in Genetic Mechanisms of Speciation in Insects.
Symposia held at the XIVth International Congress of Entomology, Canberra Australia, August 22-30, [1972] sponsored by the Australian Academy of Science and the Australian Entomological Society, Ed. M.J.D.White

Phylogenetic relationships of Hawaiian Drosophilidae based on morphology

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INTRODUCTION

Concerning problems in the systematics of Drosophilidae, Sturtevant (1939) states that '... it is desirable that there be available a satisfactory arrangement of species into some scheme of classification that can be taken as indicating their degree of genetic relationships.' He discussed in detail the methods in analyzing and selecting characters which are important in showing phylogenetic relationships between species. It is clear that Sturtevant's description of taxonomic methodology in the classification of the genus *Drosophila* more than 30 years ago has remained a most important contribution in the biosystematics of *Drosophila*.

There are several lines of evidence which show that the present taxonomic status of the Hawaiian Drosophilidae may give a misleading interpretation of the phylogenetic relationships between species. This group of species has undoubtedly undergone explosive evolutionary radiation in a geologically short period of time. Currently there are approximately 500 described species (the endemic fauna may ultimately total upwards of 800 species) divided into eight endemic genera. Throckmorton (1966), based on a comparative study of the internal anatomy, states that there are only two major lineages in the evolution of Hawaiian Drosophilidae: the 'drosophiloids' and the 'scaptomyzoids.' → 'Scaptoids' Corroborating observations on the mating behavior patterns by Spieth (1966) show that there are two basic behavior patterns in the Hawaiian drosophilids: a very elaborate, species-specific courtship in the drosophiloids and a simple 'assault' courtship in the scaptomyzoids. Based on observations of the metaphase karyotypes, Clayton (1966, 1968) summarizes that the endemic species of Hawaiian Drosophilidae fall into two chromosomal groups which correspond with the genus *Drosophila* and the genus *Scaptomyza*. Recently, Yoon *et al.* (1972), based on a comparison of the polytene chromosomal patterns, show that there is a high degree of chromosomal homology between the genus *Drosophila* and the genus *Antopocerus* and conclude that these two genera have a common ancestor.

In this paper, there will be a brief discussion in the use of male genitalic structures as an important tool in studying the phylogenetic relationships of the species in the Hawaiian fauna. There will also be a discussion of how an analysis of various isolating mechanisms is important in the taxonomic treatment of the endemic drosophilids.

PHYLOGENETIC RELATIONSHIPS BASED ON GENITALIC STRUCTURES

Snodgrass (1957) states: 'The great diversity in structural detail of the genitalia gives these organs a value for the identification of insect species almost equal to that of fingerprints for identification of human individuals.' In most of the continental drosophilids, a comparative study of male genitalic structures plays an important role in showing species differentiation. There are many examples of pairs or groups of *Drosophila* species (e.g., *melanogaster* and *simulans, pseudoobscura* and *persimilis*, etc.) which are very similar and/or indistinguishable based on external morphological characters other than the genitalia; but for the most part, these 'sibling species' have been shown to be readily distinguishable based on structures of the male genitalia. As A. H. Sturtevant (1919) recognized over 50 years ago, the external male genitalia of Drosophilidae can be used as an important taxonomic tool in distinguishing between closely related species.

A comparative study of the phallic organs of the picture-winged species group of Hawaiian *Drosophila*, however, shows that there is very little structural diversity between closely related species (Kaneshiro, 1969). In most cases, one cannot distinguish between species within a species subgroup based on a comparison of phallic structures. It became clear then, that a study of the genitalic structures of the picture-winged species group could be used as an important tool in showing phylogenetic relationships between species, but that the phallic structures cannot be used to differentiate between closely related species. Based on genitalic characters, the picture-winged group of species is divided into nine species subgroups (Kaneshiro, 1969) which, for the most part, parallel very closely the phylogenetic relationships shown by cytological (Carson *et al.*, 1967, 1968a, 1968b, 1968c, 1969; Carson, 1971; and Clayton *et al.*, 1972), biochemical (Johnson, W. E., unpublished data), ethological (Spieth, 1966) and ecological (Heed, 1968 and Montgomery, 1972) data. In a few cases, a comparison of genitalic characters provides supplemental information as to the true relationships of species which are chromosomally 'homosequential' (Carson *et al.*, 1967), i.e., having the same banding patterns on all five long arms of the polytene chromosomes. This situation is illustrated in the case where *vesciseta* (Figure 1C) is shown to be chromosomally homosequential with *pilimana* and *glabriapex* (Figures 1A and 1B respectively) but is found to be more closely related to *virgulata* and *hexachaetae* (Figures 1D and 1E respectively) on the basis of genitalic characteristics. Carson and Stalker (1968a: 344) show that *vesciseta* differs from *virgulata* by one fixed chromosomal inversion and from *hexachaetae* by two fixed inversions.

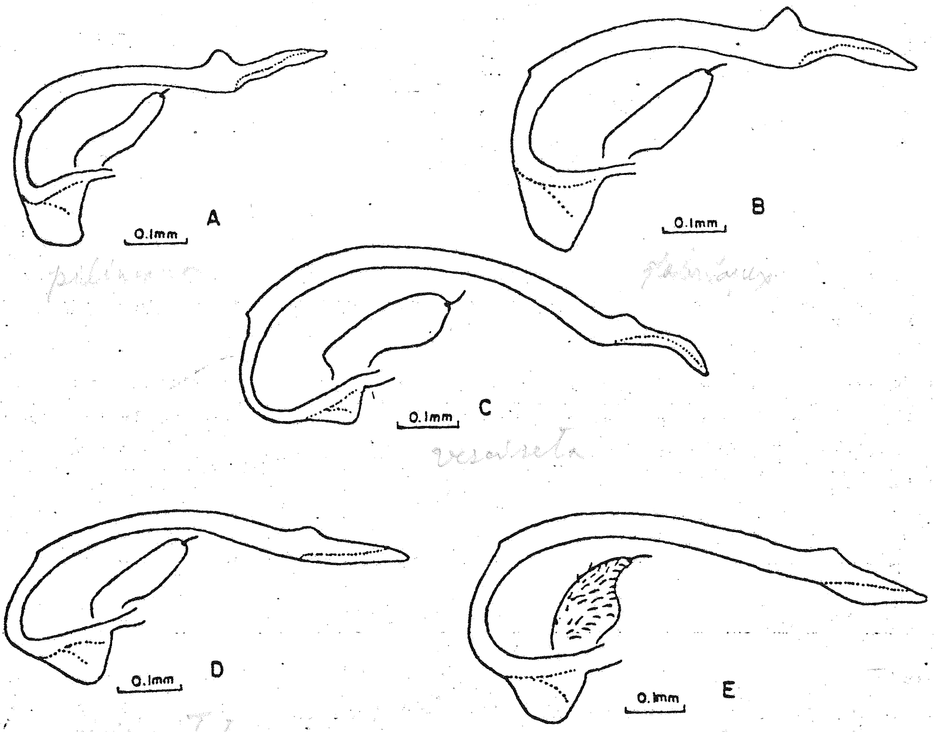


Figure 1

Based on the data on the picture-winged species group, it is possible to make comparisons of the genitalic structures of the other major groups in the endemic fauna and show phylogenetic relationships of the generic groupings. The original taxonomic treatment of the endemic species divide the fauna into nine endemic genera. A preliminary investigation of the male genitalia of representatives of the nine genera show that the species grouped in the various genera are probably only species complexes or at the most subgeneric groupings of only two genera: the genus *Drosophila* and the genus *Scaptomyza*. It became clear that a biosystematic study of Hawaiian Drosophilidae based strictly on external morphological characters can give a misleading impression of evolutionary divergence.

In the drosophiloids, which include the genera *Drosophila*, *Antopocerus*, *Nudidrosophila*, *Ateledrosophila* and what was formerly the genus *Idiomyia*, the various characters used to differentiate between the genera can be shown to be not important as generic characters. The species previously described in the genus *Idiomyia* Grimshaw are characterized by the presence of an extra crossvein in cell R5 in the wings of both sexes (Figure 2D). This is a very distinctive character and would appear to be a bona fide generic character. However, Carson *et al.* (1967) presented chromosomal evidence which indicate that the genus *Idiomyia* is congeneric with the genus *Drosophila*. They showed that two of the species, *clavisetae* and *neogrimshawi*, which have the extra crossvein in

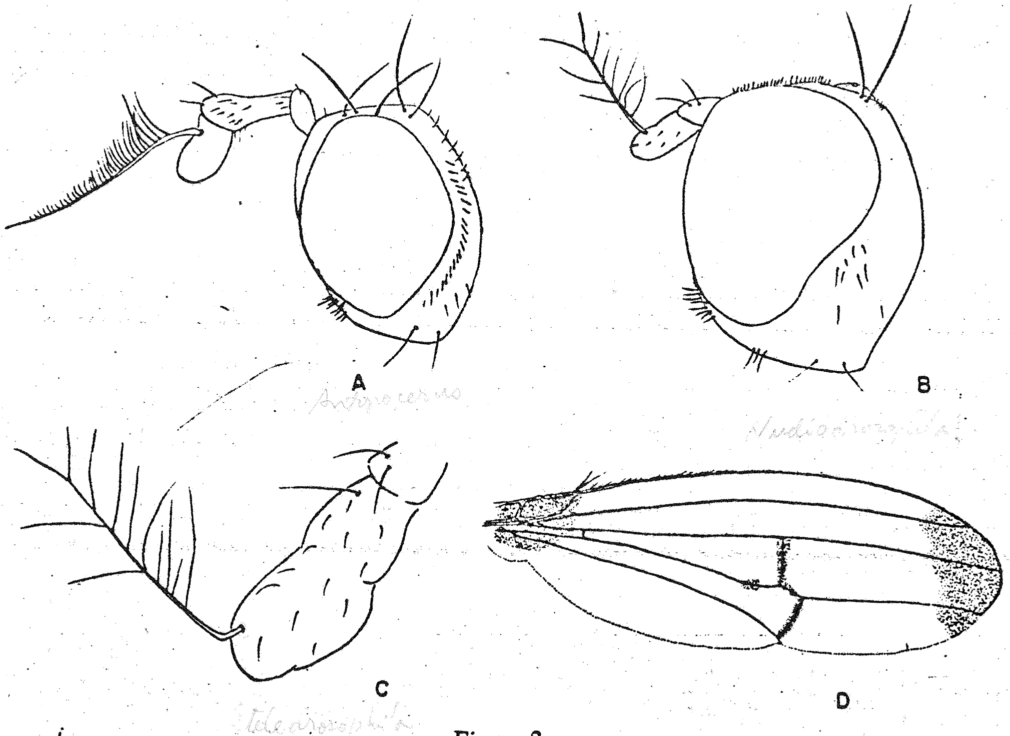


Figure 2

cell R5, differed from several species (i.e., *adiastola* subgroup species) which are typical *Drosophila* species by only five fixed inversions. The other 'idiomyia' species are 25+ inversions away from *clavisetae* and *neogrimshawi*. The phallic structures of *clavisetae* and *neogrimshawi* (Figures 3C and 3D respectively) are shown to be similar to species in the *adiastola* subgroup (Figures 3A and 3B) as reported by Kaneshiro (1969) while the phallic structures of the remaining idiomyia species (e.g. Figures 3E and 3F) are distinctly different and more closely resemble those of *setosifrons* and *picticornis* (Figures 3G and 3H respectively). It is apparent that the extra crossvein in cell R5 arose independently in the two lineages and therefore is not a valid generic character.

The key characters of the remaining three drosophiloid genera are mainly secondary sexual structures found only in the males and are structures which are used in the elaborate courtship behavior patterns (Spieth, 1966). The endemic genus *Antopocerus* Hardy consists of nine described species and is characterized by the large porrect antennae of the males (Figure 2A). The genus *Nudidrosophila* Hardy consists of five described species and is characterized by the males lacking the orbital and ocellar bristles and having microscopic pubescence or setae on the front (Figure 2B). The genus *Ateledrosophila* Hardy consists of two described species and is characterized by the males having the arista preapical in position (Figure 2C) and also by lacking the orbital and ocellar bristles. In most cases, the females of the species in these three genera cannot be distinguished

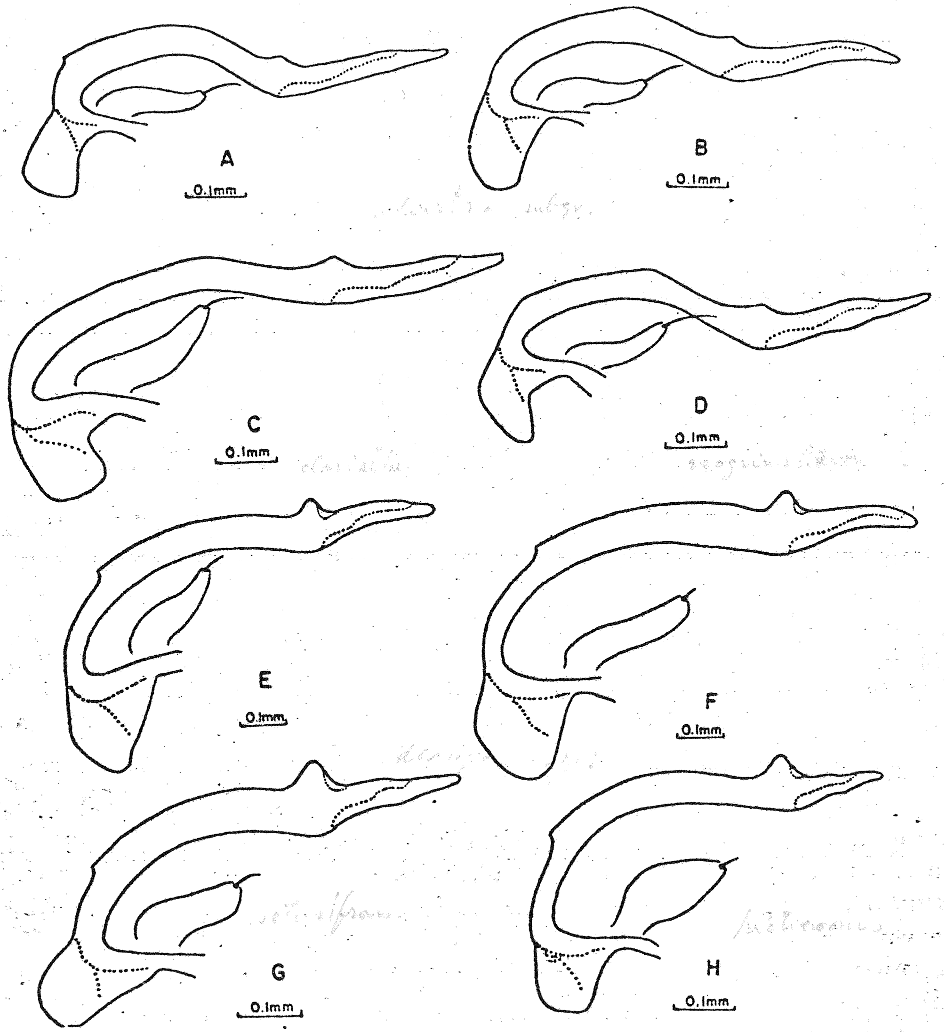
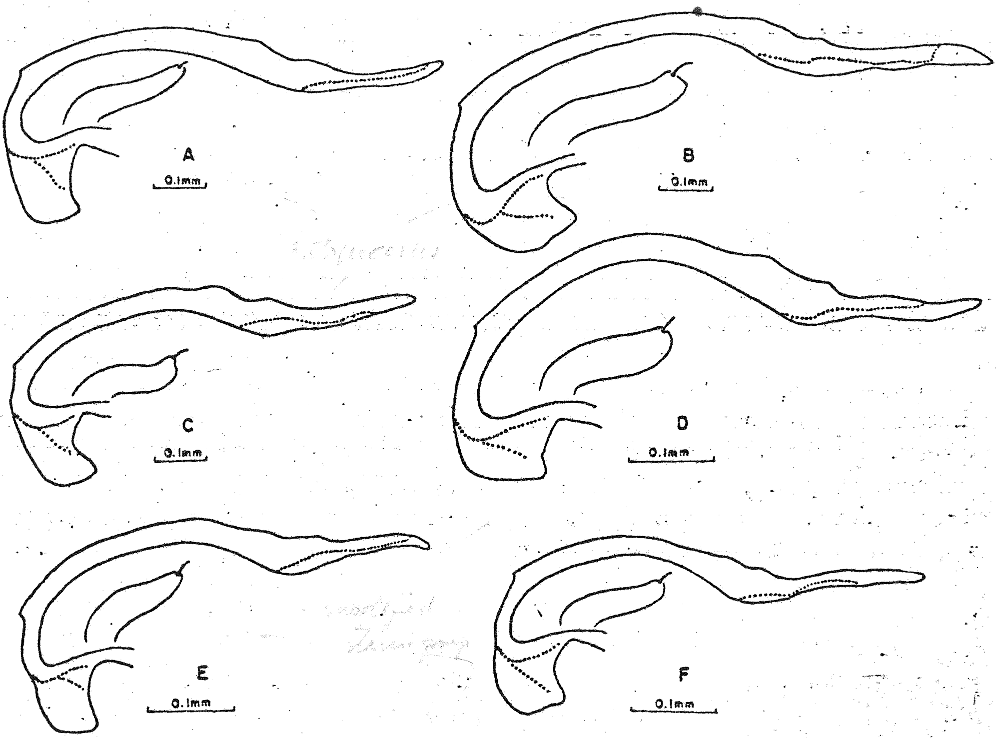


Figure 3

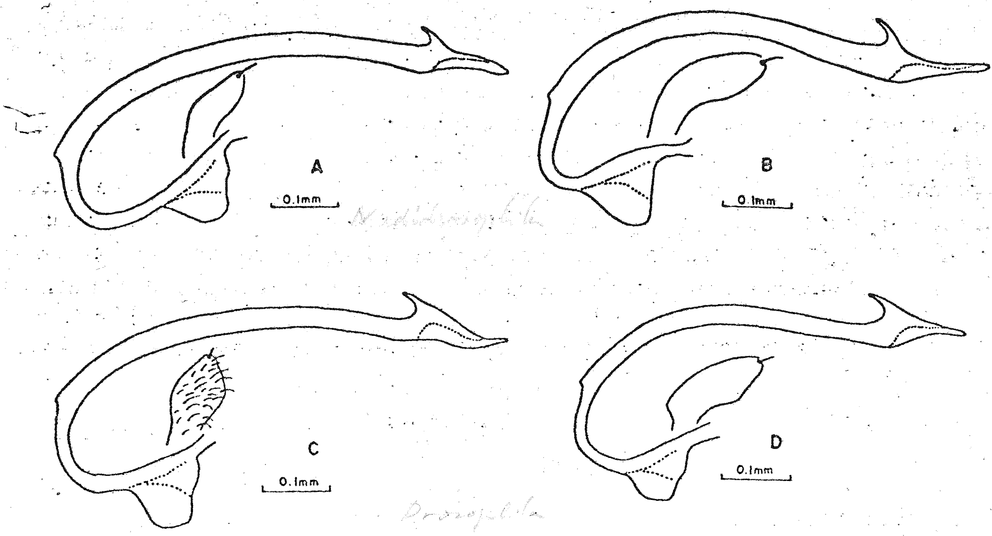
from females of typical *Drosophila* species. Also, there are *Drosophila* species which have phallic structures which are very similar to those of the species in these three genera. The modified tarsi group of species (Figures 4D, 4E, and 4F), for example, have very similar phallic organs as those of the *Antopocerus* species (Figures 4A, 4B and 4C). The aedeagus of *Nudidrosophila* species has a characteristic hook-like structure near the apex (figs. 5A and 5B) and for a time, it appeared that this character could possibly be used as a good generic character. However, it was found that there are two species in the genus *Drosophila* which have this same hook-like preapical structure on the aedeagus (figs. 5C and 5D). It is evident, then, that the conventional morphological characters which most Diptera taxonomists might have used as key generic characters are not alway reliable when studying the phylogenetic relationships of Hawaiian drosophiloids.



Antopocerus

modified tarsus group

Figure 4



Nudidrosophila

Drosophila

Figure 5

The data on the scaptomyzoid group of species which include the genera *Scaptomyza*, *Celidosoma*, *Grimshawomyia*, and the spider egg parasite, *Titano-*

chaeta, is incomplete so that this group will not be discussed at length at this time. However, it is observed that the scaptomyzoids are exactly the opposite of the Hawaiian drosophiloids in that lek behavior is absent and mating behavior is relatively simple. Therefore, there has not been any selection for the development of secondary sexual structures as in the drosophiloids and there is very little diversity in the external morphology between closely related species. The scaptomyzoids have instead evolved a highly complex genitalic apparatus which can be used to differentiate between closely related species.

THE 'SIBLING SPECIES' OF HAWAII

Another important taxonomic problem we have encountered in our evolutionary study of the drosophilid fauna of Hawaii is in the concept of 'sibling species.' The classical definition of 'sibling species' is a group of species which are morphologically similar or identical natural populations that are reproductively isolated (Mayr, 1971). *D. pseudoobscura* and *persimilis, melanogaster* and *simulans,* and *mulleri* and *aldrichi* are classical examples of sibling species pairs in *Drosophila.* In all of these cases, the external morphology, excluding the male genitalic structures, is nearly identical. However, there are good differentiating characters in the genitalic apparatus so that one could easily separate *pseudoobscura* from *persimilis, melanogaster* from *simulans* and *mulleri* from *aldrichi.* Now, in the evolution of Hawaiian *Drosophila,* elaborate courtship and mating behavior has played a very important role as a premating isolating mechanism between species (Spieth, 1966). Therefore, there is a high degree of diversity in the external morphology which is manifested mainly by the secondary sexual structures found only in the males of the species. The females of closely related species are usually indistinguishable. For the most part, even one who may be totally unfamiliar with the *Drosophila* fauna of Hawaii may be able to readily distinguish between males of closely related species. However, the phallic structures of closely related species are very similar and in most cases, indistinguishable. This is a complete reversal of the situation found in the continental sibling species where you have little or no morphological diversity but usually with good genitalic differences; whereas in Hawaiian *Drosophila* you have tremendous morphological diversity but with little or no genitalic differences.

There are preliminary evidence from some unpublished hybridization experiments that sibling species in the classical sense do exist in the Hawaiian fauna. All of these, however, are pairs or groups of species which are morphologically extremely close even in genitalic characteristics and are found on separate islands. In these cases, geographic isolation has apparently played the major role in reproductive isolation so that there has not been selection for differentiation of the secondary sexual structures found in sympatric species pairs. To the present, only one case of sympatric sibling species pair as described by the classical definition of sibling species has been found in Hawaii. *D. primaeva* and *attigua* occur sympatrically in isolated areas on the island of Kauai and can be differentiated by only minor differences in the phallic structures.

It is evident then, that if one were to determine and to take into consideration the actual isolating mechanisms which are operating between species, the concept of sympatric sibling species could be broadened to include some of the closely related species of Hawaiian *Drosophila* even though the species are morphologically readily distinguishable.

SUMMARY AND CONCLUDING REMARKS

It is obvious that the endemic fauna of Hawaiian Drosophilidae represents a classical example of evolutionary radiation on oceanic islands. This remarkable group of species has speciated profusely over a relatively short span of geological history. The data accumulated by various investigators based on cytology, behavior, electrophoresis, ecology and morphology indicate that the endemic drosophiloids make up a group of closely related species despite the tremendous morphological diversity that is so characteristic of this unique fauna. Furthermore, the data presented by comparisons of the male genitalic apparatus show that even species originally described in separate genera are only species complexes or at the most subgeneric groupings of the genus *Drosophila.* The key generic characters which are conventionally used by most Diptera taxonomists are apparently of no phylogenetic importance in the biosystematic study of Hawaiian drosophiloids. It is clear that a careful study of the biological factors responsible for reproductive isolation between species is essential. In the Hawaiian drosophiloids, the evolution of an elaborate, species-specific courtship and mating behavior has played an important role in the reproductive isolation between species. This type of premating isolating mechanism is strongly reflected by the tremendous diversity in the external morphology of these species. Therefore, these key 'adaptive' characters which have been used to differentiate between species and also to group species into separate genera are not important in showing phylogenetic relationships between species or group of species.

On the basis of the evidence presented by the various investigators discussed above and the comparisons of the male genitalic structures, it is clear that the drosophiloids of Hawaii represent a very close knit group of species which probably evolved from a common ancestor. Therefore, it is probable that the genera *Antopocerus* Hardy, *Nudidrosophila* Hardy, and *Ateledrosophila* Hardy are congeneric and should be synonymized with the genus *Drosophila.* A more detailed presentation of the various evidence which document this conclusion is being considered in a dissertation by the author.

It is quite clear that the Drosophilidae of the Hawaiian Archipelago presents taxonomists with a group of animals which is undoubtedly speciating at an accelerated rate and taxa at all stages of incipient speciation can be found. A careful study of these species and an analysis of their speciation mechanisms are crucial in the understanding of the evolutionary process. In the study of the evolution and genetics of Hawaiian Drosophilidae, various basic concepts in the field of systematics and taxonomy are being tested and with the efforts of a team of investigators in various fields of biology, new concepts will undoubtedly be formulated.

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