

SYSTEMATICS, MORPHOLOGY AND PHYSIOLOGY

Cytogenetics Studies in Thirteen Brazilian Species of Phaneropterinae (Orthoptera: Tettigonioidae: Tettigoniidae): Main Evolutive Trends Based on their Karyological Traits

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Estudos Citogenéticos em Treze Espécies Brasileiras de Phaneropterinae (Orthoptera: Tettigonioidae: Tettigoniidae): Principais Tendências Evolutivas Baseadas em suas Características Cariológicas

RESUMO - As treze espécies de Phaneropterinae estudadas neste trabalho podem ser organizadas em quatro diferentes grupos tomando como referência suas características cariotípicas. Todas possuem sistema cromossômico de determinação sexual do tipo $X0♂$, $XX♀$. O cromossomo X é sempre heteropicnótico durante a prófase I, tem dimensões e morfologias variáveis nas diferentes espécies mas é sempre o maior elemento do cariótipo, além de apresentar segregação precoce durante a anáfase I. O número cromossômico fundamental (NF) varia de 21 a 32. Neste trabalho, são discutidos os significados evolutivos das variações cariotípicas encontradas e suas correlações filogenéticas com outros grupos de espécies pertencentes à mesma subfamília.

PALAVRAS-CHAVE: Cariótipo, cromossomo, evolução

ABSTRACT - The thirteen species of Phaneropterinae here studied can be arranged in four different groups according to their basic karyological traits. All of them share the same kind of chromosomal sex determining mechanism with $X0♂$ and $XX♀$. The X chromosome differs among species and always appears heteropycnotic during prophase I, it is the largest in the set and segregates precociously during anaphase I. Among the species, the karyotypes varies in fundamental number between 31 to 21. The meaning of these significant changes in the karyotypes in relation to the phylogeny within some large taxonomic group of species is discussed.

KEY WORDS: Karyotype, chromosome, evolution

The family Tettigoniidae includes approximately 1,070 genera and 6,000 species arranged according to different authors, in 14 to 24 subgroups [Kevan 1976, 1977, 1982; Rentz 1985, 1995 (apud Warchalowska-Śliwa 1998); Eades *et al.* 2002].

The subfamily Phaneropterinae comprises a large number of species with wings that mimic leaves. The species are easily recognized by the lack of lateral grooves in the first and second tarsal segments and also because the females show a very short ovipositor curved upwards. The subfamily is found all around the world but it is particularly common in the tropical and subtropical zones.

After the first karyological studies of the Phaneropterinae species, published in the beginning of the 20th century, few progresses were ensued if compared with other orthopteran groups. Except for the subfamily Tettigoniinae, the Phaneropterinae species are the best known cytologically within the family Tettigoniidae. The karyology of 86 species are known including those of the present paper. A recent revision was published by Warchalowska-Śliwa (1998) but

the chromosomes of three species studied by Ferreira *et al.* (1976) were not included in the paper: *Thomazia borgmeire* (Piza, 1977) and *Ferreiraia nigropunctata* (Piza, 1977) both with $2n♂ = 31$ and *Viadana delicatula* (Piza, 1977) with $2n♂ = 27$, the three species with all the chromosomes acrocentric. Several species described by Warchalowska-Śliwa *et al.* (1987, 1992a, 1992b, 1995, 1996) and Warchalowska-Śliwa (1998), as belonging to Phaneropterinae were more recently included in Odonturinae by the same author in 1998.

Most published papers deal basically with the description of chromosome number, morphology, behavior and sex-determination mechanisms during meiosis, using conventional methods of staining. More recently, Warchalowska-Śliwa *et al.* (1996) and Warchalowska-Śliwa & Heller (1998) included sophisticated techniques to study the chromosome structure to detect C bands and Ag-NOR besides the use of quantitative approaches.

The literature shows that species of Phaneropterinae present a large chromosomal morphological and numerical variability, and their extreme limits in number of chromosomes

are $2n♂ = 16$ and $2n♂ = 33$ (Ferreira 1969). The majority of its species are $2n♂ = 31$ with all the chromosomes acrocentric or a derived number, originated mainly by tandem fusions, robertsonian changes and pericentric inversions.

The X chromosome is the largest of the set, heteropicnotic during prophase I but its size is different among species. The sex determining mechanism is $X0♂ - XX♀$ in the majority of species. Only six species are $neoXY♂ - neoXX♀$ and one of the $X_1X_2Y♂ - X_1X_1X_2X_2♀$ type (Dave 1965; White *et al.* 1967; Ferreira 1969, 1976; Alicata *et al.* 1974).

In this paper the karyotypes of thirteen species of Phaneropterinae from different Brazilian localities were studied.

Material and Methods

The species studied and respective collection sites are in Table 1.

The specimens were dissected in the field and the testes fixed in Carnoy and preserved at low temperature in the same fixative during thirteen days.

In the laboratory the tissues were macerated during two minutes in acetic acid 45% and then transferred to a slide with a drop of lacto-propionic orcein 1% before squashing. The meiotic first metaphases were photographed and each bivalent and the sex chromosomes drawn from photographic images.

Results

The thirteen species here studied can be arranged in four different groups according to their basic karyological characteristics. All of them have an $X0♂ - XX♀$ kind

of sex-determining mechanism. The X always migrates towards a pole ahead of the autosomes, what delays its pole movement due to the occurrence of chiasmata in the bivalents.

The different groups are as follows:

Group I. *T. catalao*, *T. jahyrae*, *P. modesta*, *Phylloptera* sp., *M. phyllacantha*, *Diplophyllus* sp. and *P. maculifemora*, have $2n♂ = 31$ acrocentric chromosomes (NF = 31). During prophase I the autosomes form 15 bivalents that can be organized in three groups according to their sizes: two large (L), seven or eight medium size (M) and five or six small (S). Normally, two chiasmata are observed in the large and in some of the medium size bivalents and one in the remaining pairs (Figs. 1 and 7, respectively).

Group II. *P. infumata*, *A. chellata*, *A. linguata* and *P. verrucosa* have $2n♂ = 31$ similar to the group I but with the X submetacentric (NF = 32). The X chromosome is particularly large in *P. verrucosa* (see Figs. 8 and 11, respectively).

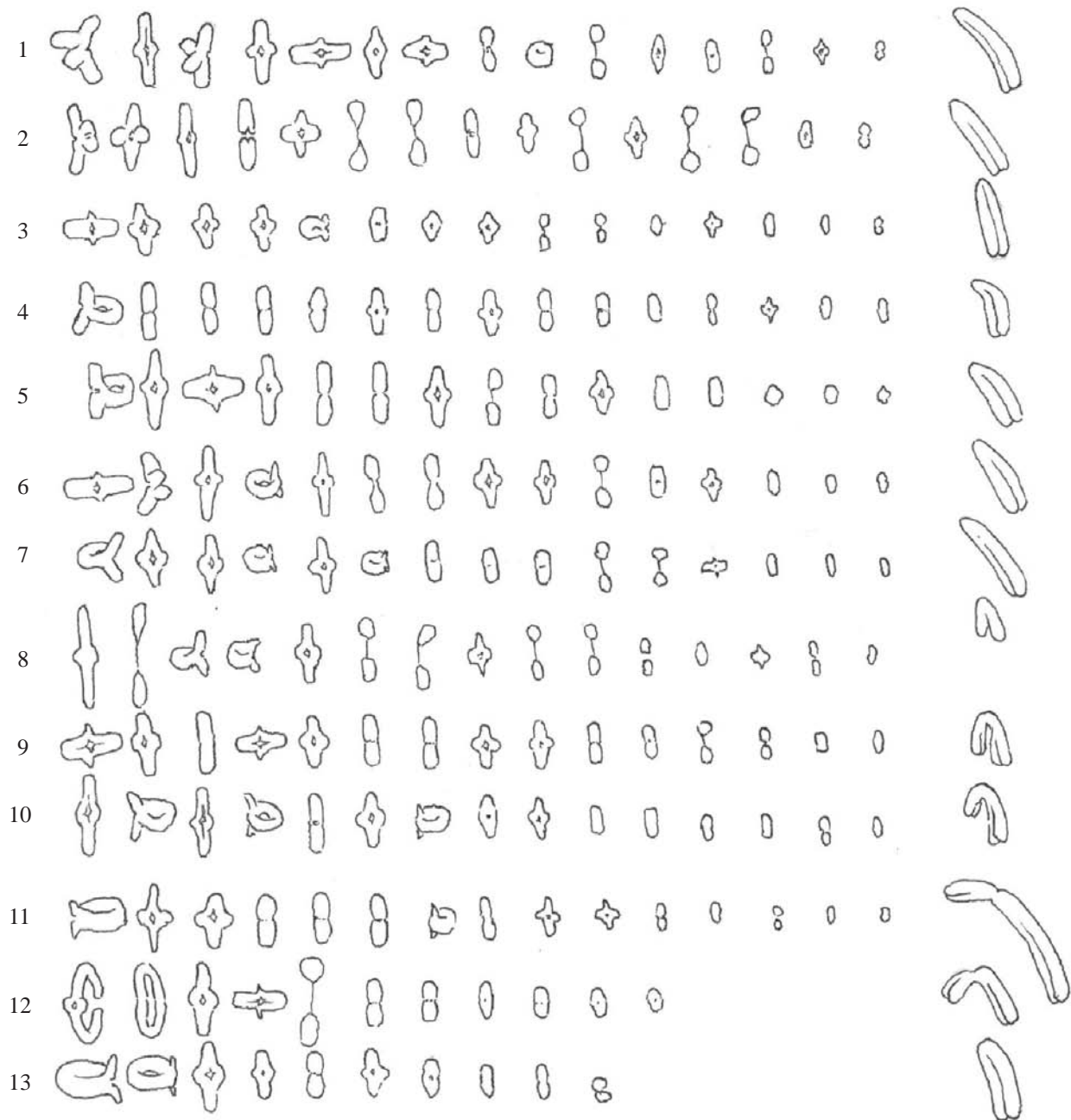
Group III. *A. brasiliae* is $2n♂ = 23$. The two largest autosomal pairs L_1 and L_2 are formed by metacentric autosomes that show two chiasmata whereas the remaining pairs have only one. The X is submetacentric (NF = 28), Fig. 12.

Group IV. *A. ferracioui* has 21 acrocentric chromosomes ($2n♂ = 21$ and NF = 21). In metaphase I, three pairs of large chromosomes are observed: three medium-sized and four small. The bivalents of the groups L form three chiasmata and the remaining bivalents a single one (Fig. 13).

Table 2 summarizes the main karyological characteristics of the species studied.

Table 1. Species studied and respective collecting sites.

Species	Collecting sites	
<i>Theudoria catalao</i> Piza	Goiás	50 km north of Catalão
<i>Theudoria jahyrae</i> Piza	Goiás	1700 m south of Cristalina
<i>Phylloptera modesta</i> Piza	Rio de Janeiro	Itatiaia National Park
<i>Phylloptera</i> sp. Piza	Rio de Janeiro	Itatiaia National Park
<i>Machyma phyllacantha</i> Brum	São Paulo	Center of Biological Studies at Boracéia
<i>Diplophyllus</i> sp.	São Paulo	Center of Biological Studies at Boracéia
<i>Paracora maculifemora</i> Piza	Rio de Janeiro	Itatiaia National Park
<i>Phaneropterella infumata</i> Piza	Goiás	Vicinity of Cristalina
<i>Anaulacomera chellata</i> Brunner v. W.	São Paulo	Center of Biological Studies at Boracéia
<i>Anaulacomera linguata</i> Piza	São Paulo	Center of Biological Studies at Boracéia
<i>Paraphidnia verrucosa</i> Brunner v. W.	Goiás	Vicinity of Cristalina
<i>Anaulacomera brasiliae</i> Piza	Goiás	Vicinity of Brasília
<i>Aniarella ferracioui</i> Piza	Rio de Janeiro	Itatiaia National Park



Figs. 1-13. First metaphase of: 1 - *Theodoria calatao*; 2 - *Theodoria jahuræ*; 3 - *Phylloptera modesta*; 4 - *Phylloptera* sp.; 5 - *Machyma phyllacantha*; 6 - *Diplophyllus* sp.; 7 - *Paracora maculifemora*; 8 - *Phaneropterella infumata*; 9 - *Anaulacomera chellata*; 10 - *Anaulacomera linguatta*; 11 - *Paraphidnia verrucosa*; 12 - *Anaulacomera brasiliae*; 13 - *Aniarella ferracioui*. For each species, the chromosomes were organized in decreasing order of size from left to right, with the X at the right end.

Discussion

The variability in chromosome number and morphology found among the Phlebotominae is by far larger than in the remaining subfamilies, their extremes going from $2n♂ = 33$ to $2n♂ = 16$ (Pearson 1929, Dave 1965, Ferreira 1969, Cisneros-Barrios *et al.* 1990). Between those extremes, species with $2n♂ = 32, 31, 30, 29, 28, 27, 25, 23, 21, 20, 19$, and 17 chromosomes were studied. Among the five species described

with $2n♂ = 33$, three show fundamental number (NF) = 33 (Mc Clung 1902, Pearson 1929) and two NF = 34 (Cisneros-Barrios *et al.* 1990) due to the presence of a submetacentric X. Dave (1965) published the karyotype $2n♂ = 32$ for *Isopsera* sp. and a sex-determination mechanism of the type $neoXY♂ - neoXX♀$, originated by an X-A centric fusion.

The karyotype $2n♂ = 31$ was observed in 48 of 86 species studied and half of them show only acrocentric chromosomes with a NF = 31, collected in several localities

Table 2. Number, morphology and sex determining mechanisms in thirteen species studied.

Taxa	2n♂	NF	Sex	Morphology
<i>T. catalao</i>	31	31	X0	All acro
<i>T. jahyrae</i>	31	31	X0	All acro
<i>P. modesta</i>	31	31	X0	All acro
<i>Phylloptera</i> sp.	31	32	X0	All acro
<i>M. phyllacantha</i>	31	31	X0	All acro
<i>Diplophyllus</i> sp.	31	31	X0	All acro
<i>P. maculifemora</i>	31	31	X0	All acro
<i>P. infumata</i>	31	32	X0	L ₁ -S ₁₅ acro, X submet
<i>A. chellata</i>	31	32	X0	L ₁ -S ₁₅ acro, X submet
<i>A. linguata</i>	31	32	X0	L ₁ -S ₁₅ acro, X submet
<i>P. verrucosa</i>	31	32	X0	L ₁ -S ₁₅ acro, X submet
<i>A. brasiliae</i>	23	28	X0	L ₁ ,L ₂ metac, X submetata, rest acro
<i>A. ferracioui</i>	21	21	X0	All acro

around the world except in Australia, Japan (Ohmachi 1935), Brazil (Ferreira 1969, 1976, 1977; Ferreira *et al.* 1976), Canada (Beaudry 1973), Italia (Messina *et al.* 1975), Poland (Warchalowska-Sliwa 1984), Mexico (Cisneros-Barrios *et al.* 1990), India (Aswatharayama *et al.* 1996), and South Korea (Warchalowska-Sliwa 1998).

T. catalao, *T. jahyrae*, *P. modesta*, *Phylloptera* sp., *Paracora maculifemora*, *Machima phyllacantha* and *Diplophyllus* sp., studied in the present paper, show the kind of karyotype with 2n♂ = 31 with all the chromosomes acrocentric.

This kind of karyotype was considered by Ferreira (1977) as the ancestral for the majority of Phaneropterinae, and those different from the basic one derived by mean of different kind of rearrangements. The 2n♂=21 karyotype with all the chromosomes acrocentric, seems to be another branch of ancestry but not too recent since it was found in Australia and South America thought an independent origin can not be put aside.

P. infumata, *A. chellata*, *A. linguata* and *P. verrucosa*, belong to the second group, together with four species of the genus *Caedicia* (Ferreira 1977) and two of the genus *Amblycorypha* (Beaudry 1973) all of them with 2n♂ = 31 and NF = 32 due to a pericentric inversion of the X chromosome.

A. brasiliae belongs to the third group and it is the only species known with 2n♂ = 23 and NF = 27. It maintains the characteristic submetacentric X, present in the remaining studied species of the genus. The two pairs of metacentric chromosomes of the species were formed by two independent centric fusions engaging four large pairs of acrocentric chromosomes. Yet, the presence of a low NF = 23 only could be explained by the occurrence of tandem fusions or centric fusions followed by pericentric inversions. Both situations have been documented by Warchalowska-Sliwa *et al.* (1998) in the species *Isophya hemiptera* Bey-Bienko.

The reduction in the number of chromosome arms by the integration of autosomal chromatin in the Phaneropterinae was already observed by Ferreira (1969) in *Tinzeda albosignata* Brunner von Watternwyl, an Australian species with 2n♂ = 25 acrocentric chromosomes and by Mesa & Ferreira (1977) in *Dichopetala brevihastata* Morse collected in USA, with 2n♂ = 23 acrocentric chromosomes. Both species have in common a very large pair of chromosomes comprising nearly half of the whole autosomal chromatin, with a high number of chiasmata, well out of the normal if compared with other chromosomes in Tettigoniidae. As a consequence, the movement of this chromosomes to the poles in anaphase I is delayed while the remaining pairs are already moving to opposite poles. The larger size of those chromosomes could be explained by the occurrence of several centric fusions followed by pericentric inversions or by a series of tandem fusions.

The giant autosomic pair found in *D. brevihastata* by Mesa & Ferreira (1977) can be easily identified in three other species of the genus studied by Cisneros-Barrios *et al.* (1990) in *D. tauriformis* Rehn & Hebard (2n♂ = 23), *D. femorata* Brunner von Watternwyl (2n♂ = 27) and *D. mexicana* Brunner von Watternwyl (2n♂ = 17). Unfortunately, those authors do not mention the morphology of the chromosomes which make difficult to explain the origin of the karyotypes 2n♂ = 17 from those 2n♂ = 23 acrocentric ones. Yet, the process of chromatin integration that originated the giant autosomal pair needs to be quite old since it is present in four species studied in that genus.

A. ferracioui belongs to the group IV and it is the only species known outside the Australian territory to show a karyotype 2n♂ = 21 with all the chromosomes acrocentric.

Prosagoga sp. collected in Cruzeiro do Sul, Acre, Brazil, is 2n♂ = 19 with two submetacentric autosomal pairs surely originated by centric fusions involving medium and small autosomes from a karyotype similar to that of *A. ferracioui* (Ferreira 1977).

Except for *T. albosignata* (Ferreira 1969) all the six Australian species studied are $2n\♂ = 21$ with the chromosomes acrocentric. Three species of the genus *Caedicia* show derived karyotypes from $2n\♂ = 21$ to $2n\♂ = 16$ due to X-A centric fusion (*Caedicia marginata* Brunner von Watternyl and *Polichne parvicauda* Stål) or between autosomes (*P. parvicauda*) or to two centric fusions followed by inversions [*Torbia viridissima* (Brunner)]. Within those extremes there are consequently species with $2n\♂ = 20, 19$ and 16 .

Despite the scarcity of cytological information available, it is possible to evaluate the mean chromosomal mechanisms that take place in the karyotypic evolution of Phaneropterinae species. The subfamily basic karyotype $2n\♂ = 31$ and NF = 31 (White 1973, Ferreira 1977) is prevalent in other eleven subfamilies of Tettigoniidae found all around the world. This karyotype, however, has not been observed in species of Mecopodinae, Heterodinae, Nedubinae and Glyphonotinae (Warchalowska-Śliwa 1998).

The analysis of the chromosomal variability in Phaneropterinae species shows preponderance of tandem fusions in the origin of derived karyotypes. From 86 species studied in Phaneropterinae 25 have karyotype with all chromosomes acrocentric but with number smaller than 31 and most probably originated by tandem fusions events. These species were studied by several authors and found in many regions of the world as India, Canada, Korea, Japan, Brazil, Italy and Mexico and the decreasing order of numbers are $2n\♂ = 29$ (11 spp.), $2n\♂ = 27$ (9 spp.), $2n\♂ = 25$ (3 spp.) and $2n\♂ = 23$ (2 spp.).

In *T. albosignata*, $2n\♂ = 27$; *D. brevihasta*, $2n\♂ = 25$; *D. tauriformis*, $2n\♂ = 23$; *D. femorata*, $2n\♂ = 27$ and *D. mexicana*, $2n = 17$, it was possible to infer the presence of tandem fusions by the increase in length of some chromosome, as published by Ferreira (1969), Mesa *et al.* (1977) and Cisneros-Barrios *et al.* (1990). The karyotypic bimodality observed in those species seems to indicate that some chromosomes are more prone to breaks than others which tend to remain unchanged in length.

The occurrence of centric fusions is not relevant in Phaneropterinae, but predominant in Tettigoniinae and Bradyphorinae (Warchalowska-Śliwa 1998). Within Phaneropterinae, six species are known to have neoXY♂ or X₁X₂Y♀ sex-determining mechanisms (Dave 1965; White *et al.* 1967; Ferreira 1969, 1977) involving X and autosomal chromosomes in species originally X0♂.

Centric fusions between autosomes were already described in five species (Dasgupta 1961; Ferreira 1969, 1977; Muthu 1988) besides *A. brasiliae* here studied. It is interesting to note that among these six species, five are originated in species $2n\♂ = 21$ with NF = 21 considered to be the second basic number in Phaneropterinae (Ferreira 1969, 1977).

Pericentric inversions that modify the centromere position thus changing the acrocentric chromosomes to metacentric or submetacentric, were detected in six species all of them involving the X chromosome (Pearson 1929; Beaudry 1973; Ferreira 1977; Piza 1945; Muthu 1987, 1988). From these six species, three (*P. infumata*, *A. chellata* and *A. linguata*) were here studied. There is no information about autosomal pericentric inversions in Phaneropterinae. The occurrence of this kind of inversions in the X chromosome seems to confer

adaptability to the species because when they take place they spray by speciation among the species of a genus as happens in *Amblicorypha* and *Anaulacomera*.

The occurrence of more than one chromosomal rearrangement in a single species was observed in *A. brasiliae* where two independent centric fusions took place and where a tandem fusion reduced the karyotype from $2n\♂ = 23$ to $2n\♂ = 28$.

The presence of species $2n\♂ = 21$ described by Ferreira, (1969), Dasgupta, (1961), and like *A. ferracioui* in this paper, could not be explained for a while from species $2n\♂ = 31$ and NF = 31 and the strong reduction in number and arms probably took place long time ago, and gave rise to the second ancestral karyotype for Phaneropterinae. The further reductions of this second ancestral karyotype to $2n\♂ = 20, 19$ and 16 were surely due to mechanisms of chromosomal rearrangements.

The study of chromosome number, centromere position and sex-determining mechanisms provides basic information on the karyotypes, and according to Warchalowska-Śliwa (1998), they allow to understand only partially the number, nature and sequence of chromosomal rearrangements. For a better understanding of the karyological evolution in Tettigoniidae it will be necessary to increase the number of species studied and to use more elaborated techniques like banding and localization of Ag-NOR's. The knowledge of the species karyotypes is particularly insufficient in subfamilies as Mecopodinae, Heterodinae, Nedubinae and Glyphonotinae. This lack of information allows to a fragmentary understanding of the filogenetic relationships within Tettigoniidae based on karyology.

Drastic changes in karyotype structures may occur even between closely related species. In grasshoppers the ancestral number is $2n = 23$ (males) with acrocentric chromosomes. Three closely related grasshopper species of the genus *Dichroplus* (*D. obscurus* Brunner, *D. pratensis* Brunner and *D. silveiraguidoi* Lieber) show however three strongly different karyotypes, whose structures were necessarily acquired in recent times. *D. obscurus* has $2n = 18$ males due two A-A and X-A centric fusions but with NF = 23 (Mesa *et al.* 1982). *D. pratensis* has $2n = 19$ males with all the chromosomes acrocentric (NF = 19) but with three heterozygote independent A-A centric fusions which provide the species with 27 different karyological combinations with the smallest numbers in males of $2n = 13$ (Mesa *et al.* 1982). *D. silveiraguidoi* reached the most reduced number among the acridids, with $2n = 8$ males and NF = 13 (Saez 1956), the mechanism of this strong reduction in NF being still unknown.

Two species closely related of an undescribed new genus (genus new H sp. n. 1) of a New Zealand gryllacridid belonging to the circumantartic subfamily Macropathinae, separated by the Cook Strait, show two extremely different karyotypes. That of the northern side of the South Island is $2n$ (males) = 45 that is the ancestral number for the subfamily according to studies carried out in Australia, New Zealand and South America (Mesa 1965, 1970, 1971; Mesa *et al.* 1968, 1969). Specimens collected in the South shore of the North Island (Gen nv H, sp nv 2) are instead $2n = 27$ (males). Again the mechanism of such a large and fast change is unknown.

The final inference based on these particular examples among Orthopteran insects is that drastic changes in karyotype structure are not always an indicative of old karyological lineages if large and numerous groups of species are not involved.

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