Chromosome Size Differences May Affect Meiosis and Genome Size

John Wang,[1]* Pei-Jiun Chen,[2]† George J. Wang,[3] Laurent Keller[1]*

Transmission distortion has been identified by deviations from the equal representation of parental alleles in the progeny (*1*). Weak transmission bias and violations of the independent assortment of chromosomes are harder to detect, however, because large broods and a careful examination of the transmission ratios are necessary. We investigated whether weak violations of chromosome transmission or assortment exist in the nematode *Caenorhabditis elegans*, which is characterized by an XX/XO sex determination system.

We crossed males heterozygous for *mIs10* [an integrated transgene on chromosome V expressing green fluorescent protein (GFP)] to wild-type hermaphrodites and found sex-biased inheritance of *mIs10* (Fig. 1A, $P = 9.8 \times 10^{-189}$, χ^2 test). Sons were more likely to inherit the *mIs10* allele, whereas hermaphrodite daughters were more likely to receive the wild-type (*wt*) allele. This was not due to the preferential transmission of one particular chromosomal allele, because the number of total offspring inheriting *mIs10* was not different from that inheriting *wt* ($P = 0.39$, binomial test). We also ruled out mortality of males bearing the *wt* allele and of hermaphrodites bearing the *mIs10* allele, because we observed no dead larvae and only a few dead eggs. Thus, there is preferential segregation of the longer *mIs10*-bearing chromosome away from the X chromosome and of the shorter *wt* chromosome with the X. We refer to this phenomenon as skew.

To exclude the possibility that skew for *mIs10* was specific to this genetic construct or chromosome V, we investigated segregation patterns for large insertion transgenes on the other four autosomes. All four insertion transgenes also preferentially segregated away from the X chromosome (Fig. 1B) with significantly differing magnitudes of skew among the insertion lines ($P < 2.2 \times 10^{-16}$, χ^2 test) and with transmission bias ratios ranging from 1.42 (*mIs13*) to 6.55 (*mIs10*). Skew also occurred in males heterozygous for large deletions (Fig. 1C, *nDf24 I* and *tDf1 IV*).

Because these insertions and deletions (indels) are relatively large (range ~615 kb to ~7.3 Mb, table S1), we tested whether smaller indels also exhibited skew by using a small insertion (*ruIs38*, ~33 kb) and three single-gene deletions (*unc-30*, *unc-47*, and *unc-63*, range from ~1 to ~1.5 kb). In the four cases, the shorter chromosome also segregated with the X chromosome, the skew being significant for *ruIs38*, *unc-47*, and *unc-63* (fig. S1). The magnitude of bias for these four indels (1.02 to 1.21) was smaller than for the larger indels. We also observed no difference regarding the parent of origin of an indel on skew (*2*). Overall, there was a significant positive correlation between indel size and transmission bias ratio (fig. S2, $P = 0.006$, Spearman's rank correlation test).

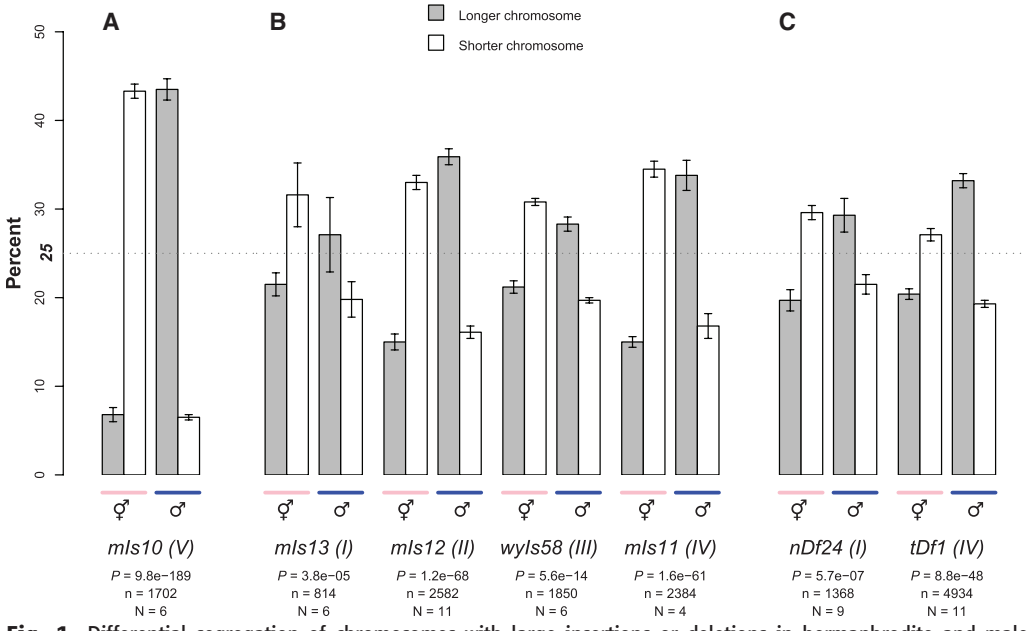

Fig. 1. Differential segregation of chromosomes with large insertions or deletions in hermaphrodite and male offspring. (**A**) *mIs10* transgene, (**B**) transgenes on chromosomes I to IV, and (**C**) deficiencies. The 25% line indicates expected values with no segregation bias. Error bars are SEM. Transgene or deficiency names and their chromosomal locations (roman numerals) are below respective bar plots. *P* values, χ^2 tests assuming random segregation of the two alternate chromosomes by sex. *N*, number of males tested; *n*, total individuals scored.

Skew may affect genome evolution and genome size. Given that hermaphrodites tend to inherit the shorter chromosome and because new populations of *C. elegans* are frequently initiated by hermaphrodites (*3*), genome size reduction may occur over evolutionary time. Simulations of hermaphroditic mating, hermaphroditic selfing-only, and gonochoristic mating systems (*2*) (fig. S3) showed that skew led to a significant reduction in genome size in the hermaphroditic mating system ($P = 2.5 \times 10^{-13}$, one-sample *t* test) but not in the gonochoristic or hermaphroditic selfing-only systems (both $P > 0.27$, one-sample *t* test).

These observations of insertion disjoining from the X, causing genome size reduction in male/hermaphrodite relative to gonochoristic mating systems, is consistent with genome sizes in the genus *Caenorhabditis*. Hermaphroditism within the genus has evolved independently at least twice (*4*). All three male/female species tested have genome sizes of >130 Mb, whereas both sequenced hermaphroditic species have genome sizes of ~100 Mb (*5*–*7*). Thus, in at least two cases, the evolution of hermaphroditism was associated with a convergent reduction in genome size relative to the ancestral male/female species.

References and Notes

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8. We thank W. Herr, P. Gönczy, A. W. Murray, and A. M. Villeneuve for comments on the manuscript; S. K. Kim and R. E. Ellis for discussions; W. Herr, in whose laboratory the experiments were performed; the *Caenorhabditis* Genetics Center, funded by the NIH National Center for Research Resources, for strains; the University of Lausanne Cellular Imaging Facility; and the Vital-IT Center for high-performance computing. Supported by grants from the Swiss National Science Foundation to L.K. and W. Herr. L.K. thanks S. Leibler for hosting him during his sabbatical at Rockefeller University.

Supporting Online Material

www.sciencemag.org/cgi/content/full/329/5989/293/DC1
Materials and Methods
SOM Text
Figs. S1 to S3
Table S1
References

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[1]Department of Ecology and Evolution, University of Lausanne, CH-1015 Lausanne, Switzerland. [2]Center for Integrative Genomics, University of Lausanne, CH-1015 Lausanne, Switzerland. [3]Howard Hughes Medical Institute and Department of Biology, Stanford University, Stanford, CA 94305–5020, USA.

*To whom correspondence should be addressed. E-mail: John.Wang@unil.ch (J.W.); Laurent.Keller@unil.ch (L.K.)
†Present address: TopoGenomics Incorporated, Taipei, Taiwan.