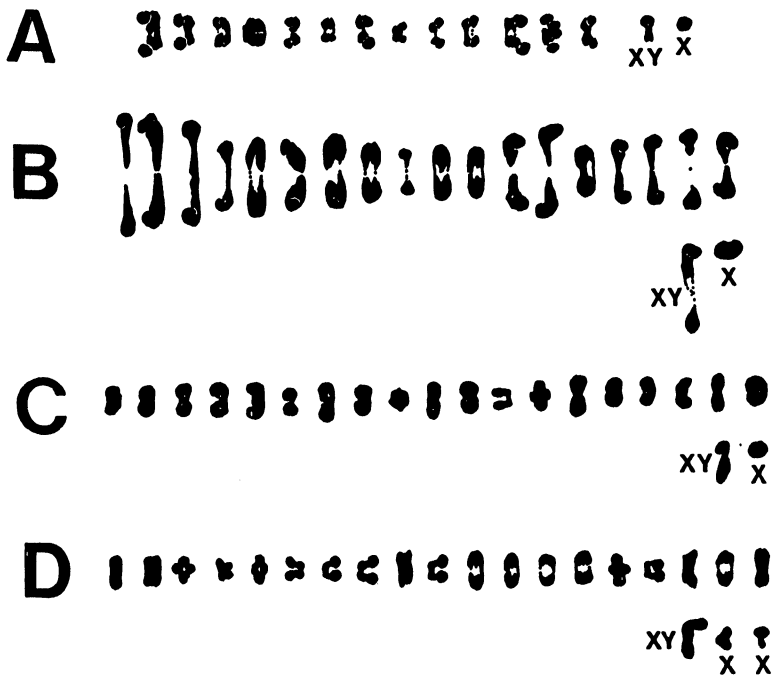


Fig. 1. Meiochromosomes of some Puerto Rican Disonychina. A. *Disonycha spilotrachela*,  $13+X_1y+X_2$ . B. *D. comma*,  $18+X_1y+X_2$ . C. *D. leptolineata*,  $19+X_1y+X_2$ . D. *D. eximia*,  $19+X_1y+X_2+X_3$ .

Meiochromosome (Fig. 1B) and M I (Fig. 2C):  $18+X_1y+X_2$ . All autosomes are metacentric and most are capable of forming ring bivalents, a sign of more than one crossover on a chromosome.

Karyogram (Figs. 4, 5):  $2n=40(4X)$  on females,  $2n=39(2X,y)$  on males. All autosomes and, at least,  $X_1$  are metacentric.

#### *Disonycha leptolineata* Blatchley

Formerly unknown from Puerto Rico, this species became quite abundant in the Ponce region some years ago (J. Micheli 1990 *pers. comm.*) but it is seldom seen nowadays. This population growth pattern suggests a recent invasion, followed by a rapid increase, and an effective checking by natural enemies (van den

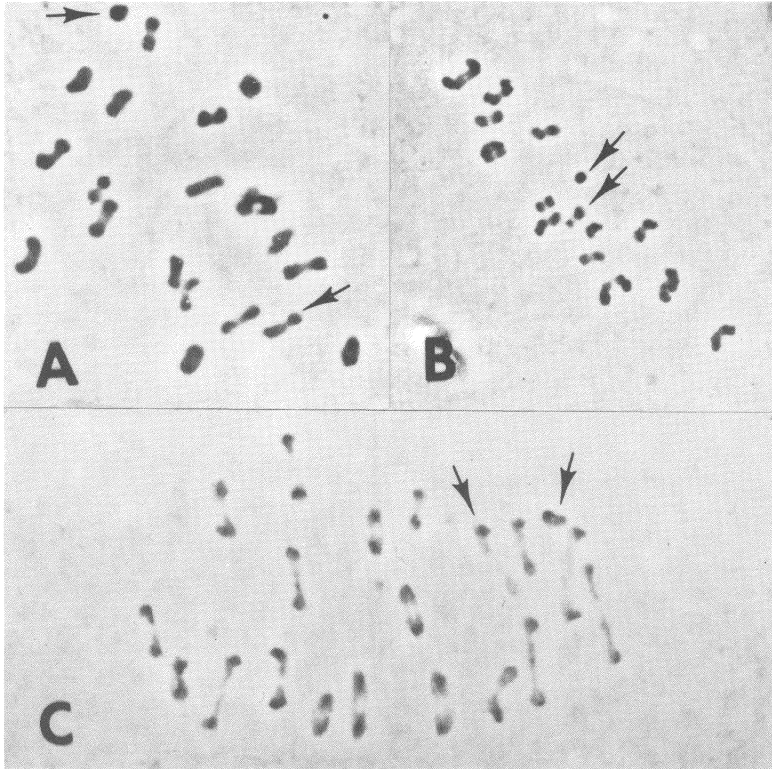


Fig. 2. First meiotic metaphase in three *Disonycha* spp. Phase contrast. On A and B, the lowermost arrows point the  $X_1y$ ; on C, the right hand arrow. A. *D. leptolineata*,  $19+X_1y+X_2$ . (1435 $\times$ ) B. *D. spilotrachela*,  $13+X_1y+X_2$ . (1168 $\times$ ) C. *D. comma*,  $18+X_1y+X_2$ . (1205 $\times$ )

Bosch, *et al.* 1982). This species is known from the U.S.A. to Mexico and Guatemala.

Meiogram (Fig. 1C) and M I (Fig. 2A):  $19+X_1y+X_2$ . This is an amendment of the former preliminary count  $18+X_1y+X_2$  (Virkki 1988b). The "telephone-handle" shape of many bivalents suggests that they are formed by metacentric autosomes. Segregation to  $21(2X)$  and  $20(y)$  is confirmed by M II (Fig. 3A and B).

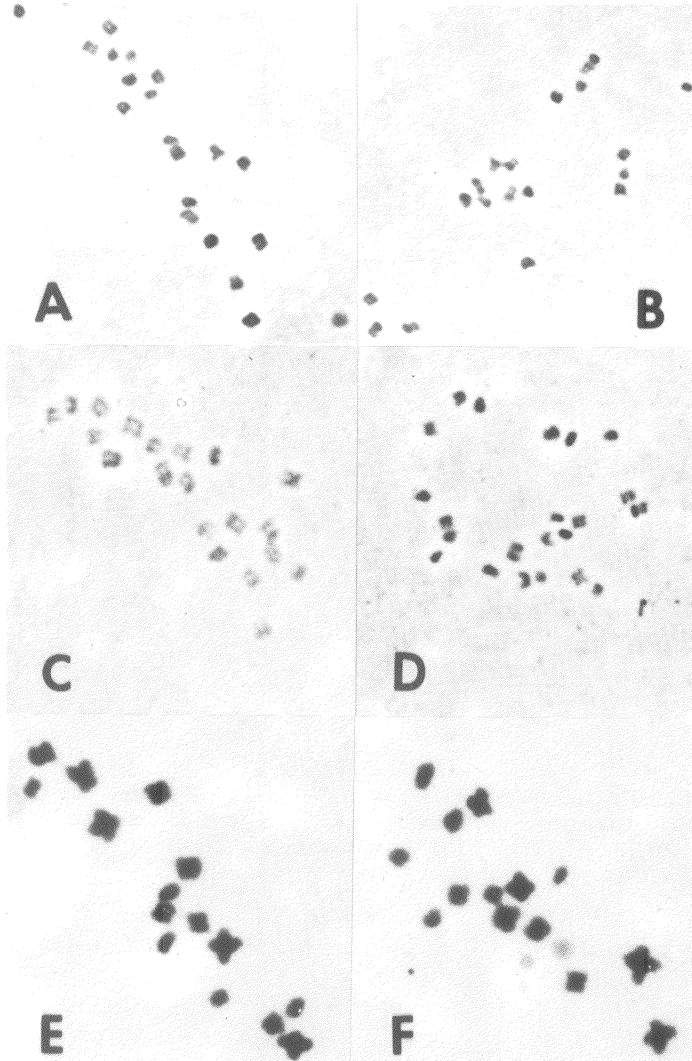


Fig. 3. Second meiotic metaphase in three *Disonycha* spp. Phase contrast. Identification of the sex chromosomes is not attempted. A and B. *D. leptolineata*. (1264 $\times$  and 1018 $\times$ , respectively.) A shows 21 chromosomes (19 autosomes, two X chromosomes); B, 20 chromosomes (19 autosomes and one Y chromosome). C and D. *D. eximia*. (1018 $\times$ ) C shows 20 chromosomes (19 autosomes and one Y chromosome); D, 22 chromosomes (19 autosomes and three X chromosomes). E and F. *D. spilotrachelata* 1791 $\times$ ) E shows 15 chromosomes (13 autosomes and two X chromosomes); F, 13 autosomes and one Y chromosome.

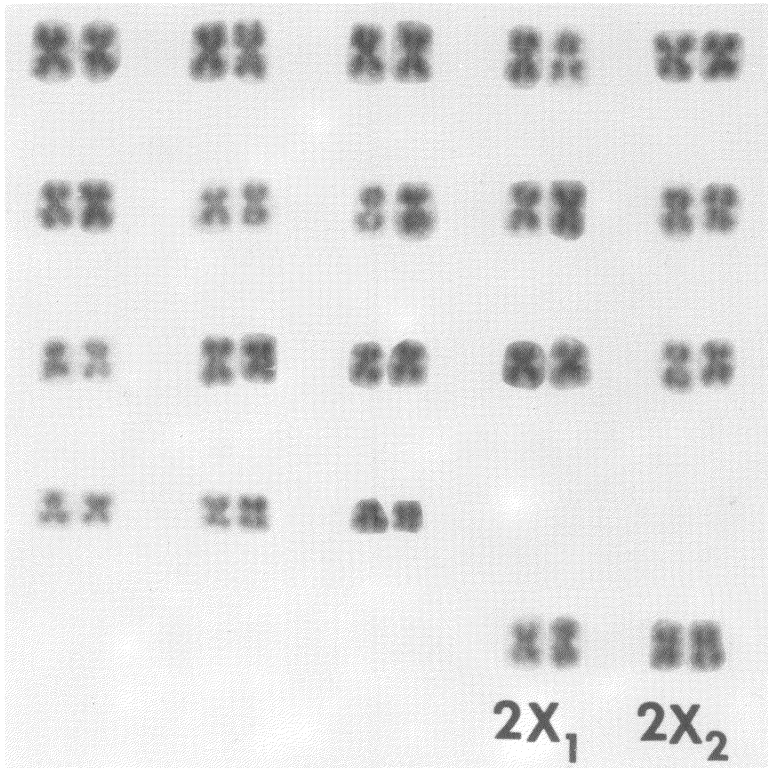


Fig. 4. Karyogram of female *D. comma*.  $2n=40(4X)$ .

#### *Disonycha eximia* Harold

Apart from *D. chlorotica* (Olivier) and *D. weisei* Csiki, both of which likely belong in other genera and neither of which has been recognized in recent years, this is the only non-vittate *Disonycha* (Blake 1955) known from Puerto Rico. This species is distributed from Costa Rica to Panamá. Wolcott (1948) suspected that this species may have arrived from Hispaniola in Puerto Rico early in the century. Undoubtedly, this species is now well established in Puerto Rico.

Meiogram (Fig. 1D) and M I (Virkki 1988b):  $19+X_1y+X_2+X_3$ . This is the highest chromosome number among Puerto Rican *Disonychini*. In closely related species with low and higher chromosome numbers, high numbers tend to be associated with the

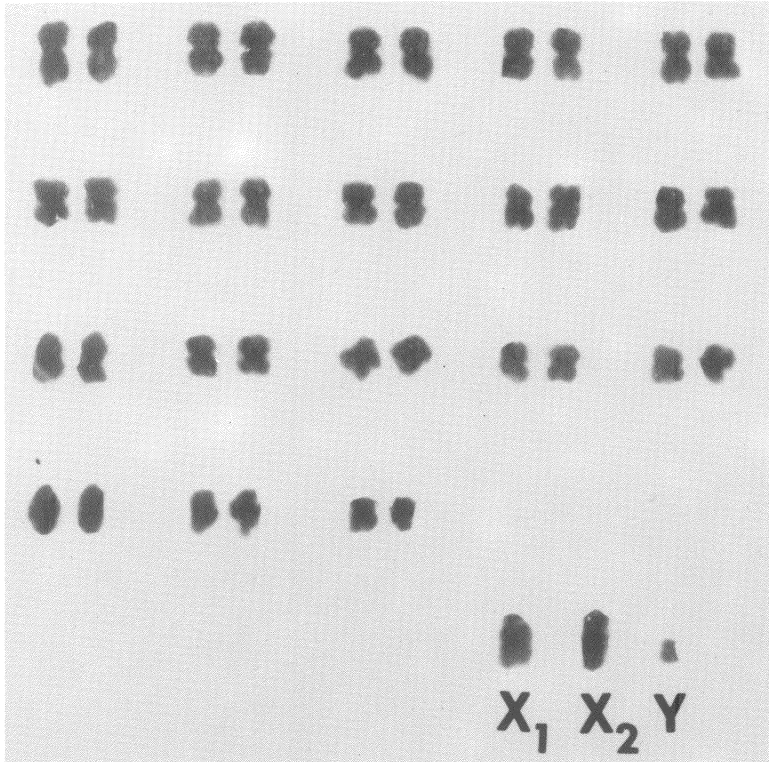


Fig. 5. Karyogram of male *D. comma*.  $2n=39(2X,y)$ .

existence of acro- or telocentric chromosomes (Robertson's rule), but in this species most chromosomes look metacentric and are capable of ring bivalent formation. The segregation to  $22(3X)$  and  $20(y)$  is confirmed by M II (Fig. 3C and D).

Karyogram (Virkki 1988b):  $2n=44(6X)$  on females,  $2n=42(3X,y)$  on males.

**Oedionychina.** This Pantropical subtribe has several Neotropical genera cytologically characterized as follows: typically with  $2n=22(X,y)$  and  $10+X+y$  in males (Petitpierre *et al.* 1988), giant sex chromosomes segregating from a "distance bivalent" in male meiosis, 16 spz/b, the lowest number known in Coleoptera, and very large spermatocyte I (Smith and Virkki 1978, Virkki 1985, Virkki and Denton 1987). Aggregation of nuclear pores to "nuclear



sieve complexes" (Virkki and Kimura 1978) in the growing spermatocyte I characterizes *Alagoasa* spp. and many other Neotropical genera formerly included in *Oedionychus* spp. (Virkki 1976). The inferred polarity (Stephens 1980) of the latter character points to *Alagoasa* and "*Oedionychus*" as more derived than *Omophoita*, which shows random distribution of nuclear pores in their spermatocyte I.

The orientation and segregation of the giant univalent sex chromosomes, as well as the growth of spermatocyte I in Oedionychina, have theoretical and phylogenetic implications (Smith and Virkki 1978, Virkki 1970, 1988a).

#### *Omophoita cyanipennis cyanipennis* (Fabricius)

This oligophagous beetle feeds principally on the verbenaceans *Clerodendrum aculeatum* and *Phyla nodiflora*, especially on borders of mangroves and other wetlands where the host plants are sympatric (Virkki 1980). It has a West Indian to southern North America distribution (Wilcox 1983). Puerto Rican samples are largely comprised of individuals with unicolored elytra; individuals with white spots are rare (Virkki 1980). A spotted color morph *O. c. octomaculata* (Crotch) prevails from Texas to Florida (U.S.A.), and perhaps on some of the other Caribbean islands (Blake 1931, Wilcox 1983).

Meiogram (Fig. 6A) and M I (Virkki 1979b): 10+X+y. Spermatogonial metaphases show  $2n=22(X,y)$  (Virkki 1979b). As found for many *Omophoita* spp. (Virkki 1983), the Y chromosome is acrocentric or submetacentric, having, in contrast to X, unequal arms. Profiles of autosomal bivalents show all chromatids united by what may be a chiasma terminalized during a preceding diffuse diplotene, if not an original terminal contact. Cross or ring bivalents have never been observed. Each chromatid shows a "telephone-handle" shape in the large bivalent closest to the sex chromosomes, but, where the free arm is short, it projects polewards leaving the centric gap equatorialwards from it. Jamaican samples of *O. c. octomaculata* have the same karyotype as *O. c. cyanipennis* from Puerto Rico (Virkki, *unpubl.*).

Idiogram, based on measurements of A II chromosomes. Sex chromosomes assume nearly 53% of total karyotype length, all chromosomes are metacentric (Virkki 1979b).

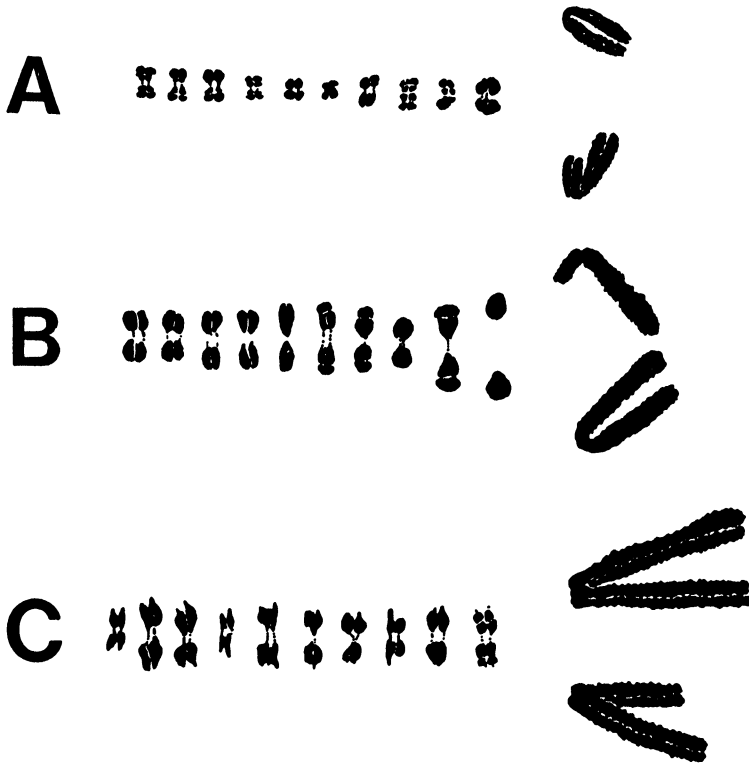


Fig. 6. Meiochromosomes of three Puerto Rican Oedionychina.  $10+X+y$ . A. *Omophoita cyanipennis*. B. *O. albicollis*. C. *Alagoasa bicolor*.

#### *Omophoita albicollis* (Fabricius)

This beetle lives in drier habitats and it is more sporadically found than *O. c. cyanipennis*. It has been found feeding on *Stachytarpheta jamaicensis* (Verbenaceae) near the air strip of Mona Island and in the abandoned military air strip at Tortuguero. *Heliotropium indicum* (Boraginaceae) is a secondary host (Virkki 1980).

Meiochromosomes (Fig. 6B) and MI (Smith and Virkki 1978):  $10+X+y$ . The Y chromosome has even more unequal arms than in *O. c. cyanipennis*. A desynaptic autosome pair depicted closest to the sex

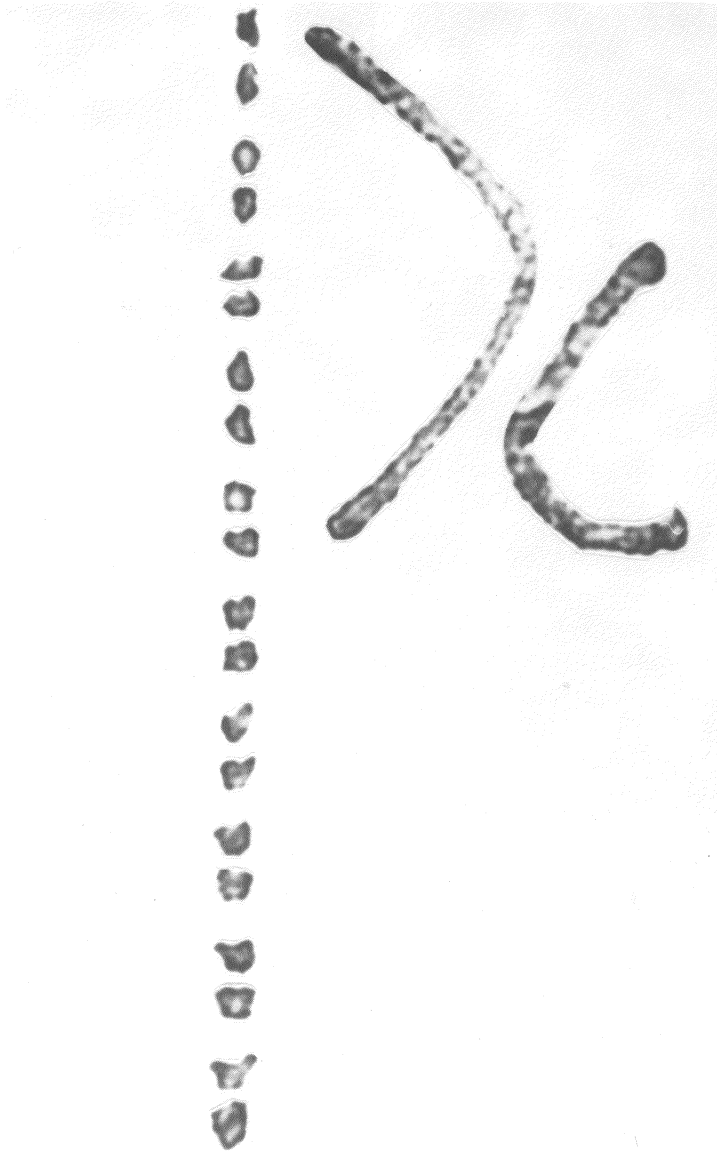


Fig. 7. Karyogram of *A. bicolor*.  $2n=22(X,y)$ .

chromosomes (Fig. 6B) is often seen in *Oedionychina* from the Puerto Rico region. Because such univalents do not move to the poles but remain facing one another not far from the equator, they may show incipient distance pairing rather than asynapsis or precession.

*Alagoasa bicolor* (L.)

Compared to *O. c. cyanipennis* and *O. albicollis*, this is a sedentary species that seldom leaves its host plant. It is sympatric with *O. c. cyanipennis*, and it feeds on *C. aculeatum* and *Aegiphila martinicensis* (both Verbenaceae), the latter not associated with wetlands. In spite of published records from other islands, the distribution of this species is probably limited to Puerto Rico and the Virgin Islands (Blake 1940). Some aspects of the life history, ecology, and behavior of this species in Puerto Rico have been studied (Virkki 1979a, 1980; Virkki and Zambrana 1980, 1983).

Meiogram (Fig. 6C) and M I (Virkki 1970, 1989a): 10+X+y. Both sex chromosomes are nearly mediocentric, X slightly larger than Y. All autosomes look acro- or telocentric.

Karyogram (Fig. 7) and spermatogonial mitosis (Virkki 1970):  $2n=22(X,y)$ . The autosomes, which have distal collochores (Virkki 1989a) in meiosis, do not show proximal collochores in these mitoses either, but their chromatids do not immediately open to stop at the final contact on the telomeres. There are some "sticky bridges" that slow down the separation of the chromatids. We have studied a sample taken from *C. aculeatum* in Emmaus, St. John (United States Virgin Islands), that shows the same karyotype as the Puerto Rican sample.

Idiogram. The sex chromosomes comprise 52% of the total karyotype length, all autosomes are telocentric (M. Mojica 1990 *pers. comm.*). M II chromosomes are currently being studied.

#### DISCUSSION

The cytological, hypothetical synapomorphic characters of *Oedionychini* (*Disonychina* and *Oedionychina*) are summarized in Fig. 8. It should be noted that a 10+X+y meioformula has appeared in *Omophoita* and in *Alagoasa*, constituting a parallelism. Also, the status of the nuclear pore distribution in *Asphaera* is uncertain (Virkki 1976); morphological characters (Scherer 1983) seem to

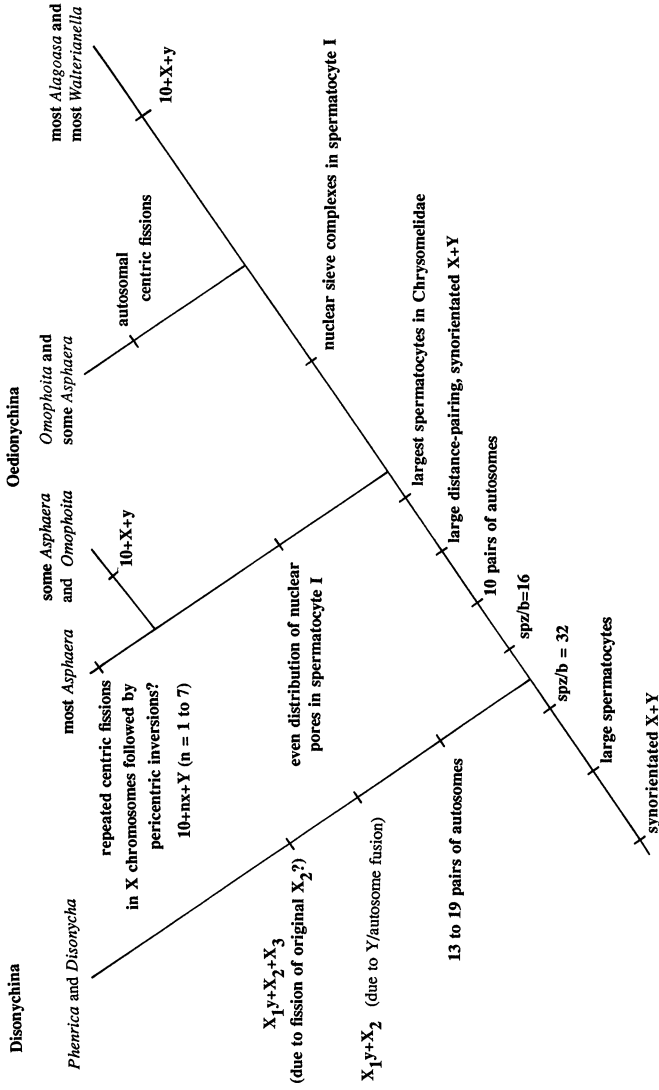


Fig. 8. Hypothetical cladogram of Oedionychini (Disonychina and Oedionychina) based on cytological characters of the male meiosis.

support our hypothetical placement. Virkki (1970, 1988a) suggested that the evolution of these Disonychina and Oedionychina can be tracked to some genera related to *Altica* and *Syphraea*, the putative primitive "tribal groupings" Alticini and Hermaeophagini, where male meioformulae  $11+X+y$  occur. It should be noted that the use of tribal names in the Alticinae is highly suspect and not well founded at this point (D. Furth 1991 *pers. comm.*). A common ancestor for Disonychina and Oedionychina should be looked for among relatively remote forms having karyotypes like those in *Stenophyma* sp., with unpaired, synorientated sex chromosomes of moderate size (Virkki 1970). A translocation of such a Y chromosome on an autosome would immediately produce a neo-system  $X_1y+X_2$ , as found in Disonychina. Oedionychina would have evolved without such translocation, under enormous increase in the size of both sex chromosomes. It seems feasible that a simultaneous increase of the spermatocyte size occurred in response to the increasing size of the Y chromosome, which has bands active in the diplotenic growth stage of spermatocyte I (Virkki and Denton 1987). Cell size and genome size increase have been positively correlated in succulent plants (De Rocher *et al.* 1990). Intraspecific variation of these parameters is similarly correlated in *Tribolium* (Coleoptera: Tenebrionidae), a genus showing spermatocytes of conventional size (Alvarez-Fuster, *et al.* 1991). Since the very large spermatocytes of Oedionychina would not fit in a cyst formed by only two or four cyst wall cells, alternative rearrangements became necessary: either to enlarge the cyst through additional cell growth or multiplication of the cyst wall cells, or to reduce the number of spermatocytes per cyst. The latter alternative was realized, in continuation of a trend already established on this inferred evolutionary lineage. Among the chromosomally most advanced Oedionychina are *Asphaera* spp., where distance sex multivalents occur (Petitpierre *et al.* 1988, Vidal 1984). These were usually noted  $X+ny$  ( $n=1-7$ ), but since females became available for study, the X chromosome was found to be multiple:  $nx+Y$  (Virkki and Santiago-Blay, *unpubl.*). The multiple chromosomes are relatively small but of different size, suggesting a repeated sequence of centric fissions of formerly large chromosomes followed by pericentric inversions. Other advanced genera are *Walterianella* Bechyné, where autosomal centric fissions have

led to  $22+X+y$  karyotypes (Petitpierre *et al.* 1988), and an undescribed *Alagoasa* with  $5+X+Y$  due to autosomal centric fusions (Virkki and Santiago, *unpubl.*).

The chromosomal and cytological unorthodoxies of Oedionychini, and especially of Oedionychina, warrant a comparative study of alleged related genera (see Seeno and Wilcox 1982, pp. 139–141), particularly the Old World *Oedionychus*.

#### SUMMARY

The Puerto Rican beetles of the tribe Oedionychini are cytologically typical of the inferred sister subtribes Disonychina and Oedionychina. In four Disonychina (*Disonycha spilotrachela*, *D. comma*, *D. leptolineata*, and *D. eximia*), metacentric autosomes prevail. Interspecific differences are expressed mainly in the diploid number, from  $2n=30(4X) \text{♀} / 29(2X,y) \text{♂}$  to  $2n=44(6X) \text{♀} / 42(3X,y) \text{♂}$ . The sex chromosome association in male meiosis is either  $X_1y+X_2$  or  $X_1y+X_2+X_3$ . *Disonycha leptolineata* and *D. comma* are new records for Puerto Rico. In contrast, the three species of Oedionychina (*Omophoita c. cyanipennis*, *O. albicollis*, *Alagoasa bicolor*), have  $2n=22(X,y)$ , with a simple distance sex bivalent in male meiosis ( $X+y$ ). The interspecific differences are mainly due to a different centromere position. We suggest that karyotypes as those encountered in contemporary *Stenophyma* gave rise to Oedionychini by increase in size of sex chromosomes and/or by chromosomal rearrangements.

#### RESUMEN

Los escarabajos puertorriqueños de la tribu Oedionychini son citológicamente típicos de las subtribus hermanas inferidas Disonychina y Oedionychina. En cuatro Disonychina (*Disonycha spilotrachela*, *D. comma*, *D. leptolineata*, y *D. eximia*), estudiadas, prevalecen los autosomas metacéntricos. Las diferencias interespecíficas ocurren mayormente en el número diploide, desde  $2n=30(4X) \text{♀} / 29(2X,y) \text{♂}$  hasta  $2n=44(6X) \text{♀} / 42(3X,y) \text{♂}$ . La asociación de cromosomas sexuales en la meiosis de los machos es  $X_1y+X_2$  o  $X_1y+X_2+X_3$ . *Disonycha leptolineata* y *D. comma* son nuevos registros para Puerto Rico. Por contraste, las tres especies de Oedionychina (*Omophoita c. cyanipennis*, *O. albicollis*,

*Alagoasa bicolor*), tienen  $2n=22(X,y)$ , con un bivalente sexual de distancia sencillo en la meiosis del macho ( $X+y$ ). Las diferencias interespecíficas se deben mayormente a las deferencias en la posición del centrómero. Sugerimos que cariotipos como los encontrados en *Stenophyma* contemporáneos originaron *Oedionychini* mediante el crecimiento de los cromosomas sexuales y/o las reordenaciones cromosómicas.

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