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A Phylogeny of Robber Flies (Diptera: Asilidae) at the Subfamilial Level: Molecular Evidence

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Robber flies (Diptera: Asilidae) comprise one of the largest groups of extant flies (Hull, 1962). Asilids constitute more than 500 genera (Woodley, 1989) and more than 5500 species (Lehr, 1988) with a worldwide distribution except Antarctica. Species range in size from less than one centimeter to nearly eight centimeters in length, and their prey consist of both small and large insects caught largely in flight. Asilid color patterns are simple: usually black, gray, or bronze, although some more colorful species appear to mimic bees and wasps. All members of the group, including the problematic group Leptogastrinae (thread-waisted robber flies), form a well-supported group by many distinct shared characters. The most prominent feature being the row or group of stout bristles along the lower edge of the face (mystax); and adult predatory behavior (Woodley, 1989). Phylogenetic relationships of Asilidae with other families in Asiloidea have been recently investigated by molecular and morphological phylogenetic analyses (Weigmann et al., 1993; Yeates, 2002). These analyses focused primarily on the monophyly of Asiloidea, a group including the families Asilidae, Apioceridae, Therevidae, Scenopinidae, Mydidae, Bombyliidae, and Apsilocephalidae (Yeates, 2002).

Despite the considerable popularity of robber flies, and a rich history of extensive research on asilid morphology, taxonomy, and behavior (Bromley, 1932; Karl, 1959; Hull, 1962; Martin, 1968; Oldroyd, 1969), a quantitative phylogenetic hypothesis for the subfamilies has yet to emerge. Recent attempts to produce a phylogenetic hypothesis at this level have been based solely on intuition (Papavero, 1973; Woodley 1989) and have not received universal acceptance. Moreover, the characters used to define subfamilies have never been assessed across the entire diversity of robber flies, and many groups do not fit well within these subfamilial groupings (Carrera, 1949).

Our research included multiple exemplars representing 10 of the 11 subfamilies (all except Dioctriinae) and 18 tribes for a total of 26 ingroup taxa. Outgroups were selected from five closely related families (Yeates, 2002) within the superfamily Asiloidea: Mydidae (*Mydas clavatus*), Therevidae (*Ozodiceromyia costalis*), Bombyliidae (*Hemipenthes jaenickeana*), Apioceridae (*Apiocera* sp.), and Scenopinidae (*Scenopinus fenestralis*).

We based our phylogeny on four genes: 16S rDNA, 18S rDNA, 28S rDNA and cytochrome oxidase II. These genes are found to be suitable for the higher level questions of subfamilial relationships that were posed.

Leptogastrinae is resolved as sister to the remaining Asilidae (Bremer support 15; Bootstrap 100) under all analyses. The sensitivity analysis shows that the basal placement of Leptogastrinae is relatively sensitive. However, a portion of this sensitivity is due to outgroups nesting within the ingroups as described above. Overall, the basal placement of Leptogastrinae appears to be well supported via molecular data, with nearly 47% of the signal originating from 16S rDNA, whereas the other genes provide positive but lower support values. Note that the clade

Leptogaster + *Psilonyx* is extremely well supported in this analysis, which further supports the monophyly of Leptogastrinae. Our result reinforces Martin's opinion (1968) that this lineage is distinct from that of other asilids, and places it specifically as the most basal asilid group.

Wood (1981) and Papavero (1973) suggested that Laphriinae + Laphystiinae is sister group to a presumably monophyletic dasypogoninae-group, defined as ((*Dasypogoninae* + (*Trigonimiminae* + *Stenopogoninae* + *Stichopogoninae*)). In our analyses, the dasypogoninae-group is never monophyletic. The group Laphystiinae + Laphriinae is supported under maximum likelihood (ML) and a subset of cost ratios under parsimony. However, in ML Laphystiinae + Laphriinae is sister group to a paraphyletic assemblage of *Stenopogoninae* and *Stichopogoninae*, rather than to the dasypogoninae-group.

The only higher level relationship suggested by Papavero (1973) supported in our analysis was the monophyly of the asilinae-group. This relationship is supported by high bootstrap (100) and Bremer support (44) values, is relatively robust to all analysis. All gene partitions support this relationship, with the majority of the signal originating from 18S rDNA and 16S rDNA. That molecular data support the monophyly of the asilinae-group suggests that the closed marginal wing cells and slender antennae used to characterize this group are valid synapomorphies. Within the asilinae-group our analysis supports two major lineages: Asilinae + Ommatiinae and Apocleinae. The former clade is again well supported in all analyses. An interesting result is the placement of the subfamily Trigonimiminae as the sister group to the asilinae-group, since morphology suggests a placement within the dasypogoninae-group (Papavero, 1973). However, our data indicate that the dasypogoninae-group is paraphyletic, and hence the morphological characters defining this group are not homologous.

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