J. mar. biol. Ass. India, 1973, **15** (1) : 270-273

EVOLUTION OF THE HAWAIIAN DROSOPHILIDAE (INSECTA: DIPTERA)[1,2]

D. ELMO HARDY

Department of Entomology, University of Hawaii, U. S. A.

ABSTRACT

It is a well known fact that evolution has proceeded at an accelerated pace on various oceanic islands and the rich faunas of some of these islands offer unusual opportunities for evolutionary research. Because of special attributes some groups of Diptera are ideal for obtaining information concering evolutionary processess and speciation rates. In the Hawaiian Islands the family Drosophilidae is especially well suited for such studies.

The dipterous family Drosophilidae is most remarkably developed in Hawaii and represents one of the most striking examples of "explosive" evolution known in animal kingdom. We have now described approximately 500 species (97% endemic) and estimate that the total fauna may number 700 species. The Hawaiian species are unique among drosophilids in many different ways. They have structural peculiarities and picturesque wing markings which are extraordinarily diverse. They exhibit striking sexual dimorphism and elaborate courtship and mating behavior, including lek behaviour in the males. They have radiated into a great variety of habitats and their food and breeding requirements differ from those of species from other areas of the world. The fauna exhibits a high degree of endemicity by islands. It appears probable that 90-95 per cent of the species are restricted to single islands.

This amazing fauna has been under intensive study since 1963 by a team of about 20 senior scientists and over 100 assistants attempting to unravel some of the complexities in the extraordinary evolution of this group. These investigations have been aimed at determining the factors responsible for the evolution of such a large number of species in these islands, why they have developed such an array and diversity of morphological and biological characteristics, why this adaptive radiation has occurred at such a rapid rate, the possible time required for speciation, the pattern of evolutionary development and spread of species and groups over the islands, and probable numbers of progenator species and their possible home land.

We have now determined the most primative, ancestoral type, species in the genus *Drosophila* and have traced the evolutionary paths of various groups from the oldest island (Kauai, ca 8-10,000,000) to the youngest island (Hawaii, ca 800,000 years and still volcanically active) and have documented the Founder Principal.

Evolutionary data have been obtained by the following types of studies: cytogenetics, hybridization, courtship and mating behaviour, ecology, biology, external and internal morphology, nutrition biochemistry, and ovarian transplantation. The results of these studies will provide a better understanding of evolutionary process under insular conditions and will have world wide application.

INTRODUCTION

IT is a well known fact that evolution has proceeded at an accelerated pace on various oceanic islands and the rich faunas of some of these islands offer unusual

1. Presented at the "Symposium on Indian Ocean and Adjacent Seas—Their Origin, Science and Resources" held by the Marine Biological Association of India at Cochin from January 12 to 18, 1971.

2. Published with the approval of the Director of the Hawaii Agricultural Experiment Station as Journal Series No. 1284. This research has been supported by National Institutes of Health Grants GM 10640, GM 11609, and National Science Foundation Grants GB 711 and GF 152.

opportunities for evolutionary research. Compared to continental areas the biotic factors affecting speciation are rather simple in oceanic island situations. The Hawaiian Islands are, in many respects, uniquely suited for evolutionary studies, many groups of animals, as well as plants, have speciated profusely during a relatively short period of geological history.

The Hawaiian Archipelago presently consists of a series of atolls, reefs, islets, and Islands extending for 2500 kilometres along a northwest to southeast axis between 154°41′ to 171° 75′ W longitude and 18°54′ to 28°15′ N latitude with a total land area of 16,667 sq. kilometers. These are volcanic islands which are still building toward the southeast. The older islands of the chain have worn down to reefs and small pinnacles and have a very impoverished biota while the younger islands are relatively high, ranging from a maximum altitude of 1,000 metres for Lanai to nearly 4,200 metres for the island of Hawaii, and have a comparatively rich, and in many ways unique, fauna and flora. These are the most isolated of oceanic islands, they lie in the warm tropical region of the Pacific Ocean 3,200 kilometres from the nearest continental land mass. The habitats are extraordinarily diverse, ranging from dry deserts, alpine windswept meadows, to high rainfall tropical forests.

The six largest islands vary in age from about 5,000,000 years for Kauai, the westernmost island, to 800,000 years and less, for Hawaii. The latter still has active volcanoes and is growing to the southeast.

Terrestrial life came to Hawaii by chance from all directions, with the majority an ancestoral species originating in Asia or the southwest Pacific. Over the last five million years these islands have been populated by an unique biota and many groups of plants and animals have evolved at a rapid rate. Zimmerman (1948:94) stated that there are 3,722 known species of endemic insects and that these could have arisen from between 233 and 254 ancestoral species. This would mean that the founder species arrived at the rate of one every 20,000+years. It now seems evident that the total number of endemic insects in the Hawaiian Islands must be near 7,000 species. It also seems that Zimmerman's original estimate of the number of probable ancestral species is still as accurate as any guess which can presently be made.

EVOLUTION OF HAWAIIAN DROSOPHILIDS

Because of special attributes such as ease in culturing under laboratory conditions, short life cycle, presence of polytene chromosomes, and other factors some groups of Diptera are ideal for obtaining data concerning evolutionary processes and speciation rates. For over thirty years since the pioneer work of Th. Dobzhansky, the late J. T. Patterson, W. S. Stone and others, *Drosophila* flies have served as almost ideal material for the study of patterns of evolution in higher organisms. The Dipterous family Drosophilidae is most remarkably developed in Hawaii and represents one of the most striking examples of "explosive evolution known in the animal kingdom. We presently have approximately 500 named species and estimate that the total fauna may number 700 species, this is the greatest known concentration of these flies in the entire world; also the Hawaiian species exhibit more morphological and biological diversities (Carson, *et. al.*, 1970:450-469) than are known over the rest of the world. They show unusual sexual dimorphism with peculiar and striking characters developed on the legs, mouthparts, and genitalia of the males and with picturesque wing markings in a large number of species. Along with the unusual morphological characters the species of *Drosophila* exhibit elaborate

courtship and mating behaviour, including lek behaviour (Spieth, 1966, 1968a-b; Carson, *et. al.*, 1970:482-492). They have radiated into a great variety of habitats (Heed, 1968; and Carson, *et.al.*, 1970: 469-482) and for the most part their food and substrate preferences differ from those of species from other areas. They breed in an assortment of situations such as decaying leaves, stems, bark, flowers and fruit fleshy fungi; pollen feeders in morning glory flowers; miners in fern leaves;slime fluxes; plant hairs of *cyrtandra* and as predators in spider egg cases.

The fauna shows a high degree of endemicity by islands. It appears probable that 90-95% of the native species are restricted to single islands. It is interesting to note, however, that many of the insects, that have been accidently introduced into Hawaii from other areas have spread rapidly over the main islands. The introduced species of insects, as well as plants, have completely taken over the low land areas throughout the islands and the native insects are, almost without exception restricted to rather limited habitats at elevations above 500 metres where native plants are found.

This remarkable group of flies has been under intensive study since 1963 by a team of about 20 senior scientists and over 100 research assistants attempting to unravel some of the complexities in the extraordinary evolution of this group. These investigations have attempted to determine the factors responsible for the development of such large numbers of species in these small isolated islands; why and how such an array and diversity of morphological and biological characters have arisen; and the time required for speciation to occur. For a review of the results of this research and references see Carson, *et. al.* (1970).

The major concentration of efforts to date have been with a large group of species with maculations in their wings. The picture-winged species are now better known than any other Hawaiian drosophilids. These are the largest, most elaborate and unusual *Drosophila* known in the entire world (Hardy, 1965). Some species have a wing spread of 18-20 mm. The field and laboratory techniques have been perfected so that we know the breeding habitats and food preferences of these flies and have been able to culture 125 or more species in artificial media. These have proved ideal for our team approach to evolutionary research. We have determined the primative ancestral species on the Island of Kauai and have constructed detailed phylogenies on most of the picture-wings by combining results of comparative studies of chromosomes and other genetic techniques, behavourial, ecological and morphological studies. The migration routes of founder species have been charted, the main centers of adaptive radiation have been determined and the Founder Principal has beend ocumented (Carson, 1970a, 1970 b). These studies indicate that the major center for adaptive radiation has been the island of Maui, that the ancestral types migrated from Kauai in several well documented cases direct to Maui, bipassing Oahu; subsequently many species groups developed on Maui and dispersed to other islands.

A number of factors appear to be responsible for the evolution of the extraordinary number of species. The major factors would appear to be the spartan nature of the food supply which resulted in the evolution of a low reproductive rate, relatively long lived adults and consequently small population sizes. The infrequent but repeated migrations from each island to adjacent islands, which resulted in effective isolating barriers. The added effects of volcanic and meteorological action which further isolated small areas such as "kipukas" (islands of vegetation in the lava). The evolution of lek behaviour, and the utilization of specialized food sources such as decaying leaves, fleshy fungi, spider eggs, etc. (Heed, 1968).

One of the most remarkable features of the Hawaiian *Drosophila* is that many of the species groups have homosequential chromosomes (Carson, *et. al.*, 1970: 514), that is they have identical polytene chromosome banding sequences in all of the chromosomes. One would normally assume that such species are siblings but this is obviously not the case in Hawaiian species. These show distinct and constant morphological and behaviourial differences and hybrids are infertile. In some cases the homosequential species are morphologically diverse and show little or no external relationships. This clearly demonstrates that much evolutionary change occurs at the submicroscopic or molecular level (Carson, 1970b : 1416) and points up the fact that it is impossible to determine polygenies of taxa like Hawaiian *Drosophila* based upon external morphological characters alone.

Internal morphology studies have demonstrated that the internal systems are remarkably stable and are much more reliable for determining gross relationship than are external characters. The immediate results of these studies showed that the two major groups, *Drosophila* Fallén and related genera (drosophiloids) and *Scaptomyza* Hardy and related genera (scaptomyzoids) intergrade in Hawaii and the borderline species can be differentiated only by internal characters, egg structure, and behaviour. This leads to the implication that the total Hawaiian drosophilid fauna could have originated from only one ancestoral species and that the genus *Scaptomyza* originated in Hawaii. The latter implication is most startling and even though circumstantial evidence from many different sources points to this definite espousal of the "one introduction" over the "two introduction" hypothesis seems premature. To the present time we know about 350 native species of *Drosophila*, this represents approximately one-third of the total world fauna in this genus. The situation is even more unusual in *Scaptomyza*, 132 species have been described to date (this is probably about half the total number which occurs here) whereas about 75-80 species are known for the world outside Hawaii. To make the latter picutre even more complex, however, we now know 87 species of *Scaptomyza* (*Trogloscaptomyza*) Frey from the entire world, 86 of these occur only in Hawaii. The type of the subgenus, *S. brevilamellata* (Frey)was described from the island of Tristan da Cunha, in the middle of the Atlantic Ocean. The group is unknown elsewhere in the world, except Hawaii.

REFERENCES

CARSON, H.L. 1970a. Chromosomal Tracers of Founder Events. *Biotropica*, 2 (1):3-6.

————1970b. Chromosome Tracers of the Origin of Species. *Science*, 168 : 1414-1418.

————, D.E. HARDY, H.T. SPIETH, AND W. S. STONE 1970. The Evolutionary Biology of the Hawaiian Drosophilidae. Essays in: *Evolution and Genetics in Honour of Theodosius Dobzhansky*, a suppl., to *Evol. Biol.*, Appleton-Century-Crofts, New York. pp. 437-543.

HARDY, D.E. 1965. *Insects of Hawaii*, vol. 12. Diptera: Cyclorrhapha II, Series Schizophora, Section Acalypterae I. Family Drosophilidae. Univ. Hawaii Press, Honolulu. 814 pp.

HEED, W.B. 1968. Ecology of the Hawaiian Drosophilidae. *Univ. Texas Publ.*, 6818: 387-419.

SPIETH, H.T. 1966. Courtship behaviour of Hawaiian Drosophilidae. *Ibid.*, 6615 : 245-313.

————1968a. Evolutionary implications of sexual behaviour in Drosophila. *Evol. Biol.*, Appleton-Century-Crofts, New Yourk. pp. 157-193.

————1968b. Evolutionary implications of the mating behaviour of the species of Antopocerus (Drosophilidae) in Hawaii. *Univ. Texas Pub.*, 6818 : 319-333.

ZIMMERMAN, E.C. 1948. *Insects of Hawaii*, vol. 1. Introduction. Univ. Hawaii Press, Honolulu. 206. pp.