Amer. Nat. 70:574–584 (1936)

OBSERVATIONS ON THE SPECIES RELATED TO NEW FORMS OF *DROSOPHILA AFFINIS*, WITH DESCRIPTIONS OF SEVEN

PROFESSOR A. H. STURTEVANT
AND
PROFESSOR TH. DOBZHANSKY
W. G. KERCKHOFF LABORATORIES, CALIFORNIA INSTITUTE OF TECHNOLOGY

INTRODUCTION

Drosophila affinis Sturtevant (1916, p. 334) has been recorded from many localities, ranging from New Hampshire and Illinois, south to Florida and west to Texas and Kansas (Sturtevant, 1921). We find that there are forms in Alaska, the northwestern United States and the Mexican plateau that also will fit the published descriptions of affinis; but these represent distinct species, and careful study shows that the original material is itself a mixture of several species. The members of this group are clearly closely related to the forms that have gone under the name of *Drosophila obscura*. This is also a complex group, containing at least four European species and the western American *Drosophila pseudoobscura* (Frolowa and Astaurow, 1929) and *Drosophila miranda* (Dobzhansky, 1935).

KEY FOR PINNED MALES OF THE SPECIES OF AFFINIS GROUP

The key given herewith is to be taken as an expansion of the first line of couplet 4 in the key given by Sturtevant (1921, p. 67), or of the first line of couplet 5 in that given by Malloch and McAtee (1924, p. 34). The descriptions of the species include only those respects in which they differ. For other characters, common to all of them, see the descriptions cited.

It should be added that all members of the group have a single tooth of a second sex-comb (Fig. 1) on the second tarsal segment, where there is a fully developed comb in members of the obscura group. We have found no differences among the eight forms in the internal genital ap-

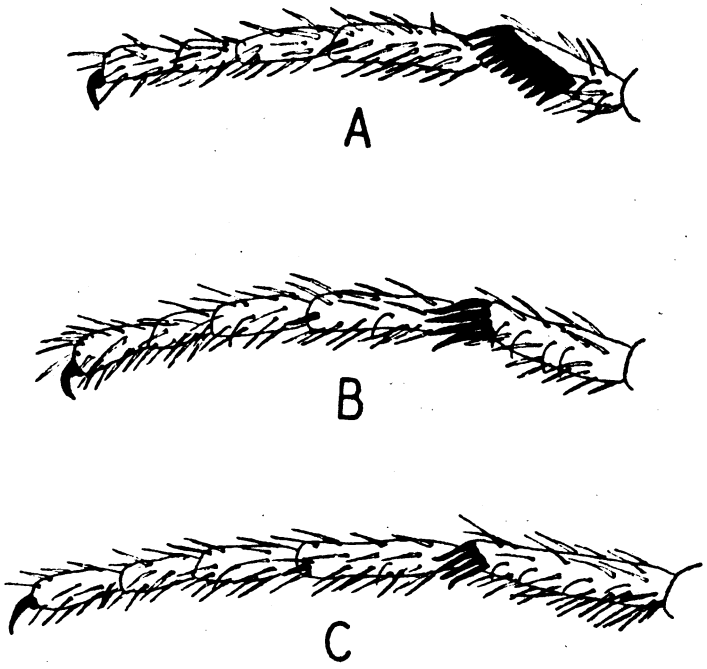

FIG. 1. Tarsi of A– *Drosophila algonquin*, B– *D. affinis* and C– *D. athabasca*.

paratus of either sex, while all of them have spiral testes different from the ellipsoidal ones present in species of the obscura group.

1. Sex-combs with 8–10 teeth, nearly parallel to axis of the tarsal segment; large species, more brownish than others ..... **algonquin**
– Sex-combs with 4–6 teeth, more oblique 2
2. Frons slightly pollinose when viewed laterally; sex-combs short 3
– Frons scarcely pollinose 4
3. Frons not pollinose when viewed from vertex; mesonotum not uniformly pollinose, with indistinct longitudinal stripes ..... **seminole**
– Frons pollinose when viewed from vertex; mesonotum uniformly pollinose ..... **narragansett**
4. Sex-combs longer (Fig. 1B) ..... **affinis**
– Sex-combs shorter (Fig. 1C) 5
5. Mesonotum with four relatively distinct longitudinal less pollinose stripes (two inside and two outside the dorsocentral lines) ..... **azteca**
– Mesonotum with two relatively less distinct dark longitudinal stripes (inside the dorsocentral lines) 6
6. Legs distinctly brownish ..... **athabasca**
– Legs wholly yellow ..... **mahican**

DESCRIPTION OF SPECIES

Drosophila algonquin, sp. n.

♂. Frons dull, light brown. Mesonotum light brown, indistinctly longitudinally striped. Legs yellow; sex-combs with 8 to 10 teeth (Fig. 1A), larger

than in affinis. Male genitalia (Fig. 2A) with a short and broad eighth sternite and a blunt distal end of the penis. The anterior margin of the eighth sternite rounded and not thickened.

♀. Abdomen indistinctly banded.

Distribution. Massachusetts: Woods Hole (type locality), East Falmouth, Waquoit; New Jersey: Mendham, Sparta; Michigan: Detroit; Indiana: North Manchester; Illinois: Flat Rock.

Drosophila affinis Sturtevant

♂. Frons dull brown. Mesonotum brown, with faint indications of longitudinal stripes anteriorly. Legs yellow; 4 to 6 teeth per sex-comb (Fig. 1B). Medium size. Genitalia (Fig. 2B) with an elongate eighth sternite whose anterior margin is not thickened. Penis acuminate.

♀. Abdomen distinctly banded.

Distribution. New Jersey: Morristown (one specimen); South Carolina: Greenville; Florida: St. Augustine, Lakeland; Alabama: Kushla (type locality); Louisiana: Baton Rouge; Texas: Houston, Florence.

Duda (1927, p. 135) has recorded D. affinis from Paraguay. This record requires confirmation, since experience shows that this author sometimes misinterprets American locality labels; if a member of the present group occurs so far south, we can only suggest that azteca or an undescribed form may be concerned.

Drosophila affinis subsp. *iroquois*, subp. n.

Differing from the typical affinis in that it has darker frons, mesonotum, and pleurae. Legs somewhat brownish, especially apices of femora and bases of tibiae.

Distribution. Massachusetts: Woods Hole (type locality); New York: Staten Island; New Jersey: Fort Lee, Sparta, Mendham, New Brunswick; Mississippi: Agricultural College (1 specimen).

Drosophila athabasca, sp. n.

♂. Frons dull, dark brown. Mesonotum dark brown, with a pair of faint longitudinal stripes just inside the dorsocentral lines. Legs yellow, apices of femora and bases of tibiae brown; sex-combs with four teeth, very small (Fig. 1C). Medium size. Genitalia (Fig. 2C) with an elongate eighth sternite thickened and blunt on its anterior margin.

♀. Abdominal banding indistinct.

Distribution. Alaska: Gravina Island (type locality), Ketchikan, Juneau, Chitina; British Columbia: Quesnel, 150-mile House, Pavilion, Lake Shuswap, Arrowhead, Nakusp, Kaslo, Campbell River, Lake Cowichan; Washington: Cape Flattery, Brinnon; Oregon: Reedsport; Wyoming: Grand Teton, East entrance to Yellowstone Nat. Park, Big Horn Mts., Sundance; South Dakota: Black Hills; Colorado: Cache la Poudre Canyon, Grand Lake, Estes Park, University Camp.

Drosophila athabasca subsp. *mahican*, subsp. n.

Differs from typical athabasca in somewhat paler frons and thorax; legs yellow, not brownish.

Distribution. New Hampshire: Hanover (type locality); Massachusetts: Middleboro, Woods Hole; New Jersey: Mendham.

Drosophila azteca, sp. n.

♂. Frons dull, dark brown. Mesonotum dark brown, a relatively darker shining longitudinal line just inside each dorsocentral row, and a similar but less distinct and narrower line lateral to each dorsocentral row. Legs yellow, slightly brownish; sex-combs with 4 to 5 teeth, small. Size medium. Genitalia (Fig. 2D) with eighth sternite thickened and acuminate on the anterior margin. Penis acuminate.

♀. Abdominal banding indistinct.

Distribution. Oaxaca: Cerro San Jose (type locality); Morelos: mountains north of Cuernavaca; Durango: Otinapa, Aserraderos.

Drosophila seminole, sp. n.

♂. Frons brown, paler anteriorly; strongly pollinose when viewed laterally but not when viewed from vertex. Mesonotum brown, with indistinct longitudinal stripes. Legs yellow; sex-combs as in athabasca or azteca. Medium size. Genitalia unknown.

♀. Abdominal banding indistinct. Frons not pollinose.

Distribution. Alabama, Mobile County: Kushla (type locality), Whistler.

Drosophila narragansett, sp. n.

♂. Frons strongly pollinose when viewed either laterally or from vertex. Mesonotum brown, grayish dusted, longitudinal stripes faint or absent. Legs yellow, slightly brownish; sex-combs small, similar to those of athabasca or azteca. Somewhat smaller than affinis. Genitalia (Fig. 2E) with the eighth sternite smoothly rounded on the margin.

♀. Frons not pollinose.

Distribution. Massachusetts: Woods Hole (type locality); Connecticut: Darien.

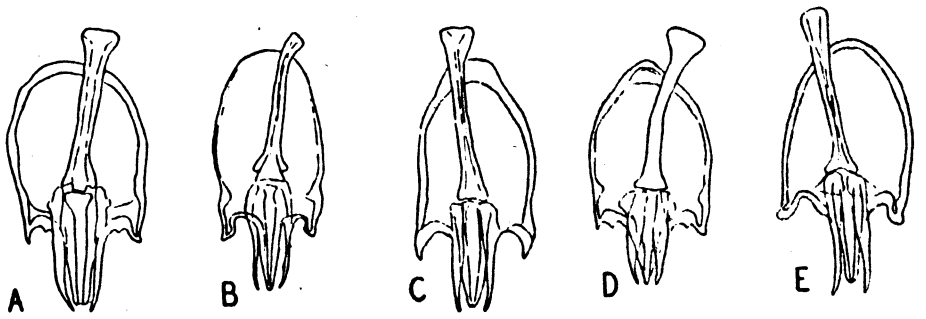

FIG. 2. The eighth abdominal sternite and the penis apparatus of A– *Drosophila algonquin*, B– *D. affinis*, C– *D. athabasca*, D– *D. azteca*, E– *D. narragansett*.

The types of all the species and subspecies here described are deposited in the American Museum of Natural

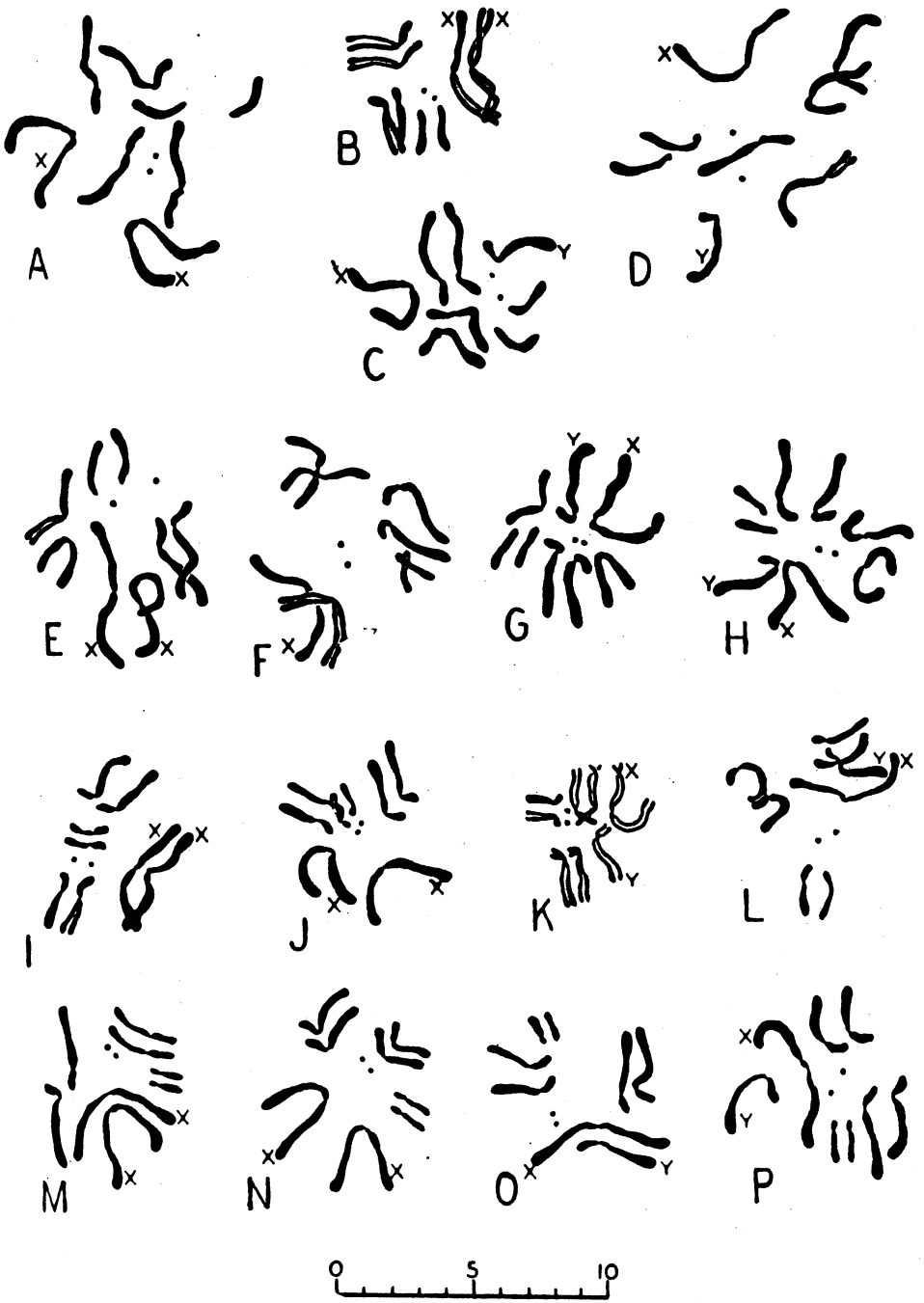

FIG. 3. Metaphase plates in the cells of the larval nerve ganglia in A and B– *Drosophila algonquin* females, C and D– *Drosophila algonquin* males; E and F— *D. affinis* females and G and H males; I and J— *D. athabasca* females and K and L males; M and N– *D. azteca* females and O and P males. X– the X-chromosome; Y– the Y-chromosome. The scale below represents 10 micra.

History, New York, which also contains the types of *affinis* and *miranda*.

Chromosomes

Metz (1916, A, C) found in *Drosophila affinis* five pairs of chromosomes. The X–chromosome is V–shaped and the Y is J–shaped. Among the four autosomes two have distinctly subterminal spindle fiber attachments, one, the shortest, is rod-shaped, and the fifth is very small, dot-like. Since among the species studied by Metz no other except affinis had a chromosomal group with such characteristics, he isolated it into a special "type K" containing affinis as the sole representative. At present we know, however, that at least six distinct species were confused under the name "affinis." We have studied the chromosomes of four of them (Fig. 3), using the acetocarmine smear preparations of the larval ganglia and picking out the division figures in the giant nerve cells. Comparing Metz's figures with ours, it seems most probable that the species he was dealing with was not the true affinis, but *Drosophila algonquin*.

All the species which we have studied have the essential characteristics of the type K of Metz. However, chromosomes of *Drosophila affinis* differ from those of its relatives in that one of its autosomes (Figs. 3 E–H) has a very nearly median spindle fiber attachment. In algonquin, athabasca and azteca the seemingly homologous chromosome has the fiber attachment in a distinctly subterminal position. *Drosophila athabasca* and *azteca* appear to have identical metaphase plate chromosomes (Figs. 3 I–P), but they differ from algonquin and the true affinis, since the shortest autosome has a subterminal fiber attachment instead of the apparently terminal one found in the latter two species. It must be mentioned, however, that this difference is reasonably clearly visible only in favorable plates: it is, for instance, not noticeable in the smaller nerve cells. Thus, among the four species of the affinis group studied cytologically three are distinguishable in the metaphase plate configurations.

No detailed study of the salivary gland chromosomes of the species of the affinis group has as yet been made. Preliminary information is available only on athabasca and azteca. In these the salivary gland nuclei contain five long and apparently three short strands attached to a common chromocenter. In males two of the long strands are pale. The provisional interpretation of this condition is as follows. The two long strands that are pale in the male are the two limbs of the X–chromosome. The remaining three long strands are the longer limbs of the autosomes having subterminal fiber attachments. The three short strands correspond—one to the dot-like autosome and two to the shorter limbs of the two autosomes in which the fiber attachment is clearly subterminal. The short limb of the autosome having more nearly terminal attachment (see above) is probably inert.

Ecological Data

Our collecting west of the Mississippi has been done almost exclusively by the use of trap bottles containing fermented banana, exposed in forested areas and examined for adult specimens at about sunset. Most of this collecting (all the records for azteca and athabasca) has been done by one of us (Dobzhansky). The collecting in the eastern United States has been done largely by Sturtevant, using the banana trap method and also (more extensively) sweeping tree trunks with a net and collecting individual specimens found on bleeding trees. These various methods do not appear to affect the relative frequencies of the species concerned.

At Woods Hole the commonest species of the group is iroquois, followed by algonquin and mahican, with narragansett very rare. In southern Alabama affinis is somewhat commoner than seminole. Professor J. T. Patterson informs us that in central Texas affinis is more frequent than pseudoobscura. In Alaska only athabasca was found, frequently in great abundance. The distribution of this form and of pseudoobscura overlap in the region from British Columbia to the Rocky Mountains of north-

ern Colorado, but in this overlapping zone athabasca is clearly commoner as one proceeds north and northeast, and pseudoobscura south and southwest. That is to say, one species replaces the other rather rapidly as one moves at right angles to the boundaries of their distribution. For instance, at Yale and Merritt, British Columbia, only pseudoobscura was found among large numbers of flies collected. Further north, at Pavilion, athabasca appeared as an admixture to the population consisting predominantly of pseudoobscura; near 150-mile House athabasca decidedly predominates, and near Quesnel a single pseudoobscura was found among a mass of athabasca. Occasional specimens of either species may, of

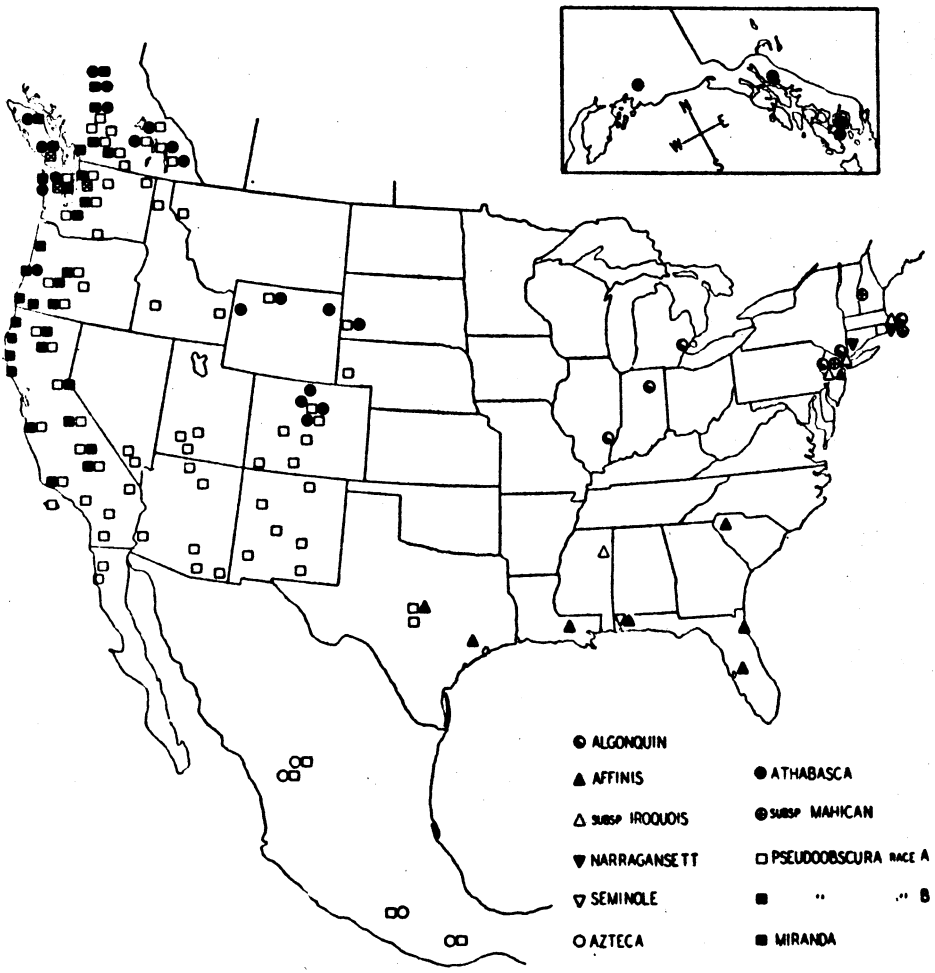

FIG. 4. The known records of species of *Drosophila affinis* and *pseudoobscura* groups. The insert map above represents a part of Alaska.

course, appear well within the range occupied by the other species—a single athabasca individual found at Reedsport, Oregon, does in fact represent such an isolated occurrence (Fig. 4). In the northern Rocky Mountains pseudoobscura is more frequent at lower elevations, and athabasca in the subalpine zone (although further south, at the tree line on Pike's Peak only pseudoobscura was found). All these facts suggest that athabasca and pseudoobscura are ecologically nearly equivalent. It does not appear from our present information that such a replacement in a relatively narrow zone occurs for any other species here discussed, but in many of the areas where this might happen we have little or no data. It may be surmised that when such data are available similar cases will be found, and also that additional species will be discovered.

Azteca and athabasca may be crossed (see below), and a number of facts indicate that they are very closely related. One is tempted to conclude that they have only recently diverged. In this connection it is of interest that the distribution areas of these two species are separated by a broad zone that is occupied exclusively by pseudoobscura, and as shown above pseudoobscura and athabasca do not seem to both survive in a given region (Fig. 4). The conclusion seems to be clear; azteca and athabasca were separated by an eastward extension of the range of pseudoobscura—a conclusion concerning the history of the latter species that is consistent with the results of studies now in progress, on the geographic distribution of inversions in the third chromosome of pseudoobscura.

INTERRELATIONS OF THE FORMS DESCRIBED

The eight forms concerned here are so similar in appearance that we have been unable to devise satisfactory methods of distinguishing pinned females. That the types listed as species are really distinct follows from laboratory experiments. We have kept strains of all of them at one time or another, and have made many attempts at interspecific crosses. Affinis (or iroquois—in most cases

both) has been tried with all the others; algonquin with narragansett, athabasca and azteca; seminole with mahican; and azteca with athabasca. With the exception of the last named, these crosses produce no offspring whatever. Affinis, algonquin, athabasca and azteca have also been tested with both races of pseudoobscura, with negative results.

In living material some differences not mentioned in the above descriptions are apparent. The females of affinis and algonquin have distinctly banded abdomens; in athabasca, azteca, seminole and mahican this banding is much less distinct, the pattern resembling that of pseudoobscura; narragansett has not been seen alive since this character was noted. Affinis, iroquois, algonquin and azteca are relatively easy to breed by the usual maize meal—molasses—agar technique, though more difficult than pseudoobscura; athabasca, mahican, seminole and narragansett are much more troublesome to maintain, and appear to be more sensitive to high temperature.

These facts leave no doubt that we are here concerned with "good" species. The relation of the two forms described as subspecies is less certain. Iroquois is only slightly different from affinis in color, and is fully fertile with it (strains from Texas, Alabama and Florida have been crossed to Woods Hole ones and have given fully fertile offspring of both sexes). However, since the variation is clearly a geographical one, it has seemed desirable to recognize and name the two types. Mahican and athabasca have not been compared in living material; but the only difference we can see is in color. Even the male genitalia are identical. It remains uncertain whether the range is a continuous one, since records are absent for the greater portion of the Canada-United States border, where they are needed for this purpose.

Drosophila azteca and *athabasca* may be crossed in either direction. Neither mating is as often successful as are matings within either species; that of athabasca ♀ × azteca ♂ is particularly difficult to obtain. All the

hybrids produced are sterile, and have rudimentary gonads. In the male hybrids the testis size is variable, apparently depending in part on which strains of the parent species are used (*cf.* the results of Dobzhansky and Boche, 1933, on the hybrids of the two races of pseudoobscura). In females the ovaries contain egg chambers only. All the females observed have been about the same size and proportions as the parent species, but all have had some macrochaetae markedly reduced in size. The males from the reciprocal crosses are strikingly different. Those from the azteca ♀ × athabasca ♂ are larger than their sisters or parents and have relatively very large wings of a characteristic shape. Those from athabasca ♀ × azteca ♂ are dwarfs, with relatively small wings; they are also much less numerous than their sisters on account of low viability. Neither type of males has reduced macrochaetae. The hybrid between azteca and athabasca is the fourth example of sterile hybrid in the genus Drosophila. The examples known previously are the melanogaster × simulans and the pseudoobscura × miranda hybrids. The hybrids between the A and B "races" of *Drosophila pseudoobscura* may be placed in the same category.

LITERATURE CITED

Dobzhansky, Th.
1935. *Genetics*, 20: 201–213.

Dobzhansky, Th., and R. D. Boche
1933. *Biol. Zentrbl.*, 53: 314–330.

Duda, O.
1927. *Arch. Naturgesch.*, 91A, Heft 11–12, 229 pp.

Frolowa, S. L., and B. L. Astaurow
1929. *Zeits. Zellf. mikr. Anat.*, 10: 201–213.

Malloch, J. R., and W. L. McAtee
1924. *Proc. Biol. Soc. Washington*, 37: 25–42.

Metz, C. W.
1916a. *Jour. Exp. Zool.*, 21: 213–279.

Metz, C. W.
1916b. AMER. NAT., 50: 587–599.

Sturtevant, A. H.
1916. *Ann. Entom. Soc. America*, 9: 323–342.

Sturtevant, A. H.
1921. "The North American Species of Drosophila," Carnegie Inst. Washington, Publ. 301, 150 pp.