Theor Appl Genet (1985) 70:213–221

A new mechanism for altering chromosome number during karyotype evolution

I. Schubert and R. Rieger

Zentralinstitut für Genetik und Kulturpflanzenforschung der Akademie der Wissenschaften der DDR, DDR-4325 Gatersleben, German Democratic Republic

Received October 30, 1984; Accepted December 27, 1984
Communicated by F. Mechelke

Summary. A new mechanism for changing chromosome numbers (preserving the fundamental number of long chromosome arms) during karyotype evolution is suggested. It includes: 1) Occurrence of individuals heterozygous for two interchanges between different arms of three chromosomes (a metacentric and two acrocentric ones). 2) Formation in heterokaryotypes of multivalents during meiosis between the chromosomes involved in the interchanges and their unchanged homologues. 3) Mis-segregation of chromosomes from these multivalents resulting in hypoploid (n−1) and hyperploid (n+1) simultaneously instead of euhaploid gametes. 4) Fusion of n−1 or n+1 gametes which gives rise to (zygotes and) individuals representing homokaryotypes with changed number of chromosomes (2n+2 or 2n−2), but preserves (as compared to the parental karyotypes) the number of long chromosome arms. Under definite conditions, chromosome numbers of the progeny may be changed by this process in both directions (upwards and downwards). The mechanism is free of the difficulties associated with the explanation for such changes by direct Robertsonian interchanges (see "Discussion"), which are usually considered to be responsible for such alterations in chromosome number. The above-mentioned process has been experimentally documented in *Vicia faba* and it probably also occurred naturally within the *Vicia sativa* group.

Key words: Chromosome numbers – Karyotype evolution – Interchange heterozygotes – Multivalent segregation – *Vicia faba* – Pseudoaneuploidy – Robertsonian exchanges

Introduction

Though the knowledge concerning karyotype evolution is still rather incomplete, some basic mechanisms are known (for reviews, see John and Lewis 1968; Stebbins 1971; White 1973; Kaina and Rieger 1979; Holmquist and Dancis 1980) which may be classified as the following:

1) Structural rearrangements of chromosomes without quantitative changes of chromosome number: i.e., para- and pericentric inversion, symmetrical reciprocal translocations, intra- and interchromosomal segment transpositions, duplications or deletions due to unequal sister chromatid exchange or crossing over, crossing over in inversion heterozygotes, erroneous replication or asymmetrical interchanges, and random breakage of the dicentric products during mitosis.

2) Centric fusion of acro- or telocentric chromosomes (Robertsonian interchanges) and centric fission of metacentrics resulting in pseudoaneuploidy. Under these circumstances, the fundamental number of the karyotype, i.e., the number of long chromosome arms, remains constant while the chromosome number changes.

3) Addition or loss of whole chromosomes (aneuploidy) or whole chromosome sets (polyploidy and haploidy, respectively).

In different groups of organisms these mechanisms are, individually or in specific combination, of varying importance in karyotype evolution.

The present paper deals with the generation of pseudoaneuploid changes of chromosome numbers via aberrant multivalent segregation in individuals heterozygous for two reciprocal translocations (interchanges)

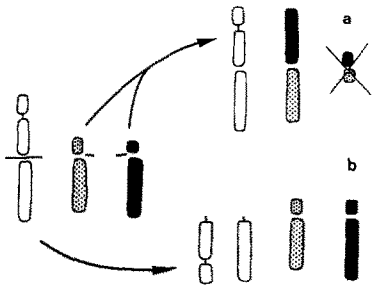

Fig. 1. Change in chromosome number via Robertsonian interchanges. **a** Reduction of chromosome number by centromere fusion: two acrocentrics give rise to one metacentric composed of the long and another composed of the short chromosome arms; the latter is usually lost. **b** Increase of chromosome number by centromere fission (dissociation): a metacentric gives rise to two telocentric chromosomes each representing one arm of the former metacentric (for further explanation see text)

involving three chromosomes. Mechanisms of this kind, for which experimental evidence is presented, may in fact represent one route of karyotype reconstruction and karyotype evolution.

Change in chromosome numbers through heterozygosity for multiple translocations and mis-segregation of multivalents

Theory

Up to the level of a haploid chromosome number of two, only true Robertsonian exchanges (centromere fusion or fission, see Fig. 1) or derived processes as postulated by Holmquist and Dancis (1980) result in changes in chromosome numbers. However, with

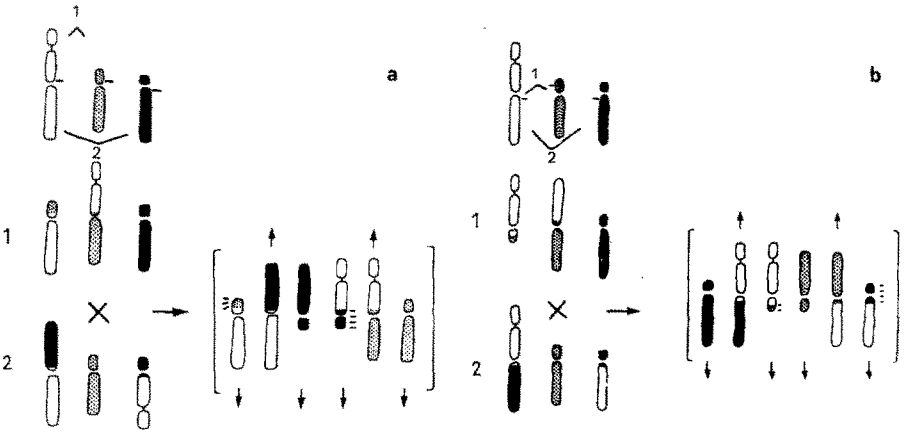

Fig. 2 a–j. Various possibilities of interchanges between the arms of one metacentric and the arms of two acrocentrics in a hypothetical karyotype with three chromosomes, and the hexavalents (in brackets) which can be formed in double heterozygotes after crossing of two different interchange lines (1×2) involving all three chromosomes. Mis-segregation from these hexavalents may result in n − 1 = 2 and n + 1 = 4 gametes as indicated by *arrows;* duplications and deletions, respectively, in pseudoaneuploid gametes are labelled; duplication and deletions of complete long arms are supposed to be lethal (**2 e–j**) and therefore interchange combinations producing them are excluded as an acceptable basis for changing chromosome numbers. **a** Interchanges between the satellite arm of the metacentric and the short arm of one and the long arm of the other acrocentric; n + 1 gametes with the labelled regions duplicated should be viable. The corresponding n − 1 gametes with the two new metacentrics are expected to be only viable when the deletions of the corresponding regions do not contain essential genes (see text). There are two variants of this type of interchange combination depending on which of the acrocentrics is involved in the interchanges with the long arm and which with the short arm; **b** The same as (**a**) but both interchanges involve the second (instead of the satellite) arm of the metacentric (also two variants are possible); **c** Interchanges involving both arms of the metacentric and the short arms of both acrocentrics. Two variants are also possible depending on which acrocentric receives the satellite and which one the second long arm of the original metacentric; **d** As (**c**) but instead of the short arms, the long arms of both acrocentrics are involved in the interchanges. In such case (two variants) the hyperploid gametes contain a deletion of the centromere of the original metacentric in addition to the centromere and short arm duplications; again the opposite is true for the hypoploid gametes with the two new metacentrics; **e** The satellite arm of the original metacentric is interchanged with the short arms of both acrocentrics (one variant only in this case). Hypo- and hyperploid gametes contain both deletions and duplications of the complete long chromosome arms and are therefore assumed to be lethal and thus not contributing to changes of chromosome number; **f** The satellite arm of the metacentric is interchanged with the long arms of the acrocentrics. The consequences are the same as in (**e**). The same is inferred for (**g**) and (**h**) where the second arm of the original metacentric is interchanged with either the long (**g**) or the short (**h**) arms of both acrocentrics. Interchange combinations between the satellite arm and the long arm of an original acrocentric on the one hand, and the second arm of the metacentric and the short arm of the other acrocentric on the other (**i**), or vice versa (**j**), would also result in inviable hypo- and hyperploid gametes due to the above-mentioned duplications and deletions of complete long arms; (**i**) and (**j**) may both occur in two variants

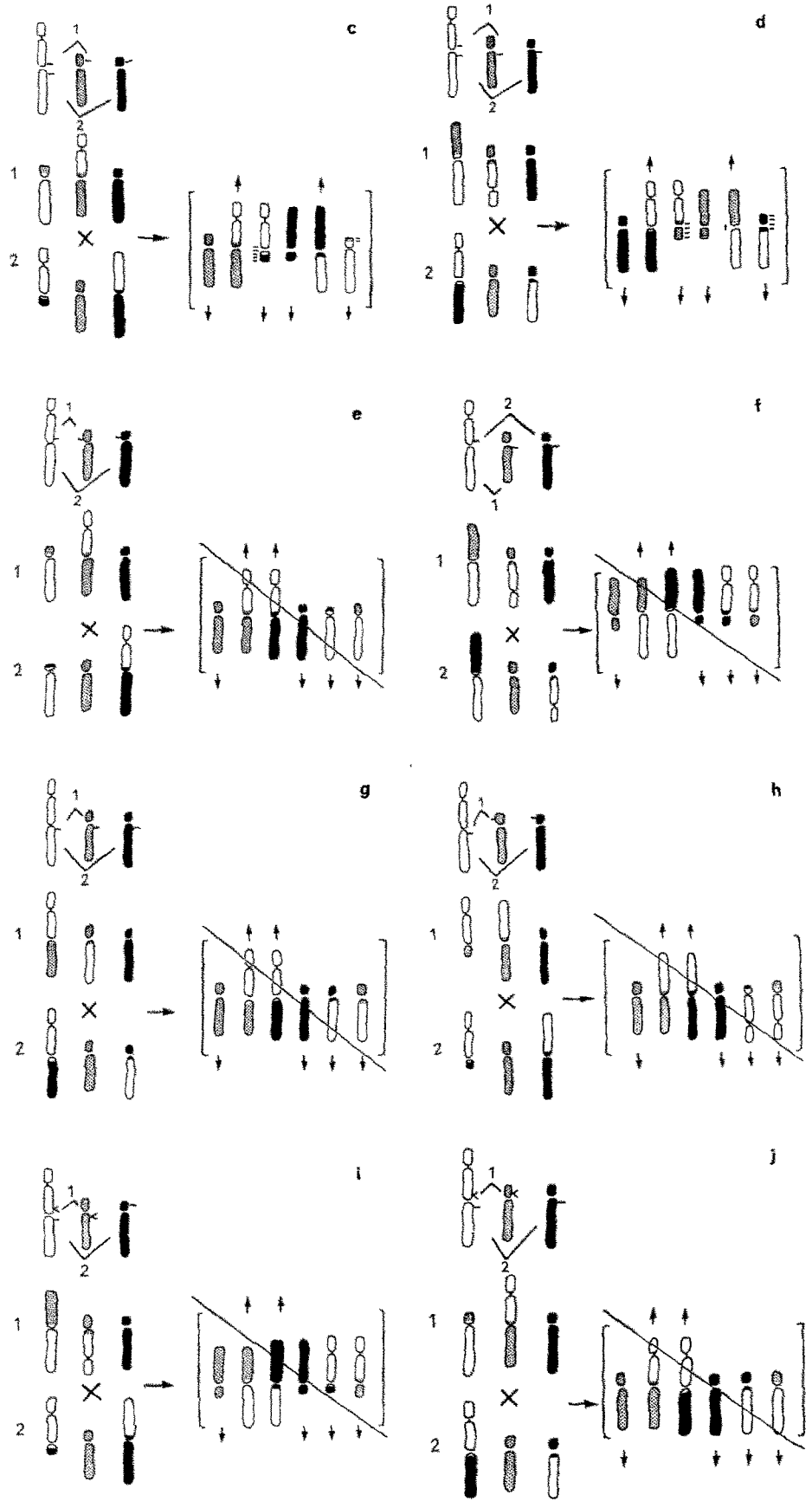

Fig. 2c–j

haploid chromosome complements consisting of three or more chromosomes another mode of altering chromosome number (Fig. 2) becomes possible provided the following prerequisites are fulfilled:

a) Presence of at least one metacentric chromosome in the original karyotype.

b) Availability of two reciprocal symmetric interchanges – each of them with one translocation point located in the same or in opposite arms of the original metacentric and the other in one of two different acrocentrics (see Fig. 2). The translocation breakpoints should be located near the centromeres.

c) Production by appropriate crossing of heterokaryotypes for the above-mentioned interchanges and formation, at meiosis, of one hexavalent or two trivalents involving the chromosomes which participated in the interchanges and the structurally unchanged acrocentric homologues.

d) Aberrant segregation (mis-segregation) of the chromosomes which participate in the multivalent(s) resulting not in euhaploid gametes but in hypoploid (n−1) gametes with both reconstructed metacentrics and hyperploid (n+1) gametes containing the four arms of the translocated metacentrics as acrocentrics (two original and two translocated chromosomes) (Fig. 2).

e) Fusion of two n+1 gametes or of two n−1 gametes giving rise to homozygous karyotypes with new chromosome numbers. These are either higher (2n+2) or lower (2n−2) in chromosome number than the original karyotype.

In the karyotype with 2n+2 chromosomes there is one metacentric chromosome less than in the original karyotype. The missing metacentric is replaced by two acrocentric chromosomes whose long arms are derived from the two arms of the original metacentric chromosome, for example in the following way (Fig. 2a, b): one of these acrocentrics contains one arm and the centromeric region of the original metacentric plus the telomeric region of the short arm of its original acrocentric interchange partner. This telomeric region therefore represents a duplication. The other new acrocentric contains, in addition to the second arm of the original metacentric, the centromere and short arm of its original acrocentric interchange partner as a duplication.

Just the opposite is true for the 2n−2 karyotypes. They contain one metacentric more than the original karyotype and lack those regions being duplicated in the corresponding hyperploid karyotypes.

If both the above-mentioned duplications and the corresponding deletions are tolerated (or even selected for), changes in chromosome number in both directions may occur simultaneously in the progeny. Deletions may be tolerated provided the deleted material is either nonessential, redundant or even dispensable in the sense discussed by Marks (1983). When only duplications are being tolerated, the described mechanism results exclusively in an increase in chromosome number (Fig. 2a–c) up to the level at which sufficient redundancy of genetic material allows also reduction of chromosome number (Fig. 4h).

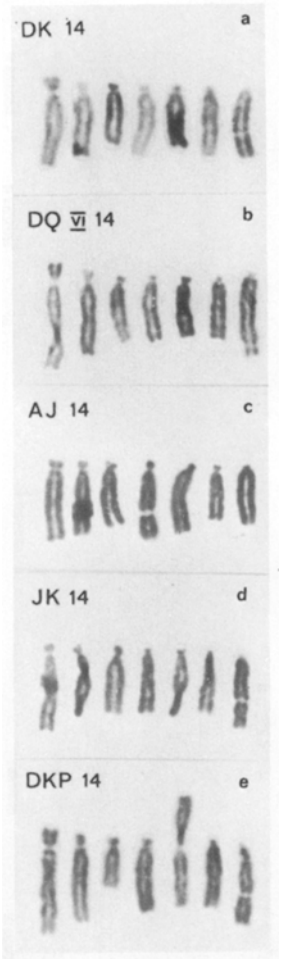

Fig. 3a–e. Haploid chromosome sets of 5 karyotypes of *Vicia faba* with 14 instead of 12 chromosomes which resulted from mis-segregation of multivalents in karyotypes heterozygous for two interchanges between the satellite arm of the original metacentric chromosome I and short (chromosome III in **a, b, e;** chromosome V in **c** and **d**) and long (chromosome VI in **a, b, d, e,** and chromosome III in **c**) arms of different acrocentrics. Only karyotype DKP_{14} (**e**) contains a metacentric chromosome (V) due to a pericentric inversion followed by reciprocal translocation between the short arm of this chromosome and the long arm of chromosome III. For further details see Schubert et. al. (1982, 1983) and Fig. 4 (concerning **e**)

Experimental evidence. The standard karyotype of *Vicia faba* (2n = 12) consists of one pair of metacentric satellited chromosomes and 5 pairs of acrocentric chromosomes. Among the progeny of "open field pollination experiments" involving different translocation lines between the satellite arm of the standard metacentric and the short or long arms of various standard acrocentrics, karyotypes with 7 pairs of homologous acrocentric chromosomes have been found (see Figs. 3 a, b, 4 d and Schubert et al. 1982).

In order to obtain evidence as to the origin of these karyotypes along the routes described above (Figs. 2 a, 4 a–d) other suitable translocation lines were crossed. They gave rise to similar karyotypes (2n = 14, about 4% of the total progeny, see Figs. 3 c–e and Schubert et al. 1983).

No examples of karyotypes having originated from (n–1) gametes with two metacentrics were observed, neither in homozygous (2n = 2) nor in heterozygous (2n–1) condition, indicating that these gametes did not function.

Currently, an attempt is being made to change the fundamental chromosome arm number of *Vicia faba* from 7 to 8 (2n = 16). This is based on karyotype DKP14 (2n = 14, see Figs. 3 e and 4 f) containing a new metacentric chromosome which originated by two sequential reconstructions of the standard chromosome V (Fig. 4): a pericentric inversion transformed chromosome V from an acrocentric into a submetacentric chromosome (Fig. 4 e), and a reciprocal translocation between the short arm of this chromosome and the long arm of chromosome III transformed chromosome V into a metacentric (Fig. 4 f). Selection and crossing of interchanges involving one arm of chromosome V and the long arm of one and the short arm of another acrocentric chromosome would again lead to double heterozygous individuals offering the possibility of mis-segregation from the multivalents during the meiosis giving gametes with 8 and 6 chromosomes, respectively.

Our efforts are directed towards selection of interchanges allowing not only the production of karyotypes with 2n = 16 chromosomes but, simultaneously, karyotypes with 2n = 12, which may survive since these are, though different in chromosome structure from the standard karyotype, identical in genetic content to the standard (2n = 12) karyotype.

This is to be expected when the two chromosomes involved in the interchanges, which already gave rise to meiotic mis-segregation eventually resulting in the 2n = 14 karyotype (e.g. those acrocentrics representative of both arms of the original metacentric (Fig. 4 g)), participate in interchanges with the metacentric chromosome V of karyotype DKP14. Provided the breakpoints are more or less identically located in both groups of interchanges (one resulting in the 2n = 14 karyotype, the other in the 2n = 16 karyotype), the karyotype with 2n = 16 would contain, in hexasomic state, one centromere plus a short arm and one telomeric region (Fig. 4 h_2) while the corresponding deletions connected with the reduction of chromosome number from 14 back to 12 would concern the same regions which are duplicated in the 2n = 14 karyotype and thus return to the disomic state again (Fig. 4 h_1).

There are indications that such changes may have occurred during evolution of the *Vicia sativa* group. Among *Vicia sativa* populations there are at least two different karyotypes with 2n = 12, two different karyotypes with 2n = 10, and one karyotype with 2n = 14 (Mettin and Hanelt 1964; Hanelt and Mettin 1966; Ladizinsky 1978). The karyotypes with 10 and 12 chromosomes probably represent varieties, while the 2n = 14 karyotype is evolutionary more advanced and represents an new subspecies or even a species (*V. amphicarpa*). Both morphological and ecological criteria suggest that 2n = 12 is the original chromosome number and karyotypes with 10, and probably also those with 14 chromosomes, have been derived from it (Ladizinsky 1978).

Discussion

Robertsonian exchanges have been observed in different groups of organisms. They frequently occur in rodents and other animals (for review, see White 1973) and also in some plants (see Table 1). Only in one case observed in *Tradescantia* is the increase in chromosome number evidently not based on simple centromeric fission (Östergren and Östergren 1983). In some cases, however, it might be difficult to find out whether the change in chromosome number occurred by Robertsonian interchange or by the mechanism described here, since the main effect, a change in chromosome number but conservation of the number of long chromosome arms, is the same in both situations. Even though Robertsonian interchange, at first view, seems to be the simpler and more straightforward way of altering chromosome number, there are features more easily explainable by meiotic mis-segregation of multivalents in double interchange heterozygotes:

1) Robertsonian fusion *sensu strictu* can only occur when exclusively telocentric chromosomes are present in the karyotype. In all other cases (acrocentrics), the generally observed absence (loss) of the second translocation product, the small centric fragment (Fig. 1 a), which renders this process irreversible, is still a matter of discussion. Holmquist and Dancis (1980) circumvent this problem by the assumption that the metacentric is in fact dicentric due to an assymmetric interchange with one of the centromeres becoming inactive while Marks (1983) considered the lost material to represent unwanted chromatin and Robertsonian exchange to be a mechanisms for discarding it.

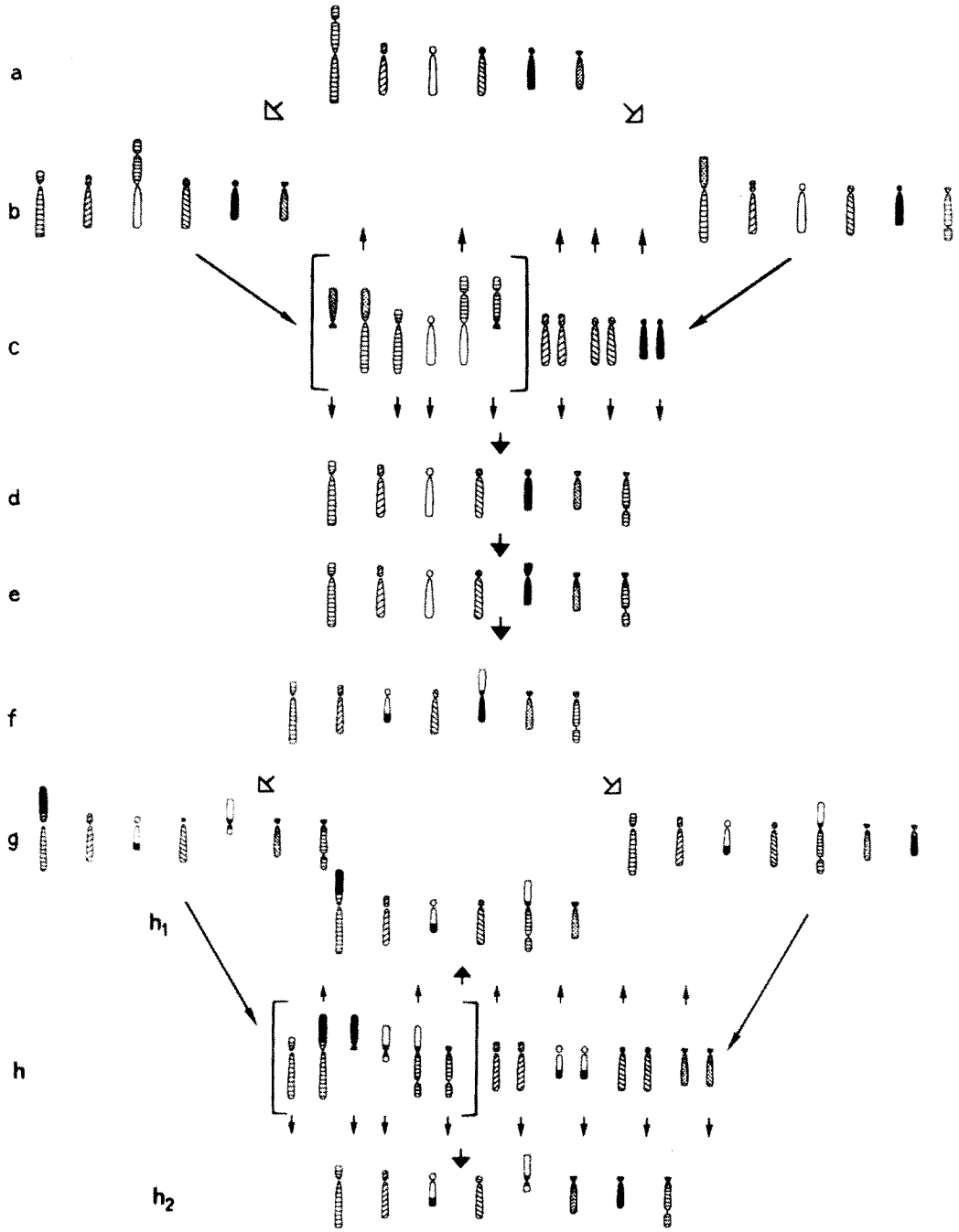

Fig. 4a–h. Observed (**a–f**) and expected (**g–h**) steps in changing chromosome numbers in *Vicia faba* (schematically). **a** Haploid standard chromosome set of *V. faba* (2n = 12) consisting of one metacentric satellite chromosome and five acrocentrics; **b** Left: interchange between the satellite arm of chromosome I and the short arm of chromosome III (= karyotype D). *Right:* interchange between the satellite arm of chromosome I and the long arm of chromosome VI (= karyotype K); **c** Potential meiotic pairing configuration in double heterozygotes obtained after crossing of interchange lines D and K: three bivalents plus a hexavalent (in brackets) involving the two interchange metacentrics and the four wildtype or interchange acrocentrics whose long arms are homologous to the arms of the metacentrics. Small arrows indicate mis-segregation resulting in gametes with n – 1 = 5 (*above*) and n + 1 = 7 (*below*). The n – 1 gametes are probably not viable because of small deletions concerning the centromere and short arm of chromosome VI and the tolemeric region of chromosome III; compare legend d); **d** Fusion of two n + 1 gametes from (**c**) results in karyotype DK14 with 14 chromosomes. Two of these represent the two arms of the original metacentric as two separate acrocentrics. In this situation, the centromere and short arm of chromosome VI and the telomeric region of chromosome III are duplicated; **e** Pericentric inversion resulted in a submetacentric chromosome V (= karyotype DKB14); **f** Interchange between the short arm of the submetacentric

2) In addition, centric fission of a metacentric resulting in two functional chromosomes is also not easily explainable. It can only function when the centromeres of metacentrics represent functionally duplicated structures prior to the dissociation of arms since each new telocentric chromosome needs its own active centromere which simultaneously must function as a telomere (Fig. 1 b), otherwise a donor of both organelles or their de novo appearance must be postulated (Holmquist and Dancis 1980). These problems do not exist in the case of mis-segregation from interchange multivalents (Figs. 2 and 4).

The way of changing chromosome number described in this paper is also different from that suggested by Darlington (1937) and modified by Stebbins (1950, 1971) (Fig. 5):

1. According to Darlington and Stebbins, reduction in chromosome number implies the loss of the small centric translocation product, similar to the situation in other cases of Robertsonian fusion.

2. Increase in chromosome number requires, according to Stebbins, two subsequent translocations within the same individual, the second one involving the small centric translocation product of the first.

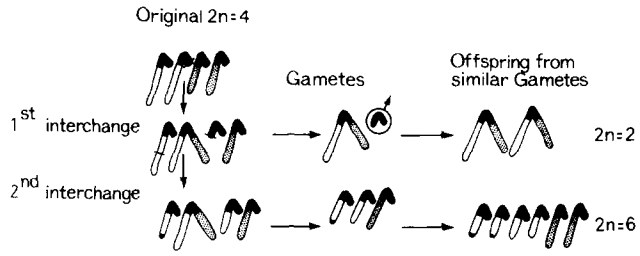

Fig. 5. Changing of chromosome numbers by means of reciprocal translocation(s) of unequal chromosome segments. Based upon Darlington 1937, modified from Stebbins 1971

According to the way proposed in our paper, both translocations arise independently of each other in different parental organisms, and may only after appropriate crossing result in individuals heterozygous for both translocations.

3. In our model (n−1) and (n+1) gametes arise simultaneously. In spite of the fact that this is not explicitly shown in the corresponding diagram of Stebbins (Fig. 5) it might theoretically be possible that also in his case (n−1) and (n+1) gametes arise simultaneously via mis-segregation (1 metacentric : 3 acrocentrics) at meiosis when two suitable consecutive translocation events provide the appropriate chromosomal basis.

If such a mechanism could be proved experimentally it would allow changes in chromosome numbers in both directions even on the basis of two acrocentric chromosomes.

Evolutionary significance of the process described here, which is coupled to the simultaneous occurrence of reciprocal translocations between preexisting meta- and acrocentric chromosomes, may be postulated for populations sufficiently small and isolated as to allow the appearance of double interchange heterozygotes. The chance for development of homozygous organisms with a new chromosome number should be especially high when self-fertilization also occurs.

A relatively high frequency of suitable translocations may be caused by environmental mutagenic influences or by processes analogous to transposon-mediated 'hybrid dysgenesis' as observed in *Drosophila melanogaster* (Engels and Preston 1981). The existence of hot spot segments for chromosome structural changes, as observed in *Vicia faba* near the centromeres (Schubert et al. 1981), is an additional factor increasing the probability of evolutionary changes of chromosome number via the mechanism described here.

chromosome V and the long arm of chromosome III renders chromosome V metacentric (=karyotype DKP14); **g** *Left:* interchange between the long arm of chromosome V and the short arm of chromosome I. *Right:* interchange between the long arm of chromosome V and the long arm of the acrocentric satellite chromosome (note that both interchange partners of chromosome V represent the acrocentric substitutes of the original metacentric due to the two interchanges, which resulted in karyotype DK14 (**a–d**)); **h** Potential meiotic pairing configuration in double heterozyotes obtained after crossing of both karyotypes shown in (**g**) with four bivalents and one hexavalent containing the new interchange metacentrics and their acrocentric homologues. *Small arrows* indicate mis-segregation resulting in a hypoploid n=6 gamete with two metacentrics and four acrocentrics ($\mathbf{h_1}$) and a hyperploid gamete with eight acrocentrics ($\mathbf{h_2}$); $\mathbf{h_1}$ The n=6 karyotype (DKP12) is viable since the deletions, connected with the formation of two metacentrics instead of one (in karyotype DKP14), concern those regions which are duplicated in karyotype DK14 (see **a–d**). These regions now revert to the disomic state provided the breakpoints of the interchanges in (**b**) and (**g**) were more or less identical in position (*hot spots*). Thus, this karyotype is genetically identical to, but structurally different from, the standard karyotype (**a**); $\mathbf{h_2}$ Since the centromere and the short arm and the telomeric region, which became duplicated during increase in chromosome number from 14 to 16, are identical to those duplicated when the chromosome number increased from 12 to 14 (**a–d**), these regions are in hexasomic state in karyotype DKP16. The hypothetical steps **f** to **h** (which are under investigation now) demonstrate simultaneous increase ($\mathbf{h_2}$) and decrease ($\mathbf{h_1}$) of chromosome number (provided there is enough redundancy permitting the latter) by meiotic chromosome mis-segregation in karyotypes heterozygous for two interchanges, and show how the fundamental number of long chromosome arms of the original karyotpye (**a**) can be changed from seven into eight (**f–h**).

Table 1. Higher plant species with presumed Robertsonian fusions or fissions and changes of chromosome numbers possibly due to Robertsonian interchanges[a]

Plant	Observation and chromosome no(s)	Reference
Godetia (= Clarkia) whitneyi	X = 7 → X = 8 (connected with 2 interchanges)	cited from Sybenga 1972
Oxalis dispar	Centric fission and loss of a short arm of an A 2n = 12	Marks 1983
Apium graveolens	Fusion of long arms of acrocentric chromosomes 3 and 8; loss of short arm of chromosome 3 2n = 22	Marks 1983
Tradescantia paludosa	X-raying of pollen resulted in two stable As from one SM; 2n → 2n + 2 (sometimes dicentrics, isochromosomes, or restitutions of the original SM were found in the progeny)	Östergren and Östergren 1983
Alisma plantagoaquatica	2n = 12M → 2n = 10M + 2A + 2T (or vice versa)	cf John and Lewis 1968 (see Jones 1978)
Haplopappus gracilis	2n = 6 → 2n = 4 (fusion of 2As)	cf John and Lewis 1968
Nothosordum fragans (inodorum)	2n = 16M → 2n = 13M + 6T	cf John and Lewis 1965 but see also Jones 1978
Nigella doerfleri	2n = 12 → 2n = 14 (fission of 1M)	Strid 1968
Campanula persicifolia	2n = 16 → 2n = 18 (fission of 1M)	Darlington and La Cour 1950
Gibasis schiedeana	2n = 10 (X = 5) → 4n = 16 (X = 4) fusion of 2As	cf Jones 1978
Tradescantia andreuxii	2n = 12M → 2n = 11M + 2T	Jones 1978
Cymbispatha commelinoides	2n = 14M/2 = 13M + 2T	cf Jones 1978
Crocus minimus	2n = 24 (6M + 18SM) → 2n = 25, 26, 27 28, 29, 30 (by fission of Ms)	cf Jones 1978
Miersia chilensis	2n = 20 (2M + 18A)/2n = 21 (1M + 20A)	cf Jones 1978
Crocus aff. danfordiae	2n = 10 ($2M_l + 8A$) 2n = 10 ($3M_l + 1M_s + 6A$) (centric fusion)	Jones 1978
Aloe rabaiensis	2n = 14 ($8A_l + 6A_s$) 2n = 14 ($1M_l + 1M_s + 6A_l + 6A_s$) (centric fusion)	Jones 1978

M = metacentric; A = acrocentric; T = telocentric; SM = submetacentric; l = long; s = short

[a] Some related species differing with respect to chromosome number and ratio of metacentrics to acro-/telocentrics but showing the same fundamental number of long chromosome arms were found in genera *Lycoris, Fritellaria, Podocarpus, Dacrydium* (cf John and Lewis 1968) or among *Gibasis, Zebrina* and other genera of *Commelinaceae* (see Jones and Kenton 1984). Such changes in chromosome numbers are probably due to Robertsonian fusions or fissions

Acknowledgements. We are grateful to Dr. G. E. Marks (John Innes Institute, Norwich, England), Dr. G. P. Holmquist (Baylor College of Medicine, Houston, Texas, USA) and Prof. J. Sybenga, Agricultural University, Wageningen, The Netherlands) for their critical review of the manuscript and helpful suggestions.

References

Darlington CD (1937) Recent advances in cytology, 2nd edn. J & A Churchill, London, p 559

Darlington CD, La Cour LF (1950) Hybridity selection in *Campanula.* Heredity 4:217–248

Engels WR, Preston CR (1981) Identifying P factors in *Drosophila* by means of chromosome breakage hotspots. Cell 26:421–428

Hanelt P, Mettin D (1966) Cytosystematische Untersuchungen in der Artengruppe um *Vicia sativa* L. 2. Kulturpflanze 14:137–161

Holmquist G, Dancis BM (1980) A general model of karyotype evolution. Genetica 52/53:151–163

John B, Lewis KR (1965) The meiotic system. In: Alfert M, Brauer H, Harding CN, Sitte P (eds) Protoplasmatologia, vol VI. Springer, Wien New York

John B, Lewis KR (1968) The chromosome complement. In: Alfert M, Bauer H, Harding CN, Sandritter W, Sitte P (eds) Protoplasmatologia, vol VI. Springer, Wien New York

Jones K (1978) Aspects of chromosome evolution in higher plants. Adv Bot Res 6:119–194

Jones K, Kenton A (1984) Mechanisms of chromosome change in the evolution of the tribe *Tradescantieae (Commelinaceae).* In: Sharma AK, Sharma A (eds) Chromosomes in evolution of eukaryotic groups, vol II. CRC Press, pp 143–168

Kaina B, Rieger R (1979) Chromosomenmutationen, Karyotyp-Polymorphismus und Speciation. Biol Zentralbl 98: 661–697

Ladizinsky G (1978) Chromosomal polymorphism in wild population of *Vicia sativa* L. Caryologia 31:233–241

Marks GE (1983) Evidence for the occurrence of dispensable and disadvantageous chromatin. In: Kew Chromosome Conf II. Allen & Unwin, London, pp 269–272

Mettin D, Hanelt P (1964) Cytosystematische Untersuchungen in der Artengruppe um *Vicia sativa* L. 1. Kulturpflanze 12:163–225

Östergren G, Östergren K (1983) An X-ray induced Robertsonian fission in *Tradescantia* that gave rise to transmissible dicentric chromosomes. In: Kew Chromosome Conf II. Allen & Unwin, London, p 357

Schubert I, Michaelis A, Rieger R (1981) Effects of chromosome repatterning in *V. faba* L. 5. Influence of segment transposition on maleic hydrazide specific aberration clustering in a heterochromatin containing chromosome region. Biol Zentralbl 100:167–179

Schubert I, Michaelis A, Rieger R (1982) Karyotype variability and evolution in *Vicia faba* L. Biol Zentralbl 101:793–806

Schubert I, Rieger R, Michaelis A (1983) A method for directed production of definite aneuploids of *Vicia faba* L. Faba Bean Inf Serv 7:13–18

Stebbins GL (1950) Variation and evolution in plants. Columbia University Press, New York, p 446

Stebbins GL (1971) Chromosomal evolution in higher plants. Arnold, London

Strid A (1968) Stable telocentric chromosomes formed by spontaneous misdivision in *Nigella doerfleri (Ranunculaceae).* Bot Not 121:153–164

Sybenga J (1972) General cytogenetics. North Holland/American Elsevier, Amsterdam

White MJD (1973) Animal cytology and evolution, 3rd edn. Cambridge University Press, London