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Asymmetrical Mating Success and the Phylogeny of *Drosophila*

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ABSTRACT Mating successes among five species of the *virilis* group of *Drosophila* have been examined by the 'no choice' method. In every reciprocal cross, one-sided (asymmetrical) mating success was detected, from which a unidirectional evolutionary sequence (the relative age of the species) can be postulated, *i. e.*, females of older species mate relatively well with males of younger species but females of younger species do not mate well with males of older species. However, the real phylogeny of the species group is not always unidirectional but often diversely branched. The degree of genetic similarity must be taken into account to search for the immediate ancestor of each species. These two components, the relative age of the species and the immediate ancestor of each species, allow us to postulate the phylogenetic tree of related species in *Drosophila*. (*Zool. Mag.* 90: 317-324, 1981)

The phenomenon of one-sided mating success has been observed since Darwin (1859). He cited a certain variety of the four o'clock plant, *Mirabilis jalapa* which was easily fertilized by the pollen of *M. longiflora* but the reciprocal cross was very difficult. This phenomenon was reported in *Drosophila* by Sturtevant (1920) for *D. melanogaster* and *D. simulans*, Dobzhansky (1944) for *D. sturtevanti* and Patterson *et al.* (1947) for the *D. virilis* group. Recently, Yoon *et al.* (1972), Ahearn *et al.* (1974), Kaneshiro (1976) and Ohta (1978) have also detected asymmetrical mating preferences among sibling species of Hawaiian *Drosophila*. The mating preferences exhibited in reciprocal matings of related species are species specific characters which have probably been acquired by each species and conservatively maintained.

Watanabe and Kawanishi (1979) have proposed a hypothesis that the direction of evolution in some *Drosophila* species groups may be ascertained by the mating preferences between sibling species. If we find a difference in reciprocal matings between two species, the species whose females more often fail to mate with

males of the other is the derived (new) species and the species whose females more often mate with alien males is the ancestral (old) species. However, this hypothesis is the reverse of that Kaneshiro (1976) postulated from studies of Hawaiian *Drosophila*. He hypothesized that females of ancestral species strongly discriminate against males of the derived species while females of the derived species readily accept males of ancestral species. Kaneshiro's hypothesis is supported by karyological data together with the geohistorical relationship among the Hawaiian Islands. He supposed that a new species in a younger island descended from a founder population which had migrated from an old island.

The mode of speciation which has been widely held by evolutionary biologists is the geographical theory of speciation: A subpopulation spatially isolated from the remainder of the ancestral species establishes new barriers of reproductive isolation which block gene flow between the two populations. During the period of geographical isolation, the reproductive isolation develops by the accumulation of genetic differences occurred in each population. There-

after the new subpopulation can survive as an independent species even though the geographical barrier was removed and live sympatric with the ancestral species, because they were already reproductively isolated.

However, many subpopulations must have been exterminated before they became a full species, since the geographical isolation was not always guaranteed for a long enough such as 10 million years (Nei, 1975) to complete the reproductive isolation. Sibling species or semi-species are often found sympatrically though they are not completely isolated in their reproductive systems. These closely related species groups seem to be in the process of speciation in which finally they become a full species but now they live sympatrically with the incomplete reproductive barrier.

Then we considered that the relation between the speciation and mating success among sibling species was as follows in Fig. 1: When small subpopulations which had been geographically isolated from the ancestral population A, rejoined partially with the ancestral large population, both subpopulations might have some reproductive isolating barriers though they were incomplete but they partially suppressed random mating between the subpopulation (B or B') and the ancestral population (A). Further development of speciation of the sympatric subpopulations depends primarily on the genetic differences already gained during the geographical isolation. If the genetic differences behaviorally work to lessen the gene flow from the old (ancestral) population to the new (derived) subpopulation, the subpopulation can survive against the danger of mixing and contamination with genes from the old population.

In the case of the subpopulation B', whose males do not mate with the females of the old population A but the B' females easily accept the A males, the breakdown of the new subpopulation B' will occur because the genes of A population are easily introduced into the B' subpopulation by the A males. On the other hand, subpopulation B, whose females do not

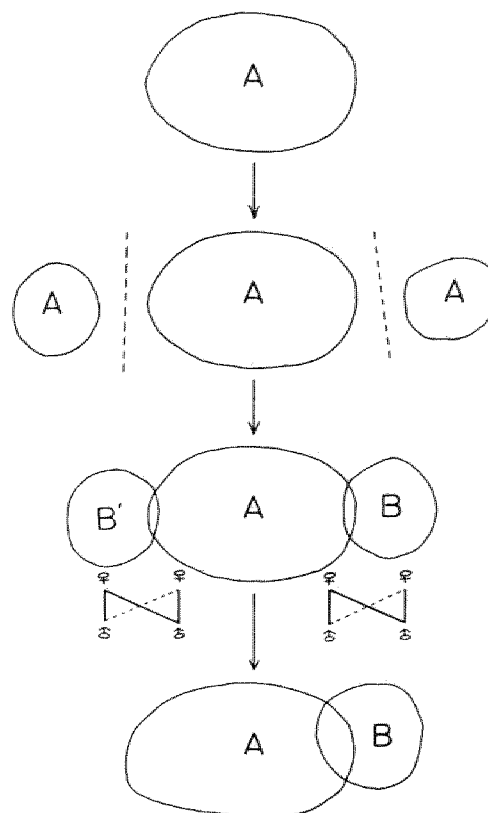


Fig. 1. Schematic relationship of mating preferences in speciation according to the hypothesis that new species evolves in contact with old species. —: more successful mating,: less successful mating.

mate with the old males though B males easily mate with the A females, is protected from the gene flow through the A males. Migration of B males into the A population has little effect, for the minority of genes introduced in this way will be swamped by the much larger number in A and perhaps will be eliminated by normalizing selection.

The above behavioral difference in mating success between the sibling species is perfectly effective for the plant speciation in which only males (pollens) migrate between the border of two populations. In *Drosophila*, although males are more active than females, females also can

migrate across the border to mate and lay eggs there. It means that genes can flow from the old A population to the new B subpopulation, by hybridization between the migrated old females and the new subpopulation males. However, if gene(s) which suppress the mating between the old males and the new females is located in the X chromosome or it is recessive to the old gene when located in the autosomes, hybrid males prefer to mate with females carrying genes of the old population. This mechanism prevents the gene flow from the old to the new in case of old A-new B relation but does not work in case of old A-new B' relation. In fact, this kind of mating preference was found in several pairs of sibling species; *D. pseudoobscura*-*D. persimilis* (Tan, 1946), *D. pallidosa*-*D. ananassae* (Futch, 1973), and *D. melanogaster*-*D. simulans* (Kawanishi and Watanabe, 1981). Hybrid males of the above pairs preferred to mate with the former (ancestral) species females such as *D. pseudoobscura*, *D. pallidosa* and *D. melanogaster*. Thus, even though the migrated females from the old population produced hybrid males by the mating with the new males, genes once introduced into the new again flow back to the old population by the mating preference of the hybrid males which perhaps prevents further gene flow from the old to the new population in the case of old A-new B relation.

Moreover, distantly colonized (allopatric) populations are not always geographically isolated. Every subpopulation is more or less exposed to the danger of invasion by a few migrants from the old ancestral population. Therefore, unsuccessful mating between the old males and the new females is the minimum request for the first step of speciation which finally allows both populations to diverge into different species. This leads to the prediction that, when there is a difference in the success of matings reciprocally, the species whose females most often fail to mate with males from the other is the new (derived) species.

The present paper proposes a phylogenetic

interpretation of the observed asymmetrical mating success in *Drosophila*. Although the directions are opposite, both hypotheses, Kanehiro's (1976) and ours (1979), postulate a uni-directional interpretation of the phylogeny of some *Drosophila* species group. However, the real phylogeny of most species group is not always uni-directional but often diversely branched. Two evolutionarily important components, the relative age of a species and the immediate ancestor of each species, are deduced from data of mating successes in the *Drosophila virilis* group.

Materials and Methods

The following strains of five species of the *Drosophila virilis* group were used.

- (1) Texmelucan, Puebla (Mexico) strain of *D. virilis* (No. 1801.1).
- (2) Chaco (Argentina) strain of *D. virilis* (No. 1999.1).
- (3) San Antonio, New Mexico (USA) strain of *D. novamexicana* (No. 1714.1).
- (4) Patagonia, Arizona (USA) strain of *D. novamexicana* (No. 2358.6).
- (5) South Hero, Vermont (USA) strain of *D. americana* (No. 1893.10).
- (6) Halsey, Nebraska (USA) strain of *D. americana* (No. 2515.3).
- (7) Tallahassee, Florida (USA) strain of *D. texana* (No. 2007.6).
- (8) Chestview, Florida (USA) strain of *D. texana* (No. 2301.5).
- (9) Swedish strain of *D. littoralis* (No. 1026).
- (10) Finnish strain of *D. littoralis* (No. 1061).

The eight American strains were supplied by Dr. M. R. Wheeler. The numbers after the species names are the stock number of the University of Texas collection. The two Scandinavian strains, (9) and (10), were supplied by Dr. S. Lakovaara and the stock number are those of the University of Oulu.

The mating experiments employed the 'no-choice' method by Spieth (1968). Virgin females and males were collected from each strain and were separately aged for four days. On the

fifth day, ten females and ten males were put together in a vial (3×10 cm) containing standard medium. They were left there for three days except for the crosses using *D. littoralis* which needed two more days for satisfactory mating, even for the cross within the species. After the period of mating, all females were dissected to determine whether or not they had been inseminated. The experiment was replicated from eight (80 females) to twenty (200 females) times. Since we used two lines for each species, the same number of replicates for each cross was made.

All experiments were carried out at 25°C

under a fluorescent lamp. A corn meal, agar, brown sugar and brewer's yeast medium was used.

Results and Discussion

Asymmetrical mating success between reciprocal interspecific crosses: The results of the mating experiments are shown in Table 1. Since there was no significant difference among strains of each species, within-species data were pooled. The percent of successful matings within species crosses ranged from 91.3 to 100 %, suggesting that the mating period of 3 days (5 days mating for *D. littoralis*), seemed to be

Table 1. Percent of successful matings among five species of the *Drosophila virilis* group

Female	Male	No. of females dissected (n)	No. of females inseminated	Percent of successful matings (P)	(Mean)	Z*	D**
virilis	virilis	120	120	100			
littoralis	littoralis	100	92	92			
novamexicana	novamexicana	120	117	97.5			
americana	americana	160	155	96.9			
texana	texana	160	146	91.3			
virilis	littoralis	100	52	52	(30.5)	7.47	0.94
littoralis	virilis	100	9	9			
virilis	novamexicana	100	87	87	(60.0)	9.34	0.24
novamexicana	virilis	100	33	33			
virilis	americana	100	88	88	(49.0)	17.66	0.24
americana	virilis	100	10	10			
virilis	texana	100	83	83	(47.0)	14.73	0.47
texana	virilis	100	11	11			
littoralis	novamexicana	100	40	40	(20.0)	8.16	1.09
novamexicana	littoralis	100	0	0			
littoralis	americana	100	45	45	(23.0)	8.67	0.88
americana	littoralis	100	1	1			
littoralis	texana	80	35	43.8	(22.6)	7.47	1.14
texana	littoralis	80	1	1.3			
novamexicana	americana	100	97	97	(55.0)	22.28	0.24
americana	novamexicana	100	13	13			
novamexicana	texana	100	90	90	(53.0)	15.62	0.43
texana	novamexicana	100	16	16			
americana	texana	200	193	96.5	(93.8)	2.29	0.43
texana	americana	200	182	91			

*Z: $Z = (P_1 - P_2) / \sqrt{P_1(1 - P_1)/n_1 + P_2(1 - P_2)/n_2}$. If the Z is greater than 1.96, the difference between the pair is significant at the 5% level.

**D: Genetic distance reported by Nei (1971).

appropriate for the *virilis* group.

Interspecific crosses exhibit great variation in frequency of successful matings from 0 to 97%. The differences between pairs of reciprocal interspecific matings were also remarkable. Females of *D. virilis* were always more successful in mating with males of *D. littoralis*, *D. novamexicana*, *D. americana* and *D. texana* than the reciprocals. Males of *D. texana* were the more successful in mating with females of all species than the reciprocals. Every reciprocal pair of the ten combinations of the five species showed significant difference in the mating success. These results are very similar to the classical studies of Patterson and Stone (1949) and Patterson (1952), which had been done by 'male-choice' method.

Postulated phylogeny of the virilis species group: The differences in successful matings

between pairs of reciprocal interspecific matings observed in Table 1 are graphically presented in Fig. 2. The five species are arranged according to the following scheme: if the females of species A mated more often the males in a cross with species B, species A was put to the left of the species B. The most parsimonious order is *virilis* → *littoralis* → *novamexicana* → *americana* → *texana*.

The interpretation of this order is that females of the species on the left readily accept males of the species on the right while the females of the species on the right reject males of the species on the left. Alternatively, it can be said that males of the former species hesitate to court females of the latter species while the males of the latter species readily court females of the former species. Some behavioral and experimental observations suggest that the

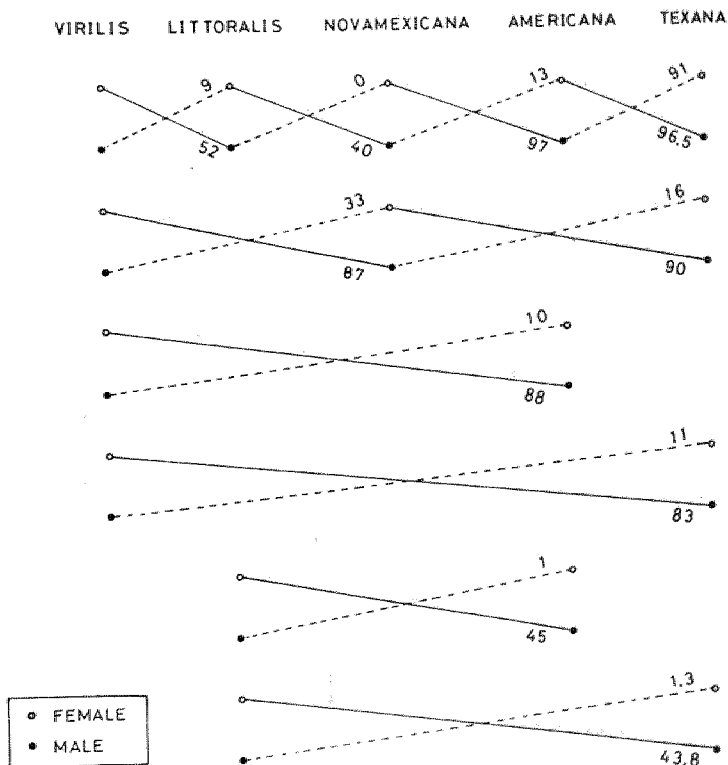


Fig. 2. Schematic relations of mating success (%) between reciprocal crosses of the *D. virilis* group.

females more often exercise the discrimination (Mayr 1946; Streisinger 1948), but some others suggest the males discriminate more often (Wood and Ringo 1980).

Here we propose two components of species evolution. One is the relative age of a species and the other is the immediate ancestor of each species. The former is the evolutionary sequence which means the emergence order of species as presented above. The most probable immediate ancestor of a species must be genetically close to the species. The genetic closeness between the species may be measured by the average percent of successful matings. Incidentally, genetic similarity due to enzyme variation was highly correlated with the degree of mating success. In Table 1 the genetic distance (D) between species obtained by Nei (1971) are also presented. Nei's D, the number of electrophoretically detectable amino acid differences per protein, was estimated from the data of Hubby and Throckmorton (1965). Correlation between the D value and the mean percent of successful matings was significantly negative, $r = -0.754$ (d. f. = 8, $0.05 > P > 0.01$).

The relation between the two components, the relative age of a species and the immediate ancestor of each species, are shown in Fig. 3. The emergence order of species is the same for the both cases (A→B→C). However, in case of a, B is the immediate ancestor of C and A is the immediate ancestor of B so that the relation of A-B-C is like a grandmother-mother-daughter. But in case of b, A is the immediate ancestor of both B and C so that the relation of A-B-C is like a mother-elder sister-younger sister. For the emergence of the third species, C, females of C must always be reproductively isolated from males of both A and B. Or, when the species C was reproductively isolated from the species A, the species C might be automatically isolated from the elder species B, since the B had ever been the A in the evolutionary past. Of course, every species ever been should not have survived, then the predicted immediate ancestor means only the most probable candidate

for the immediate ancestor among the tested species.

The emergence order of the first three species is *D. virilis*→*D. littoralis*→*D. novamexicana* as predicted in Fig. 2. However, the *D. novamexicana* seemed to have arisen from *D. virilis* not from *D. littoralis* since the *D.*

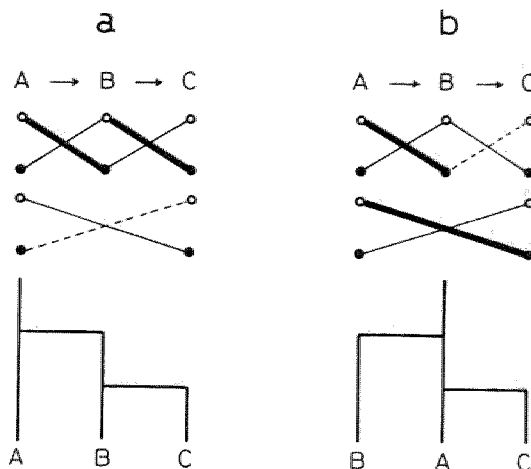


Fig. 3. Relationship between the evolutionary sequence (→) and the phylogenetic tree. —: more successful mating, — —: fairly successful mating, ····: less successful mating.

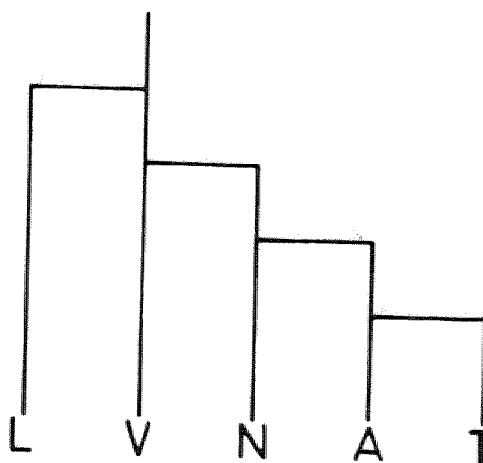


Fig. 4. Postulated phylogenetic tree of the *D. virilis* group. L: *littoralis*, V: *virilis*, N: *novamexicana*, A: *americana*, T: *texana*.

novamexicana is reproductively closer to *D. virilis* (60%) than to the *D. littoralis* (20%). The remaining species, *D. americana* and *D. texana*, seemed to have arisen from *D. novamexicana* (55%) and *D. americana* (93.8%) respectively. Figure 4 summarizes the results. Although *D. americana* was tentatively postulated as an older species than *D. texana*, they are reproductively very close to each other. At any rate, they are the youngest among the five species.

The chromosomal phylogeny of the *virilis* group has been reported by Stone (1962). His result is very consistent with the present phylogeny based of mating preferences. Even though Stone's phylogeny had been established by the subjective assumption that *D. virilis* was the probable ancestral species, the two different studies include two directional branches: *D. virilis*→*D. littoralis* and *D. virilis*→*D. novamexicana*→*D. americana*→*D. texana*. Our previous report (Watanabe and Kawanishi, 1979) also pointed out two branches, one from *D. virilis* to *D. novamexicana* and the other from *D. virilis* to *D. lacicola* or *D. montana*. The phylogeny of the *virilis* group based on the electrophoretic studies has been proposed since Hubby and Throckmorton (1965). Nei (1971) estimated the divergence time between the pairs of related species from the protein identities. His evolutionary tree showed that *D. littoralis* diverged earlier than *D. novamexicana* and *D. americana* among the *virilis* group which is consistent with the present phylogeny.

The present study has extended our previous hypothesis (Watanabe and Kawanishi, 1979) by considering two components in speciation, the relative age of the species and the immediate ancestor of each species. That is, females of older species mate relatively well with males of younger species but females of younger species do not mate well with males of older species. The evolutionary sequence drawn by the asymmetrical mating preferences only suggests the relative age of each species. Therefore, it resulted in a unidirectional se-

quence.

The skeleton of phylogeny can be postulated by the above sequence but it must be revised by the degree of genetic similarity between the pair of each species. In the present paper, we used the average mating success as a measurement of genetic closeness. Genetic distance obtained from electrophoretic data is of course useful for the measurement. In any case, this procedure improves the phylogeny from unidirectional one to diversely branched, more realistic one.

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