POPULATION GENETICS IN THE AMERICAN TROPICS XXXIX, ASYMMETRY AS A DIVERGENCE FACTOR IN DEMES OF *DROSOPHILA PSEUDOOBSCURA* IN THE CUNDIBOYACENSE ALTIPLANO OF COLOMBIA

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ABSTRACT

High-resolution statistical analysis from *Drosophila pseudoobscura's* external parameters; sexual combs, claspers and vaginal bristles from hundreds of specimens representing the central part of its geographic distribution (many collections from Davis, California) and from specimens representing isolated and marginal demes from Colombia, South America (Cundinamarca-Boyacá altiplano) have been shown astonishing differences in symmetry, according to statistical analysis (anovas, simple and multiple regressions). The most striking resùlts in perfect agreement with demic theory (Hoenigsberg, 1988) has been the amazing symmetry maintained throughout central populations of California U.S.A. and, at the same time, an equally amazing total asymmetry (right vs. left, up vs. down) in the marginal isolated samples of demes from the Colombian high altiplano.

RESUMEN

Análisis estadísticos de alta resolución para caracteres cuantitativos externos de *Drosophila pseudoobscura;* peines sexuales, abrochadores y quetas vaginales de cientos de especímenes representantes de la parte central de su distribución geográfica (muchas colectas de Davis, California) y de especímenes representantes de los demos marginales y aislados de Colombia (Altiplano Cundiboyacense), han mostrado diferencias sorprendentes en la simetría, de acuerdo a los análisis estadísticos (Anovas, Regresiones múltiples y simples). La mayoría de los resultados están de acuerdo con la teoría démica (Hoenigsberg, 1988), muestran total simetría para la población central de California, U.S.A. y al mismo tiempo una total asimetría (derecha-izquierda, arriba-abajo) para las muestras de los demos marginales y aislados del Altiplano de Colombia.

INTRODUCTION

Observations at different levels of structural organization give us different forms of access to knowledge of the mechanisms governing processes which promote and produce differences between population groups that eventually become different species. It is well-known that genetic and environmental variation are to be found among and between populations. From this source of variation, natural selection and/or drift, probability distribution and/or effective population size can cause spatial divergence when distance and isolation help separate local demes (Hoenigsberg & Rodríguez, 1987).

Variations between populations can be detected in a number of ways: allozyme frequency, polymorphism, and genetic distance are three of them. The data for the demes of *Drosophila pseudoobscura* in the Cundinamarca-Boyacá altiplano of Colombia (= the Cundiboyacense altiplano) show divergence between demes which are close to each other, in non-homozygotic populations with little variability (Hoenigsberg *et altri*, 1988). In populations such as ours it may be very desirable to know if Mayr's 'genetic revolutions' due to distance and isolation have produced deep changes in phenotypes affecting development and morphogenesis. In order to detect disturbances in the basic genome of our demes on the altiplano, we have chosen meristic characteristics which could be significant. So far, we have found that there are at least four sterility patterns in male F_1 hybrids from crossings of certain demes such as Aguas Calientes/Davis, Recreo/Davis, Sochagota/Davis and Potosí/Davis. It is therefore necessary to understand something about the morphogenesis and adult plenotype of the flies which in the stages of larva, pupa formation and pupa have shown sterility crises and as adults are totally sterile F_1 males. It is as if, from our point of view, the various manifestations of sterility in altiplano *Drosophila pseudoobscura* and Davis *Drosophila pseudoobscura* are based on the epigenetic system responsible, at the centre of the distribution of the species, due to the viability of the hybrids itself and to symmetry, so that breaks could be considered as epigenetic crises resulting in a serious threat to the morphogenesis of the population structure.

The locations and demographic characteristics of the demes have already been described (Hoenigsberg & Dobzhansky, 1987; Hoenigsberg *et altri*, 1988) and we shall therefore be describing only what happened to the morphological characteristics studied.

As we are dealing with polygenic characteristics, measurement of these characteristics is affected by genetic and non-genetic factors. It is generally assumed that the meristic characteristics reflect some hidden tendency: they are a continuous variable but one which can only be expressed in whole numbers. For example, the number of hairs on *Drosophila* may reflect a continuous development trend, producing complete hairs; and we can postulate a threshold which has to be crossed for each complete hair to appear (Merell, 1981).

Geographic variation may lead to discontinuity, separating species into discrete intra-specific entities like ecotypes or subspecies. Often, however, the trend is towards gradual and continuous change over large areas - clines, measured over a geographical transect (Merell, 1981). This was the basis of Prevosti's work in 1954 and 1955, following Monclus (1953), on *Drosophila subobscura* a species widely distributed over Europe. The quantitative characteristics considered were the sexual combs and claspers on the males, the vaginal bristles of the females, and wing dimensions as a gauge of the size of each individual. The morphological differences between a number of populations of the species were analyzed, precisely where speciation is most evident, through transects and clines, correlated along climatic gradients.

Observation of the variation in the number of teeth in the sexual combs and in the claspers of the male, and the number of vaginal bristles in the female *Drosophila pseudoobscura,* can show whether there are important differences between populations, particularly between the population representing the central distribution of the species and the populations of the Cundiboyacense altiplano, as well as between different altiplano populations. Statistical parameters can describe the quantitative behaviour of the characteristics of the populations studied. The population context of the locations should be taken into account: those of the altiplano are singular since they are isolated and peripheral, an apparent example of genetic insularity (Prakash, Lewontin & Hubby, 1969). The effective size of the altiplano populations is small (Cárdenas, 1988), which provides the conditions for peripatric speciation proposed by Mayr (1954), where the divergence processes arise from genetic revolution, due to a population size so small that foundation effects may occur. Also, environmental conditions are very different from those of the central distribution of the species. Their isolation, with little or no migration, promote the permanence of changes in gene constitution arising from all the conditions mentioned. The central distribution, however, behaves in a typical fashion, due to its location and large population effective size: the effects of stochastic processes are reduced, and an important co-adaptation of the whole genome in that population can be expected. This will allow us to make valid comparisons to determine whether in the altiplano populations some divergence processes are taking place and can be detected from quantitative differences in the morphological characteristics studied.

MATERIALS AND METHODS

Five demes were studied, four of them in the Cundiboyacense altiplano (Recreo, Potosí, Sochagota and Aguas Calientes, see Fig. 1). Collections were made in September-November, 1987; November, 1987; September, 1987 and September-November, 1987 respectively, using a network of banana traps pre-fermented four days earlier. Following earlier experiences reported and demonstrated (Polanco & Hoenigsberg, 1983) traps were placed on leaves in the open without preparing the surrounding flora and without trying to find locations with the native Quercus oak (Huertas & Camargo, 1976). Indeed, none of the altiplano locations (Recreo, Potosi, Aguas Calientes, Sochagota) have, or have ever had Quercus species, according to the Natural Sciences Institute of Universidad Nacional (Huertas & Camargo, 1976).

Figure 1 shows the locations and Figure 2 the distances on the 300 km. scale reported in Hoenigsberg & Dobzhansky (1987). In their work the authors described the characteristics of momentary and permanent colonization in the four demes studied here. From the grid used in the 1987 work (Hoenigsberg & Dobzhansky) genetically successful colonies of the 16 areas studied over 12 years were selected. In Aguas Calientes, these were colonies 7 and 9, in Recreo No. 7, in Sochagota Nos. 1 and 11 and in Potosi, Nos. 1, 2, 3, and 4 (see Figure 2). The catch in the traps on successful Nos., for example, 7 and 9 in Aguas Calientes (the other 14 colonies passed through periods of successive colonization and extinction over many years, and still follow this classical natural cycle) were mixed together as a single sample in order to obtain a sufficient number of isolines, since in some cases there were very few. We are aware that mixing samples from localized and perhaps highly specialized demes may establish a spurious variance of genetic structure, greater than would naturally occur.

All collections were made in the same period, September-November, 1987. Individuals were sexed at the place of collection to avoid problems of sexual selection in confinement. The females were counted into isolines from the collection in cultivation media suited to *Drosophila pseudoobscura*, made of banana and agar, enriched with yeast. In the laboratory they are rapidly placed in incubators at 22°C ± 1°C and every few days they are checked for development. All traces of contamination by oospores

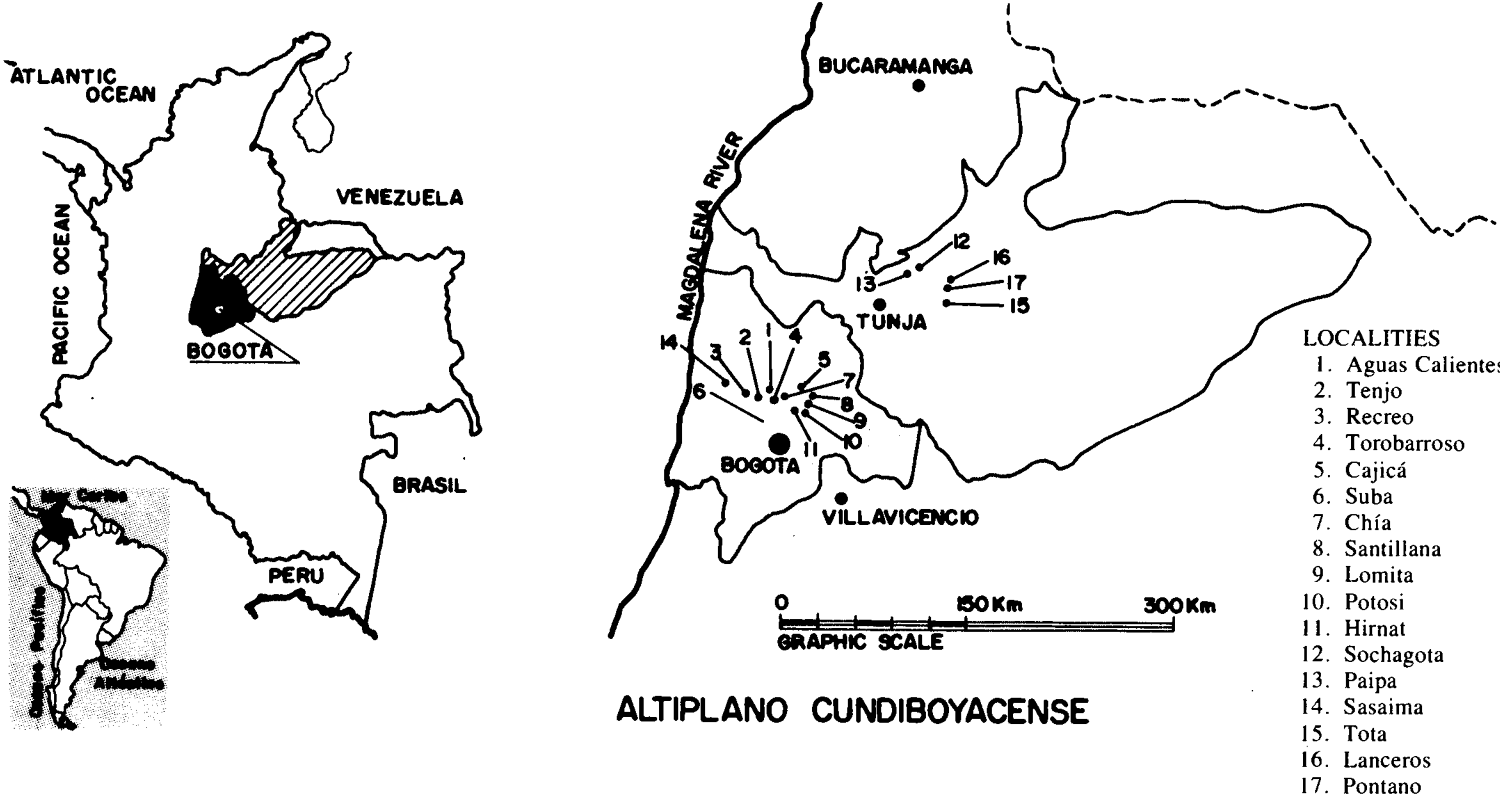


FIGURE 1. Colonization attempts by *D. pseudoobscura* in the Cundiboyacense altiplano. *D. pseudoobscura* was found at 17 locations. Data were collected by Dobzhansky and Hoenigsberg between 1971 and 1975, and by Hoenigsberg between 1975 and 1983.

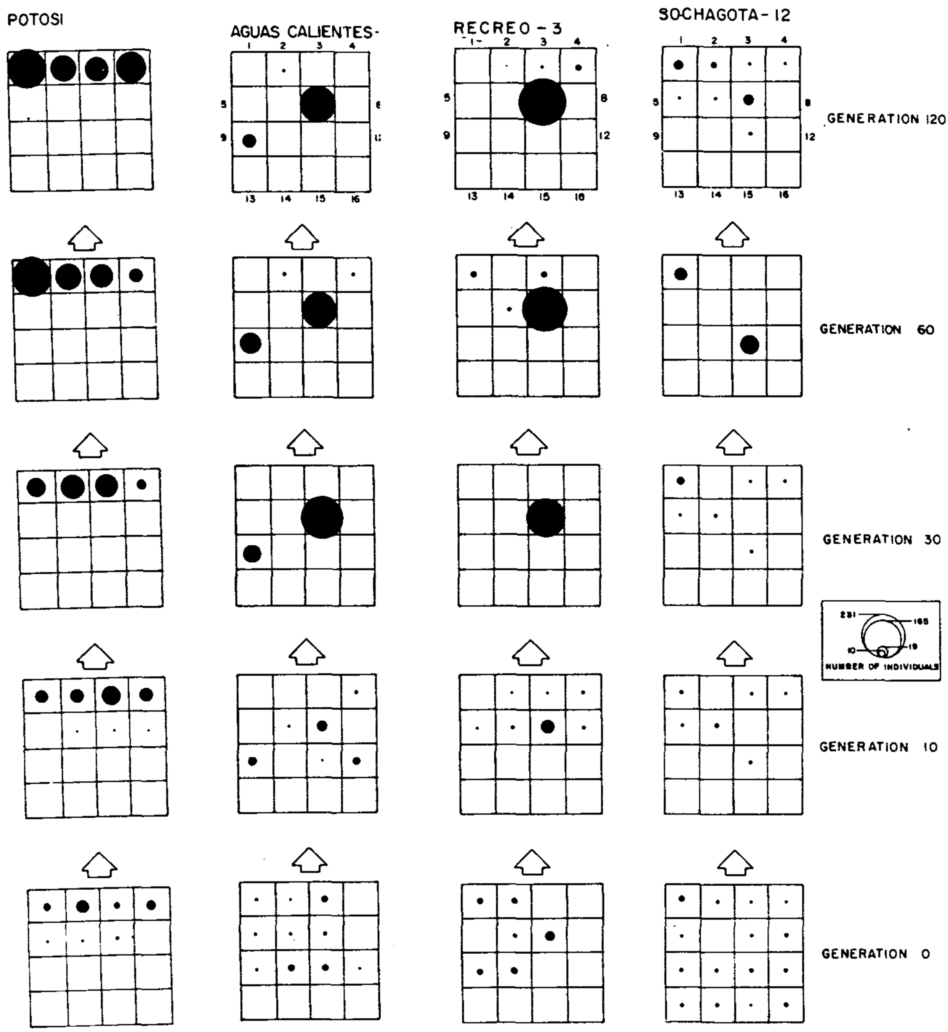


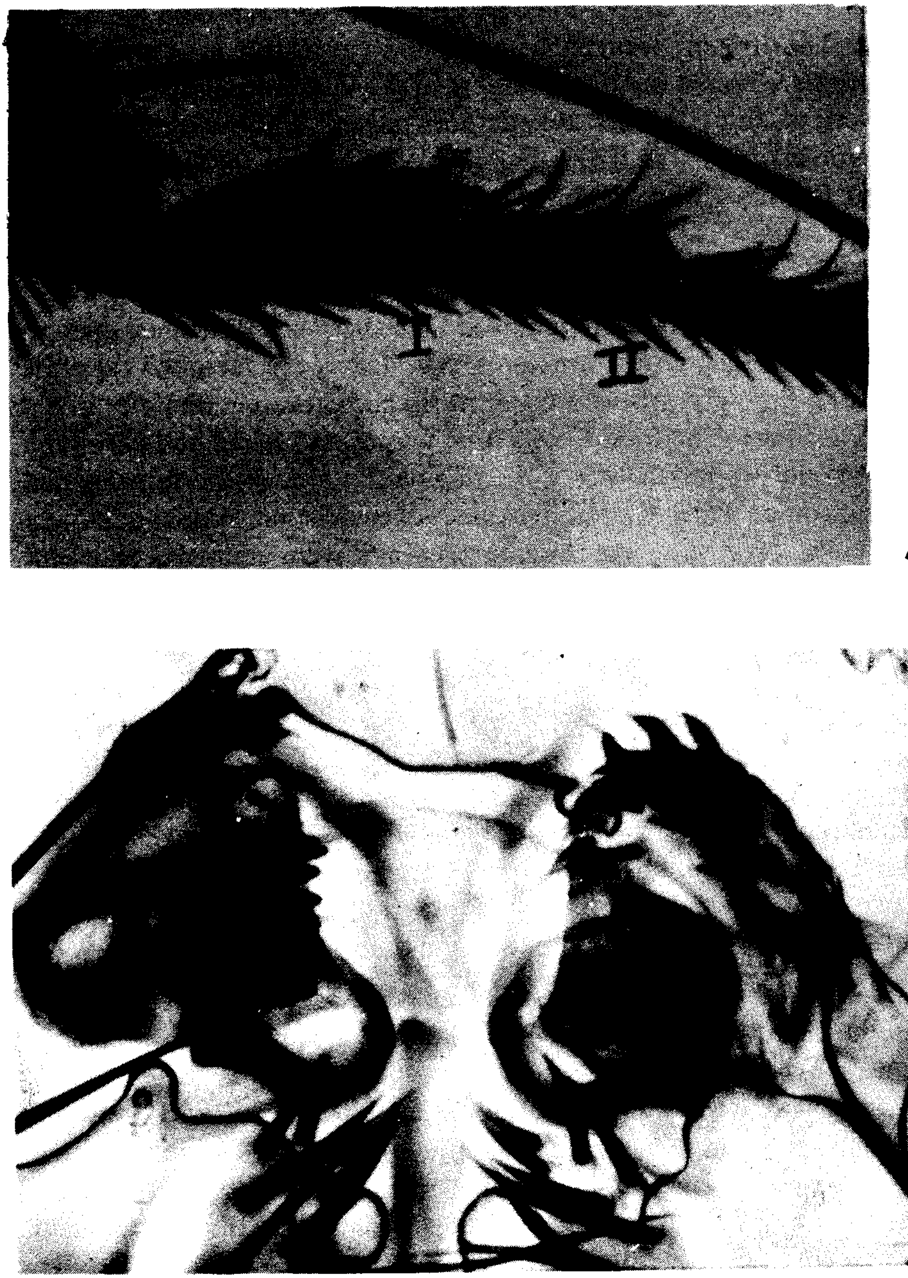
FIGURE 2. Four colonization attempts by *D. pseudoobscura* in the Cundiboyacense altiplano. The total area of the study is 16 sq. km. The surface of each circle is exactly equivalent to the number of individuals in the colony. The numbers 0, 10, 30, 60 and 144 show the number of generations sincc the original collection (= 0). Demographically successful colonies are shown. The studies were conducted by Dobzhansky and Hoenigsberg between 1971 and 1975 and by Hoenigsberg since 1975.

or penicillium involve immediate removal of the jar. Isolines are sometimes put into new jars on day 5 of deposition, in order to stimulate greater deposition of eggs. This treatment is identical for all demes analyzed. The progeny from each isoline cultivated were used to measure sexual combs, vaginal bristles, claspers and wing dimensions. Measurements were made by the first two authors named, and biologists Martha Lucía Pardo and Eleonora Uribe. Our thanks go to them for their important work and for their contribution to this study. Figures 3 and 4 show the structures analyzed.

For the study of the combs, the prothoracic legs of male progeny of the isolines of each deme were removed with sharp needles, small enough not to dissect neighbouring structures. The legs were mounted on glass plates with a little glycerin and water to fix and preserve humidity in the structure. Natural dehydration over time was thus delayed and permitted the tooth count to be made. For the vaginal bristles of the females and the claspers of the males bred from isolines of each deme, similar treatment was provided. For wing measurement, wings were removed and kept carefully as right or left but not glycerin hydrated. Water was used to fix the structure on the plate.

Measurements were taken simultaneously for each individual from each location with stereoscopes and/or microscopes with optical micrometers, giving precise and repeatable measurement. The Davis population (California, U.S.A.) was used as a representative sample of the central distribution of the species (Hoenigsberg, 1986). Isolines received the same treatment in mounting, hydration and measurement. 200 individuals were analyzed (5 per isoline per sex) for each of the altiplano demes and 400 individuals (5 per isoline per sex) for the central (Davis) population.

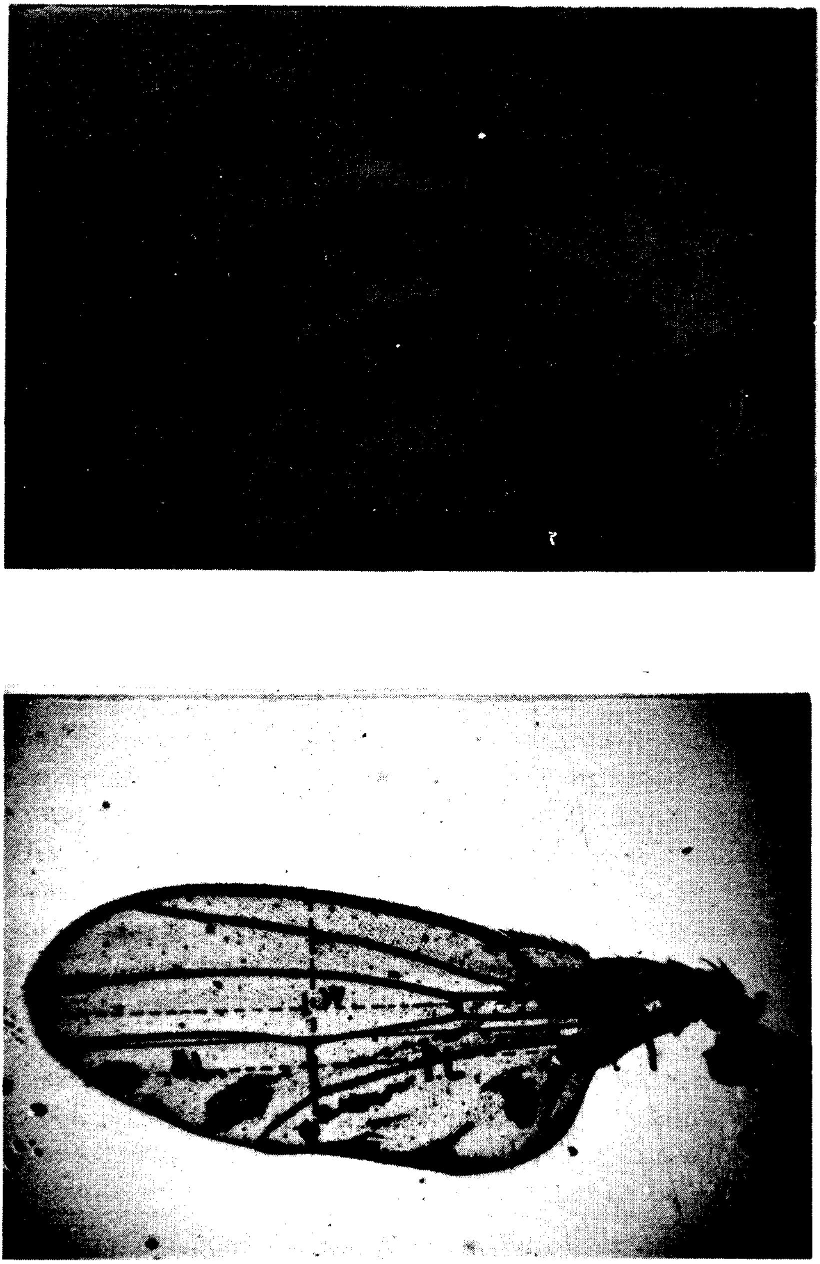
A question arising in a study of this kind is, what is the most convenient procedure for structural measurements to provide the best estimate of aberrant ontogenetic mechanisms? The problem is similar to that of the taxonomist who wishes to establish the degree of similarity between individuals in a taxon. A degree of reliability can be expected of the operative taxonomic units (O.T.U.) beyond the individual level in the hope of clarifying species, genus, family, etc. Should we, then, be content with no more than the study of individuals to uncover ontogenetic crises which morphological construction uses to signal the destructuction produced by deme structure in individuals, and anticipates an initially primary degree of divergence? But, if not all individuals can be analyzed, can we rely on the study of samples? The study of samples, when properly representative, enables us to make inferences of probability. Such inferences can lead us to define or presume statistical parameters essential to



A

B

FIGURE 3. Photographs of two male morphological characteristics of *D. pseudoobsura* in populations of Cundiboyacense altiplano and central Davis population. (A) Sexual combs of males on the prothoracic legs, I = first comb, proximal to thorax; II = second comb, distal to thorax. (B) Claspers teeth located on anal plates.



A

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FIGURE 4. Photographs of two morphological characteristics used in the study (A). Vaginal bristles located on the vagional plate of the female. * = inner bristles, ** = outer bristles. (B) Wing dimensions to estimate body size. P.L. = proximal length, D.L. = distal length, W = width.