

## SHORT PAPER

### Stasipatric speciation in *Drosophila*

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(Received January 8, 1983)

#### ABSTRACT

Geographical distribution of some sibling species of *Drosophila* was explained by the direction of evolution based on the mating preferences and White's stasipatric speciation. The *D. bipectinata* complex and the *D. takahashii* complex distributed in the Oriental-Australian biogeographic zones are good examples for the speciation model in which the sibling species repeatedly evolved in the center near Borneo and expanded radially, eliminating the old species.

Two opposing models have been proposed for predicting the direction of evolution from asymmetrical mating preferences among sibling species of *Drosophila*. Kaneshiro (1976, 1980) proposed that males of derived species were not readily accepted by females of the ancestral species because the derived males have lost some courtship properties which are required for successful mating with ancestral females. On the contrary, Watanabe and Kawanishi (1979, 1981) proposed that it was the females of the derived species which discriminated and rejected the males of the ancestral species because the newly derived species population must be protected from gene invasion by the males of the ancestral species. A fundamental difference between the models came from the postulated situation when the new species was formed. Kaneshiro constructed his model according to an allopatric model, while we assumed sympatry. Kaneshiro's asymmetrical isolation is a consequence of the allopatric speciation, while our asymmetrical isolation is a possible cause of sympatric speciation.

Wide fluctuations of population size are common in nature. When a population dwindles into a few individuals, a rare mutation can be fixed in a few generations. Genes affecting mating preferences must be included in this process. Powell (1978) and Markow (1981) easily detected such changes in experimental populations of *D. pseudoobscura* and *D. melanogaster*. Since the mutations occur randomly, some new populations carry an old (ancestral)-female-rejecting gene and some an old-male-rejecting gene to lessen the mating between the old and new populations. If either population increases in

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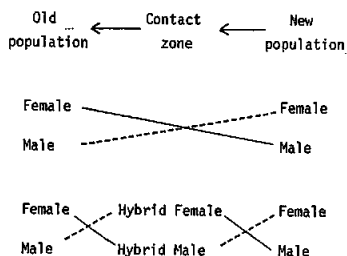


Fig. 1. One-way street-like contact zone formed by the old and new populations according to the Watanabe-Kawanishi's asymmetrical isolation model. Hybrid progenies are derived from the more productive of the reciprocal parental crosses. ( $\leftarrow$ ), gene flow; (—), more successful mating; (----), less successful mating.

number, they come in contact with each other and share the same niche. Mating will occur in the contact zones according to individual preferences.

If the new population carries the old-female-rejecting gene, mating between ancestral females and new males will be suppressed in the contact zone, but the reciprocal mating between old males and new females will occur, producing hybrid progeny (Kaneshiro's model). On the contrary, if a new population carries the old-male-rejecting gene, mating between old males and new females will be suppressed, although the mating between old females and new males will produce hybrid progenies (Watanabe-Kawanishi's model). Using data on mating preferences of the hybrid progenies, we develop our hypothesis as follows.

Fig. 1 shows the mating preference of individuals in the contact zone of the old and new populations according to our model. A population whose females discriminate and reject alien males was postulated to be the new (derived) population. Population growth due to adaptation to the environment, intrinsic fitness, and migratory activity were supposed to be equal between the populations. Mating preferences of hybrid females among the corresponding parental males have been tested by many *Drosophila* workers. Among them, Bock (1978) clearly showed that hybrid females of *D. malerkotliana* ♀ × *D. parabiopectinata* ♂, *D. pseudoananassae* ♀ × *D. parabiopectinata* ♂, and *D. pseudoananassae* ♀ × *D. malerkotliana* ♂ preferred to mate with males of the paternal species rather than with those of the maternal species. These parental crosses were more successful than the reciprocal crosses, so that the paternal species were postulated as the derived species according to our model (Fig. 2). That is, hybrid females accept more easily the derived males rather than the ancestral males which allows gene flow from the new population to the contact zone but not in the reverse direction. On the other hand, hybrid males produced by *D. melanogaster* ♀ × *D. simulans* ♂, *D. pseudoobscura* ♀ × *D. persimilis* ♂, and *D. pallidosa* ♀ × *D. ananassae* ♂ preferred to mate

with females of the maternal species rather than with those of the paternal species (Kawanishi and Watanabe 1981; Tan 1946; Futch 1973). Therefore, the maternal species of these crosses were classified as the ancestral species according to our model. Then, gene flow from the contact zone to the old population through the hybrid males is more likely than from the contact zone to the new population. Mating preferences of the hybrid progenies presented here are genetically understandable if the mating genes fixed in a new population are recessive to the old (original) genes, or are semidominant.

Thus, the contact zone is very similar to a one-way street allowing relatively free passage of genes from the new population to the old population via hybrid progenies in the contact zone, but holding back gene flow in the other direction. This concept is analogous to the White's stasipatric speciation model (White 1968; Key 1968) proposed by the karyological studies of a Morabine grasshopper species group. That is, a new species arose within the old species range and took over whatever area it could by eliminating the old species. In case of the Morabine grasshopper, isolation was reproductive (post-mating) and the contact zone (tension zone) moved to the less adapted population. In the present case of *Drosophila*, isolation is pre-mating and the contact zone moves to the ancestral population when the derived population carried an old-male-rejecting gene, even if the both populations are equally adapted to the environment.

Fig. 2 illustrates the mating preferences and the distribution of the *bipectinata* complex of *Drosophila* according to Bock (1978). The direction of species evolution of the complex was predicted by our model to be *pseudoananassae* → *malerkotliana* → *bipectinata* → *parabipertinata*. The geographical distribution of the oldest species (*pseudoananassae*) is from Thailand and Borneo to New Guinea and Australia. The youngest species (*parabipectinata*) is around Borneo. All the four species now coexist in Borneo which seems to be the center of this group. While *D. parabipectinata* was evolving in Borneo, the other older species might have been extending their populations in other directions such as New Guinea (*pseudoananassae*), India (*malerkotliana*), and Japan or Fiji (*bipectinata*). When the speciation proceeds further, the older species will be eliminated from Borneo.

Fig. 3 shows a more advanced case of species evolution and the geographical distribution. The mating crosses were made by us; 'No Choice' method of introducing ten females and ten alien males in a vial and dissecting the females after two days to measure the insemination rate. Replication was made more than five times using two strains of each species. The species distributions are from Bock and Wheeler (1972). According to our model the four species belonging to the *takahashii* complex of *Drosophila* evolved in the sequence *pseudotakahashii* → *trilutea* → *lutescens* → *takahashii*. Both reciprocal matings between *pseudotakahashii* and *lutescens* or *takahashii* were unsuc-

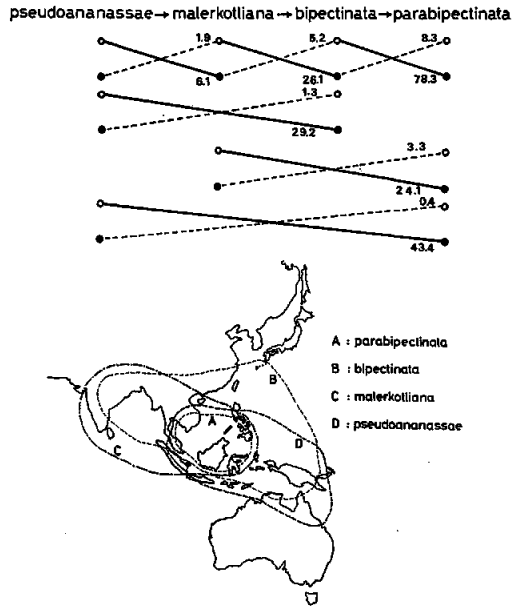


Fig. 2. Asymmetrical mating success (%) predicting the direction of evolution (→) and the distribution of the *D. bipectinata* complex according to Bock (1978). (○), female; (●), male.

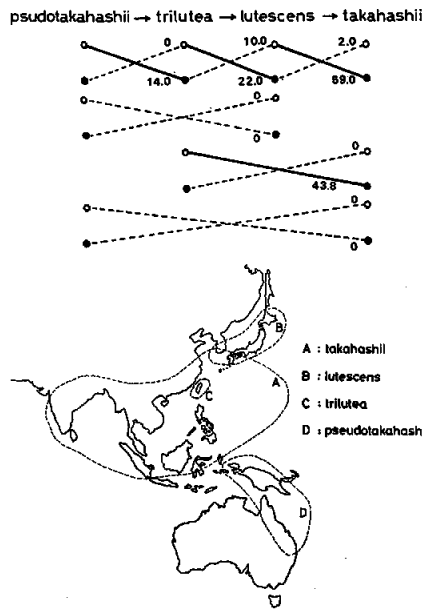


Fig. 3. Asymmetrical mating success (%) predicting the direction of evolution (→) and the distribution of the *D. takahashii* complex. (○) female; (●) male.

cessful. This probably means that both species pairs have already evolved so far that they strongly discriminate against each other. However, 14% of the *pseudotakahashii* females still accepted *trilutea* males because they are closest species. The present distribution of the four *takahashii* complex is geographically restricted to some specific areas, more so than the *bipunctinata* complex. The oldest species, *pseudotakahashii*, is found in New Guinea-Australia region, the next oldest *trilutea* is restricted to Taiwan, and *lutescens* lives in Far East. The youngest species, *takahashii*, is distributed in a wide area from India, Borneo to Japan. If we suppose that each species has evolved near Borneo (center) and expanded its population according to the one-way street action by the hybrid progenis, finally eliminating the older species from the center, the separate distribution of the four species is understandable. Now *Drosophila takahashii* has almost replaced the other siblings in South East Asia.

In conclusion, the species groups of *Drosophila* have evolved near Borneo, which is the center of many *Drosophila* species, and have expanded radially either by chance or according to the adaptive potential of each species. At the initial stage of species formation, old-male-rejecting gene fixed in a new population must have played an important role among many isolating genes, since they act as a defense of a small new population (Watanabe-Kawanishi's model). On the contrary, even if an old-female-rejecting gene were fixed in the new population but no discrimination occurred between old males and new females, old genes inevitably flow into the new population through the contact zone (Kaneshiro's model). At the contact zone, only when the new population was established according to the Watanabe-Kawanishi's model, will hybrid progenies behave like a one-way street which allows the gene flow from the new to the old through the contact zone but holding back reverse gene flow. This condition is analogous to the White's stasipatric speciation model. Thus, if we take both Watanabe-Kawanishi's model and White's model into consideration, the geographical distribution of many *Drosophila* species can be understood as an evolutionary process.

We thank Dr. J. F. Crow for reading and criticizing the manuscript. *D. trilutea* was supplied by Dr. F. J. Lin, Taiwan and *D. pseudotakahashii* by Dr. M. R. Wheeler, Texas. Contribution No. 1406 from the National Institute of Genetics, Mishima, Japan.

#### REFERENCES

- BOCK, I. R. (1978) The *bipunctinata* complex: A study in interspecific hybridization in the genus *Drosophila* (Insecta: Diptera). *Aust. J. Biol. Sci.* **31**, 197-208.
- BOCK, I. R. and WHEELER, M. R. (1972) The *Drosophila melanogaster* species group. *Univ. Texas Publ.* **7213**, 1-102.
- FUTCH, D. G. (1973) On the ethological differentiation of *Drosophila ananassae* and *Drosophila pallidosa* in Samoa. *Evolution* **27**, 456-467.

- KANESHIRO, K. Y. (1976) Ethological isolation and phylogeny in the *planitibia* subgroup of Hawaiian *Drosophila*. *Evolution* **30**, 740-745.
- KANESHIRO, K. Y. (1980) Sexual isolation, speciation and the direction of evolution. *Evolution* **34**, 437-444.
- KAWANISHI, M. and WATANABE, T. K. (1981) Genes affecting courtship song and mating preferences in *Drosophila melanogaster*, *Drosophila simulans* and their hybrids. *Evolution* **35**, 1128-1133.
- KEY, K. H. L. (1968) The concept of stasipatric speciation. *Syst. Zool.* **17**, 14-22.
- MARKOW, T. A. (1981) Mating preferences are not predictive of the direction of evolution in experimental populations of *Drosophila*. *Science* **213**, 1405-1407.
- POWELL, J. R. (1978) The founder-flush speciation theory: An experimental approach. *Evolution* **32**, 465-474.
- TAN, C. C. (1946) Genetics of sexual isolation between *Drosophila pseudoobscura* and *Drosophila persimilis*. *Genetics* **31**, 558-573.
- WATANABE, T. K. and KAWANISHI, M. (1979) Mating preference and the direction of evolution in *Drosophila*. *Science* **205**, 906-907.
- WATANABE, T. K. and KAWANISHI, M. (1981) Asymmetrical mating success and the phylogeny of *Drosophila*. *Zool. Mag. (Tokyo)* **90**, 317-324.
- WHITE, M. J. D. (1968) Models of speciation. *Science* **159**, 1065-1070.