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Does an x-autosome centric fusion in Acridoidea condemn the species to extinction?

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Abstract

Based on analysis of more than fifty species of neotropical grasshoppers with a neo XY sex determining mechanism, the authors suggest that species acquiring such mechanisms are finally extinct at the end of a relatively short evolutionary process.

Key words

Sex determination, grasshoppers, Acridoidea, species extinction, chromosomes

Introduction

The basic X0-XX (male-female) sex determining mechanism of Acridoidea is substituted, with some frequency, by a neo XY-XX (male-female) system, by means of an X-autosome centric fusion. Once the new mechanism is established in all the individuals of the species, it starts an evolutionary process (Saez 1963) that consists in the progressive heterochromatinization of the neo Y chromosome and limitation of the crossing-over to the distal end of the ex-homologous chromosomes. For a time, during first meiotic prophase, XR (the autosomal arm of the neo X) remains euchromatic, but at the end of the process even this arm appears heterochromatic. The neotropical grasshoppers are very rich in species with a neo XY sex determining mechanism, in comparison to acridid faunas of other regions, and up to now, more than fifty such species have been detected (Mesa *et al.* 1982, Mesa unpub.).

Results

Among several hundreds of neotropical grasshopper species cytologically analyzed (Mesa *et al.* 1982), the following three show recently established neo XY sex determining mechanisms with full Y-XR pachytene pairing: *Neuquenina ficator* (Rehn) (Mesa 1960), *Tetrixocephalus* (= *Calcitrena*) *willemsei* (Gurney & Lieberman) (Mesa 1973, Mesa & Ferreira 1977) and *Leiotettix sanguineus*, Bruner (Figs 1-5) (Mesa & Mesa 1967).

Six species are at the end of the neo XY evolutionary process, with both X and Y wholly heterochromatic during first prophase: *Atacamacris diminuta* Carbonell & Mesa (Figs

17, 18) (Mesa & Sandulsky 1971, Carbonell & Mesa 1971, Mesa *et al.* 1982), *Dichroplus maculipennis* (Blanchard) (Figs 15, 16) (Mesa *et al.* 1982), *Dichroplus vittigerum* (Blanchard) (Figs 8-14) (Mesa 1973, Mesa *et al.* 1982), *Zygoclistron nasicum* (Gerstaecker) (Ferreira *et al.*, 1979), *Z. falconicum* (Gerstaecker) (Mesa *et al.* 1982) (Fig. 23) and *Z. trachystictum*, (Rehn) (Figs 19, 20) (Mesa *et al.* 1982).

Intermediate stages were observed in nearly forty other species. One of these cases occurs in an undescribed species of the genus *Dichroplus*, with XR being euchromatic during diplotene (Fig. 6) and diakinesis (Fig. 7) stages, and Y heterochromatic. The single XR-Y chiasma or a simple end-to-end contact is already strictly distal, as observed in both figures (arrows).

All the six species with old neo XY mechanisms have bivalents with ample loops during first prophase that give them a peculiar wavy appearance, as observed in Figs 13-19 and 23 a-c. Normal diplotene and diakinesis stages do not present such characteristics: see Figs 21 and 22 from the X0-XX (male-female) species *Xestotrachelus robustus*, (Bruner). *Zygoclistrum* and *Aleuas* are two closely related genera and both of them include species that share the presence of a large pair of metacentric autosomes, as well as neo XY sex determining mechanisms.

In species of *Aleuas* during diplotene there is always present a large segment of euchromatic XR arm, as observed in *A. lineatus* (Fig. 24 a'), *A. brachypterus* (= *A. vitticollis*) (Fig. 24 b'), *A. n.sp.* Corrientes (Fig. 24 c'), *A. n.sp.* Caaguazú (Fig. 24 d') and *A. gracilis* (Ferreira 1975), while in species of *Zygoclistron*, XR is always entirely heterochromatic. Four of the above mentioned species of *Aleuas* have a metacentric or submetacentric Y chromosome due to a more recent pericentric inversion. In *A. sp.n.* from Caaguazu, this chromosome remains acrocentric (Fig. 24 d).

Discussion

It is assumed that X-autosome centric fusions took place at a more or less constant rate in the evolutionary history of the Acridoidea. Therefore, it is expected that the earlier ones gave the species involved time enough to speciate, giving rise to higher taxa. Consequently, at present, large taxo-



Figs 1-7. *L. sanguineus*. 1 and 3, early diplotene stages of neo XY pair. 2. *idem.* during late pachytene. 4. Middle diplotene with interstitial chiasma between XR and Y. 5. *idem.* during first metaphase. *Dichroplus* n.sp. 6 and 7, Neo XY pair with XR and Y connected by a single distal chiasma (arrows). Y chromosome clearly heterochromatic and XR euchromatic; diplotene (6), diakinesis (7). Scale bar 10 μ m.

nomic groups such as genera, tribes and even subfamilies could have all their species with neo XY sex determining mechanisms. Instead, in the majority of cases, only isolated species within a genus are neo XY (Mesa *et al.* 1982). Cases where all the species of the genus are neo XY as in *Zygoclistron* and *Aleuas*, are rare (Mesa *et al.* 1982). A particular event seems to have occurred among the species of the genus *Aleuas*, closely related to *Zygoclistron*, where all five species analyzed are neo XY (Mesa *et al.* 1982, Ferreira 1975). In these species, the meiotic connection between XR and Y does not seem to be chiasmate and during diplotene and diakinesis stages a relatively long chromosomal segment of the X, probably XR, remains euchromatic (Fig. 24). The neo X chromosomes of *Aleuas* species deserve a more accurate analysis.

Species of the genus *Zygoclistron*, on the other hand, show XY mechanisms at the end of their evolutionary process, with XR wholly heterochromatic during first prophase. Whether the X-autosome centric fusion that connected the X chromosome to an autosome has a single origin in a common ancestral species of both genera, or took place twice independently in the origin of each genus, is an unresolved question, though the presence of a long euchromatic XR segment in species of *Aleuas* points toward the second hypothesis. However, the absence of XR-Y chiasmata and the presence of a long euchromatic XR segment in *Aleuas*, could mean that even with a single origin of the X-A centric fusion, a relatively recent change in the chiasmatic behavior of its species avoided the negative consequences observed in the *Zygoclistron* species with the full heterochromatinization of XR.

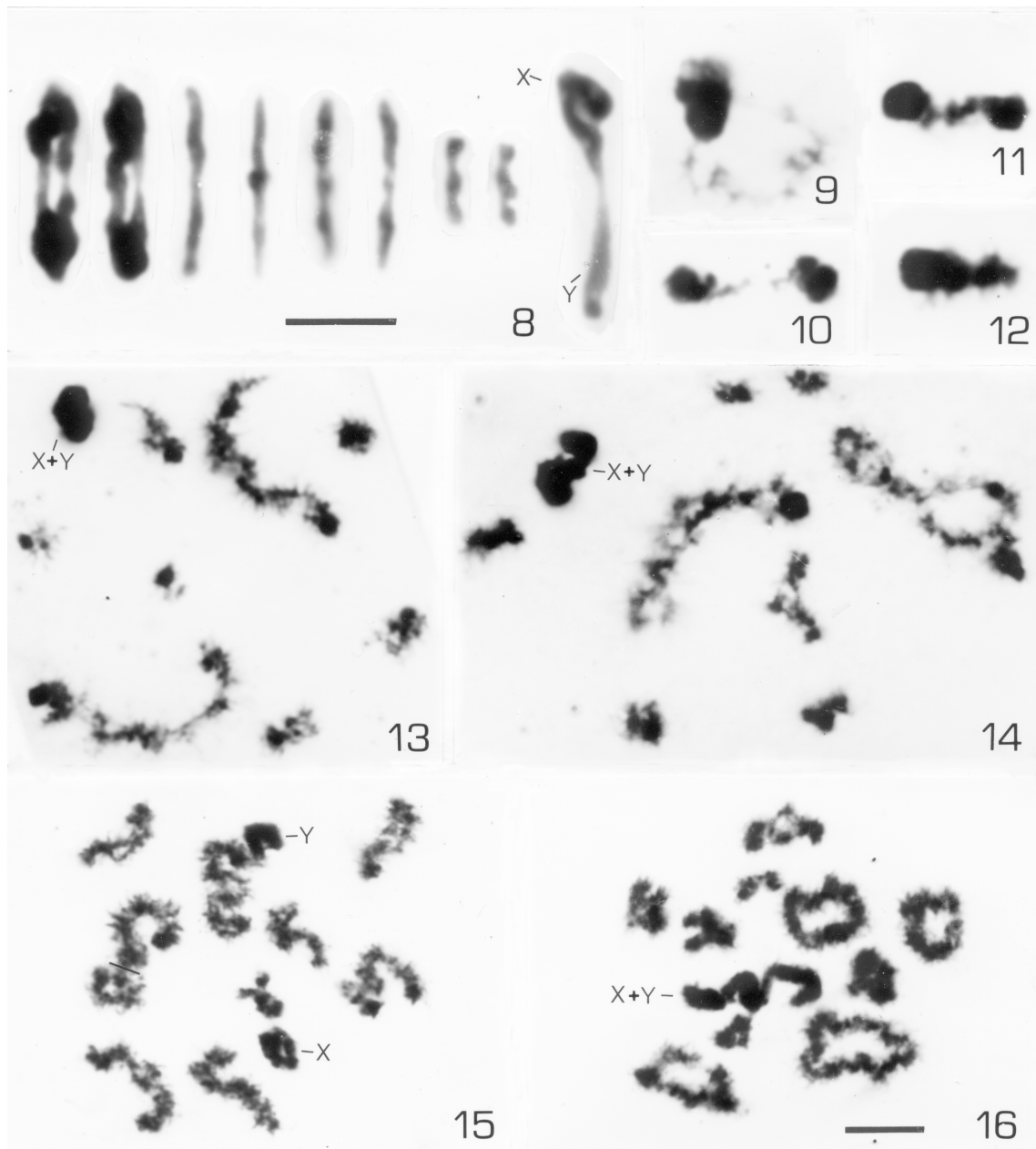
Another genus that includes all its species with X-A centric fusion is *Eurotettix*. In this case a second centric fusion between the neo Y and a second pair of autosomes

took place, transforming the males into X1X2Y and the females into X1X1X2X2. Four species of this genus, *E. lilloanus*, *E. schrottkyi*, *E. sp. n. 1* and *E. sp. n. 2* (Mesa *et al.* 1982) have X1X2Y males. *E. minor* has XY males, but judging from the morphological characters, this species probably belongs to a different genus.

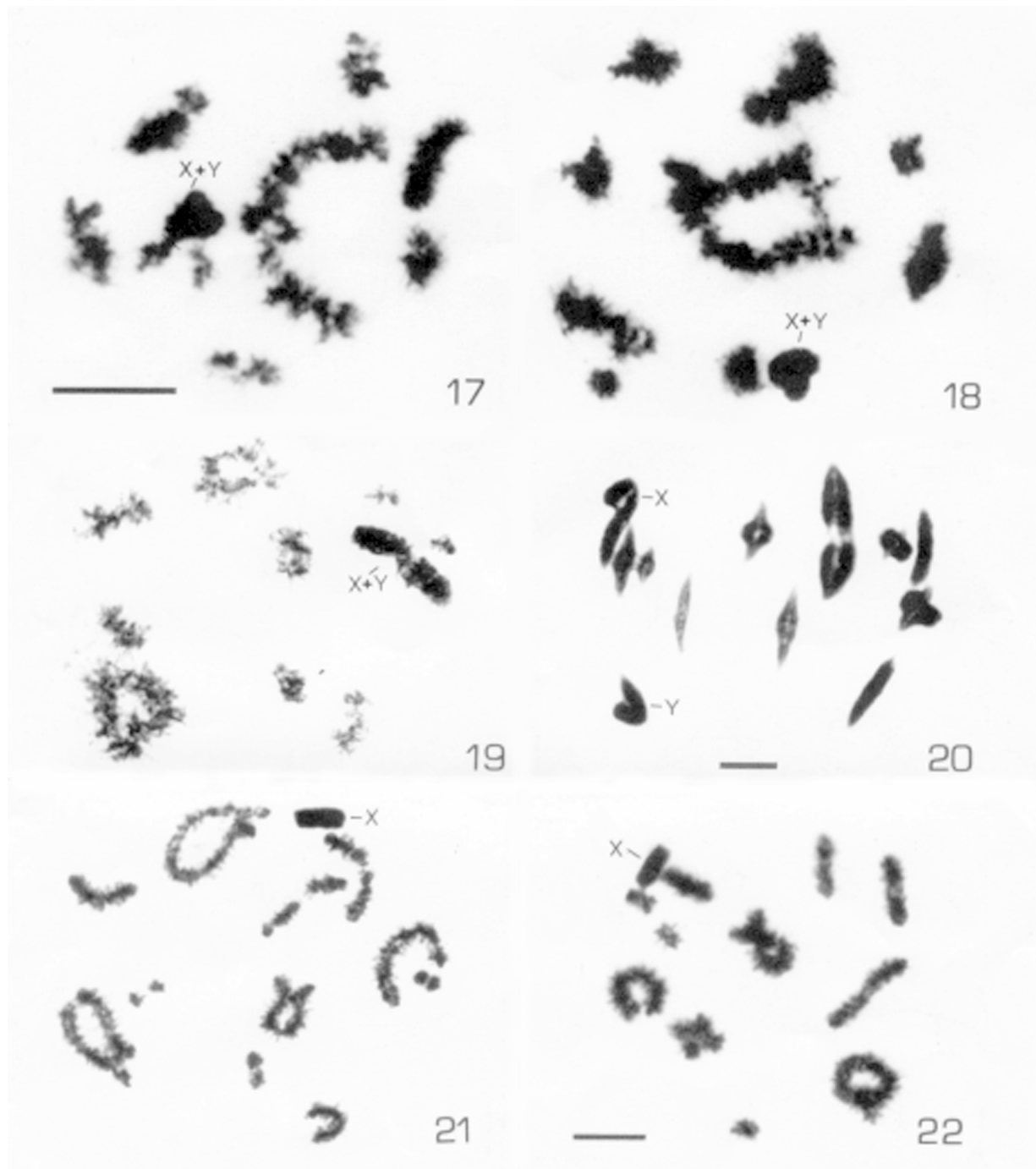
The whole process from a recent to an ancient neo XY mechanism needs to take place in a relatively short period of time, since X0 and old neo XY species sometimes coexist within the same genus, as in species of *Dichroplus* (Mesa *et al.* 1982). If the process ends with the whole heterochromatinization of the neo XY pair, an accumulation of species with this kind of mechanism would be expected, but this does not occur. In the approximately fifty species with neo XY mechanisms discovered in the neotropical region (Mesa *et al.* 1982), three species are at the beginning of the process, six at the end and the remaining species are in intermediate stages.

Since there is no accumulation in the number of species with old mechanisms and no higher taxon than genus which has all its species with neo XY mechanisms of a single origin (except perhaps the *Aleuas*, *Zygoclistron* group), it is logical to infer that the species with neo XY mechanisms may be extinct at the end of the process.

The meiotic structural changes observed in the bivalents during first prophase could be an indication of meiotic disorders that finally conduce the species to a deficit in the number and fertility of male gametes, starting then the consequent species decay. An early and whole condensation of the XR arm in male first meiotic prophase, compromising the control of a normal meiotic process, could be the reason for the difficulties that lead the species to extinction.



Figs 8-16. *D. vittigerum*. 8. First metaphase with neo XY at the right end. Autosomal bivalents with waxy outlines. 9. XL and Y tightened, connected and with XR forming a short euchromatic loop. 10. XL and Y separated and connected by a short segment of XR. 11 and 12. *Idem.* during diakinesis, with XR more compact. 13. Late pachytene with unusual bivalent waving and X and Y compacted in a single mass. 14. *Idem.* at diplotene. *D. maculipennis*. 15. Failure of pairing between X and Y at diplotene, due to an extreme reduction of the XR-Y pairing region. 16. Late diplotene with distal XR-Y pairing and XR heterochromatic. Both stages showing waxy contours of their bivalents. Scale bars 10 μ m.



Figs. 17-22. *A. diminuta*. 17. Early diplotene with waxy outline and XY tightly packed; 18. *Idem.* during middle diplotene. *Z. trachystictum*. 19. Diplotene with unusual extended chromosomal rings and with XR heterochromatic. 20. Late metaphase I. *X. robustus*. Species with X0 males, normal diplotene (21) and diakinesis (22). Scale bars 10 μ m.

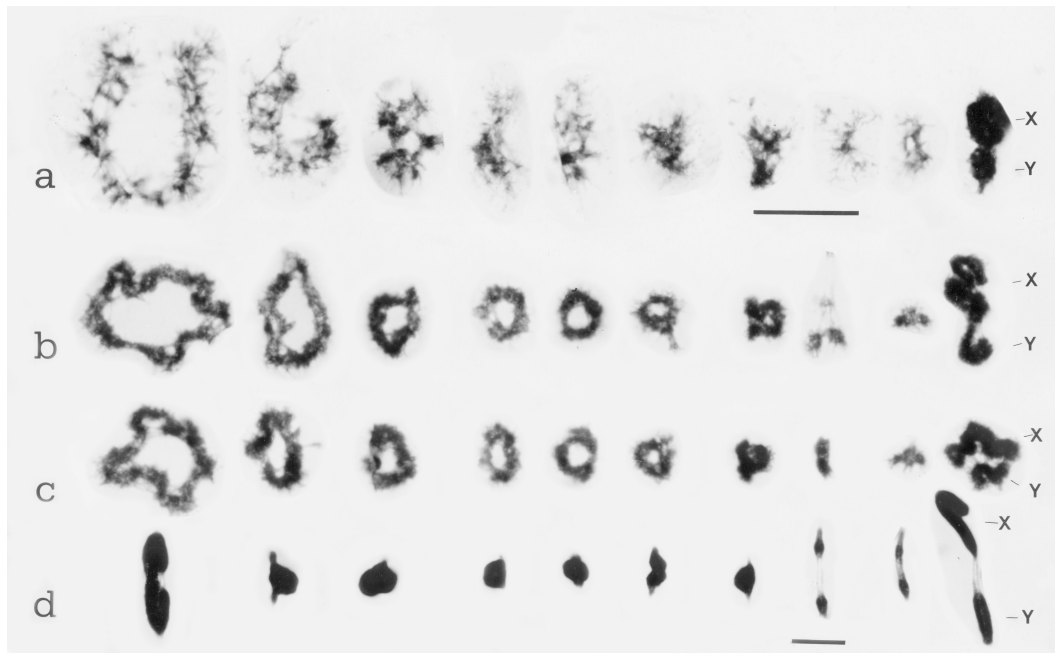


Fig. 23. *Z. falconicum*. a: late pachytene with XR heterochromatic; b, c: diplotenes. In c with X and Y connected by non-chiasmatic threads; d: first metaphase. Scale bars 10 µm.

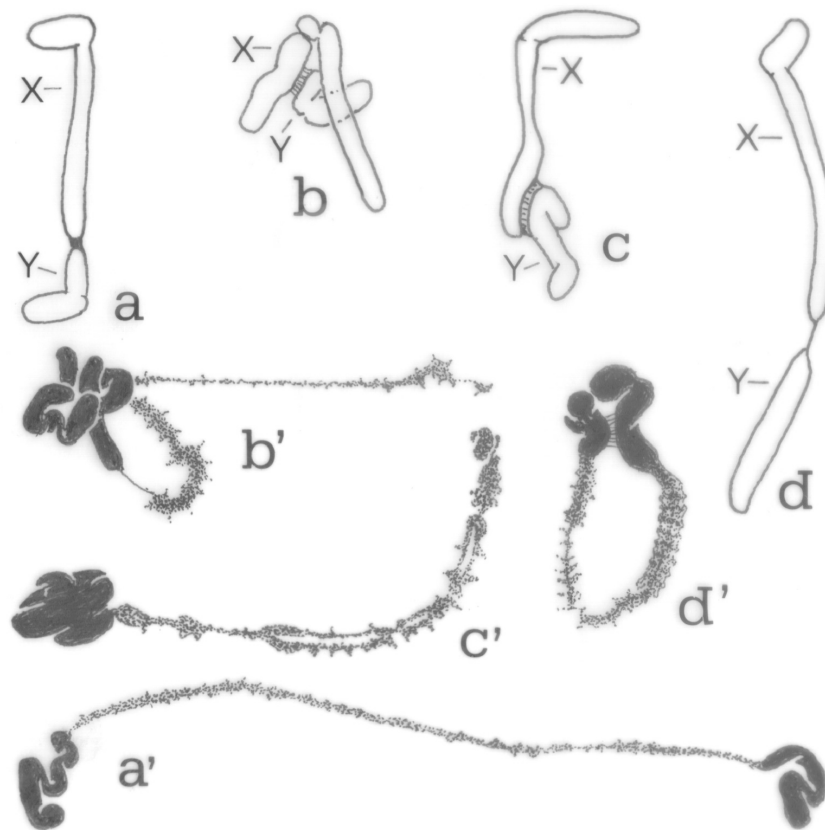


Fig. 24. Neo XY sex chromosomes of four species of the genus *Aleuas*. a, a': *A. lineatus*; b, b': *A. vitticollis* (= *brachypterus*); c, c': *A. sp.n. 1* from Corrientes Province (Rep. Argentina); d, d': *A. sp. n. 2* from Caaguazu (Paraguay). a, b, c and d during first metaphase. a', b', c' and d' during diplotene.

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