

Drosophila lowei, a New American Member of the *Obscura* Species Group^{1,2}

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ABSTRACT

A new species, *Drosophila lowei* (Diptera: Drosophilidae), from the mountains of Arizona and Colorado, is described. The species is of particular interest because it is the 5th American species to be described in the *obscura* subgroup of the *obscura* Fallén species-group, subgenus *Sophophora*, and is clearly related to *D. pseudoobscura* Frolowa and *D. persimilis* Dobzhansky & Epling. *D. lowei* may usually be distinguished from *D. pseudoobscura*, with which it is sympatric, by its smaller size,

proportionately longer wings, and its darker eye color. The chromosomes of *D. lowei* differ from those of *D. pseudoobscura* by a pericentric inversion in chromosome II. Hybrids between the 2 species are sterile. Ecologically *D. lowei* prefers the more temperate and cooler habitats above 7000 feet elevation and has its population peak in late summer and fall. There is evidence that the species undergoes a reproductive diapause at that time.

At present there are 4 American species of *Drosophila* in the *obscura* subgroup of the *obscura* Fallén species-group, in the subgenus *Sophophora* (Diptera: Drosophilidae). They are *D. pseudoobscura* Frolowa, *D. persimilis* Dobzhansky & Epling, *D. miranda* Dobzhansky, and *D. frolovae* Wheeler (Patterson and Stone 1952, Buzzati-Traverso and Scossiroli 1955).

The present report describes the 5th American species in the *obscura* subgroup, *D. lowei*, n. sp., first encountered by one of us (W.B.H.) in the Santa Catalina Mountains near Tucson, Ariz., in 1960 (Heed et al. 1962). The species is smaller, with proportionately longer wings and darker eyes than *D. pseudoobscura*. Detailed examination showed that it was distinctly different from *D. pseudoobscura* in several respects, but closely related to it. Several cultures of *D. lowei* were established after the species was recognized, but none could be maintained for longer than 1 year. During 1960 and 1961, data on the chromosomes and hybrids with *D. pseudoobscura* were collected. On July 15, 1961, the species was

¹ Diptera: Drosophilidae.

² Endorsed and communicated by Floyd G. Werner. Accepted for publication July 8, 1968.

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encountered again in a collection from Rustler's Park, Chiricahua Mountains, Ariz., by Th. Dobzhansky, Charles Lowe, and one of us (W.B.H.). It was later learned that the same species had been collected in August 1950, by Marshall R. Wheeler and Charles Stephens in northern Arizona (personal communication and specimen comparison). In 1967, one of us (D.W.C.) encountered what was recognized as an unknown species of the *obscura* group in Colorado. Direct comparison of specimens from Colorado with those from Arizona showed them to be conspecific. The metaphase chromosomes are also the same.

Drosophila lowei, n. sp.

EXTERNAL CHARACTERS OF IMAGOS.—Arista with 2–4 dorsal and 2 ventral branches in addition to the terminal fork. Front dark brown, lighter anteriorly with medial hairs forming a V. Carina narrow, slightly longer than 3rd antennal segment and broadening at clypeus. Greatest cheek width $\frac{1}{4}$ – $\frac{1}{3}$ greatest diameter of eye. Proclinate orbital bristle about 0.8 as long as posterior reclinate. Anterior reclinate 0.5–0.7 as long as proclinate. Eye dark red. One stout oral bristle. Palpi with 1 stout subapical lateral bristle.

Acrostichal hairs in 7–8 complete rows inside dorsocentral rows. Anterior scutellars convergent. Mesonotum blackish with a bronzelike sheen; *D. pseudoobscura* does not have this combination. Anterior sternopleural bristle $\frac{1}{2}$ as long as posterior; midsternopleural bristle very short. Legs dark. Proximal sex comb (males only) on basitarsus of front leg with 4–6 teeth, distal sex comb on 2nd tarsus with 3–4 teeth. *D. pseudoobscura* from the Santa Catalina Mountains has respectively 6–8 teeth and 5–6 teeth on the proximal and distal sex combs. Wings clear. Costal index varies from 2.3–2.5; 4th vein index 1.8–2.2; 5x index 1.9–2.2. Third costal section with stouter bristles on basal 0.4. Abdomen black, semishining.

The total body length (etherized flies) of *D. lowei* is significantly shorter than for *D. pseudoobscura* in both sexes, although their ranges overlap considerably. The wing length of *D. lowei* is significantly longer than the length of the body in both sexes and is about the same as wing length of *D. pseudoobscura*. Wing and body lengths in *D. pseudoobscura* are not significantly different in either sex. A sample of 31 *D. lowei* ♂ and 31 ♀ collected Oct. 13, 1961, from Mt. Bigelow (8400 ft), Santa Catalina Mountains, and 26 *D. pseudoobscura* ♂, collected simultaneously, were measured. Also a sample of 20 ♂ and 20 ♀ of *D. pseudoobscura* was measured from a collection, July 6, 1961, near the Radar Station (9100 ft) at the top of the Catalina Mountains. The following measurements are in millimeters and give the mean $\pm 2 \times$ SE, and the range. *D. lowei* male body: 2.20 ± 0.056 (1.9–2.5); wing: 2.45 ± 0.072 (2.0–2.8); female body: 2.45 ± 0.066 (2.0–2.7); wing: 2.69 ± 0.088 (2.1–3.0). *D. pseudoobscura* male body: 2.38 ± 0.070 (2.1–2.7); wing: 2.41 ± 0.082 (2.1–2.8). *D. pseudoobscura* from the July 6 collection, male body: 2.55 ± 0.098 (2.1–

2.9); wing: 2.55 ± 0.092 (2.2–2.9); female body: 2.84 ± 0.102 (2.2–3.2); wing: 2.72 ± 0.114 (2.0–3.1).

INTERNAL CHARACTERS OF IMAGOS, AND GENITALIA.—Testes orange-red, deepening to very dark red in older flies, elliptical. There is consistently less testicular bulk than in *D. pseudoobscura* males. Lower tip of anal plate constricted, and clustered with 8–14 bristles. Extension of genital arch (toe) with 5–6 very long bristles extending its length, with 8–12 secondary bristles. Forceps with 9–11 primary teeth in straight row and 1–2 secondary teeth immediately outside this row; *D. pseudoobscura* has 6–7 primary teeth and 3–4 secondary teeth on forceps. Margin of forceps with many bristles which come around on upper surface. Posterior gonapophyses short, extending about $\frac{3}{4}$ distance to tip of anterior gonapophyses and are included within the margins of the aedeagus in the majority of slide preparations (Fig. 3). Aedeagus extending $\frac{1}{2}$ distance between tips of anterior and posterior gonapophyses. Hypandrium with 1 pair of paramedian bristles mounted on a prominent novasternum (Fig. 6). Bristles extending $\frac{1}{2}$ – $\frac{2}{3}$ distance to tip of aedeagus. Compared with *D. pseudoobscura*, the aedeagus and posterior gonapophyses of *D. lowei* are shorter (Fig. 1, 3), and the hypandrial bristles and novasternum are much more prominent (Fig. 4, 6). Spassky (1957) illustrated the minuteness of the hypandrial bristles for *D. pseudoobscura* and *D. persimilis*.

The penis index (Rizki 1951) of *D. lowei* is the same as for *D. pseudoobscura*. The width of a single lamina in ocular units ($n = 11$) is 0.51 ± 0.009 and length is 4.33 ± 0.016 giving a mean index of 8.49. This index is almost identical to that of several strains of *D. pseudoobscura* (Rizki 1951) and also to 3 specimens we examined from the Santa Catalina Mountains. The 3 last-mentioned specimens showed lamina width 0.60, and length 5.0, 5.1, and 5.2, giving a mean index of 8.50. Spermatheca small and round, darkly chitinized. Ventral receptacle a short tube. Ovipositor plate rounded, with 15 teeth.

EGG.—One pair of filaments, slightly blunted at tip and about $\frac{1}{2}$ as long as egg.

CHROMOSOMES.—The metaphase chromosomes were identified from specimens from the Santa Catalina Mountains, 3 miles N of Tucson, Ariz., and Williams Canyon, 6 miles NW of Colorado Springs, Colo. The larval brain cells show 2 pairs of medium length rods, 1 pair of medium sized V's, and 1 pair of dots for autosomes. The X is a large, slightly acrocentric V with a prominent secondary constriction in the longer arm. Other constrictions are occasionally seen in both arms. The Y is J-shaped and slightly longer than $\frac{1}{2}$ the total length of the X chromosome (Fig. 7, 9). Fig. 8 is an anaphase from an F_1 male hybrid larval brain cell of *D. lowei* ♀ × *D. pseudoobscura* ♂. The homologue of the autosomal V (*D. lowei*) is a rod (*D. pseudoobscura*).

The salivary gland analysis was made from cultures established, and since lost, from the Santa Catalina Mountains, 1960 and 1961. They show 6 arms and a dot, indicating that the autosomal V re-

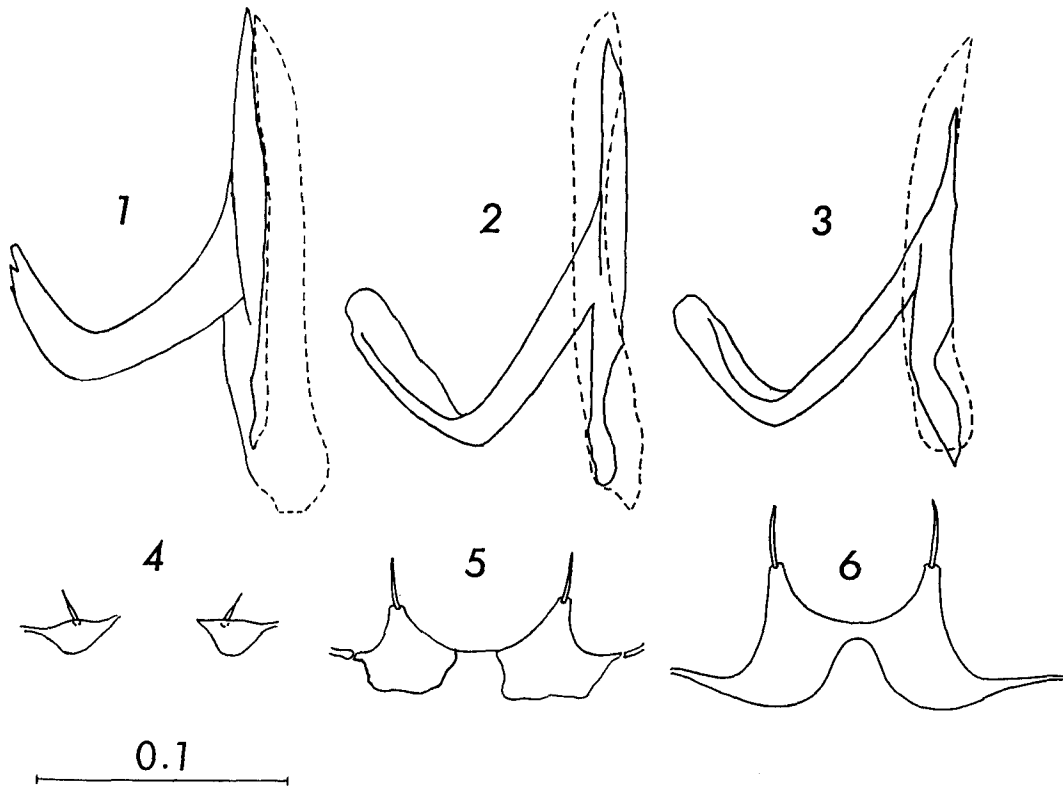


FIG. 1.—Ventral view of left posterior gonapophysis (solid line) and left half of aedeagus (dotted line) of *D. pseudoobscura* (scale is in mm). FIG. 2.—Same of *D. lowei* ♀ × *D. pseudoobscura* ♂ hybrid. FIG. 3.—Same of *D. lowei*. FIG. 4.—Ventral view of novasternum bristles of *D. pseudoobscura*. FIG. 5.—Same of *D. lowei* ♀ × *D. pseudoobscura* ♂ hybrid. FIG. 6.—Same of *D. lowei*.

sulted from a pericentric inversion. The arms have been homologized with *D. pseudoobscura* and later proved to be correct by pairing partners, even though incomplete, in hybrid larvae (*lowei* ♀ × *pseudoobscura* ♂). Therefore, it is known that *D. lowei* differs from *D. pseudoobscura* by a pericentric inversion in chromosome II. Chromosome III in *D. lowei*

is polymorphic for inversions, as are the right and left arms of the X (Fig. 10). This situation is similar to the inversion polymorphism in *D. pseudoobscura* where the majority of inversions occur in chromosome III, with most of the remainder in the X. In a hybrid slide, chromosome IV paired in 6 regions, chromosome III usually did not pair, and chromosome

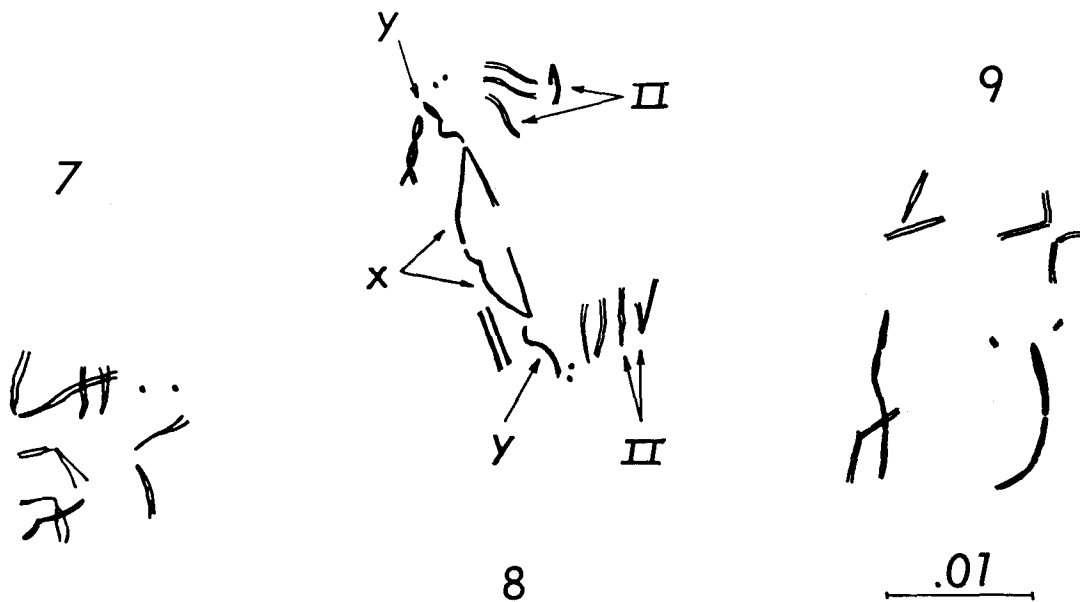


FIG. 7.—Larval brain cell metaphase of *D. lowei* male from Mt. Lemmon, Santa Catalina Mountains, Ariz. (see text). FIG. 8.—Male larval brain cell anaphase of *D. lowei* ♀ × *D. pseudoobscura* ♂ hybrid (see text). FIG. 9.—Larval brain cell metaphase of *D. lowei* female from Williams Canyon, Rampart Range, Colo. (see text).



FIG. 10.—Larval salivary gland chromosome III of *D. lowei* from Mt. Lemmon, Santa Catalina Mountains, Ariz., showing heterozygosity for overlapping inversions.

II paired in 1 region on 1 *D. lowei* arm and in 1 region on the other *D. lowei* arm.

Geographic Distribution and Types.—ARIZONA: Santa Catalina Mountains, Chiricahua Mountains, and the Mogollon Rim above 7000 ft. COLORADO: Pikes Peak area near Colorado Springs and NE to the Black Forest and along the Palmer Divide to within about 20 miles SW of Byers, Colo. Collected between 6,500 ft and 11,400 ft in vicinity of Pikes Peak, and as low as 6000 ft near Byers.

Holotype ♂, 4 paratype ♂, and 3 paratype ♀ from collection A19.2, Mt. Lemmon, Santa Catalina Mountains, Tucson, Ariz., by W. B. Heed, September 1960; 5 paratype ♂ and 2 paratype ♀ from collection 2056.1, along Mogollon Rim Road about 38 miles W of Heber, Ariz., by M. R. Wheeler and Charles Stephens, August 1950. Types are deposited in the Genetics Foundation Collection, University of Texas.

Ecology in Arizona.—In the Santa Catalina Mountains *D. lowei* prefers the more moist fir forests and has its population peak in September and October. *D. pseudoobscura* is most frequent during the summer months and apparently does equally well in pine and fir forests. The following collection records support these statements. The collecting habitats have been described (Patton et al. 1966). The flies were collected in 5-gal lard cans containing fermenting bananas. From Sept. 16 to 29, 1960, *D. lowei* made up 6.0% of 268 *D. lowei* + *D. pseudoobscura* in a predominantly ponderosa pine forest with scattered Gambel and silverleaf oak at 7800 ft elevation (Or-

ganization Ridge). At the same time it made up 96.2% of 291 *D. lowei* + *D. pseudoobscura* in a predominantly white fir and Douglas fir forest with scattered bigtooth maples, quaking aspen, and Gambel oak at 9000 ft (Mt. Lemmon). From June 20 to July 8, 1961, 8054 individuals of both species, of which *D. lowei* made up 1.1%, were collected in the same fir forest (9000 ft). Moreover, *D. lowei* prefers rotting mushroom bait, collected in situ, to banana bait. On Oct. 6, 1961, in a white fir-Douglas fir forest on Mt. Bigelow (8400 ft), 6 banana traps attracted 204 individuals of both species, of which *D. lowei* made up 13%, while 2 mushroom traps attracted 57 individuals consisting of 83% *D. lowei*. A single trap with a mixture of banana and mushroom attracted 106 flies consisting of 45% *D. lowei*.

D. lowei is the 3rd species in abundance coming to banana-baited trap cans in the Santa Catalina Mountains above 6000 ft (2.4%). The 2 commoner species are *D. pseudoobscura* (71%) and *D. hamatofila* Patterson & Wheeler, in the *repleta* Wollaston species-group, (6.0%) among 26,773 flies of the Drosophilidae (Heed et al. 1962).

Ecology in Colorado.—Collections were made along a 65-mile transect from the Pikes Peak area (12,000 ft) to about 20 miles SW of Byers, Colo. (6000 ft) from Aug. 7 through Sept. 11, 1967, using fermenting banana in small buckets. *D. lowei* was the commonest species collected at the 2 following localities on the Rampart Range road, NW of Colorado Springs, (1) Williams Canyon (7800 ft), a ponderosa pine forest, and (2) Ridge Crest (9400 ft), a pine-spruce-fir forest. *D. lowei* was collected at Williams Canyon Aug. 16 (355 ♂, 134 ♀) and Sept. 8 (106 ♂, 219 ♀). The species was collected at Ridge Crest Aug. 17 (698 ♂, 160 ♀) and Sept. 9 (154 ♂, 461 ♀). *D. lowei* represented 90-93% of the *Drosophila* from all 4 collections. *D. pseudoobscura* was not present in any of the 4 collections. In fact it was not collected above 7000 ft in 1967, even though Professor Th. Dobzhansky collected *D. pseudoobscura* at 11,500 ft on Pikes Peak on July 23, 1935. In 1967 *D. lowei* was collected at 11,400 ft in the vicinity of Pikes Peak but the species was not common above 10,000 ft. Two attempts to collect *D. lowei* at the 12,000 ft tree-line elevation on Pikes Peak were unsuccessful.

Along the remainder of the transect from the Garden of the Gods NE to the Black Forest and the Palmer Divide, *D. lowei* and *D. pseudoobscura* were collected together. The number of *D. lowei* exceeded that of *D. pseudoobscura* in all localities, but at the 6000-ft end of the transect, near Byers, the latter species was almost as frequent as *D. lowei*. In the Black Forest *D. lowei* was about 3× as frequent as *D. pseudoobscura* in August, while it comprised about 98% of the mixture collected in September.

The summer of 1967 was relatively cool and moist in Colorado, but the preceding summer was hot and dry. The year 1966 was one of the driest on record.

Therefore the distribution and relative abundance of *D. lowei* and *D. pseudoobscura* as indicated by the 1967 data may not be typical. However, the data from Colorado agree with those from Arizona in suggesting that *D. lowei* is more abundant at higher elevations and later in the summer, whereas *D. pseudoobscura* prefers lower elevations and midsummer conditions.

From the limited data, *D. lowei* appears to replace *D. pseudoobscura* at higher elevations in the southern Rocky Mountains in the same manner that *D. athabasca* Sturtevant & Dobzhansky replaces *D. pseudoobscura* at higher elevations in the northern Rocky Mountains (Dobzhansky and Epling 1944, Patterson and Stone 1952). *D. athabasca*, a member of the *affinis* subgroup, has not been collected in Arizona. *D. lowei* is the 2nd species of the *obscura* subgroup to span, at least marginally, both the Colorado and Mexican plateaus. The presence of *D. lowei* in the Chiricahua Mountains indicates that the species may extend into Mexico along the Sierra Madre Occidental.

Reproductive Physiology.—*D. lowei* is a very difficult species to maintain in the laboratory. Part of the difficulty lies in the increasingly low fecundity of females collected in August and September. Of 26 ♀ collected in mid-August in Colorado and dissected in New York, 12 ♀ (46%) contained rudimentary ovaries. Of 40 ♀ collected in early September in Colorado and dissected in New York, 31 (78%) contained rudimentary ovaries. In the mid-August sample, 12 of the 26 ♀ (46%) contained no motile sperm. In the 2nd sample, 28 of the 40 ♀ (70%) contained no motile sperm. The increasing frequency of females without motile sperm suggests a decrease in mating activity or possibly sperm expulsion or deactivation. The condition of the ovaries suggests an adult reproductive diapause similar to that found by Carson and Stalker (1948) for *D. robusta*, and Basden (1954) for several species of *Drosophila*. In a series of experiments by one of us (DWC), cold shocks lasting from 1 week to 1 month at 5°C and lower induced egg laying and subsequent larval development in at least a part of the surviving females which previously had laid no eggs. In some instances the females had not been with males since their capture, indicating the presence of viable sperm derived from natural matings. Cold shocks have been successfully used to break reproductive diapause in other species of *Drosophila* (Basden 1954).

Hybrids.—We made many attempts to obtain hybrids of *D. lowei* with *D. pseudoobscura*. However, only a single case was successful. There is also an instance of hybridization in nature, or soon after collection, and data on this instance follow in the description of laboratory hybrids.

Sixteen *D. lowei* females, collected Sept. 26, 1960, from the Santa Catalina Mountains, were placed on banana medium where they remained for 22 days without producing a single larva. On Oct. 18, many *D. pseudoobscura* males from the same general area were introduced with the females. By Nov. 12, pupal

cases were present. Four very large ♂ and 2 normal size ♀ emerged. The males were placed with 9 virgin *D. pseudoobscura* ♀ from Nov. 17 to Dec. 14 at which time they were dissected and found to contain no sperm in their testes, which were small. The backcross produced no progeny. The 2 ♀ were placed with 6 *D. pseudoobscura* ♂ from a laboratory culture with the Standard gene arrangement Nov. 17, and then with 15 *D. pseudoobscura* ♂ from Mt. Lemmon on Nov. 30. A few eggs were laid but no larvae emerged. On Dec. 21, the females were dissected and contained sperm in either the ventral receptacle or the spermathecae. There was no more than 1 mature egg in each ovary. There is little doubt that the males were hybrid, but the 2 ♀ had no measurable characteristics to prove that they were hybrid.

The characteristics of the 4 hybrid ♂ are: average wing length 3.45 mm which is 1.4× longer than *D. lowei* and 1.35× longer than *D. pseudoobscura*. Six of the 8 proximal sex combs had 6 teeth, 1 had 5 teeth, and 1 had 7 teeth. Seven of the 8 distal sex combs had 4 teeth, 1 had 3 teeth. Thus the proximal comb is intermediate to the 2 species and the distal comb is like *D. lowei*. The primary teeth on the forceps ranged from 9 to 11, as in *D. lowei*, and the secondary teeth were 1–3, which is intermediate between the 2 species. The hypandrial bristles and those of the novasternum were intermediate in size and they extended $\frac{1}{3}$ the length of aedeagus (Fig. 5). The posterior gonapophyses and aedeagus were somewhat intermediate between the 2 species (Fig. 2). The average penis index was 8.56 which is not different from either parental species.

The unusually large size of the hybrid males enables one to spot naturally occurring hybrids. On June 20, 1961, 33 ♀ and 8 ♂ of *D. lowei* were collected among 2314 *D. pseudoobscura* from Mt. Lemmon and placed on laboratory medium in several vials. Only 1 vial produced *D. lowei* progeny, but also after a delay of 1 week 5 vigorously bobbing (pumping up and down of the abdomen) females and 5 very large males emerged from the same vial. The males were undoubtedly of hybrid origin since they possessed exactly the same characteristics as the laboratory hybrids. It is not known, of course, whether the mating, presumably *D. lowei* ♀ × *D. pseudoobscura* ♂, occurred in nature or within the collecting vial after capture.

D. lowei is now the 3rd species that has produced hybrid adults with *D. pseudoobscura*. However, it is the 1st species to produce giant male hybrids. In the cross *D. miranda* ♀ × *D. pseudoobscura* ♂, the hybrid males are abnormal in many respects but they are no larger than the parents (Dobzhansky 1937). In the cross *D. persimilis* ♀ × *D. pseudoobscura* ♂, the hybrid males are apparently little different from either parent in size (Lancefield 1929, Dobzhansky and Epling 1944). However, Sturtevant and Dobzhansky (1936) did report giant hybrid males from the cross *D. azteca* Sturtevant & Dobzhansky ♀ × *D. athabasca* Sturtevant & Dobzhansky ♂. The 2 last-mentioned species are in the *affinis* subgroup.

ACKNOWLEDGMENTS

The species is named in honor of Professor Charles H. Lowe, Department of Biological Sciences, University of Arizona, for his interest and encouragement in the field of *Drosophila* genetics and biogeography. We thank Dr. Th. Dobzhansky and Mr. B. Spassky for their advice about the preparation of the manuscript, and Dr. M. R. Wheeler for the loan of specimens from his collection. The work is supported by Grants G17177 and GB-1607 of the National Science Foundation to W. B. Heed, and U. S. Public Health Service Research Career Award, 5K3 HD-9033-04, to L. Ehrman. It is published with the approval of the Director of the Colorado Agricultural Experiment Station as Scientific Series Paper no. 1332.

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Reprinted from the

ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA
Volume 62, Number 2, pp. 388-393, March 1969