

MORPHOMETRIC EVIDENCE FOR INCIPIENT SPECIATION IN *DROSOPHILA SILVESTRIS* FROM THE ISLAND OF HAWAII

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Carson and Bryant (1979) reported a case of variability in a secondary sexual character of males of *Drosophila silvestris*, a giant fly endemic to the high-altitude rainforests of the geologically very new island of Hawaii. In populations from the north and east (N&E) parts of the island, the tibia of the male foreleg was found to possess on its dorsal surface an extra, that is, intermediately-positioned, row of large, long hairs (cilia). This character is not found in populations to the south and west (S&W); it is wholly lacking in females and shows high heritability in crosses (Bryant and Carson, 1979). Both chromosomal and electrophoretic distances among populations of *silvestris* are negligible and *silvestris* has therefore been considered a clear example of a single biological species (Carson and Bryant, 1979; Craddock and Johnson, 1979).

The evidence for differentiation in the N&E populations of *D. silvestris* is more compelling than Carson and Bryant indicated in their preliminary report. Not only do these flies possess extra, centrally-located cilia but the rows of cilia bordering the new row are themselves differentiated. Further, the evidence suggests that the genetic basis of this evolutionary event is unstabilized, that is, it may still be in an active dynamic state.

In this paper we explore the phylogenetic background of these characters by examining the legs of males of four additional, closely related species; three of these are allopatric to *silvestris* and are endemic to separate, geologically older islands. The data support the notion that the radical new burst of evolutionary change has occurred relatively recently and solely within the N&E populations of

D. silvestris, and that we are observing a case of incipient speciation.

The discovery of a species *in statu nascenti* is not in itself unusual. Many examples of incipient species are known. The exciting implication of the *D. silvestris* situation is that here we have an example of the beginning of the development of a morphological character which is intimately concerned with sexual behavior. Male tibial cilia have a clearly-defined biological importance: the only function of this leg surface appears to be a ritualized stimulation of the female's abdomen during the final and crucial stage of courtship (Spieth, 1978). Although such a character might first arise simply in response to altered sexual selection in the population, the same character might later serve as an ethological barrier to hybridization. With newly-formed full species which are sympatric, it is impossible to know whether ethological barriers to interbreeding arose in allopatry or upon secondary contact (Futuyma, 1979). We are left to speculate. In present-day communities, where rich "species swarms" appear to be maintained through prezygotic mating barriers, we can only surmise that these barriers arose in the absence of gene flow. In *D. silvestris*, we see a mechanism by which behaviorally-related reproductive isolation may arise in allopatry.

MATERIALS AND METHODS

Tibial cilia counts have been obtained from the males of five species of the *planitibia* subgroup of the picture-winged group of Hawaiian *Drosophila*. The distribution of the species and the 19 specific localities from which samples were obtained are given in Figure 1; the samples

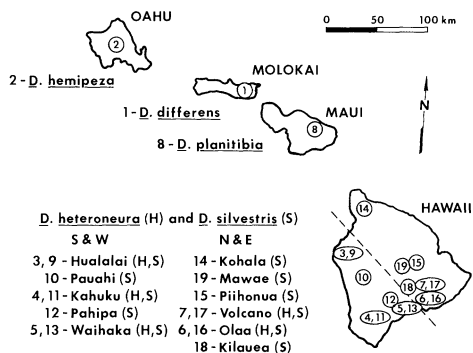


FIG. 1. Distribution of species and populations studied from the southeastern Hawaiian Islands. Numbers refer to samples reported in Table 1 and Figs. 2–5. The diagonal line across Hawaii separates the S&W populations from those on the N&E.

are numbered 1–19 in Table 1. At five of the localities on the island of Hawaii, *D. silvestris* and *D. heteroneura* occur sympatrically. Most samples are of wild males captured in nature during a single collecting period of at most one week. Allochronic samples at a locality are designated “-1” and “-2” in Table 1.

To facilitate comparison with the samples of Carson and Bryant (1979) and other published work on these flies, we provide the following detailed information on the samples presented in Table 1. Wild-caught males carry a simple code (e.g., U84G or T81) whereas data obtained from F_1 males reared from a single wild-caught female (iso-female line) carry an arabic number at the end of the code (e.g., U69G1). A sample derived from an established laboratory stock is indicated by the use of \$ sign as a suffix. Samples corresponding to 1–19 in Table 1 are as follows: 1, U43V1\$; 2, museum specimens from Palikea and Pupukea (collected between 1966 and 1977; from collection of Department of Entomology, University of Hawaii); 3, U51Y40\$; 4a, U26T16\$; 4b, U26B52\$; 5, U52B10\$; 6, Q71G12\$; 7, T94B18\$; 8a, U84G, U84G1\$; 8b, U89L and museum specimens (collected between 1964 and 1966); 9, U5B; 10, T89, T90; 11, T96V; 12, U27T1–7; 13, U52, U69, U69G1; 14a, T89B; 14b, U34B4\$; 15, U57G, U57V; 16, U13B; 17, T81; 18, T92; 19, U18. Dates of these collections were as follows: U51–U89, 3/78–7/79; U5–U43, 5/76–8/77; T81–T96, 10/75–4/76; Q71, 1/72.

Counts of the number of cilia located on the dorsal surface of the tibia were made by separating the right foreleg of each specimen from the body of the fly by cut-

ting through the extreme distal end of the femur. The leg was then laid on a coverslip and covered by a drop of Euparal. A second overslip was added, forming a sandwich; care was taken to move the leg so that the dorsal surface of the tibia was clearly displayed.

The cilia on the dorsal surface are deployed in two major marginal rows. The outer, postero-lateral row, is designated as No. 5 and the antero-medial row as No. 6. Between these two rows the rest of the dorsal surface is mostly bare but, as mentioned above, the N&E populations of *silvestris* show an additional irregular row of cilia which occupies this region (Row No. 5a). Details of these arrangements are illustrated in Carson and Bryant (1979).

Counts of these rows (by HLC and FCV) were done scrupulously according to the following scheme. Counting was carried out under the compound microscope (300 \times). Row 6 was counted first, starting at the distal end and running all the way to the proximal end. The most proximal cilium on the tibia was always included in the row 6 count. Row 5 is then counted out to the distal end where it tends to curve slightly over towards row 6. The cilia lying in this curve were included in row 5 counts. All cilia on the dorsal surface which lie between these two rows were recorded as belonging to the intermediate row (row 5a).

OBSERVATIONS AND ANALYSES

Table 1 presents the basic data of this study. For each sample and locality, the sample size, mean, range and standard error of the mean are given for each of the three dorsal rows of tibial cilia. A graphic plot for each row is given in Figure 2. A summary is presented in Figure 3. Some of the data of Table 1 are identical to those given in Carson and Bryant (1979) but in some instances samples have been augmented by new collections and four new species have been added. Carson and Bryant studied only *D. silvestris*.

From Table 1 it can be seen that the mean number of bristles in row 6 is always

TABLE 1. *Variability of foreleg cilia of males of five species of the Drosophila planitibia subgroup at various localities in the Hawaiian Islands.*

| Locality | Sample | | Row 5 | | | Row 5a | | | Row 6 | | |
|-----------------------|--------|------|-------|-------|------|--------|-------|------|-------|-------|-----|
| | No. | Size | Mean | Range | SE | Mean | Range | SE | Mean | Range | SE |
| <i>D. differens</i> | | | | | | | | | | | |
| Molokai | 1 | 20 | 15.0 | 14–17 | .22 | 0.4 | 0–2 | | 18.8 | 15–22 | .37 |
| <i>D. hemipeza</i> | | | | | | | | | | | |
| Oahu | 2 | 15 | 15.1 | 12–18 | .39 | 1.0 | 0–2 | | 18.9 | 16–23 | .49 |
| <i>D. heteroneura</i> | | | | | | | | | | | |
| Hawaii | | | | | | | | | | | |
| Hualalai | 3 | 15 | 18.0 | 15–21 | .38 | 0.3 | 0–1 | | 24.3 | 18–29 | .93 |
| Kahuku-1 | 4a | 20 | 14.1 | 12–18 | .27 | 0.1 | 0–1 | | 20.5 | 16–25 | .46 |
| Kahuku-2 | 4b | 19 | 16.2 | 13–20 | .37 | 0.2 | 0–1 | | 22.6 | 15–26 | .55 |
| Waihaka | 5 | 20 | 14.0 | 12–16 | .25 | 0.2 | 0–1 | | 20.4 | 18–24 | .33 |
| Olaa | 6 | 20 | 15.7 | 14–17 | .23 | 0.1 | 0–1 | | 21.5 | 19–25 | .37 |
| Volcano | 7 | 20 | 15.4 | 12–19 | .37 | 0.4 | 0–1 | | 22.2 | 19–24 | .32 |
| <i>D. planitibia</i> | | | | | | | | | | | |
| Maui | | | | | | | | | | | |
| Waikamoi-1 | 8a | 24 | 18.8 | 17–24 | .37 | 0.4 | 0–2 | | 21.5 | 18–25 | .38 |
| Waikamoi-2 | 8b | 29 | 19.7 | 17–24 | .28 | 0.4 | 0–2 | | 22.1 | 19–25 | .28 |
| <i>D. silvestris</i> | | | | | | | | | | | |
| Hawaii | | | | | | | | | | | |
| (S&W) | | | | | | | | | | | |
| Hualalai | 9 | 20 | 22.5 | 19–27 | .55 | 0.4 | 0–2 | | 27.8 | 23–31 | .54 |
| Pauahi | 10 | 21 | 21.0 | 18–24 | .44 | 0.4 | 0–2 | | 26.3 | 23–31 | .42 |
| Kahuku | 11 | 20 | 23.0 | 18–27 | .48 | 0.2 | 0–2 | | 28.3 | 24–32 | .52 |
| Pahipa | 12 | 45 | 19.9 | 15–26 | .29 | 0.3 | 0–2 | | 23.0 | 17–29 | .44 |
| Waihaka | 13 | 22 | 21.5 | 18–25 | .36 | 0.5 | 0–2 | | 27.8 | 24–32 | .52 |
| Hawaii | | | | | | | | | | | |
| (N&E) | | | | | | | | | | | |
| Kohala-1 | 14a | 10 | 31.1 | 28–36 | 1.11 | 23.3 | 17–31 | 1.66 | 26.5 | 24–30 | .64 |
| Kohala-2 | 14b | 24 | 29.5 | 23–34 | .50 | 20.2 | 11–28 | .89 | 28.5 | 25–33 | .38 |
| Piihonua | 15 | 46 | 30.4 | 23–44 | .59 | 21.4 | 10–33 | .65 | 29.2 | 25–36 | .42 |
| Olaa | 16 | 20 | 34.4 | 28–42 | 1.01 | 26.1 | 12–37 | 1.71 | 31.3 | 26–36 | .72 |
| Volcano | 17 | 18 | 33.7 | 29–41 | .79 | 30.4 | 22–42 | 1.41 | 31.1 | 26–37 | .64 |
| Kilauea | 18 | 17 | 33.1 | 26–41 | 1.01 | 32.5 | 21–40 | 1.45 | 30.5 | 25–36 | .62 |
| Mawae | 19 | 20 | 35.2 | 29–43 | 1.02 | 32.5 | 16–45 | 1.70 | 31.0 | 25–38 | .80 |

greater than the mean number in row 5 for all populations except those with the extra bristle row 5a. In these latter populations there are on average more bristles in row 5 than row 6. A two-way analysis of variance (ANOVA) paired comparisons test demonstrated that for the 15 samples without row 5a, the difference between the population means of rows 5 and 6 was statistically significant ($F = 153.1$; $d.f. = 1,13$; $P \leq .001$). Similarly, for the seven samples with the extra row, the difference (in the opposite direction) was also significant ($F = 29.2$; $d.f. = 1,13$; $P < .001$). An examination of the *individual* counts

showed that 90.6% of the *D. silvestris* individuals without the middle row (S&W) have more bristles in row 6 than row 5, while only 26.9% of the individuals with the middle row (i.e., N&E *D. silvestris*) have more in row 6 than 5. For the other species examined (all without the middle row), 93.2% of the individuals have more bristles in row 6 than 5. Furthermore, a posteriori tests (to be discussed in more detail below), demonstrate that the total numbers of bristles in both rows 5 and 6 are significantly greater in the populations with the extra bristles than in those lacking this extra row.

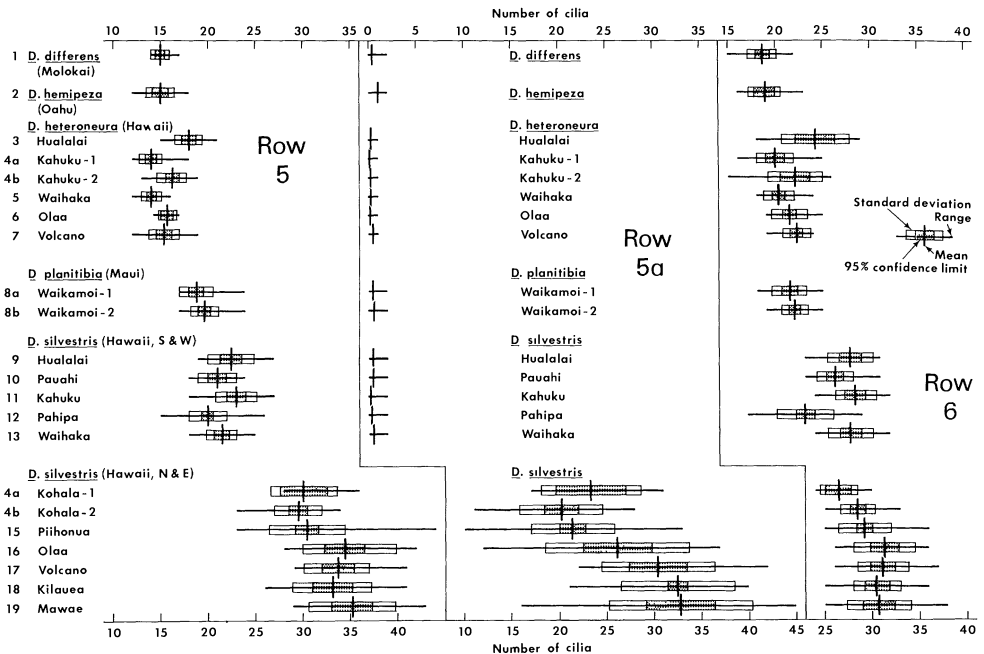


FIG. 2. Cilia numbers in Rows 5, 5a and 6 of the male tibia for five species. Means, 95% confidence limits, standard deviations and ranges of each sample are given.

Considering the possibility that there might be some correlation between the number of bristles in rows 5 and 6 in an individual, we examined the data for 11 *D. silvestris* populations but found no significant product moment correlation.

The three bristle rows differ not only in the number of cilia but also in the degree to which they vary in number within and among populations (analyzed by single classification ANOVA each row). Before these analyses and the tests presented below were carried out, the data were transformed, using logarithms, to equalize variances. The number of bristles in row 5 is most stable at the population level with 90.4% of the total variation being among as opposed to within populations. For row 6, 74.8% of the total variation of row 6 was among populations, whereas row 5a—the extra row—was least stable with only 42.8% of its total variation among populations. The fact that row 5a has greater within than among population variability suggests that it may not be fully canalized; it may still be evolving.

To examine among population variability more closely, a series of a posteriori Student-Newman-Keuls (SNK) tests were performed (Fig. 4). The SNK tests partitioned the populations into homogeneous subsets. The patterns are not simple. For row 5, nine homogeneous subsets were distinguished. *Drosophila differens*, *D. hemipeza*, and *D. heteroneura* (except Hualalai) are separated from the other flies. The N&E populations of *D. silvestris* are separated from all other flies and fall into two homogeneous groups (Figs. 1 and 5: populations 14–15 versus 16–19). Populations 14–15 also group together in the SNK analysis of the middle bristle row, as do populations 17, 18 and 19. In both rows 5 and 5a, there is a clear separation between *D. silvestris* populations on the N&E versus S&W sides of Hawaii.

The SNK test of row 6 reveals a complex pattern of overlapping populations. There is no clear differentiation between N&E and S&W populations of *D. silvestris* as there is in rows 5 and 5a. Note that all *D. silvestris* except Pahipa are sepa-

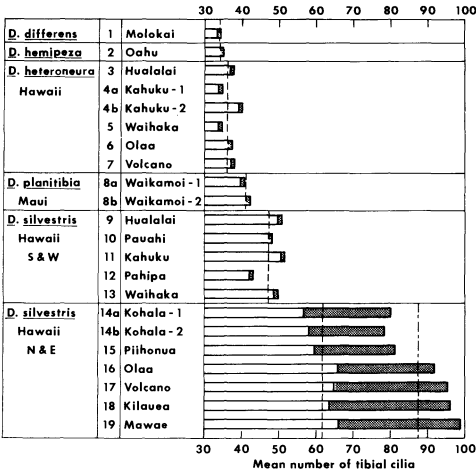


FIG. 3. Mean numbers of cilia on the dorsal surface of the tibia of the male foreleg. Vertical broken lines represent weighted means of population means of rows 5 and 6; the vertical line at the right of N&E *silvestris* represents the mean with row 5a added. Cross-hatching in bars represents cilia from row 5a.

rated from all the other species in the row 6 analysis.

Separate SNK tests were carried out for *D. silvestris* and *D. heteroneura* (the only two species in this study which are found on the island of Hawaii). The results are diagrammed on outline maps in Figure 5.

Because the males of the *planitibia* subgroup probably use the tibial bristle rows as one unit in courting the females, the total number of tibial cilia may be the character of selective importance rather than the number of cilia in each row. The summary (Fig. 3) illustrates the much larger number of cilia per tibia (even without row 5a) in the N&E *D. silvestris* (our putative incipient species). An analysis of variance of total number of cilia shows significant heterogeneity among all 22 populations ($F = 488$; $d.f. = 20,454$; $P < .001$). Even without including the extra row, the among population heterogeneity is still highly significant ($F = 24.1$; $d.f. = 20,454$; $P < .001$). A SNK test of all three rows grouped the *silvestris* populations as shown in Figure 5D. This figure shows that N&E and S&W populations are distinct from each other and that on the N&E side of Hawaii there are two distinct

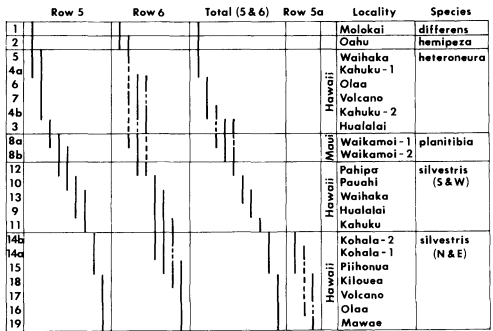


FIG. 4. Results of Student Newman Keuls (SNK) a posteriori analyses on all five *Drosophila* species. Populations are grouped into homogeneous subsets indicated by continuous bars. Dotted lines bypass populations which are not members of a homogeneous subset. Together these can be used to interpret among-population heterogeneity as found via analyses of variance.

groups. Figures 5E and 5F suggest an affinity between *heteroneura* populations in the Olaa-Volcano area and those of the extreme southwest side of the island rather than with Hualalai (Sample No. 3).

DISCUSSION

Incipient species are created by behavioral, temporal, or geographic isolation which acts as a reproductive barrier. Many examples are known. For instance, the six semispecies of *D. paulistorum* are separated by a behavioral (female choice) barrier reinforced by a semispecies-specific cytoplasmic parasite causing male sterility (Ehrman and Kernaghan, 1972). Broods of periodical cicadas are temporally reproductively isolated and have begun to develop morphological and other genetic differences (Simon, 1979, and unpubl.). Chromosomal races of, for example, *Geomys* (Selander et al., 1974), *Thomomys* (Nevo et al., 1974) and *Spalax* (Nevo et al., 1975)—all small fossorial mammals—are geographically isolated; many still hybridize in zones of secondary contact. The majority of examples involve geographic race formation. The degree of differentiation varies among taxa and it is often not obvious how this differentiation might affect gene flow upon secondary contact.

The northern and eastern *D. silvestris* populations which have diverged in bristle number are an unusual example of species incipience in that the specific changes which could be pivotal in speciation can be identified; the relevant morphological character is the secondary sexual ornamentation on the tibia used by the male to stimulate the female during courtship. Accordingly, the possible origin of this character is discussed below.

On the island of Hawaii, various lava flows have been dated by potassium-argon methods (McDougall, 1969). None has been found to exceed 700,000 years of age. As both *D. silvestris* and its close but morphologically distinct relative *D. heteroneura* are endemic to this island, the separate gene pools which comprise these species must themselves be younger than this age. The detailed time and mode of origin of these two species has been the subject of considerable difference of opinion (for various views see Carson [1971]; Kaneshiro [1976]; Craddock [1974]; and Spieth [1980]). All nevertheless agree that both species must be relatively newly-formed, i.e., constitute a pair of very similar neospecies (Carson, 1976).

In our present study of the male foreleg character, it is clear that the three species endemic to the older islands of Maui, Molokai and Oahu have a rather uniform, uncomplicated set of two rows of cilia on the tibia, separated by a bare area. In view of this it is especially striking that this same uniform, putatively ancestral, condition characterizes both *heteroneura* from all parts of the island of Hawaii and all the populations of S&W *silvestris*. Thus, it is only the N&E *silvestris* populations which show the newly-embellished bristle character. Accordingly, the latter condition clearly is a derived state, contrasting with the ancestral one found in all other populations.

Obviously, then, the origin of N&E *D. silvestris* becomes a key question, as we attempt to reconstruct the most recent evolutionary events. The inference that it arose recently from the S&W population of the same species is inescapable. We can

further inquire as to where on the Big Island of Hawaii this event could possibly have taken place. This is a reasonable question; it should be recalled that the area of the entire island is only about 10,000 km² of which only a small fraction (10% or less) provides a suitable habitat for these *planitibia* subgroup species. *Drosophila silvestris* is confined to montane rainforests on the volcano slopes from about 1,000 to 1,800 m altitude. Almost everywhere these forests are patchy; they have obviously been continually shaped by prehistoric as well as historic lava flows. This has resulted in the formation of many kipukas, that is, islands of older forest surrounded by newer lava. The host plant for this species of *Drosophila* consists primarily of trees of the genus *Clermontia* (Lobeliaceae). These plants have a comparable patchy distribution, being found particularly along the edges of newer lava flows. Certain very large areas of forest contain few *Clermontia* and such areas are correspondingly unsuitable for *silvestris*.

All of these factors have led to the concept that the different populations of all of these *Drosophila* species, especially *silvestris* and *heteroneura*, are likely to have been founded allopatrically by one or a very small number of specimens colonizing previously unoccupied areas. The vestiges of any serial genetic differentiation accompanying the colonizations might well be retained in these new patchy forests. After lava flows cease and the forests close in and become mature, the original genetic differentiations caused by founder effects might become diluted by interpopulation migrations.

There is evidence which suggests that founder events may affect the genetic basis of certain behavioral attributes. Kaneshiro (1976) and Ohta (1978) have described systematic differences in sexual behavior among various geographic strains and species of *Drosophila* from the different Hawaiian Islands. The central feature of their discovery is that females taken from populations from geologically older island volcanoes display much more dis-

crimination in mating than those from new islands. This led to the hypothesis (Kaneshiro, 1976, 1980) that the observation of a shift in mating behavior after a new founding event may be used to establish direction of evolution, even in cases where the geological history of the populations cannot be directly inferred, as it can between older and younger volcanic islands of the Hawaiian archipelago. Thus, various populations can be arranged in a sequence, reflecting the historical order of founding. Populations having females with a relatively discriminatory behavior may be designated as ancestral to more recent ones in which the females are less discriminatory.

Based on tests of sexual behavior within *D. silvestris*, Kaneshiro and Kurihara (1982) have designated the Hualalai *silvestris* population (a S&W population: No. 9, Figs. 1 and 5) as the most ancestral within the species. Newer S&W populations extend sequentially south down the island to Pauahi and ultimately Kahuku (Nos. 10 and 11, respectively, Figs. 1 and 5). Most significant for the present discussion, however, is that their data further suggest that Kohala and Piihonua (localities 14 and 15, Figs. 1 and 5) are also independently derived from Hualalai. Further tests show Olaa (No. 16, Figs. 1 and 5) to be derived in turn from Kohala-Piuhonua.

Our bristle data on these same N&E populations lend themselves to the postulation of a similar geographical seriation. Thus, Hualalai (low cilia of the S&W type) might have given rise to Kohala-Piuhonua (moderate increase in cilia on rows 5 and 5a) and ultimately to populations in the Olaa area (an additional increase of cilia in these same rows). The strong correlation between increased bristle number and a symmetrical mating preference does not prove that the change in bristle number went hand-in-hand with the change in mating behavior, but the two arguments for the derived nature of N&E populations are both strengthened by this agreement.

The evidence for incipient speciation through morphometric differentiation pre-

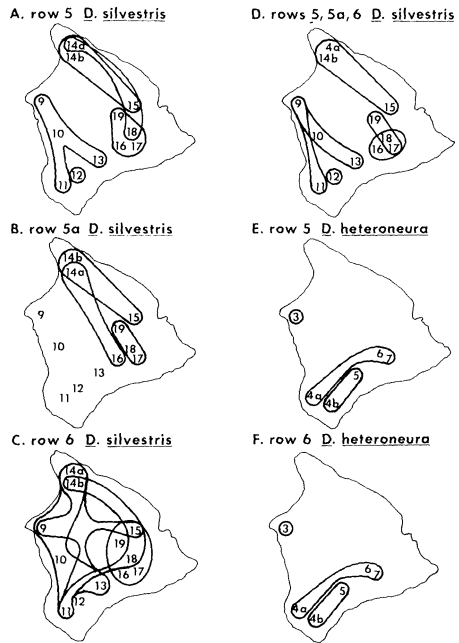


FIG. 5. Results of Student Newman Keuls a posteriori analyses for populations of *D. silvestris* alone (A-D) and *D. heteroneura* alone (E and F). Homogeneous groups are contained within single contours. Note that for *D. silvestris* (rows 5, 5a, and total), there is clear differentiation between N&E and S&W populations while for row 6 *silvestris* and rows 5 and 6 *heteroneura*, there is no such differentiation.

sented here has special interest since electrophoretic and chromosomal data are abundantly available in the case of *D. silvestris* (Sene and Carson, 1977; Carson and Bryant, 1979; Craddock and Johnson, 1979). These later data, however, are quite insensitive as a diagnostic method for species incipience (see Carson, 1976, 1978). Hybridization studies between various *silvestris* populations furthermore, have revealed no post-mating incompatibilities (Craddock, 1974; Craddock and Johnson, 1979; Ahearn, 1980). All these facts focus particular attention on courtship and mating behavior as the primary ingredient of species incipience in this instance. Population to population evolution within *silvestris* appears to have operated through a stepwise series of founder events having their principal genetic effect initially on the mating behavior system

and then, later, on morphological sexual characters which embellish or reinforce this behavior. This contrasts with theories of speciation which place adaptation to the ambient environment as the crucial feature.

Preliminary information (Bryant and Carson, 1979, and unpubl.) suggests that the genetic basis of the differences between the two bristle types is polygenic. Within a single locality, the variation among males sampled from different isofemale lines is extraordinarily large (Carson, 1979). Although genetic analysis involving a series of reciprocal crosses and backcrosses between the bristle types is still in progress, it may not be premature to propose a genetic scenario for the type of change observed between populations in this case.

We favor an interpretation along the lines of the shifting balance theory of Wright (1970, 1977, Chapter 13) in which intraspecific founder effects cause a transience (Templeton, 1980) affecting the polygenic basis for the quantitative variability impinging on mating behavior. As a result, the ancestral harmonious polygenic interaction system is disturbed by the stochastic founder event. This forces a shift away from the old polygenic balance that natural and sexual selection had established. As Templeton has argued, such a shift may not necessarily be accompanied by a loss of alleles through drift. A similar view has recently been articulated by Lande (1980) and we find ourselves in close agreement with it.

As Wright (1977) has pointed out, such shifts in polygenic systems may occur "... with little or no novel mutation and without necessarily involving any systematic environmental changes in time." Essentially, then, the newly-formed allopatric population is forced to shift from an old genetic equilibrium to a new one. This may indeed be a wholly intrapopulational phenomenon involving the genetic coadaptation of the sexes. It can occur without regard to challenges from other species or altered ambient environment.

SUMMARY

A cluster of five closely related species of Hawaiian *Drosophila* display a male secondary sexual character consisting of rows of enlarged bristles (cilia) on the dorsal surface of the foreleg tibiae. These cilia are used by the male to stimulate the female during courtship. In four of the five species, this character is conservative and stable with low variances in number; cilia are deployed in two marginal rows separated by a bare area. *Drosophila silvestris* of Hawaii Island, however, is strikingly different. In S&W populations, legs of males resemble those of the other species, but those from the N&E side of the island show a much larger number of cilia with greatly increased variance. These cilia are distributed as additions to one of the marginal rows and in a new irregular row in the area which is bare in the other species and in S&W populations of *silvestris*. Groupings identified by a posteriori tests suggest that this change took place in two stages; thus males from two N&E localities (Kohala and Piihonua) show fewer new cilia than those from the more easterly populations. Our data support the notion that Kohala is an early derivative from S&W populations, as exemplified by the present-day population on Hualalai volcano. All data suggest that N&E *silvestris* is phylogenetically new, since flies from the older islands and other populations from Hawaii lack the embellishment. We suggest that intraspecific founder effects have been conducive to a shift in the balance of the polygenes which serve as the genetic basis of the bristle character. This in turn may force the newly-formed allopatric population to shift from an old genetic equilibrium to a new one. We suggest that this shift is mediated by an altered sexual selection favoring an increase in cilia number. The change may be interpreted as one which could be important in species incipience although at first the change might have been purely an intrapopulational phenomenon involving the genetic coadaptation of the sexes.

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