

Molecular phylogenetic relationships of the *Drosophila* (*Drosophila*) *virilis* section (Diptera, Drosophilidae)

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The genus *Drosophila* within the family Drosophilidae is an extremely species-rich radiation with at least 1000 described species occurring in all major biogeographic realms (Wheeler, 1981, 1986; Ashburner, 1989). Hsu (1949) divided this subgenus into the *quinaria* section and the *virilis* section by the structure of the male genitalia. Throckmorton (1975) recognized that two major evolutionary radiations, the *virilis-repleta* radiation and the *immigrans-Hirtodrosophila* radiation, have occurred in this subgenus. The species groups of the subgenus *Drosophila* emerged in the *virilis-repleta* radiation are called as the *virilis* section. The *virilis* section is one of the best-studied groups in the genus *Drosophila*, with respect to morphological observations, geographic distribution, habitats, chromosomal analyses, and molecular phylogeny. Nevertheless, the phylogenetic relationships and the evolutionary scenario of this section have not been established.

To clarify the phylogenetic relationships for the *virilis* section, I analyzed the sequences of the *ND2*, *COI*, and *Adh* genes. The phylogenetic tree was constructed by the minimum evolution (ME) method (Rzhetsky and Nei, 1992). Furthermore, to estimate the time of divergence for the *virilis* section, I reconstructed a linearized tree for the *Adh* sequences under the assumption of a constant rate of evolution (Takezaki et al., 1995).

The phylogenetic tree obtained from the *Adh* gene sequences showed that the *virilis* section made a large monophyletic cluster, demonstrating that the *virilis-repleta* radiation, which was recognized by Throckmorton (1975), has really occurred. From the phylogenetic tree, five sub-lineages were recognized for the *virilis* section. The first sub-lineage included the *robusta*, the *melanica*, and the *quadrisetata* species groups. The second and third sub-lineages were comprised of members of the *angor* and the *virilis* groups, respectively. The fourth sub-lineage contained the *polychaeta* group and *D. hirtipes* an uncertain species distributed in the Ethiopian region. The fifth sub-lineage was composed of the Neotropical species and *D. fluvialis* an Oriental member of the *virilis* section.

The phylogenetic tree has undoubtedly showed that most species groups of the *virilis* section are monophyletic. However, the *robusta* group did not form a monophyletic group. In the phylogenetic tree, the *robusta*, the *melanica*, and the *quadrisetata* groups formed a monophyletic cluster. In this cluster, the *okadai* and the

*lacertosa* subgroups of the *robusta* group, which have adapted to streamside environments with a high humidity and a relatively constant temperature, made a cluster together with the *quadrisetata* group. On the other hand, the *robusta* subgroup and *D. unimaculata* of the *robusta* group, which have adapted to natural forests, made another cluster with the *melanica* group. This relationship suggests that the ecological character rather than the morphological and cytological characters would reflect the real picture of the evolutionary history of the *robusta* group.

Based on the geographic distribution, molecular phylogeny, and divergence times, I proposed a scenario for the evolutionary history for the *virilis* section as follows. The common ancestor of the *virilis* section would have originated probably in the Oriental region. The Neotropical species have diversified throughout the Oriental region to the Neotropical one during the early Oligocene period with the warming up of temperatures. Among the Holarctic species, the *angor* group and the *quadrisetata* group, and the *okadai* and the *lacertosa* subgroups of the *robusta* group, which have adapted to the riparian environments, extended their distribution from the Oriental region to middle geographic latitudes of the Palearctic one during the early Oligocene. On the other hand, the *virilis* group and the *melanica* group and the *robusta* subgroup, which inhabit both watersides and forests, extended their distribution range from the Oriental region to high latitudes of the Palearctic one, when the global climatic change have occurred with the warm of temperature. Thereafter, these species emigrated from the Palearctic region to the Nearctic one by way of the Bering Strait during the middle Miocene and the Pliocene, when the land bridge between the Old and the New World was constructed. The current disjunctive distribution patterns for these species would have been resulted from the climatic changes during the Tertiary period.