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SHORT REVIEW

Variation in genomic recombination rates among animal taxa and the case of social insects

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Meiotic recombination is almost universal among sexually reproducing organisms. Because the process leads to the destruction of successful parental allele combinations and the creation of novel, untested genotypes for offspring, the evolutionary forces responsible for the origin and maintenance of this counter-intuitive process are still enigmatic. Here, we have used newly available genetic data to compare genome-wide recombination rates in a report on recombination rates among different taxa. In particular, we find that among the higher eukaryotes exceptionally high rates are found in social Hymenoptera. The high rates are compatible with current hypotheses suggesting that sociality in insects strongly selects for increased genotypic diversity in worker offspring to either meet the demands of a sophisticated caste system or to mitigate against the effects of parasitism. Our findings might stimulate more detailed research for the comparative study of recombination frequencies in taxa with different life histories or ecological settings and so help to understand the causes for the evolution and maintenance of this puzzling process.
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Introduction

Recombination occurs in almost all sexually living organisms. It involves both the segregation of entire chromosomes and the genetic exchange between homologous chromosomes (crossing-over), when gametes are formed during the process of meiosis (Bell, 1982). As a consequence of meiotic recombination, the combinations of alleles in offspring differ from those found in the parents. Because the successful parental genotypes are thereby destroyed in seeming contradiction to the expectations of Darwinian natural selection, the evolutionary processes responsible for the origin and maintenance of recombination are still very controversial (Barton and Charlesworth, 1998; Otto and Lenormand, 2002). However, if variation in recombination rate is not neutral but reflects the working of natural selection, differences in recombination among different taxa, environments or life histories, can shed some light on the adaptive value of recombination. Here, we report on newly available data that elucidate – against the background of a large number of animal taxa – the importance of recombination for an especially interesting group of species, that is, the social Hymenoptera.

Social insects illustrate how besides the many advantages such as cooperative brood care or collective defence, sociality also involves several drawbacks. Social living, for example, entails a higher risk of disease transmission, facilitated by the close spatial proximity and interactions among group members. In social systems based on kin selection, parasite transmission is additionally promoted by the high genetic similarity of individuals belonging to the same society (Hamilton, 1987; Sherman *et al*., 1988; Schmid-Hempel, 1998). Additionally, some virulence effects can be of greater importance in social species when compared to their non-social relatives. In the Hymenoptera, for example, sex-ratio distorting parasites such as *Wolbachia* are prevalent. In contrast to solitary species, the fitness costs of *Wolbachia* infections can lead to dramatic fitness losses in social insects that are dependent on producing a large number of offspring, that is, the large female worker force of the social Hymenoptera. Similarly, the division of labour between non-reproducing individuals (i.e., workers, soldiers, etc.) in social insects can be constrained by low genotypic diversity within the worker force (Page *et al*., 1989). In eusocial species like the leaf-cutter ants (e.g., *Acromyrmex*) or the honeybee (e.g., *Apis mellifera*), selection also acts at the colony level (e.g., Tarpy *et al*., 2004), that is, colonies with a more efficient system of division of labour may out-compete those with a less efficient system.

Consequently, it has been hypothesized that natural selection operating on social insects should strongly favour the genotypic diversification of offspring (Crozier and Fjerdingstad, 2001), for example, by increasing the number of segregating chromosomes (Sherman, 1979) or increasing intra-chromosomal recombination rate (through crossovers) (Gadau *et al*., 2000; Schmid-Hempel, 2000). In fact, there is empirical evidence that a genotypically more diverse worker force is associated

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with improved colony growth (Oldroyd *et al*., 1992; Cole and Wiernasz, 1999), improved foraging efficiency (Oldroyd *et al*., 1993, 1994; Cole and Wiernasz, 1999), or lower parasite loads (Liersch and Schmid-Hempel, 1998; Baer and Schmid-Hempel, 1999; Tarpy, 2003). Higher chromosome numbers will additionally reduce the variance in relatedness between social group members, and thereby stabilize the society in kin-based social systems (Sherman, 1979; Templeton, 1979); an analogous argument can also be made for increased intra-chromosomal recombination rates.

Apart from the genetic means of recombination (i.e., segregation and intra-chromosomal crossovers), genotypic diversity among workers of a social insect colony is also behaviourally affected by the degree of polyandry and polygyny. Through polyandry, social insect females may generate high degrees of genotypic diversity in worker offspring (Sherman, 1979; Schmid-Hempel and Crozier, 1999). Empirical evidence indeed shows that social insect females, especially in advanced taxa, are characterized by an unusually high degree of multiple mating (e.g., in vespids and honeybees Moritz *et al*., 1995; Foster *et al*., 1999). Moreover, in ants, the degree of genotypic diversity within a colony correlates negatively with the reported parasite load of the species (Schmid-Hempel and Crozier, 1999). Although the possible adaptive values of increased polygyny and polyandry, and of increased chromosome numbers in socially advanced insect species have been tested previously (Sherman, 1979; Schmid-Hempel and Crozier, 1999), any confirmed data to evaluate the possible role of intra-chromosomal recombination rates have not come yet. In fact, it is very recently that data have become available, in the form of genetic linkage maps that allow the comparison of genomic recombination rates across many taxa.

Linkage maps are based on the probability of recombination events between known markers along the genome, yielding a recombination distance (in cM) between marker pairs, whereas the respective physical distance is given by the number of base pairs (in bp). The correlation between recombination and physical distance forms the basis of linkage mapping. However, there is ample evidence for considerable variation of recombination rate per unit of physical distance (here, we call this measure the 'recombination density', in cM/Mb) on all levels, that is, along chromosomes, between sexes, individuals and species (Baker *et al*., 1976; Brooks, 1988).

Describing the first genetic linkage map for the honeybee in Hunt and Page (1995), it was found that with a recombination density of 19.38 cM/Mb (corresponding to a ratio of physical and genetic genome size of 52 kb/cM, that is, a short physical distance for every cM of recombination distance), *A. mellifera* at that time had the highest reported genome-wide recombination rate in any of the higher eukaryotes. In the meantime, several studies have formulated hypotheses for this extremely high recombination frequency (Gadau *et al*., 2000; Schmid-Hempel, 2000; Sirviö *et al*., 2006), but till now no consensus has been reached. Now, data on genomic recombination rates in many more organisms, including several Hymenoptera and other insects, have become available. Furthermore, much of the data from previous studies had to be revised considerably. For example, the estimate of the physical genome size of the honeybee increased from an initial 178 Mb (Jordan and Brosemer, 1974) to 262 Mb (The Honeybee Genome Consortium, 2006), and from 274 Mb (Gadau *et al*., 2000) to 625 Mb in the bumblebee, *Bombus terrestris* (Wilfert *et al*., 2006) owing to more accurate analyses and the complete sequencing of the honeybee genome. Therefore, a re-evaluation of the genomic data, including recombination rates of honeybees and other social Hymenoptera as compared to other taxa, has become necessary. We have undertaken a comprehensive survey of the available data on recombination density for insects and compare them with data from other animals, fungi and protozoa.

Materials and methods

The published data on the physical genome size and the recombination length based on linkage mapping were assembled from the literature. The assembled database encompasses a comprehensive survey of the available data for insects, and examples from other animals, plants, fungi and protozoa. Care was taken to cover the full range of genomic recombination densities for these taxa. For example, for the vertebrates, we chose the animals with both the highest and the lowest recombination densities known today, the chicken *Gallus domesticus* (Groenen *et al*., 2000) and the tiger salamander *Ambystoma tigrinum* (Smith *et al*., 2005), respectively as well as recent examples from the literature.

The quality of estimates of physical genome length depends strongly on the chosen method. For example, Feulgen densiometry and flow cytometry have both been shown to be reliable and repeatable, if quality standards are met (Dolezel *et al*., 1998). The large discrepancies between previously reported and current estimates for *A. mellifera* and *B. terrestris* are because of these methodological issues. The original estimate for the honeybee was derived through CsCl-gradient centrifugation (Jordan and Brosemer, 1974), which is generally no longer considered adequate (Dolezel *et al*., 1998). Although the bumblebee estimate was derived using flow cytometry, the inaccurate honeybee estimate was used as a standard, and DAPI was used as a stain. In contrast to propidium iodide, DAPI preferentially stains AT-rich DNA and should not therefore be used to estimate DNA amounts (Dolezel *et al*., 1998). We therefore, report only data that have been produced by state-of-the art techniques such as Feulgen densitometry and Flow cytometry using DAPI staining or estimates from advanced genome-sequencing projects (see Table A1), to avoid spurious estimates of physical genome length.

If several recombination genome sizes for the same organism had been published, we chose the linkage map with the highest coverage and best quality of markers for the current analysis. For the bumblebee *B. terrestris*, for example, we chose the genome size produced by the high-coverage linkage map BBM-1 from Wilfert *et al*. (2006) for this analysis instead of the low-resolution maps BBM-2 and BBM-3 from the same study, or the RAPD-based map from Gadau *et al*. (2001).

For low-coverage maps, the number of linkage groups often exceeds the number of actual chromosomes. These excess linkage groups have to be linked so that they conform to the karyotype. In most mapping studies, the maximum recombination frequency (Φ) is set to a value between 0.3 and 0.4, which roughly corresponds to a

recombination distance of 40 cM. Therefore, we added a conservative 40 cM per gap to make those maps comparable to more saturated maps. This should prevent artefacts due to underestimation of genomic recombination rates. In Table A1, we indicate the average distance between neighbouring markers as an indicator of the quality of maps. With the current database, species and groups had to be treated as statistically independent, as there were too few species in any clade to take into account the phylogenetic relationships.

Results

Data pertaining to recombination densities are summarized in Table A1. We found that recombination density for both *A. mellifera* and *B. terrestris* differ by a small amount from the originally published estimates, as the concurrent modifications for the estimates of genetic genome sizes happened to compensate for the change in recombination length. Therefore, recombination densities had to be corrected from 3.85 (Gadau *et al*., 2001) to 4.42 cM/Mb (Wilfert *et al*., 2006) for the bumblebee, and from 19.38 (Hunt and Page, 1995) to 16.00 cM/Mb for the honeybee (based on a recombination genome size of 4′115 cM derived from a fully saturated linkage map, personal communication, M Solignac). Thus, the honeybee's genomic recombination frequency remains highest among the known values for animals.

Our analysis suggests that there are three distinct ranges of genomic recombination densities (Figure 1, Table A1). According to Table A1 the highest recombination densities are found in fungi and protozoa (with the exception of *Toxoplasma gondii*), two groups that are characterized by small physical genomes. There is some evidence that the protochordata might also have high recombination densities. The only linkage map published so far for this taxon basal to all vertebrates reports a high genomic recombination density ranging from 20 to 40 cM/Mb (corresponding to 25–49 kb/cM) in the ascidian *Ciona intestinalis* (Kano *et al*., 2006). All other taxa have consistently lower recombination densities. Nevertheless, against this general background, the social Hymenoptera have outstandingly high recombination rates. They occupy an intermediate position between the extremely high values found in the fungi and protozoa and many other higher eukaryote taxa with low values of recombination (Figure 1). As an aside, we also screened the available studies on plants and found, on average, comparably low recombination densities. A wide range of recombination densities has been reported in the plants. Some gymnosperms have recombination densities as low as 0.1 cM/Mb (Chagné *et al*., 2002). But even the plants with the highest recombination rates, for example *Arabidopsis thaliana* (Chagné *et al*., 2002), show only about one-sixth of the recombination density that characterizes the honeybee, *A. mellifera*.

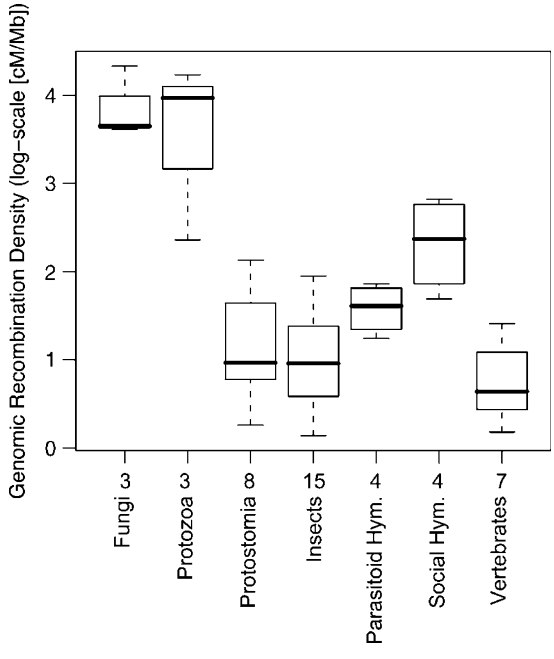

Figure 1 Average recombination densities (cM/Mb) vary across the large taxonomic groups considered in this study (c.f. Table A1) (Kruskal–Wallis $H=29.604$, $df=7$, $P=0.001$). The social Hymenoptera stand out among the eukaryotes whereas the protozoa have the highest recorded values in all. For clarity, the graph shows the ln-transformed values (ln(1 + recombination density)); the number of species per group (N) is indicated at the bottom. The horizontal line marks the median value, boxes indicate ± one quartile and vertical lines indicate the range of observations.

Among the insects, all Diptera (average: 1.03 ± 1.14 cM/Mb s.d., $n=6$ species) show very low densities, different from the Hymenoptera (7.12 ± 5.13 cM/Mb, $n=8$; *U*-test, $z=-2.969$, $P=0.003$) and from the Lepidoptera (4.74 ± 1.84 cM/Mb, $n=3$; *U*-test, $z=-2.066$, $P=0.039$) with the average value for Coleoptera occupying the middle range between these extremes (2.48 ± 1.31 cM/Mb s.d., $n=4$). As the Hymenoptera have a sex-determination system based on haplodiploid genetics, meiotic recombination is limited to the diploid females. Similar sex-restricted recombination occurs in *Drosophila* and in the Lepidopteran species included in this study. This reproductive mode may affect recombination densities, because the effect of recombination per generation is diluted. On average, insects with sex-restricted recombination (mean for all species: 5.81 ± 4.30 cM/Mb, $n=13$) indeed show significantly higher densities, than those where both sexes do recombine (1.41 ± 1.33, $n=9$; *U*-test, $z=-3.306$, $P=0.001$), which lends some support to the hypothesis that limited recombination in one sex may lead to an increase in recombination in the other.

Even with the limited set of data currently available, it thus seems that recombination densities differ considerably among major taxonomic groups (Figure 1) and that the social Hymenoptera have unusually high rates. For the social Hymenoptera, the known recombination densities range from 16.0 cM/Mb (given a recombinational genome size of 4′115 cM (personal communication, M Solignac), in the highly eusocial *A. mellifera* (defined, e.g., by their sophisticated system of division of labour, and large differences between workers and the queen), to 4.40 cM/Mb in the primitively eusocial bumblebee, *B. terrestris* (with simple division of labour and queens not very different from workers) (Wilfert *et al*., 2006). The two investigated ant species, *Acromyrmex echinatior* and *Pogonomyrmex rugosus* show intermediate values (Table A1). The solitary Hymenoptera, *Nasonia spp.* (2.5 cM/Mb for an interspecific cross of *N. vitripennis* and *N. giraulti*) and *Bracon sp. near hebetor* (3.2 cM/Mb),

by contrast, have much lower recombination rates than the average social Hymenoptera (mean: 10.26 ± 5.59 cM/Mb, $n = 4$; Table A1), even though two of the parasitoid Hymenoptera, *Trichogramma brassicae* (5.41 cM/Mb) and *Bracon hebetor* (4.85 cM/Mb), have higher recombination rates than the bumblebee (Table A1). Among these, the social Hymenoptera have a higher average recombination density than any other insects (mean: 2.55 ± 1.90 cM/Mb, $n = 19$; *U*-test, $z = -2.758$, $P = 0.006$).

Discussion

The data presented here place the recombination densities measured in the social Hymenoptera in the context of other taxa. This analysis demonstrates that the socially advanced honeybee *A. mellifera* and the ants studied to date (all of which are socially advanced) are characterized by unusually high recombination densities. For the honeybee, Beye *et al*. (2006) have shown that this high recombination density is a genome-wide phenomenon, although there is large local variation. The authors particularly showed that whereas there are weak positive correlations with GC-content and repetitive DNA, recombination densities are not influenced by chromosome size. This speaks against the stabilization of meiotic chromosome pairs as an explanation for the high recombination rate of honeybees.

Although social Hymenoptera have unusually high recombination densities among the higher eukaryotes, the highest altogether are found in protozoa and fungi (see Table A1). These organisms are often characterized by extended haploid life stages with a separate development, or by cycling through asexual phases with multiplication and their own life histories. This is true, to varying degrees, for the protozoa and fungi included in this study. We therefore propose that such life cycles and reproductive modes could favour increased recombination densities, similar to the higher densities associated with sex-restricted recombination, as these limitations dilute the effect of recombination (Hawthorne and Via, 2001). In either case, the opportunities for recombination occur less frequently during the full life cycle of the organism, for example, only in one sex or intermittently in cyclically parthenogenetic organisms. However, given the currently available data, reproductive mode alone cannot fully explain the differences. For example, the cyclically parthenogenetic pea aphid has a low density of only 1 cM/Mb (see Table A1); yet, the cyclically parthenogenetic *Daphnia pulex* has a relatively high value of 5.1 cM/Mb (Table A1). Although we have shown that insects with sex-restricted recombination show higher recombination densities, it must be noted that much of the difference between these groups is due to the mosquitoes, which are characterized by extremely low recombination densities. Therefore, a caveat mentioned earlier is that the available database does not yet allow making comparisons fully independent of phylogenetic effects. To clarify further the importance of reproductive mode for genome-wide recombination rates, taxa including species with different reproductive modes should be studied. For example, there is no recombination in females of the mosquito, *C. tritaeniorhynchus*, whereas closely related Culicidae show meiotic recombination in both sexes (Mori *et al*., 2001). Even though the data presented here suggest that sex-restricted recombination might lead to increased genome-wide recombination rates, this does not explain the difference between social and parasitoid Hymenoptera, both of which share haplodiploid sex determination system and sex-restricted recombination.

In social insects, several arguments suggest that natural selection should favour increased genotypic diversity of offspring, for example, by female multiple mating (Crozier and Fjerdingstad, 2001). Genotypic diversity is known to counter the threat posed by parasites (Sherman *et al*., 1988; Schmid-Hempel, 2000) or to stabilize the division of labour (Sherman, 1979). A similar argument pertains to recombination (Gadau *et al*., 2000; Schmid-Hempel, 2000) with an increase especially predicted for socially advanced taxa. The advanced social groups, such as the honeybees or ants, are characterized by a pronounced morphological and behavioural differentiation between queens and workers, and within the workers themselves. Typically, workers are no longer able to reproduce and are specialized to perform certain tasks, thereby forming distinct castes (Gadagkar, 1990, 1994). Additionally, their colonies are generally much larger and longer lived than those of the primitively social species such as the bumblebee included in this study. All of these characteristics assign a high premium for genotypic diversity in offspring of the socially advanced species. This prediction is met by the data presented in this study.

Alternatively to the natural-selection-based hypotheses advanced above, the exceptionally high recombination density of *A. mellifera* may be the result of domestication (Schmid-Hempel and Jokela, 2002). Domestication is typically associated with strong directional selection exerted by breeders, which is known to increase recombination rates (e.g., in Korol and Iliadi, 1994). Increased values of recombination, as measured by chiasmata frequencies, have, in fact, been observed in domesticated mammals (Burt and Bell, 1987) and plants (Ross-Ibarra, 2004). However, our data does not show this pattern in the insects. In the Hymenoptera, the ant *P. rugosus* has a recombination rate similar to the honeybee, yet has never been subject to domestication. Vice versa, the domesticated silkworm, *Bombyx mori* does not show an increase in recombination frequencies compared to other Lepidoptera (see Table A1). Note that this remains so if one prefers the higher estimate of genome size from a recent, nearly saturated SSR-based map of *B. mori* (Miao *et al*., 2005). We therefore can reject artificial selection through domestication as a consistent explanation for the increased recombination rate of the honeybee in particular and social insects in general.

Besides variation in the intra-chromosomal recombination rate through crossovers, the genotypic diversity of a mother's offspring is also affected by the number of independently segregating chromosomes. Sherman (1979) demonstrated that chromosome numbers are higher in eusocial taxa as compared to closely related solitary groups. Using colony size as an indicator of parasite load, Schmid-Hempel (1998) found that among 58 ant species chromosome number increases with the typical colony size (assumed to be an indicator of higher parasite loads and more sophisticated societies), and that this effect persisted after correcting for phylogenetic dependencies. Although our present dataset (Table A1) includes only a small fraction of the available karyotype

data, they are consistent with the results of Sherman (1979) as the social Hymenoptera included in this study indeed have higher chromosome numbers (haploid N, range 16–18 chromosomes) than their parasitoid counterparts (range 5–10; *U*-test, $z = -2.366$, $P = 0.029$).

The results reported here are encouraging in suggesting that social insects have unusually high recombination frequencies even though more data clearly are needed to thoroughly evaluate this pattern and to elucidate the importance of sociality for the evolution of recombination frequencies. Data on closely related species with varying degrees of sociality would be highly valuable in this context, including examples from the Isoptera and their non-social relatives. Moreover, the nature of the selective pressure for increased recombination in social insects is still unclear, with both, selection for sophisticated division of labour (but see Brown and Schmid-Hempel (2003)) and selection to mitigate against parasites (Fischer and Schmid-Hempel, 2005) being two major contenders. Social parasitic Hymenoptera, such as the cuckoo bumblebees or parasitic ant species that take over the worker force of a host colony, face the same parasite pressure as their host, but lack division of labour as they have lost their worker caste. The genomic recombination of these species would be particularly interesting to differentiate between the two rival functional hypotheses. With data on genomic recombination frequencies slowly accumulating now, the study of social insects has great promise to test theories on the evolution of recombination rates in a new context.

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Appendix A

Summary of genetic data used for this study. Studies are listed alphabetically within taxonomic groups. The haploid karyotype and estimates of the genetic and physical genome sizes (in cM and Mb, respectively) as well as the resulting recombination density (in cM/Mb) are indicated.

Table A1 Genomic recombination rates across different taxa

	Species	Class	Order	Family	Marker distance	Karyotype (1 N)	Genetic size (cM)	Physical size (Mb)	Density (cM/Mb)	Method[a]	Source
Social Hymenoptera	*Acromyrmex echinatior*	Insecta	Hymenoptera	Formicidae	16.5	18	2′236[b]	335	6.7	FC	Sirviö *et al*., 2007
	Apis mellifera	Insecta	Hymenoptera	Apidae	2.1	16	4′115	262	16.0	FC	Personal Communication, M Solignac;
	Bombus terrestris	Insecta	Hymenoptera	Apidae	10.3	18	2′760	625	4.4	FC	Gadau *et al*., 2001; Wilfert *et al*., 2006
	Pogonomyrmex rugosus	Insecta	Hymenoptera	Formicidae	NA	16	3′558	255	14.0	FC	Sirviö *et al*., 2007
Parasitoid Hymenoptera	*Bracon hebetor*	Insecta	Hymenoptera	Braconidae	17	10	800[b]	165	4.8	FD	Antolin *et al*., 1996; Rasch *et al*., 1977, genome size following Holloway *et al*., 2000
	Bracon sp. Near hebetor	Insecta	Hymenoptera	Braconidae	7.5	10	536	165	3.2	FD	Rasch *et al*., 1977; Holloway *et al*., 2000
	Nasonia vitripennis x giraulti	Insecta	Hymenoptera	Pteromalidae	8.4	5	765	312	2.5	FD	Rasch *et al*., 1977; Gadau *et al*., 1999
	Trichogramma brassica	Insecta	Hymenoptera	Trichogrammatidae	17.7	5	1′330	246	5.4	FC	Laurent *et al*., 1998; Johnston *et al*., 2004
Other insects	*Acyrthosiphon pisum pisum*	Insecta	Hemiptera	Aphididae	10.9	5	294	360	1.0	FD	Finston *et al*., 1995; Hawthorne and Via, 2002; Beye *et al*., 2006
	Aedes aegypti	Insecta	Diptera	Culicidae	1.4	3	205	793[c]	0.3	FD	Rao and Rai 1987; Severson *et al*., 2003
	Anopheles gambiae	Insecta	Diptera	Culicidae	1.8	3	215	278	0.8	GS	Zheng *et al*., 1997; Holt *et al*., 1992, 2002
	Armigeres subalbatus	Insecta	Diptera	Culicidae	7.6	3	182	1′215[c]	0.1	FD	Rao and Rai, 1990; Ferdig *et al*., 1998
	Bombyx mori	Insecta	Lepidoptera	Bombycidae	2.6	28	1′305[d]	510[c]	2.6	FD	Rasch 1974; Yasukochi, 1998; Yamamoto *et al*., 2007
	Culex pipiens	Insecta	Diptera	Culicidae	8.7	3	166	528	0.3	FD	Jost and Mameli, 1972; Mori *et al*., 1999
	Drosophila mauretania	Insecta	Diptera	Drosophilidae	4.2	3	463	147	3.1	FC	True *et al*., 1997; Boulesteix *et al*., 2006
	Drosophila melanogaster	Insecta	Diptera	Drosophilidae	NA	3	259	157	1.6	FC	True *et al*., 1997; Boulesteix *et al*., 2006
	Heliconius erato	Insecta	Lepidoptera	Nymphalidae	23	21	2′400	396	6.1	FC	Tobler *et al*., 2006
	Heliconius melpomene	Insecta	Lepidoptera	Nymphalidae	6.7	21	1′616	292	5.5	FC	Jiggins *et al*., 2006
	Laupala spec.	Insecta	Orthoptera	Gryllidae	15	8	2′330	1′900	1.2	FC	Petrov *et al*., 2000; Parsons and Shaw, 2002
	Leptinotarsa decemlineata	Insecta	Coleoptera	Chrysomelidae	11.1	18	1′032	450	2.3	FD	Petitpierre *et al*., 1994; Hawthorne, 2001
	Rhyzopertha dominica	Insecta	Coleoptera	Bostrichidae	4.6	9	390	476	0.8	FC	Schlipalius *et al*., 2003
	Tribolium castaneum	Insecta	Coleoptera	Tenebrionidae	1.3	10	571	199[c]	2.9	FD	Alvarez-Fuster *et al*., 1991; Lorenzen *et al*., 2006
	Tribolium confusum	Insecta	Coleoptera	Tenebrionidae	7.0	10	969	245[c]	4.0	FD	Alvarez-Fuster *et al*., 1991; Yezerski *et al*., 2004
Other protostomia	*Crassostrea gigas*	Bivalvia	Ostreoida	Ostreidae	9.2	10	1′096[d]	890	1.2	FD	Gonzalez-Tizon *et al*., 2000; Li and Guo, 2005
	Crassostrea virginica	Bivalvia	Ostreoida	Ostreidae	9.5	10	1′077[d]	675	1.6	FA	Hinegardner, 1974; Yu and Guo, 2004
	Daphnia pulex	Branchiopoda	Diplostraca	Daphniidae	7.0	12	1′206	235	5.1	FD	Rasch, 1986; Cristescu *et al*., 2006
	Heterodera glycines	Chromadorea	Tylenchida	Heteroderidae	4.5	9	687[e]	93	7.4[e]	FD	Lapp and Triantap Ac, 1972; Opperman and Bird, 1998; Atibalentja *et al*., 2005
	Penaeus monodon	Malacostraca	Decapoda	Penaidae	22.0	44	2′292[b]	2′000	1.1	FC	Chow *et al*., 1990; Wilson *et al*., 2003
	Penaeus vannamei	Malacostraca	Decapoda	Penaidae	16.4	44	4′015[d]	2′393	1.7	FC	Chow *et al*., 1990; Perez *et al*., 2005
	Pristionchus pacificus	Chromadorea	Diplogasterida	Neodiplogasteridae	2.9	6	339	100	3.4	GB	Sommer *et al*., 1996; Srinivasan *et al*., 2003
Vertebrata	*Ambystoma tigrinum*	Amphibia	Caudata	Ambystomatidae	8.0	14	5′251[f]	26′950[c]	0.2	FD	Morescalchi and Olmo, 1982; Smith *et al*., 2006
	Equus caballus	Mammalia	Perissodactyla	Equidae	3.7	32	2′772	3′087[c]	0.9	FC	Tiersch *et al*., 1989; Swinbume *et al*., 2006
	Gallus gallus	Aves	Galliformes	Phasianidae	NA	39	3′800[f]	1′225[c]	3.1	FA	Groenen *et al*., 2000
	Homo sapiens	Mammalia	Primates	Hominidae	0.5	23	3′615	3′191	1.1	GS	Kong *et al*., 2003
	Macaca mulatta	Mammalia	Primates	Hominidae	9.3	21	2′048	3′077[c]	0.7	FD	Manfredi, 1972; Rogers *et al*., 2007
	Mus musculus	Mammalia	Rodentia	Muridae	0.2	20	1′361	3′179	0.4	FC	Dietrich *et al*., 1996; Vinogradov, 1998
	Takifugu rubripes	Osteichthyes	Tetraodontiformes	Tetraodontidae	5.6	22	1′135[b,d]	365	3.1	GS	Aparicio *et al*., 2002; Kai *et al*., 2006
	Plasmodium falciparum	Aconoidasida	Haemosporida	Plasmodiidae	1.8	14	1′556	23	67.7	GS	Su *et al*., 1999; Gardner *et al*., 2002
	Toxoplasma gondii	Coccidia	Eimeriida	Sarcocystidae	2.9	14	592	65	9.6	GS	Khan *et al*., 2006
	Trypanosoma brucei		Kinetoplastida	Trypanosomaidae	9.5	11	1′358[b]	26	52.2	GS	Berriman *et al*., 2005; MacLeod *et al*., 2006
Fungi	*Cryptococcus neoformans*	Heterobasidiomycetes	Tremellales	Tremellaceae	4.8	14	1500	20	75	GS	Kullman *et al*., 2005; Marra *et al*., 2005
	Coprinus cinereus	Homobasidiomycetes	Agaricales	Agaricaceae	5.7	13	346	36	37.4	GS	Muraguchi *et al*., 2004; Kullman *et al*., 2005
	Cochliobolus sativus	Dothideomycetes	Pleosporales	Pleosporaceae	7.9	15	849	33	25.7	PFGE	Zhong *et al*., 2003

Abbreviations: FC, flow cytometry; FD, feulgen densiometry; FA, fluorescence assay; GB, genome blotting; GS, genome sequence; PFGE, pulse-field gel electrophoresis.
[a]Method used for estimating physical genome size.
[b]Minimal genome size: we added 40 cM per excess linkage group to the genetic map size provided by the original authors. The physical genome size in MB was calculated from its weight in pg as 1 pg = 980 Mb, following (Cavallier-Smith, 1985).
[c]Averaged over the sexes.
[d]Averaged estimate.
[e]Genome size estimated by original authors.
[f]Subclass.

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