The Chromosomes of *Dicranocephalus agilis* (Hemiptera : Heteroptera)

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Introduction

The establishment of a sex chromosome mechanism depends on the creation of differential segments between which there is no crossing over. Chromosome reduction normally depends on chromosome pairing: qualitatively specific and quantitatively limited pairing. The sex chromosomes of many species consist, therefore, of both pairing and differential segments. But, in some cases, the sex chromosomes are completely differential. They enjoy no gene exchange and their homology is only historical.

In such cases special mechanisms must exist to ensure the regular segregation of the sex chromosomes in the heterogametic sex. Some of these devices operate only in isolated species as in *Tipula maxima* (John 1957), others would appear to act throughout a genus, for example *Blaps* (Lewis and John 1958), but in one case the same basic mechanism, like the condition which demands it, is found in many families of a much larger group, namely, the Heteroptera. The present account deals with one species from this group, *Dicranocephalus agilis* (Scop).

Males of this species were taken at Padstow in Cornwall and we are indebted to G. E. Woodroffe for supplying the material. The testes were dissected out under saline and were fixed in 1:3 acetic-alcohol for one to three days before squashing in either aceto-carmine or acetic orcein. Both these stains are satisfactory, but the latter does not stain the nucleolus (Lewis 1957).

Observations

Mitosis

The chromosome number in the male is $2n=14$. The complement includes two very small m-chromosomes. The largest pair also can be distinguished but the remaining chromosomes, which include the sex chromosomes, are sub-equal. They cannot be classified with any certainty nor can the sex chromosomes be identified in the very contracted metaphase plates

of the gonial mitoses. The mitotic chromosomes are double along their entire length and show no longitudinal differentiation.

Meiosis

The resting spermatocyte nuclei include a positively heteropycnotic body and a nucleolus which are not associated. With the advent of division the heteropycnotic mass is resolved into two chromosomes, one slightly larger, both of which are seen to be double at zygotene. These are the sex chromosomes. By analogy with other XY heteropterans the larger chromosome is probably the X chromosome (Fig. 1).

The meiotic sequence is characterised, as in other Heteroptera, by a pre-diplotene 'diffuse stage' during which the autosomes lose their affinity for nuclear stains but the sex chromosomes remain unaffected. At diplotene, there are no chromosome gradients and no localised repulsions. Five pairs of autosomes are associated, usually by one distally localised chiasmate. The small m-chromosomes are always unpaired (Fig. 2). The nucleolus is still present and associated with one of the autosomal bivalents.

The staining reaction of the autosomes at diakinesis approaches that of the sex chromosomes; terminalisation is almost complete and the nucleolus has disappeared (Fig. 3). Usually the sex chromosomes are still associated at pro-metaphase at which time they and the autosomes cannot be distinguished by their staining reaction. There is a slight stretching of the bivalents, but this is not comparable in extent to that found in the mantids and roaches (see John and Lewis 1957).

The spindle is broad at the metaphase of first division. The autosomes co-orientate with their long axes parallel with the spindle and congress to form a ring at the periphery of the equatorial plate. The sex chromosomes may show a spurious co-orientation but this is momentary (Fig. 4). The association between them lapses and the X and Y chromosomes auto-orientate, side by side, in the peripheral ring with the autosomes (Figs. 5 and 13). At equilibrium the sex chromosomes are closer to one another than they are to the autosomes. The sex chromosomes stain less deeply than the autosomes at this time and this distinction is maintained throughout the first and second divisions of meiosis.

The m-chromosomes are unpaired during prophase but at metaphase they are associated and co-orientated at the centre of the spindle (Fig. 6). This association is often more than momentary. They become materially connected as is shown by the attenuated region between them (Figs. 13 and 14). The m-chromosomes are negatively heteropycnotic at metaphase and, as is the case with the sex chromosomes, they maintain this condition until the completion of meiosis (Figs. 5 and 6).

The first division of meiosis is reductional for the m-chromosomes as there is no evidence for crossing over between them. It is reductional also for the differential regions of the autosomes but the first division is equa-

Figs. 1-6. All figures $\times 2000$. Figs. 1, 2 and 6 stained in acetic orcein; Figs. 3, 4 and 5 stained in aceto-carmine. 1, diffuse stage. The two sex chromosomes, the larger X and the smaller Y, both heteropycnotic and clearly double. 2, diplotene. m-Chromosomes unpaired. 3, diakinesis. Five autosomal rod bivalents, two m-chromosomes, and the two sex chromosomes still associated. Terminalisation almost complete. 4, early metaphase I. Spurious co-orientation of the X and Y chromosomes. m-chromosomes 'paired' in the middle of the plate. 5, metaphase I. Auto-orientation of the sex chromosomes. m-chromosomes understained. 6, metaphase I. Polar view. Peripheral ring and centrally located m-chromosomes.

tional with respect to the sex chromosomes.

They are somewhat delayed in their anaphase separation and, at anaphase, often lie slightly outside the ring of autosomes (Figs. 7, 8, and 9). The X and Y chromatids may associate to form a sex pseudo-bivalent at any time after metaphase. Usually they do so as they converge towards the spindle pole. The first and second divisions of meiosis are not separated by a resting stage.

At the second division the autosomes again form a ring at the periphery of the equatorial plate. But the spindle is much narrower than it is at the first division and the m-chromosome and the XY

Figs. 7-12. Figs. 9 and 12 $\times 4000$, others $\times 2000$. Figs. 5 and 6 stained in acetic orcein, others in aceto-carmin. 7, anaphase I. Sex chromosomes slightly delayed and understained. 8, late anaphase I. X and Y forming a pseudo-bivalent. 9, late anaphase I. One group in polar view. Centrally located m-chromosome. X and Y slightly outside the ring of autosomes. Sex and m-chromosomes understained. 10, metaphase. Unequal sex pseudo-bivalent and m-chromosome understained and centrally located. 11, metaphase II. Side View. Reductional separation

pseudo-bivalent orientate in the centre of this spindle (Fig. 10). The second division is reductional for the sex-chromosomes (Fig. 11). Their outline is much smoother than that of the autosomes. In fact, they have a distinctly

nucleolar appearance when stained with aceto-carmine. In this connection it is interesting to note that Henking who first described these chromosomes in the Heteroptera in 1891 thought them to be nucleoli (see Hughes 1952). The sex chromosomes do not uncoil with the autosomes at telophase and can be recognised in the spermatid nuclei (Fig. 12).

13

14

Fig. 13. Met/Anaphase I. Sex and m-chromosomes shown solid. Sex chromosomes lying close together and auto-orientated in the peripheral ring. m-chromosomes 'paired' in the centre of the plate. Fig. 14. Anaphase I. Sex and m-chromosomes shown solid. Equational division of the sex chromosomes. Chromosome ends directed polewards.

organisation :—

(i) The division cycle of the chromosome as a whole is similar to that of the chromosome arms in chromosomes with a localised centromere. The property of mobility may characterise all regions or scattered regions. X-ray breakage can provide some information regarding these alternatives but the evidence is equivocal. If all fragments, however small, are functional the first possibility is favoured but if they are non-mobile the second alternative is not proved until the possibility of physiological upsets in the chromosomes and/or cytoplasm is excluded, or

(ii) The chromosomes contain a number of scattered 'centromeres' similar to localised centromeres.

Discussion

The centromere

The chromosomes in all Heteroptera are believed to have a non-localised centromere (see Hughes-Schrader 1948). That this is the case in *D. agilis* is evidenced by:—

a) The mitotic chromosomes are without constriction and are double along their entire length. There are no regions with a special cycle of division.

b) These are true also of the sex chromosomes at zygotene, and

c) There are no gradients or localised repulsions in the chromosomes at meiosis.

The behaviour of chromosomes with a non-localised centromere could be determined and explained by two kinds of structural or-

of the sex chromosomes. Note size difference. 12, early spermatid nucleus. Autosomal ring and central sex chromosome. m-Chromosome not visible.

The two systems may differ, therefore, in something more than the spacing of the spindle-organising particles: they may differ in their division cycle. (It makes no difference to the present discussion whether, in the case of localised centromeres, sister chromatids are held together by the centromere itself or by the regions adjacent to it as suggested by Lima-de Faria in 1953).

Where the organisation is 'diffuse' (Type (i)), terminalisation can be complete. But where it is 'polycentric' (Type (ii)), terminalisation will be arrested if the 'centromeres' remain undivided (Fig. 15).

The observations given above suggest that the chromosomes are of the 'diffuse' type in *D. agilis*. In the horse nematode, *Parascaris equorum*, on the other hand, the central centric segments of the chromosomes may be of the 'polycentric' type in which case these regions must be differential, i.e. no crossing over occurs in them, or the multiple centromeres divide precociously before first anaphase.

Fig. 15. Two types of structural organisation which can account for non-localised mobility. (i) Diffuse: Uniform cycle of division, (ii) Polycentric: Regions with a special cycle of division. Regions having the property of mobility are shown in outline. The possibilities given above are similar with respect of the distribution of these regions but they can differ.

The valency of the chromosomes is important in another mechanical respect because it is one of the factors determining the arrangement of the chromosomes on the spindle. And, clearly, where the centromere is diffuse, any conclusion regarding the valency of the chromosome must apply equally to the centric regions.

Arrangement of the chromosomes on the spindle

The following factors are involved:—

- a) The space available: This will depend on the size of the spindle and on the number and size of the chromosomes,
- b) General or Body repulsions: These depend partly on the size of the chromosomes and
- c) The valency of chromosomes.

These factors may operate in the same direction to accentuate differences in position or in opposite directions to obscure them. Also some of the variation within individuals may well be spurious, resulting from the observation of metaphase plates which, though flat, are not at equilibrium.

In general:—

- a) Associations with the highest valency (bivalents at first division and daughter bivalents at second division) will occupy the periphery of the spindle if space permits, and

b) Small chromosomes with small body repulsions (e.g. m-chromosomes) will occupy the centre of the spindle at metaphase.

The operation of these factors has been discussed in detail by Darlington (1939) and here they will be considered mainly in relation to *D. agilis*.

i) *The autosomes*

In the absence of localised centromeric repulsion the chiasmata are presumably terminalised by body repulsions to the ends nearer which they were localised. The bivalents are orientated with their long axes parallel with the spindle axis. In general, the Heteroptera differ in this respect from the Homoptera where the reverse holds. Among the factors controlling this difference may be included the time and place at which the chromosome spindle-fibres are organised.

In coccids it seems that these fibres are already present at diakinesis and produced along the entire length of the chromosomes (see fig. 17, Hughes-Schrader 1948). Attempts to demonstrate continuous fibres in this group have not been successful. If, therefore, the spindle is organised almost exclusively by the chromosomes, as appears to be the case, the observed arrangement at metaphase is inevitable. This does not deny the existence of cell polarity. On *a priori* grounds such a polarity must exist to control the relative orientation of the chromosomes. Moreover, the convergence of the fibres to more or less discreet poles provides *a posteriori* evidence for the existence of polar organisers.

Our preparations of *D. agilis* were made after only short periods of fixation and by methods which do not readily stain fibres. However, there were no indications of chromosome fibres until pro-metaphase. At this stage they can be seen, occasionally, at the non-chiasmate ends of the chromosomes which are directed polewards at this time as they are until the completion of anaphase. This is not regarded as evidence against the diffuse centromere but it suggests that all regions of the chromosome capable of organising fibres at mitosis are not functional at meiosis. In the same way all potential organisers of nucleoli are not functional at all times in all tissues. It will be remembered also that neocentric activity of chromosome ends, where it occurs, is operative only at meiosis and all these may be relateable phenomena (see Darlington 1951).

The autosomes in *D. agilis* behave in the orthodox Heteropteran manner. They are arranged in a peripheral ring at both first and second metaphase as is expected from both their size and their valency.

ii) *The sex chromosomes*

The sex chromosomes are distinguished by their positive heteropycnosis at prophase of meiosis I and by their non-homologous association at this stage. They are also precocious in their division. Precocity of condensation, association and division are often coincident and this has been recorded by many investigators (see Davies 1956).

The sex chromosomes remain associated after the dissolution of the nuclear membrane and 'co-orientate' coincidentally as the autosomes. This is expected on account of the size and valency of the sex 'bivalent' and on the space available. But their association lapses and they then auto-orientate side by side. Their position is instructive. They lie close together, suggesting that their mutual repulsion is reduced compared with that of the autosomes. But it must be greater than it was previously and greater than it is subsequently, for metaphase is the only time when the sex chromosomes are not associated. At prophase and anaphase their mutual 'repulsion' is so reduced that they fuse.

The side by side orientation at the metaphase of meiosis can be compared with the situation at mitosis in the Diptera where homologous chromosomes show somatic pairing at prophase and lie near one another on the metaphase plate. Here also a reduced repulsion is indicated.

Indeed, in some Heteroptera the mutual repulsion of the sex chromosomes is so reduced that they congress to the centre of the spindle even at first metaphase. This is true in *Lygaeus hospes* and *Dieuches uniguttatus* (see Manna 1951). In the former the sex chromosomes among the smallest in the complement and in the latter the X and Y chromosomes have always separated before diakinesis.

The dissociation of the X and Y chromosomes in *D. agilis* occurs when the allosomes and autosomes are indistinguishable in their staining reaction. They associate on the other hand whenever they differ in their staining reaction—when they are relatively overstained as at prophase or understained as at anaphase. The characteristic stickiness of over-condensed heterochromatin, at certain times, is well-known, but its association when under-condensed has also been recorded.

For example, Cooper (1944) found that in the dipteran, *Olfersia bisulcata*, somatic pairing was confined to particular homologous segments which were "relatively less condensed than the customarily widely separated portions". Moreover, understained segments often fail in their anaphase separation and this may be due, at least in part, to reduced repulsion (Klingstedt 1940). In this connection also, John (1957) has found that neo-centric activity—a property often associated with heterochromatin—is shown by the sex chromosomes of *Tipula maxima* only when they are understained.

These considerations concerning the sex chromosomes of *D. agilis* may apply to other members of the Heteroptera. In his cytotaxonomic investigation of Indian Heteroptera, Manna (1951) records that one or all the sex chromosomes are negatively heteropycnotic at the later stages of meiosis I in *Lygaeus hospes*. This is true also of both species of the sub-family Harpactorinae (Reduviidae) which he studied, namely, *Harpactor fuscipes* and a species of *Sycanus*. These latter have multiple sex chromosomes and the difficulty of ensuring co-orientation and disjunction are presumably increased in consequence.

In *Cimex* and in other Heteroptera however, negative heteropycnosity of the sex chromosomes has not been recorded. And, in *Cimex*, it has been found that the second division, the metaphase in particular, is of comparatively long duration. This is regarded as necessary to ensure the 'co-orientation' of the sex chromosomes (Darlington 1939).

In *Harpactor fuscipes*, on the other hand, the sex chromosomes are negatively heteropycnotic at second division also, as is the case in *D. agilis*. This suggests that interphase is absent, again, as in *D. agilis*. This may well mean that the second division as a whole is more rapid and the time available for co-orientation in *Cimex* is not available in *H. fuscipes* and *D. agilis*.

The adaptive significance of negative heteropycnosis in these organisms, therefore, may be the early association of the sex chromosomes which accompanies it. Evidently, 'co-orientation' can occur more easily and rapidly when the chromosomes are associated. In fact, Wilson (1912) found that in *Oncopeltus fasciatus* the sex pseudo-bivalent is formed during first anaphase and the first and second divisions of meiosis are not separated by a resting stage. Rao (1955), on the other hand, found that in the related species, *Oncopeltus nigriceps* (Dall), the sex chromosomes did not associate at this time: but an interphase was present.

These considerations immediately suggest an additional factor in the non-chiasmate association of the m-chromosomes at first metaphase.

iii) *The m-chromosomes*

These are unpaired at prophase but move to the centre of the spindle at metaphase I. This is in keeping with their valency and their small size. Like the sex chromosomes, they associate when they differ from the autosomes in their staining reaction. This again suggests a reduced repulsion which will facilitate their central congression. Evidence in support of this can be found in the description of *Elasmomia granulipes* (Manna 1951). He states that "unlike other species of coreids, the m-chromosomes do not show any negative heteropycnotic behaviour", and later "first division metaphase plates, in some cases, do not show the usual coreid pattern of arrangement in having the m-chromosome pair invariably in the centre". Also in *Leptocoris auger*, another coreid, the m-chromosomes are associated in only 8% of the cells at diplotene, but in 20% of the cells at diakinesis. This difference may depend on the m-chromosomes becoming negatively heteropycnotic at an earlier stage of division as, for example, in *Leptocrixa acuta*, where they are understained at diplotene and associated in 22% of the diakinesis nuclei.

Allocycl

All the chromosomes within a nucleus are subject to the same genotypic control and the same cellular conditions. During division the chromosomes have a characteristic cycle which is geared to the cell cycle. Therefore,

when a chromosome or chromosome segment differs in its behaviour from the rest of the complement, it must differ also in a way which determines its different behaviour. These causal differences are often gross structural changes as in the case of structural heterozygotes but others are not of this kind.

Differences in behaviour are often accompanied by differences in appearance. But it cannot be concluded that a causal relationship exists, necessarily, between them in the sense that the one determines the other. They may both be effects, albeit of the same cause. The visual differences may be important only in that they reflect or confirm the difference in state which must be inferred on other grounds. The validity of the inference regarding this 'causal state' will depend largely upon the particular aspect of chromosome behaviour under consideration and how well this is understood.

For example, the similarity in the reproductive cycles of the chromosomes and DNA and the genetical significance of both leaves little doubt that they are intimately related. The splitting of a chromosome into two chromatids may not coincide with its reproduction but the latter must be a necessary antecedent except in abnormal circumstances. DNA, therefore, may be the causal agent which determines the difference in the division cycles of the autosomes and the sex chromosomes. But in this connection it must be remembered that a chromosome may consist of three kinds of segment, all distinguishable in their 'charge cycle' and yet behave—as it must behave—as a unit in heredity (John 1957).

DNA has been held responsible for the other distinguishing properties of the sex chromosomes discussed earlier. This too may be more apparent than real. Changes in the quantity and distribution of polymerised DNA is one of the few convenient markers in the cell and these changes may equally be effects important only in that they provide visible proof of allocyclus.

In the same way, positive heteropycnosis *per se* cannot be held responsible for the non-homologous association of the sex chromosomes in *D. agilis* because they associate also when understained. It is not so much the 'state' which matters but the difference in state: not the cycle but the allocyclus. Of course, all allocyclus is not visually revealed. This conclusion can be reached by considering the somatic pairing and the non-chiasmate male meiosis of *Olfersia bisulcata* already mentioned.

Somatic pairing is confined to particular segments which are understained. Similarly, at meiosis, 'pairing' is confined to these same segments but at meiosis they show no differences in staining reaction. Thus, it is neither homology nor pycnosity alone which determines the association.

That timing relations are important also is shown by Callan's (1941) observations on *Forficula auricularia* (Dermaptera). Some males of this earwig have three sex chromosomes, two X chromosomes and a Y, which are positively heteropycnotic in the spermatocytes. But unless these chro-

mosomes fuse in the telophase of the last premeiotic mitosis they remain unassociated. "No further fusion of the sex chromosomes occurs after the telophase of the spermatogonial division, i.e. a bivalent and univalent condition of the sex chromosomes at leptotene persists until the anaphase of first meiosis".

Chromosomes are generally very uniform in their superficial appearance and in their behaviour in very diverse groups. Almost all inheritable differences and therefore evolutionary changes are due to differences in the chromosomes and the genes which they bear. But the exact requirements of nuclear propagation make the mechanical properties of chromosomes among the most conservative. The Hemiptera, particularly the Homoptera, however, are notoriously individual in their chromosome behaviour. For this reason it is not possible to generalise too far on the basis of these observations on *Dicranocephalus agilis*. The behaviour of the chromosomes, like their number, shape and size, will vary depending on the stage in their evolution. And in this respect it must be remembered that all properties do not evolve together or at the same rate.

The systematic position of *Dicranocephalus*

Until very recently, the genus *Dicranocephalus* Hahn was placed in the Coreoid family Alydidae. Scudder (1957), however, after studying the structure of the egg, male and female genitalia, salivary glands and other morphological characters, showed that *Dicranocephalus* represented a new family, Stenocephalidae Douglas and Scott 1865, which should be placed between Lygaeidae and Coreidae, being most closely related to Lygaeidae and occupying a position similar to Largidae.

Manna (1951) has pointed out that the Lygaeoidea have usually an XY sex chromosome mechanism and a smaller number of chromosomes, whereas Coreoidea have usually an XO sex chromosome mechanism with a large number of chromosomes. Both Coreoidea and Lygaeoidea (except Lygaeinae—Orsillini, previously placed in the Lygaeinae, are considered to represent a eeparat sub-family of the Lygaeidae, leaving Lygaeinae to include the Lygaeini only) are characterised by possessing a pair of m-chromosomes. The presence of such a pair in *Dicranocephalus* supports the inclusion of Stenocephalidae in the Lygaeoid-Coreoid complex. Further, the XY sex chromosome mechanism and the low chromosome number supports the placing of Stenocephalidae as a family of the Lygaeoidea.

Summary

1. The chromosome number in the males of *Dicranocephalus agilis* is $2n=14$. The complement includes a pair of m-chromosomes and a pair of

sub-equal sex chromosomes.

2. The first division of meiosis is reductional for the differential regions of the autosomes and for the m-chromosomes which are completely differential. It is equational with respect of the sex chromosomes.

3. The sex chromosomes are positively heteropycnotic at the prophase of meiosis I and are associated non-homologously. They are double when the autosomes pair at zygotene.

4. At metaphase of first and second division the autosomes congress to form a ring on the periphery of the spindle. This is in keeping with their size, valency and the space available.

5. At equilibrium, the sex chromosomes auto-orientate side by side in the ring with the autosomes at first metaphase. The sex pseudo-bivalent congresses in the centre of the spindle at second metaphase where less space is available.

6. The sex chromosomes become negatively heteropycnotic at first metaphase and the sex chromatids form a pseudo-bivalent during their anaphase separation. This is facilitated by their side by side orientation at metaphase (a consequence of their earlier association), their convergence as they approach the poles and their reduced repulsion.

7. The early formation of the sex pseudo-bivalent in *D. agilis* and *Oncopeltus fasciatus* is considered adaptive in the absence of an interphase which suggests a more rapid division than in *Cimex* and *Oncopeltus nigriceps* where the pseudo-obivalent forms later and the second division is of longer duration.

8. The m-chromosomes are unpaired at prophase of the first division but associate in the centre of the spindle at first metaphase when they are understained. They congress to the centre of the spindle at second division also. They, and the sex chromosomes remain understained until the completion of meiosis.

9. The differential staining of the sex and m-chromosomes compared with the autosomes is important only in that it provides a visible demonstration of allocycly which can be inferred on other grounds.

10. The centromere in *D. agilis* is diffuse. It is suggested that the time and place at which the chromosomal spindle fibres are organised are partly responsible for determining whether the first division of meiosis is reductional for the differential segments (as is general in the Heteroptera) or equational (as is generally the case in the Homoptera).

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