



Increasing the data size to accurately reconstruct the phylogenetic relationships between nine subgroups of the *Drosophila melanogaster* species group (*Drosophilidae*, *Diptera*)

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ABSTRACT

Previous phylogenetic analyses of the *melanogaster* species group have led to conflicting hypotheses concerning their relationship; therefore the addition of new sequence data is necessary to discover the phylogeny of this species group. Here we present new data derived from 17 genes and representing 48 species to reconstruct the phylogeny of the *melanogaster* group. A variety of statistical tests, as well as maximum likelihood mapping analysis, were performed to estimate data quality, suggesting that all genes had a high degree of contribution to resolve the phylogeny.

Individual locus was analyzed using maximum likelihood (ML), and the concatenated dataset (12,988 bp) were analyzed using partitioned maximum likelihood (ML) and Bayesian analyses. Separated analysis produced various phylogenetic relationships, however, phylogenetic topologies from ML and Bayesian analysis based on concatenated dataset, at the subgroup level, were completely identical to each other with high levels of support. Our results recovered three major clades: the *ananassae* subgroup, followed by the *montium* subgroup, the *melanogaster* subgroup and the oriental subgroups form the third monophyletic clade, in which *melanogaster* (*takahashii*, *suzukii*) forms one subclade and *ficuspshila* [*eugracilis* (*elegans*, *rhopaloa*)] forms another. However, more data are necessary to determine the phylogenetic position of *Drosophila lucipennis* which proved difficult to place.

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1. Introduction

The *melanogaster* species group, which includes 12 species subgroups: *ananassae*, *montium*, *melanogaster*, *suzukii*, *takahashii*, *ficuspshila*, *elegans*, *rhopaloa*, *eugracilis*, *denticulata*, *flavohirta*, and *longissima*; with more than 177 species (Throckmorton, 1975; Lemeunier et al., 1986; Grimaldi, 1991), is the crucial species group to discover the phylogeny of subgenus *Sophophora*. Recently, the phylogeny of the *Drosophila melanogaster* species group was studied based on various data, specifically, DNA sequence data. However, all analyses brought conflicting phylogenetic hypotheses (Fig. 1) (Pélandakis and Solignac, 1993; Inomata et al., 1997; Harr et al., 2000; Goto and Kimura, 2001; Kopp and True, 2002; Kastanis et al., 2003; Yang et al., 2004; Mou et al., 2005; Lewis et al., 2005; Kopp, 2006; Da Lage et al., 2007; Wong et al., 2007; Van der Linde and Houle, 2008; Van der Linde et al., 2010). By comparing the aforementioned hypotheses, the main conflicts focused on the

following: First, most investigations suggested that the *ananassae* subgroup is the basal subgroup (Pélandakis and Solignac, 1993; Inomata et al., 1997; Harr et al., 2000; Goto and Kimura, 2001; Kopp and True, 2002; Kastanis et al., 2003; Lewis et al., 2005; Kopp, 2006; Da Lage et al., 2007; Wong et al., 2007; Van der Linde and Houle, 2008; Van der Linde et al., 2010); however, Yang et al. (2004) and Mou et al. (2005) suggested that *montium* is the basal clade. Second, the phylogenetic relationships between the *melanogaster* subgroup and the oriental subgroups are still obscure; the phylogenetic positions of the *melanogaster*, *eugracilis*, and *ficuspshila* subgroups were quite different among all previous research. Third, analyses disagree as to whether the *suzukii* subgroup is polyphyletic or monophyletic. In some previous analyses, *Drosophila lucipennis* was nested within the *suzukii* subgroup (Mou et al., 2005) or grouped with some species of the *montium* subgroup (Lewis et al., 2005), but in some other analysis, which was closely related to *Drosophila elegans* (Schwaroch, 2002; Kopp and True, 2002; Da Lage et al., 2007; Van der Linde and Houle, 2008; Van der Linde et al., 2010).

The cause of the conflicting hypotheses is not known. All previous studies on the phylogeny of the *melanogaster* species group are based on different sample sizes or genetic markers. Differences in the number of taxa and the number of genes can have

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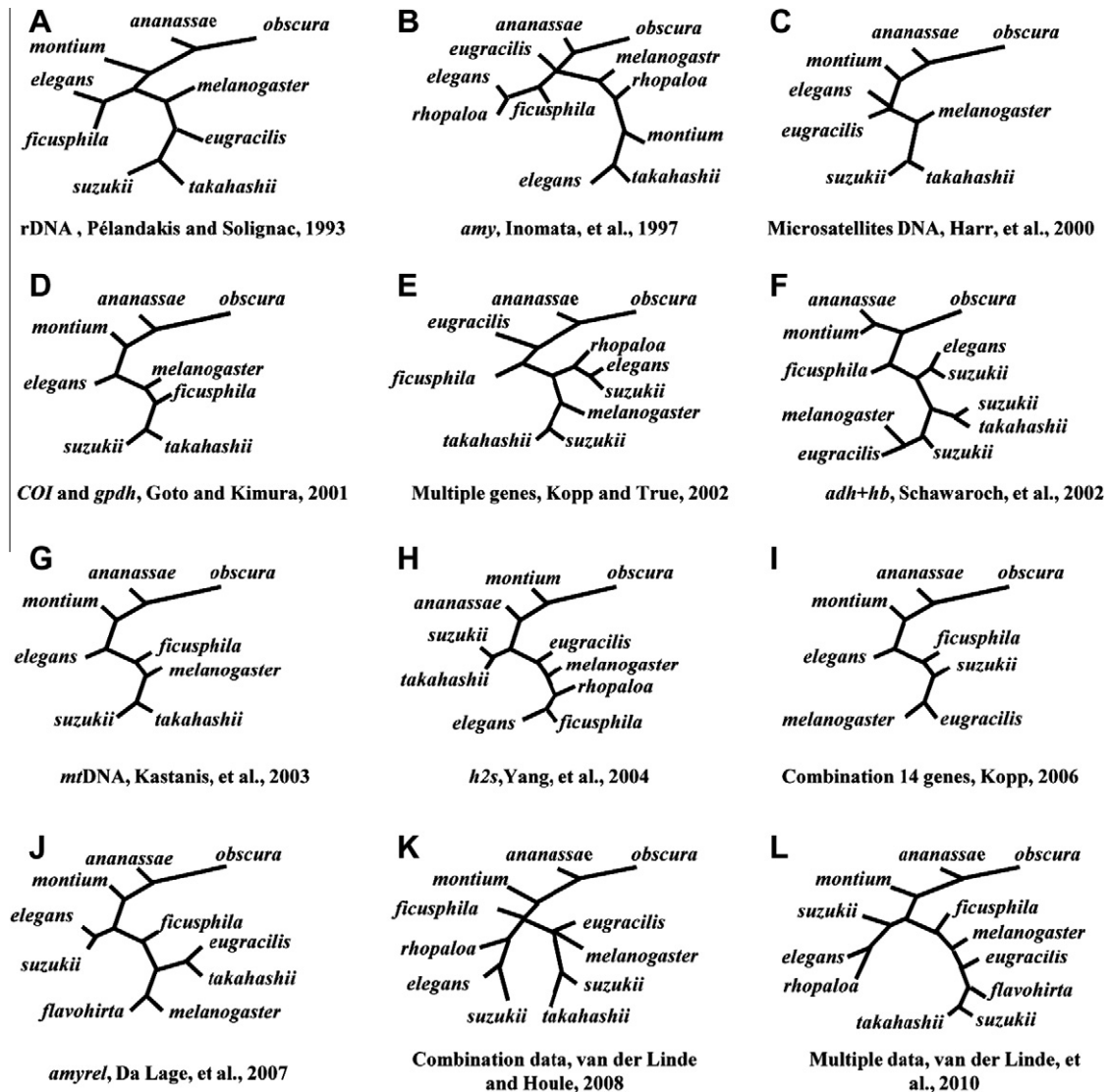


Fig. 1. Summary of the phylogeny among some subgroups in the *melanogaster* species group.

an effect on phylogenetic accuracy (Rokas and Carroll, 2005). Incomplete or insufficient taxon sampling has led to major inconsistencies in phylogenetic reconstructions (Hillis et al., 2003; Pollock et al., 2002; Zwiclk and Hillis, 2002; Schawaroch, 2002). In many previous phylogenetic treatments of this group, representatives of only eight subgroups out of 12 total or less were included, or the *rhopaloo* subgroup was ignored (Harr et al., 2000; Goto and Kimura, 2001; O'Grady and Kidwell, 2002; Kastanis et al., 2003; Kopp, 2006; Da Lage et al., 2007; Wong et al., 2007). On the other hand, differing sets of genetic markers were selected in previous studies, the conflicting hypotheses mostly resulted from limited phylogenetic information (only one gene sequence; Inomata et al., 1997; Schawaroch, 2002; Yang et al., 2004; Da Lage et al. 2007). Kopp (2006) analyzed the phylogeny of the *melanogaster* species group based on 14 loci; however, only one species was presented in each subgroup, and the *suzukii* and *rhopaloo* subgroups were ignored. For resolving complex phylogenetic problems, large data set containing more taxa and more gene sequences is more advantageous than small one (Rannala et al., 1998; Rokas and Carroll, 2005; Kopp, 2006; Pollock et al., 2002).

Comparing the previous studies, it is more advantageous to increase both the number of genes and the number of taxa to

resolve the phylogenetic relationships of *melanogaster* species group. Therefore, in this study, 17 genes from 48 species were assembled to address the phylogeny of *melanogaster* species group. The aims of this study are as follows: (1) to determine whether the *ananassae* or *montium* species subgroup is the earliest branching clade within the *melanogaster* species group; (2) to reanalyze the phylogenetic relationships of the *melanogaster* species subgroup and the oriental subgroups; and (3) to resolve the phylogenetic position of *D. lucipennis*, a species that has been difficult to place with robust support in earlier studies.

2. Materials and methods

2.1. The study taxa and sequences data

Information on the names, affiliations, and GenBank accession numbers of the specimens is given in Appendix Table A1. The previous studies (O'Grady and Kidwell, 2002; Yang et al., 2004; Mou et al., 2005; Da Lage et al., 2007) showed that the *obscura* species group is the sister group to the *melanogaster* species group. In this analysis, one species of the *obscura* group, *D. pseudoobscura*, was selected as the out group. These loci included partial genomic

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