A Chaetotaxic Study of Snowpool Aedes Larvae and Pupae with An Analysis of Variance of the Larvae of Eight Species

by

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ABSTRACT: Larval chaetotaxy is examined by analysis of variance and a multiple range test in an effort to determine affinities of one population to another and aid deduction of dispersal routes into the Southwest. Larval and pupal setal positions of all known southwestern mountain Aedes are figured.

Introduction

This study was undertaken to confirm and further elucidate the dispersal routes of snowpool₃Aedes into the American Southwest as postulated by Wolff and Nielsen (1976)³ and to determine if divergence in these marginal populations had occurred since their probable isolation at the end of the Wisconsin glaciation. The authors speculated that a simple analysis of variance of larval characters would reveal whether or not sufficient time for differentiation had elapsed subsequent to their isolation. Heretofore, little attention has been directed to quantifying the degree of morphological differentiation exhibited in isolated insect populations.

The authors further hypothesized that establishing homogeneous locality subsets of significantly varying characters would reveal dispersal routes.

Difficulties in visualizing larval chaetotaxy and lack of adequate illustrations in the literature mandated their illustration in order to make chaetotaxic determinations and comparisons. Although pupal illustrations were not necessary for the present statistical analysis, their inclusion in the manuscript appeared desirable due to the paucity of published illustrations and the utilitarian need for pupal identification keys.

Marginal populations interest biologists since interruption of gene flow may lead to the formation of evolutionary novelties. The occurrence in isolated communities of northern Aedes mosquitoes in the American Southwest suggests former Pleistocene range expansion followed by isolation when climatic conditions changed. Apparently, temperatures were sufficiently lower during

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³Wolff and Nielsen (1976) stated that both *Ae. implicatus* and *Ae. increpitus* are known only from the Neartic. Danilov (1974 and 1976), however, found these species present in the Old World.

times of glacial advance to enable species now restricted to high mountain habitats to survive at lower elevations and disperse to new areas. Warmer interglacial periods, such as at present, restrict mosquito populations to higher elevations. Evidence for such climatic change in the American Southwest is reviewed by Wolff and Nielsen (1976).

Isolated marginal populations may undergo genetic divergence and morphological differentiation. However, Mayr (1963, p. 343) states "There is perhaps no other aspect of speciation about which we know as little as its rate." Although evolutionary rates vary widely, the reviews of Mayr (1963), Briggs (1966), and others indicate that where rapid speciation occurs it has usually been in isolated, peripheral areas such as examined in the present study.

Because meristic characters permit greater accuracy than measurements, a chaetotaxic analysis of setal branching and pectin and comb scale number was chosen. Additionally, many such characters are easily studied in permanent mounts and a widely accepted system of chaetotaxic nomenclature exists.

The present study is an analysis of variation in larval chaetotaxy of peripheral populations of snowpool Aedes in the American Southwest. For the species examined here, few studies involving extensive chaetotaxi description or illustration have been published. Often, little in addition to key characters needed for species identification is described or illustrated. The large number of setal pairs recognized on the pupa and fourth instar larva, 116 and 203 pairs respectively (Belkin 1962), and the difficulties encountered in their visualization and description, has undoubtedly contributed to the slow rate of progress in this area. As understanding of variability in setal branching increases, species identification throughout their entire ranges should be facilitated. Increased understanding of geographical variation as provided by this and future studies may reveal the presence of subspecies or species previously unknown. A better understanding of culicid phylogeny will undoubtedly emerge as knowledge of the complete chaetotaxy of the immatures accumulates.

On the ten species illustrated in the present study, the only other study known to the authors in which a fairly complete larval chaetotaxy of included species was presented, was that of Novak (1971) in which the larval setal positions of Aedes communis (De Geer), Ae. hexodontus Dyar, and Ae. pullatus (Coquillett) were illustrated. Darsie (1951) described and illustrated dorsal abdominal seta, respiratory trumpets, and dorsal aspects of the paddles of Aedes cinereus Meigen, Ae. excrucians (Walker), Ae. fitchii (Felt and Young), and Ae. communis (De Geer). This paper also contained descriptions of the pupal cephalothoracic setae of these four species as well as an illustration of the pupal cephalothoracic setae of Ae. cinereus. Darsie (1957) described the pupa of Ae. hexodontus for the first time and illustrated the trumpet, metathorax, and abdomen.

Preparation of Material

Collection of snowpool Aedes has been discussed by Wolff and Nielsen (1976). All material used in this study was collected by the authors or was available in the University of Utah collection. Larvae were collected with a white enamel pint dipper and transported to the laboratory in containers

surrounded with snow or ice. Mature larvae were killed in hot water and preserved in 70% alcohol. When available for permanent mounts, at least 10 larvae of a species in a locality were placed in cellosolve for several hours. While in cellosolve the distal segments were severed with a microscalpel between segments VII and VIII to enable the siphon and anal segments to lie flat. The larvae were then mounted in Canada balsam thinned with xylene.

Illustrations

Drawings of all Southwestern snowpool Aedes immatures are original and were made with the aid of a microprojector (Figs. 2-31). One specimen was selected and the initial drawing was made in pencil. This drawing was compared with 4 or more additional specimens from the same locality and the modal condition depicted. The drawings, therefore, are composite illustrations. The immatures of most of these species have not heretofore been fully figured. Characters were critically examined in the mounted specimens with a light microscope at 120% or 480%. In examining minute hairs it was sometimes impossible to determine the exact number of branches. Such hairs were not used in the analysis. Branching of hairs not readily discernible in the mounted material were determined from unmounted preserved larvae or larval exuviae from the same locality. These hairs were not utilized in the analysis either.

Ink drawings were made on velum by tracing the penciled drawings with rapidiograph pens. The inked drawings were reproduced and reduced on a xerox machine and 9 1/2" x 11 1/2" plates were composed. Pectin and comb scales were inked on velum by tracing from photographs taken through a light microscope at 410X.

The minute ventrolateral cervical hairs are not illustrated. These setae are difficult to see in most mounted material. MacKenzie (1971, 1972) reported one such hair in Aedes cinereus. Hockman and Reinert (1974) observed, described, illustrated and proposed names (18, 19-C) for two such hairs in Ae. cataphylla, Ae. communis nevadensis, Ae. excrucians, Ae. fitchii, Ae. hexodontus, Ae. pullatus and Ae. schizopinax.

The larval and puapl setal terminology used follows the commonly used setal notational system developed by Belkin in which the setal number is followed by a hyphen and then a capital letter or Roman numeral designating body area. The body areas of the larvae and pupae figured are designated as follows:

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Α
                  - Antenna
С
                  - Head
CS
                  - Comb Scale
CT
                  - Cephalothorax
M
                  - Mesothorax
MP
                  - Metanotal Plate
Ρ
                  - Prothorax of larvae or Paddle of pupae
PT
                  - Pectin Tooth
S^{-}
                  - Siphon
                  - Metathorax
I - VIII and X - Abdominal segments 1-8 and 10.
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The chaetotaxy of the larvae and pupae of the ten snowpool Aedes found in the mountains of Arizona and New Mexico are as figured. On all subgenus Ochlerotatus larvae, upper head hairs 5-C, 6-C, and pre-antennal tuft 7-C are arranged in a triangular configuration as illustrated. On the sole representative of the subgenus Aedes found in North America and addressed in the present study (Aedes cinereus), these setae are inserted in an almost straight line (see Fig. 5). The Ochlerotatus larvae examined all have long, single or double ventral abdominals 13-III, 13-IV, and 13-V. These setae are short and multiple on Ae. (Aed.) cinereus. The Ochlerotatus pupae all have setae 9-VIII multiple. On Ae. cinereus pupae this hair is single. References to the appropriate figures of the larvae and pupae follow:

- 1. Aedes (Och.) cataphylla Dyar. Larva (Fig. 2,3) Pupa (Fig. 4). Ae. (Och.) cataphylla, Ae. (Aed.) cinereus and A. (Och.) excrucians, are the only southwestern snowpool Aedes with detached pectin teeth on the siphon. Ae. cataphylla, however, has the siphonal tuft inserted within the pectin and not beyond the pectin as present in Ae. cinereus and Ae. excrucians. As far as known, the larval and pupal stages have not been illustrated in detail.
- 2. Aedes (Ae.) cinereus Meigen. Larva (Fig. 5, 6), Pupa (Fig. 7). The larva of this species is easily distinguished using the characters discussed above and by the very small size of the mature larva. The pupa is easily distinguished using the characters discussed above, by its very small size, and by the usually short and slightly expanded respiratory trumpets.
- 3. Aedes (Och.) communis De Geer. Larva (Fig. 8, 9), Pupa (Fig. 10). The larva was first figured in detail by Novak (1971) and is separable from that of sibling species Ae. nevadensis Chapman and Barr only on the basis of comb scale shape. The pupa was first figured by Darsie (1951).
- The Ae. nevadensis pupa was figured by Chapman and Barr (1964) who found no clear-cut difference between the pupa of this species and Ae. communis. Our pupal study of Ae. communis from the American Southwest also did not reveal clear-cut differences between it and Ae. nevadensis.
- 4. Aedes (Och.) excrucians (Walker). Larva (Fig. 11, 12), Pupa (Fig. 13). The larvae had not been previously illustrated in detail. Ae. excrucians is the only southwestern snowpool Aedes of the subgenus Ochlerotatus whose larva has detached pectin teeth that do not extend beyond the siphonal tuft. The pupa, first illustrated by Darsie (1951), is very similar to Ae. fitchii and may be differentiated by key characters with some difficulty.
- 5. Aedes (Och.) fitchii (Felt and Young). Larva (Fig. 14, 15), Pupa (Fig. 16). The larva of this species, not known to have been previously illustrated in detail, is easily differentiated from that of other southwestern snowpool Aedes by the long tapering siphon, and unusually long setae. The extreme similarity of the pupa of this species, as first illustrated by Darsie (1951), with the pupa of Ae. excrucians may be due to convergent evolution resulting from the similar habitat utilized.

- 6. Aedes (Och.) hexodontus Dyar. Larva (Fig. 17, 18), Pupa (Fig. 19). The larva, first figured extensively by Novak (1971), is the only southwestern snowpool Aedes which has the anal segment completely ringed by the anal plate. The pupa first figured by Darsie (1951) is most similar to Ae. schizopinax, the only other representative of the punctor subgroup in the American Southwest.
- 7. Aedes (Och.) implicatus Vockeroth. Larva (Fig. 20, 21), Pupa (Fig. 22). The larva of this species have not been illustrated in detail previously. Seta 1-VIII is single. With the exception of the closely related Ae. cataphylla, seta 1-VII is double in all other southwestern Ochlerotatus. The pupa of this species was first illustrated by Barr (1958).
- 8. Aedes (Och.) increpitus Dyar. Larva (Fig. 23, 24), Pupa (Fig. 25). The larva of this species is not known to have been illustrated in detail previously. The pectin teeth are highly variable. The pupa has not been previously illustrated.
- 9. Aedes (Och.) pullatus (Coquillett). Larva (Fig. 26, 27), Pupa (Fig. 28). The larva were first figured in detail by Novak (1971). The pupa has not been previously illustrated.
- 10. Aedes (Och.) schizopinax Dyar. Larva (Fig. 29, 30), Pupa (Fig. 31). The larva of this species is not known to have been illustrated in detail previously. The larva may be easily separated from other snowpool Aedes of the Southwest by long 3-4 branched 1-M setae. The pupa has not been previously illustrated.

Material Studied

In selecting populations for analysis, an attempt was made to select the most peripheral population for which sufficient study materials could be obtained. Localities utilized for each species are shown in Fig. 1. Utilizing the locality code in Table 1, these are Ae. cataphylla (1, 3., 5, 6, 9); Ae. communis (1, 6); Ae. fitchii (1, 3, 4, 5, 6, 8, 9); A. hexodontus (1, 6, 7, 9); Ae. implicatus (1, 2, 9) Ae. nevadensis (7, 9); Ae. pullatus (1, 5, 6, 7, 9) and Ae. schizopinax (1, 6, 7, 9).

The sibling species, Ae. communis (De Geer) and Ae. nevadensis Chapman and Barr, presently separable in mature larvae only by comb scale shape, were examined as a single species. Ae. excrucians was not included in the present analysis as it is thought to be a species complex. Ae. cinereus and Ae. increpitus were not included due to lack of sufficient material from the American Southwest.

Collection data and number of specimens utilized follows: Aedes cata-phylla. New Mexico: Rio Arriba Co., Canjilon Lakes, IV-30-72, T. Wolff, 10. Arizona: Coconino Co., Rim of Grand Canyon, VI-V-73, L. Nielsen, T. Wolff, 10; Apache Co., Big Lake, IV-25-74, L. Nielsen, T. Wolff, 10. Utah: Salt Lake Co., Brighton, VI-V-69, L. Nielsen. G. Collett, 10

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Aedes communis. New Mexico: Rio Arriba Co., Trout Lakes, V-15-74, L. Nielsen, T. Wolff, 10. California: Alpine Co., Ebbetts Pass, VI-23-71, R. Novak, 10. Utah: Salt Lake County, Brighton, VI-V-69, G. Collett L. Nielsen, 10. Aedes fitchii. New Mexico: Rio Arriba Co., Canjilon Lakes, IV-30-72 and V-21-72, T. Wolff, 10. Arizona: Coconino Co., N. Rim of Grand Canyon, V-4-73, L. Nielsen, T. Wolff, 10; Apache Co., Chuska Mountains, IV-26-74, L. Nielsen, T. Wolff, 10; Apache Co., E. of Greer, VI-VI-73, L. Nielsen, T. Wolff, 6. California: Plumas Co., Cresent Mills. IV-24-67, S. Carpenter, 7; Nevada Co., Hobart Mills, IV-25-67, S. Carpenter, 3. Oregon: Douglas Co., Diamond Lake, VI-18-72. J. Linam, L. Nielsen, 10. Utah: Summit Co., Park City, V-18-73, T. Wolff, 10. Aedes hexodontus. New Mexico: San Miguel Co., Steward Lake, VI-22-73, T. Wolff, 10. California: Nevada Co., Nordon, VI-22-71, R. Novak, 9. Nevada: Elko Co., Lamoille Canyon, VI-18-71, R. Novak, 8. Utah: Salt Lake Co., Brighton, VII-25-71, L. Nielsen, 10. Aedes implicatus. New Mexico; Rio Arriba Co., Trout Lakes, V-27-74, L. Nielsen, T. Wolff, 10; Catron Co., Ben Lilly Camp Ground, V-11-73, L. Nielsen, T. Wolff, 10. Utah: Cache Co., Logan Canyon, V-27-67, L. Nielsen, 10. Aedes pullatus. New Mexico: San Miguel Co., Pecos, V-16-74, T. Wolff, 10. Arizona: Greenlee Co., Hannigan Meadows, VI-7-73, L. Nielsen, T. Wolff, 10. California: Inyo Co., Heart Lake, VI-21-72, J. Linam and L. Nielsen, 10. Nevada: Elko Co., Lamoille Canyon, VI-18-71, R. Novak, 10. Utah: Duchesne Co., Uintah Mountains, VII-20-47, L. Nielsen, 5; Salt Lake Co., Brighton, VI-14-44, Giles, 3 and City Creek, V-29-73, L. Nielsen, 2. Aedes schizopinax. New Mexico: Rio Arriba Co., Trout Lakes, V-27-74, L. Nielsen, T. Wolff, 10. California: El Dorado Co., Luther Pass, VI-22-71, L. Nielsen and R. Novak, 10. Nevada: Washoe Co., Hooter Lake, VI-12-59, H. Chapman, 10. Utah: Weber Co., Mountain Green, IV-27-73, T. Wolff, 10.

Study of Material

A variety of meristic characters that could be reliably determined were selected. Larval characters included are shown in Tables 2 and 3 and illustrated in Figures 2-31. With the exception of comb scale and pectin tooth counts, all characters examined were setal branchings. The nomenclature follows the interpretations of Belkin (1962).

Although variation in hair branching exists between the sides of bilaterally symmetrical larvae, it was assumed that such variation occurs randomly and that counts made from the left dorsal and ventral surfaces would provide unbiased data. When a character was missing or difficult to determine on the left side, its counterpart on the right side was examined. When a character was missing or undeterminable on both sides, a mean value was inserted after the character was determined based on the other specimens examined from the locality. When available, ten specimens were examined for all characters utilized. When less than ten specimens were available, mean values were inserted for each missing specimen. Obtaining a value for all characters examined was a requirement of the statistical package utilized.

Characters located on abdominal segment VII and structures posterior were determined from the surface mounted uppermost on the slide unless these characters were not clearly visible on that surface. When no definitive value could be obtained, mean values were inserted as described above. Since 54 characters in all were utilized, 540 values were obtained for each of the 7 species examined in each locality where they were present. Populations from 32 localities were examined, thus, a total of 18,360 values were obtained for analysis. Since both an ANOVA and Tukey Multiple Range Test were carried out for all characters examined, 108 tests were performed per species examined. Thus a total of 756 statistical examinations were made.

Statistics

A simple ANOVA and the Tukey Multiple Range test were performed to determine whether the various populations sampled differed significantly in their morphology and to establish homogeneous subsets. Both tests were carried out on 54 characters of the seven species examined. The between group classification was the locality.

These statistical procedures were found in the Standard Package for the Social Sciences-Version 6. Locality comparisons were performed by tabulating characters in common between localities. In performing these tabulations, only characters significantly different between localities at the 5% or better level and with homogeneous variances as judged by a Bartlett-Box F of 10% or more were utilized. This information is presented in Tables 4-10. Morphological stability was assessed by determining the percentage of characters examined for each species that were found to be significantly different between localities at the 5% level and the percentage of characters examined for each species without variation within or between groups. This information is presented in Table 11.

The ANOVA essentially enables one to determine whether intergroup variability is large enough in relation to intragroup variability to justify an inference that the means of the populations from which the different samples were drawn are different.

Like all statistical procedures, those utilized in this study rest on underlying assumptions. For the populations studied these are:

1. Normality of distribution. 2. Homogeneity of variance. 3. Randomness and independence of subjects drawn.

Since the material utilized in this study included museum specimens as well as collections made by the present authors, samples could not be drawn randomly. The nonrandomness of samples may be reflected in lack of sample independence, heterogeneity of variances or nonnormal distribution.

Characters with Bartlett-Box F values of 10% or less were regarded as being significantly heterogeneous to be excluded from the locality comparisons of Tables 4-10. Furthermore, characters with an ANOVA F value of 5% or less were not regarded as varying significantly between localities unless

the Bartlett-Box F was 10% or more and homogeneity of variance could be assumed. This interpretation is reflected in Table 12. Limiting locality comparisons to characters demonstrating significant ANOVA F values and lack of significant heterogeneity of variances between localities as judged by Bartlett Box F values of more than 10% enables us, we believe, to meet the assumption of homogeneity of variances.

Since variation between groups was judged at the 5% level of confidence, one would expect with the large number of determinations made in the present study, to erroneously judge random variation as significant in some cases. If all ANOVA F probablility values were at about the 5% level, this error would amount to 5% or 2.7 of the 54 characters analyzed. However, examination of Table 13 will reveal that the majority of F values used in determining interlocality variation were significant at a much higher level than the 5%. About 62% of the characters in Table 13 are significant at the 1% level of confidence or better, and only 3 characters or 5% were significant at about the 5% level. Thus, the possibility of erroneously judging random variation as significant due to the large number of ANOVAS's made is remote. racters not utilized in locality comparisons due to assumed heterogeneity of variance may reflect inherent differences in variability or increased variability due to not obtaining samples under standard conditions. In reference to the former possibility, the studies of Dobzhansky and Pavlovsky (1957) have demonstrated with Drosophila that populations which have passed through a bottleneck of small size show increased morphological variance in succeeding generations over continuously large populations, presumably due to a breakdown of genetic homeostasis.

It is evident that the assumptions underlying the ANOVA and the Tukey Multiple Range tests have not been fully met. The consequences of violation of these assumptions are discussed by McNemar (1962, p. 252) "Although these assumptions are incorporated in the mathematical deviation of the F distribution, there is ample evidence that marked skewness, departures from normal kurtosis, and extreme differences in variance (of the order 1 to 4 to 9 - it is not the numerical differences but the relative sizes of the variances that are pertinent) do not greatly disrupt the F test as a basis for judging significance in the analysis of variance."

Discussion

The present statistical analysis of larval chaetotaxy was undertaken in an attempt to obtain evidence of dispersal routes and determine if measurable evolutionary changes had occurred since the isolation of the mosquito populations. It was speculated that population affinity as assessed by an examination of morphological characters might reflect the route of dispersal. The block charts of Tables 4-10 contain tabulated homogeneous locality subsets. These subsets represent localities where means of characters studied did not significantly differ at the 5% level or better and an ANOVA F value of 5% or better was obtained with homogeneity of variances assumed as discussed earlier. Those characters determined to have significant ANOVA F values and Bartlett-Box F values of 10% or more are listed in Table 13. It should be noted that many F probability values were significant at a much higher level than 5% and Bartlett-Box F values were generally considerably higher than 10%. A discussion of the results for the seven species examined follows:

1. Aedes cataphylla Dyar. (Table 4)

The population sampled from northern New Mexico shows highest affinities to Utah and southeastern Arizona as expected on the basis of topography but shows a greater affinity to California than to North Central Arizona (Kaibab Plateau). The northern Arizona population shared 3 characters with northern New Mexico but eight with Utah and California. If the Grand Canyon presented an inimical ecological barrier to dispersal during the Pleistocene, the present populations of Ae. cataphylla on the Kaibab Plateau (North Rim) undoubtedly arrived from southern Utah or northern New Mexico. The larval chaetotaxy comparison is consistent with this interpretation although the equal number of characters shared between the Kaibab population and both Utah and that of California is unexplained. The lower percentage of characters examined with significant variation in this species, Ae. implicatus, Ae. communis and Ae. nevadensis as shown in Table 11 may bear relation to their taxonomic position. All three are members of Dyar's 1928 communis group. Ae. cataphylla is strikingly similar to Ae. implicatus in characters of the adult female and male genitalia. The larvae are, however, strikingly different and we have found them rarely to be associated in large numbers.

2. Sibling species Aedes communis (De Geer) and Aedes nevadensis Chapman and Barr. (Table 5)

In the larval chaetotaxy locality comparison of this table, the Nevada and Utah populations are Aedes nevadensis. The other localities sampled contained Ae. communis. The Utah population (Ae. nevadensis) shows closest affinity to Nevada (Ae. nevadensis). The Nevada population, however, shows greater affinity to California (Ae. communis) than to Utah, and the northern New Mexico population of Ae. communis shows a greater affinity to the Nevada (Ae. nevadensis) than to the Utah (Ae. nevadensis). No explanation is known to the authors for such apparent affinities. Reference to Table 11 shows that these sibling species, treated as a single species in the present analysis, showed less significant variation between localities than all remaining species examined except Ae. implicatus.

3. Aedes fitchii (Felt and Young). (Table 6)

This species, like Ae. cataphylla, is present on the Kaibab Plateau and is also likely to have immigrated from Utah or northern New Mexico. The larval chaetotaxy locality comparison, however, does not support this assumption. The North Central Arizona population (Kaibab Plateau) share only ten characters with the Utah population, the most likely source of immigrants. The Oregon population, an unlikely source area, shares 14 characters with the North Central Arizona population. Likewise, the northern New Mexico population shares more characters (15) with the Oregon population than it does with southeastern Arizona although the mountains of New Mexico were likely the source for immigration of this species into the White Mountains of southeastern Arizona. This species is known to vary considerably

in morphology, and the results of the present analysis showing about 20% of the characters varying significantly between localities is not unexpected. This species is widespread in the mountains and mountain valleys of the American Southwest, and the significant amount of morphological variation shown in the peripheral populations may allow for range expansion.

4. Aedes hexodontus Dyar. (Table 7)

The larval chaetotaxy comparison of this table indicated that the following populations show greatest affinity: The northern New Mexico and the Nevada primarily, and secondarily, the northern New Mexico and the California. The California population shows equal affinity to the Nevada, Utah, and northern New Mexico populations. The likely dispersal of this species into northern New Mexico from Utah through Colorado is not reflected in the locality comparison. Like Ae. fitchii, this species shows that about 20 percent of the characters examined vary significantly between localities and indicates that considerable morphological change has occurred in the different geographical populations.

5. Aedes implicatus Vockeroth. (Table 8)

From the larval chaetotaxy locality comparison, this species in northern New Mexico appears to have greatest affinity with the Utah population and secondary association with the southwestern New Mexico population. The Utah population shows equal affinities with both New Mexico populations. Since the probable dispersal of Ae. implicatus into southwestern New Mexico is from northern New Mexico, one would anticipate a greater affinity between the two New Mexico populations examined than between the southwestern New Mexico population and that of Utah. Table 11 strikingly illustrates the small percent of characters examined with significant intralocality variation and the large percentage of characters examined without variation within or between groups for this species.

6. Aedes' pullatus (Coquillett). (Table 9)

This species, the commonest snowpool Aedes mosquito in the Southwest, shows the highest percentage of characters with significant interlocality variation. Its wide altitudinal range, widespread distribution with range extension far south into Arizona, and tendency to exploit man-made excavations rapidly suggests that Ae. pullatus is extremely well adapted to the mountains of the Southwest and may be in the process of actively expanding its range. Natvig (1948) concluded that this species was of great age in Fennoscandia and probably survived the Würm glaciation in glacial refuges in northern Norway. Carpenter (1968) also concluded that the glacial refuge theory of distribution for this species seemed to provide a logical explanation for its occurrence in California.

Examination of the larval chaetotaxy locality comparison chart indicates that Utah and northern New Mexico show the greatest affinities among the populations examined, followed by the California and Utah populations. These populations are followed by the Nevada and northern New Mexico, Utah and southeastern Arizona, and Utah and Nevada populations all showing equal affinities. Northern New Mexico shows least affinity with southeastern Arizona. These locality comparisons do not appear to delineate dispersal routes since the source area for immigration into the White Mountains of southeastern Arizona is undoubtedly northern New Mexico as Aedes pullatus is not known from northern Arizona.

7. Aedes schizopinax Dyar. (Table 10)

From the larval chaetotaxy locality comparison table it is evident that the populations from the following localities have the greatest affinity for each other: the Nevada and Utah populations followed by Nevada and California. The Utah and California populations show the next greatest affinity followed by northern New Mexico and Nevada, and northern New Mexico and Utah both showing equal affinities. Examination of Table 11 show that this species exhibits a fairly high (about 20 percent) percentage of characters with significant interlocality variation in the populations studied. This species, which occurs in mountain valleys as well as mountain habitats, exhibits a wide altitudinal distribution in the American Southwest and may be in the process of extending its range. The locality comparisons do not appear to delineate dispersal routes.

Wolff and Nielsen (1976) proposed that the movement of snowpool Aedes into the Southwest occurred from the Colorado Rocky Mountain mass into northern New Mexico along the east side of the Rio Grande to the Pecos Wilderness and along the west side of the Rio Grande from the extension of the San Juan Mountains of Colorado into northern New Mexico. It was further concluded that penetration probably continued along the Rocky Mountain chain into the Gila Wilderness of southwestern New Mexico with establishment in the White Mountains and Mogollon Rim of southeastern Arizona. This dispersal pattern was suggested by the present distribution of mountain Aedes in the American Southwest as well as by evidence of past climatic conditions based on fossil finds, pollen analyses, etc.

Burger (1974) suggested a similar dispersal pattern for Rocky Mountain tabanids with a northern distribution that range south into northern New Mexico and western Arizona.

Although the present study neither confirms our previously suggested dispersal pattern nor suggests alternative ones, significant morphological variance is demonstrated in the isolated mountain *Aedes* of the American Southwest.

The present work assumes that the variance of the characters employed is largely genetic. A large amount of undetermined nongenetic variation would undoubtedly becloud deduction of dispersal routes. Environmental factors are believed to affect diverse larval structures.

The comb scale number, a character not found to vary significantly between localities in Ae. fitchii in the present study, was found to show considerable variation in this species in Minnesota by Barr (1958). Individuals from one collecting site tended to have fewer comb scales than individuals collected from the same site a week later. Mattingly (1975) discussed the setal branching of larvae attributed to Tripteroides nepenth's (Edwards) from southeastern Asia and suggested that branching of some setae of this species are environmentally determined. His review of pertinent literature suggests that this phenomena is widespread and that in some instances minute, organic matter isolated from tree hole debris is capable of inducing a change in setal branching of some species when added to the breeding water. Mattingly, in reference to such environmental factors, stated, "In the few instances which have been studied they are known or believed to be associated with the presence of particulate matter in the breeding places and to accumulate with aging of the latter, but these instances are too few to permit any generalization." Such apparently widespread environmental dosage-effect factors in Culicidae suggest that an undetermined amount of the chaetotaxic variation observed in the present study may be environmental.

Since the environments of the peripheral mountain Aedes isolates can be assumed to be somewhat different, the variation in chaetotaxy as revealed by the present analysis is not unexpected. With highly vagile and consequently panmictic organisms, inflow of genes from the main body of the species range would be expected to dilute trends toward differentiation at the range periphery. The southwestern snowpool Aedes, however, do not appear to be highly vagile. Nielsen (1951) discussed flight ranges of Rocky Mountain Aedes and concluded that their effective flight range is less than one mile. He suggested that the restriction on the flight range of some of these species (Ae. cataphylla, Ae. hexodontus, and Ae. pullatus) may be due to their predilection for subalpine and alpine habitats which are restricted to the higher elevations in the Rocky Mountains. Jenkins and Hassett (1951) reported similar findings for Aedes communis using radiophosphorus as a larval marker with recovery of radioactive adults over a six week period. It seems unlikely that passive dispersal has been an important factor in the distribution of these species. Their restriction to their present ranges appears to have been of long duration and they have apparently not been able to invade or reinvade many areas of suitable habitat in adjacent mountainous regions in the Southwest.

The possibility that the variation observed in these isolated populations of mountain Aedes could be due to drift must be considered although it seems unlikely that they passed through a bottleneck of reduced size. These species apparently arrived in the Southwest when conditions were colder and wetter and a broad dispersal corridor existed. They were then undoubtedly much more widely distributed with large populations present throughout an extensive contiguous montane forest. With a gradual amelioration of climatic conditions

their ranges in the Southwest became greatly restricted. Wherever they were able to survive, large populations, however, were apparently maintained. of observed correlation between morphological variation and either species habitat diversity or abundance lends support to this interpretation. tion, because these species are univoltine or single brooded, emerge over a short period of time and have a large breeding population, drift is unlikely to be effective. Rare species with restricted habitats would be expected due to drift to show less variability than common species utilizing a diversity of habitat. A rank order correlation of species abundance and diversity of habitat is easily prepared using the data of Table 2 of Wolff and Nielsen (1976). This table contains a frequency distribution of species collected by elevation. The class interval is 500 ft. Using this data, the seven species may easily be ranked in order of abundance based on the number of times larvae of a particular species were collected. Thus, Ae. pullatus is ranked first in abundance since it was found in 49 of the 110 collections made. Ae. cataphylla, found in 32 of the 110 collections, is ranked second. The remaining five species are similarly ranked. Diversity of habitat was determined by utilizing the range of habitats from which collections were made. Each species was ranked according to the number of 500 foot intervals over which it was altitudinally distributed. Thus, Ae. pullatus received a rank of 1 since it spanned 10 such intervals, and was followed by Ae. cataphylla which occurred over a range of seven such intervals. Assessment of diversity of habitat by range of elevations collected appears to be reasonable since a species such as Aedes pullatus which spans the Transitional, Canadian, and Hudsonian life zones is ranked higher than a species like Ae. hexodontus which does not descend below the Canadian life zone.

A rho of .750 between abundance and diversity of habitat (Table 14) is not significant at the 5% level since with an N of seven a value of .786 is required. However, a sizeable relationship exists between these variables although with a relatively small N, statistical significance was not quite reached. The correlations between diversity of habit, abundance, and amount of significant intralocality variation were not significant at the 5% level. Tables 15 and 16 contain the ranks and rank order correlation coefficients for these variables.

Since the rarest species with the most restricted habitats are not highly associated with amount of morphological variation, drift does not appear to be significant in accounting for the morphological variation obtained. A correlation between the amount of significant intralocality variation and larval self-association was obtained by utilizing data contained in Table 3 of Wolff and Nielsen (1976). Ranking for self-association was obtained by determining the percentage of larval collections containing a species in which the species was found alone. For Ae. pullatus, for example, in 19 of 33 collections made, or 58% of the time, this species was found to be non-associated. Ae. pullatus was followed by Ae. fitchii which was collected alone 42% of the time. These species were assigned ranks of 1 and 2 respectively in larval self-association. The remaining species were all found alone in a smaller proportion of collections and were assigned ranks accordingly. A rho of .929, significant at the 1% level, was found between the amount of significant intralocality variation and larval self-association as shown in Table 17. Morphological variation positively correlated with the tendency to be found alone suggests that those

snowpool Aedes which frequently are unassociated in their larval habitat are probably more variable due to reduced selective pressure from competing species.

Although our study concerned only larval morphological characters it seems likely that this variability could also extend to physiological traits in the larval stage. This could help to explain the tolerance of Ae. pullatus to an amazingly wide diversity of larval habitats (Wolff and Nielsen 1976) which makes it the most abundant and widely distributed of the snowpool Aedes in the western United States. Conversely it could also explain why species such as Ae. implicatus which have a high degree of morphological (and physiological?) stability, and occur in a much more restricted niche, may have arrived at this condition due to a more intense competition with other species. Additional studies to test this hypothesis are needed and may give some important insights into the distribution, abundance, and evolution of mosquito species.

Summary

Snowpool Aedes presently noted in the American Southwest as remnants of a mountain mosquito fauna more extensively distributed during periods of maximum glaciation were found to vary significantly in morphology between localities studied. Of seven species examined for statistically significant morphological variation, Ae. implicatus showed the least amount of morphological variation between localities with only 5.56% of characters examined demonstrating significant interlocality variation. This species also was found to possess the highest percentage of characters without variation within or between locality groups studied. Ae. implicatus was followed by other members of Dyar's 1928 communis Group: Ae. cataphylla and Ae. communis and Ae. nevadensis in lowest percentage of characters with significant interlocality variation with 16.67 character variation for Ae. cataphylla and 11.11% character variation for Ae. communis and Ae. nevadensis together. The other species examined, Ae. fitchii, Ae. hexodontus, Ae. pullatus, and Ae. schizopinax had significant interlocality character variation of 20.37 to 22.22%. Examination of homogeneous locality subsets for 54 characters did not aid confirmation of probable dispersal routes inferred from present distributional patterns.

A significant rank order correlation between interlocality variation and tendency for the larvae of a species to be found alone, and lack of significant correlation between interlocality variation and both abundance and diversity of habitat suggest that drift has not been an important factor in accounting for the morphological variation found in southwestern snowpool Aedes. Those mosquitoes frequently unassociated in their larval habitat are more variable probably due to less selective pressure from competing species.

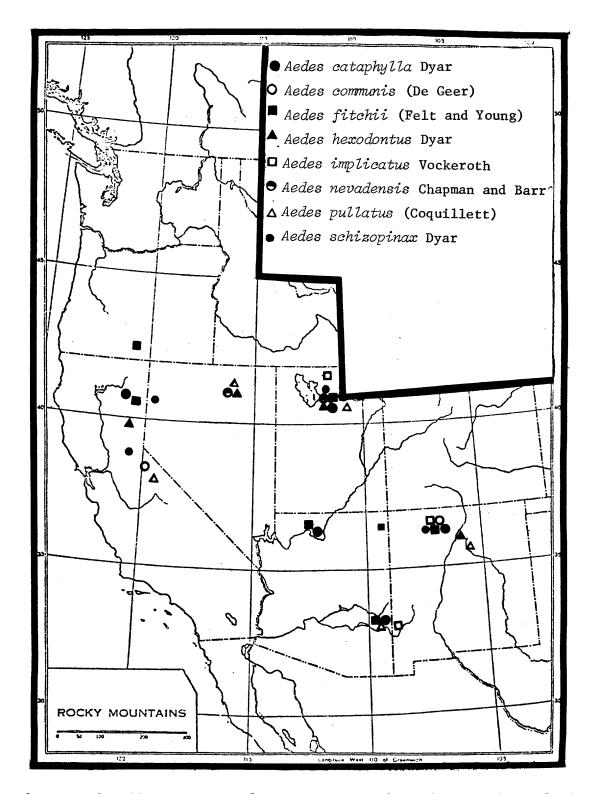


Fig. 1. Larval collection sites for specimens used in chaetotaxic analysis.

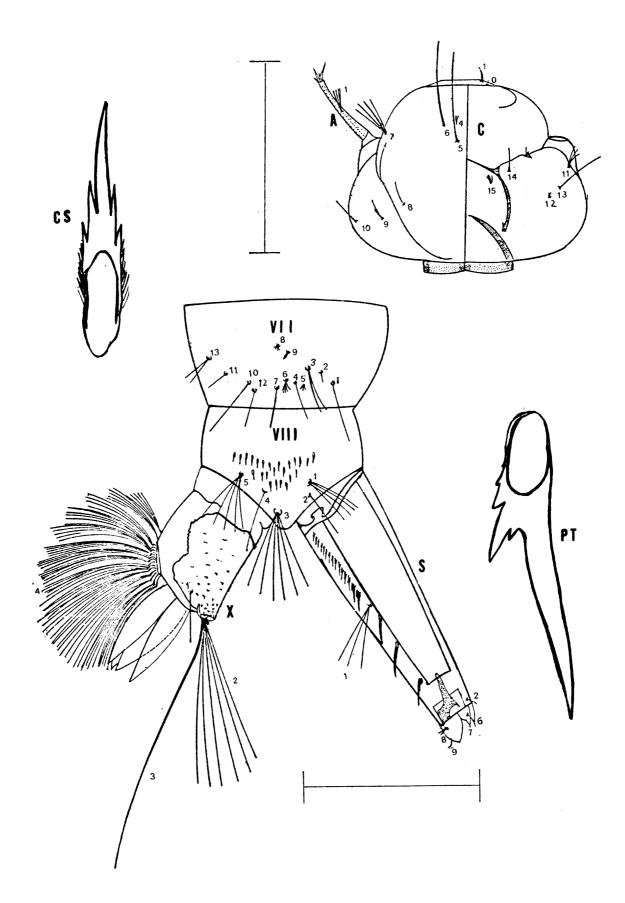


Fig. 2. Larva of Aedes (0) cataphylla Dyar.

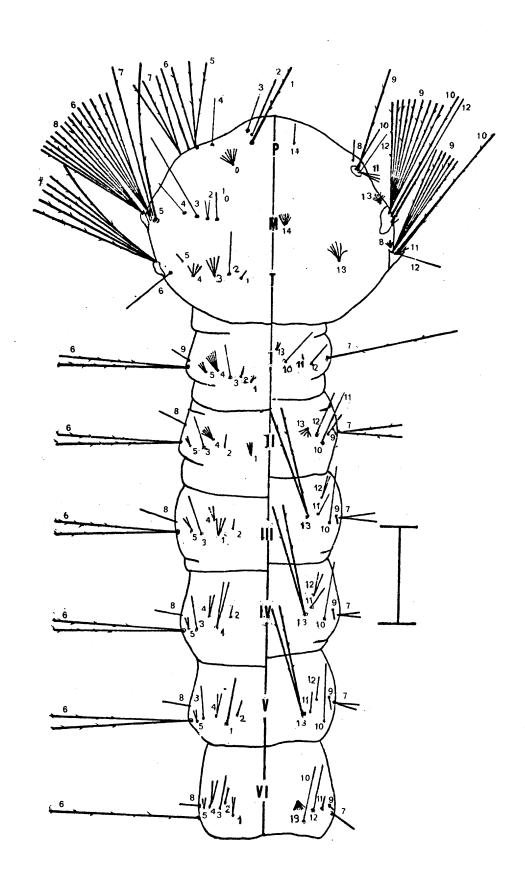


Fig. 3. Larva of Aedes (0) cataphylla Dyar.

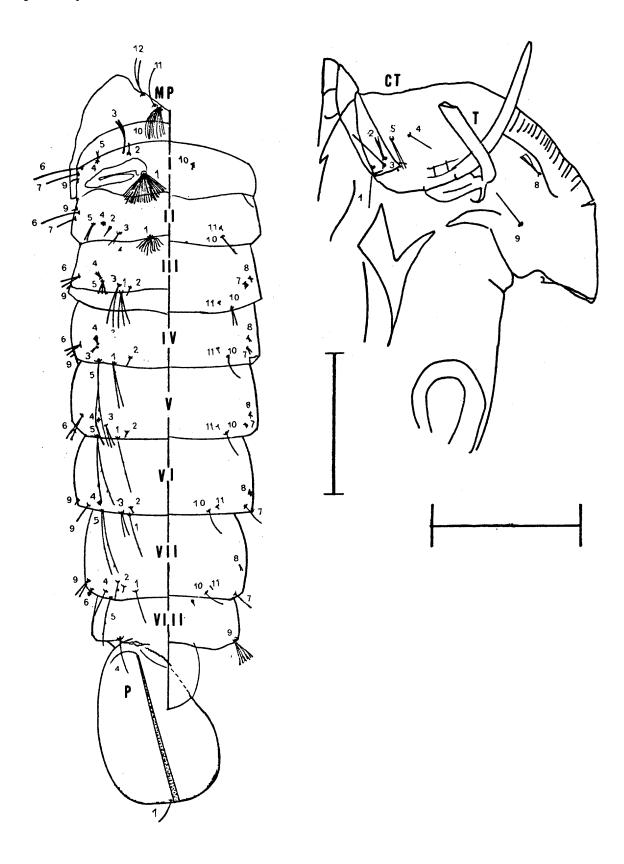


Fig. 4. Pupa of Aedes (0) cataphylla Dyar.

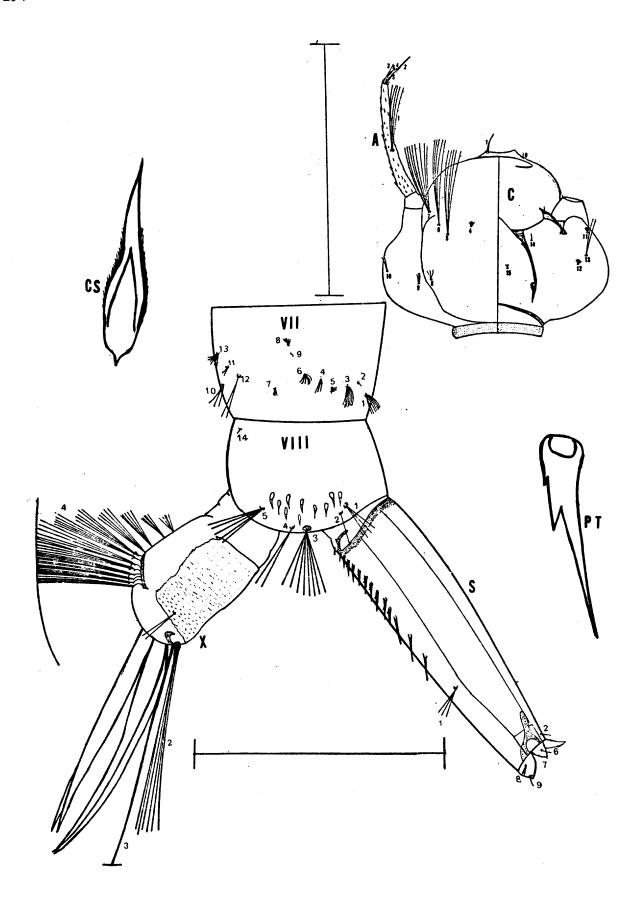


Fig. 5. Larva of Aedes (A) cinereus Meigen.

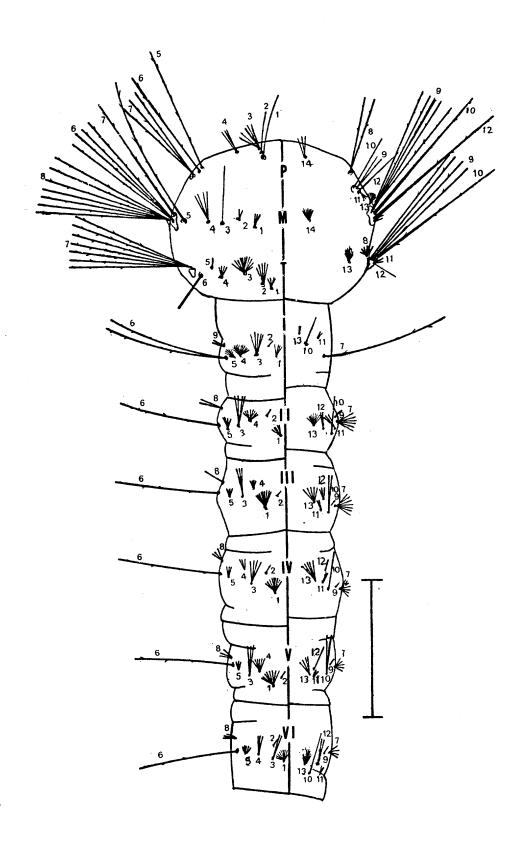


Fig. 6. Larva of Aedes (A) cinereus Meigen.

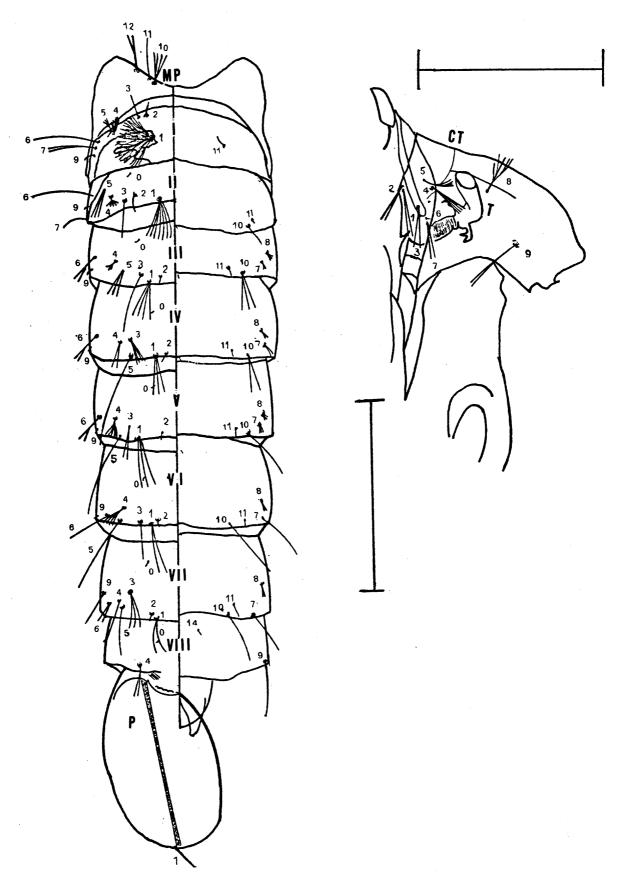


Fig. 7. Pupa of Aedes (A) cinereus Meigen.

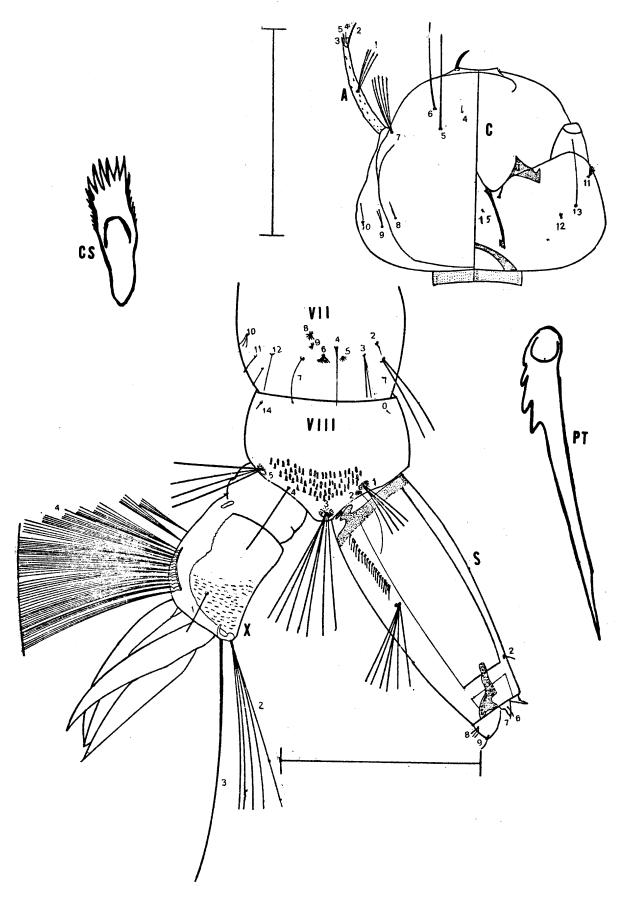


Fig. 8. Larva of Aedes (0) communis (De Geer).

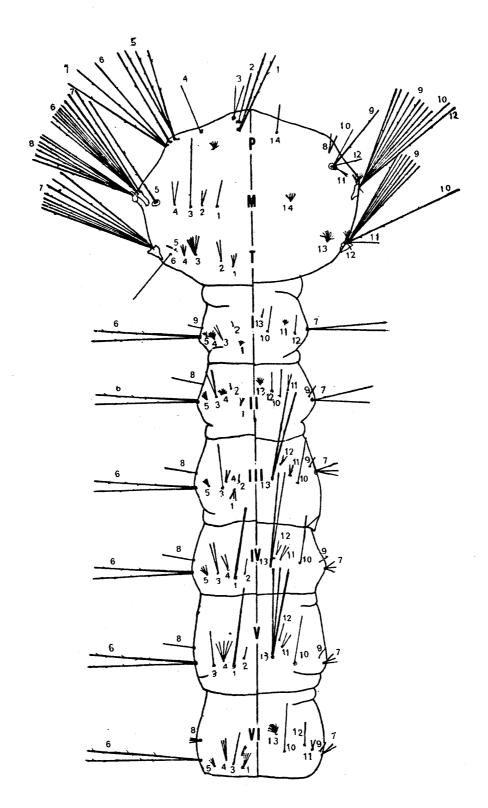


Fig. 9. Larva of Aedes (0) communis (De Geer).

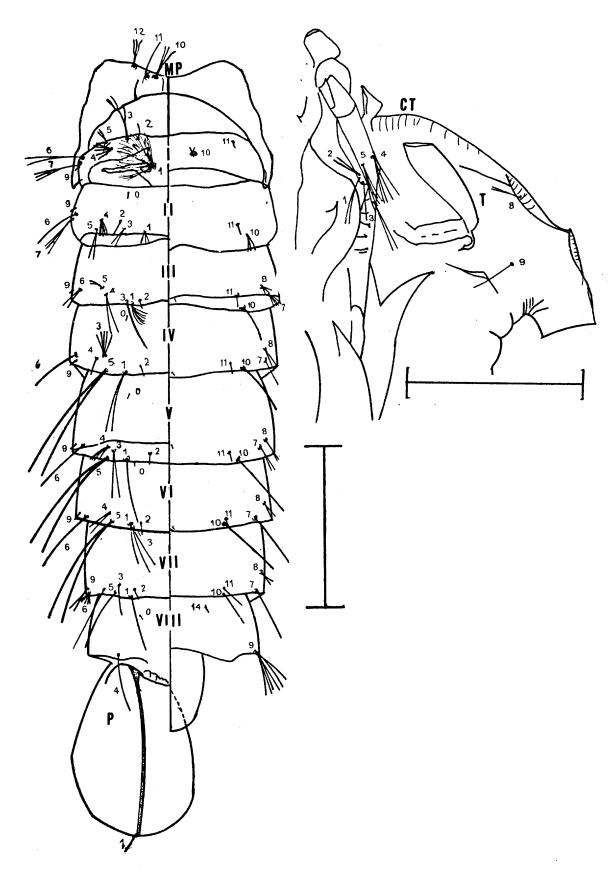


Fig. 10. Pupa of Aedes (0) communis (De Geer).

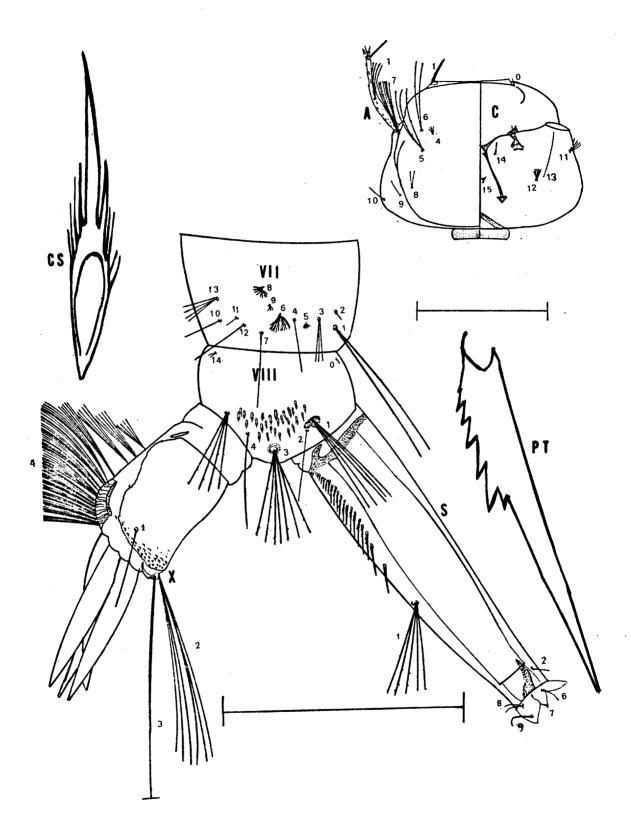


Fig. 11. Larva of Aedes (0) excrucians Walker.

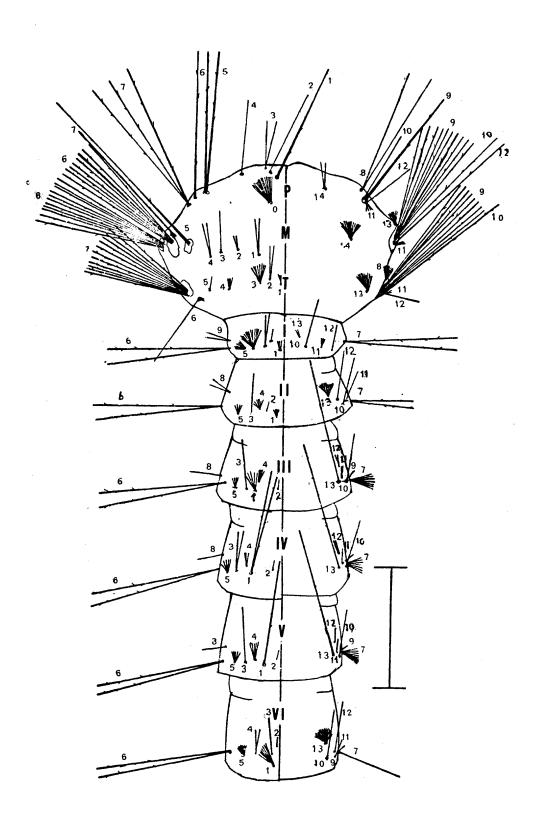


Fig. 12. Larva of Aedes (0) excrucians (Walker).

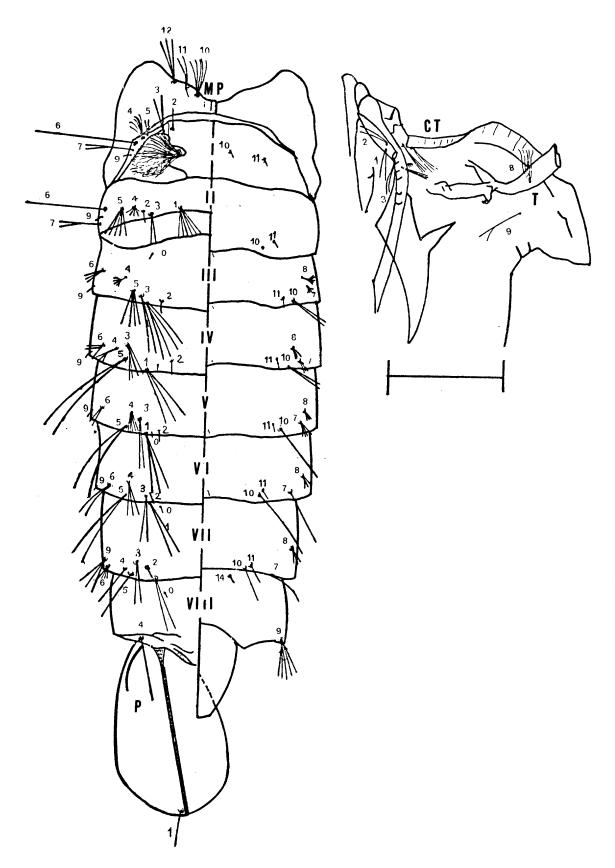


Fig. 13. Pupa of Aedes (0) excrucians (Walker).

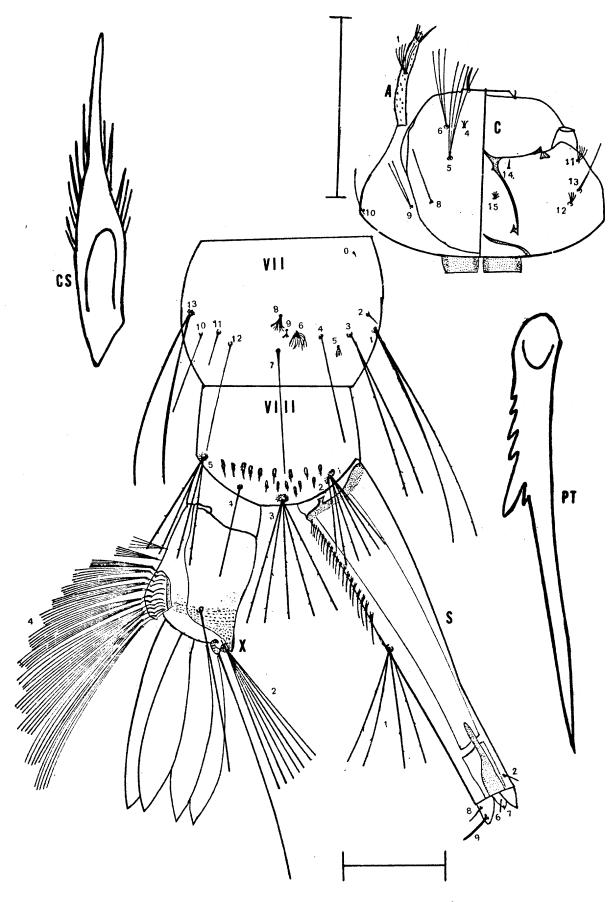


Fig. 14. Larva of Aedes (0) fitchii (Felt and Young).

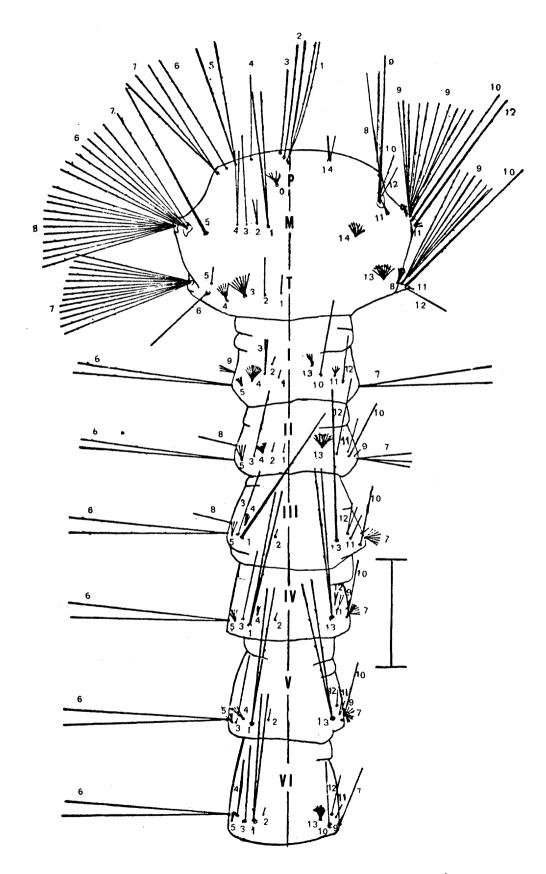


Fig. 15. Larva of Aedes (0) fitchii (Felt and Young).

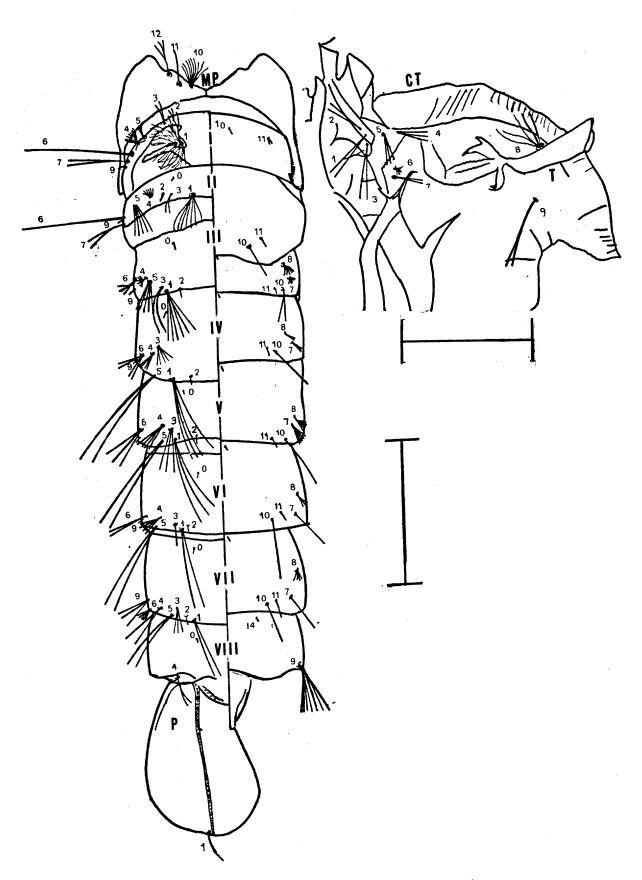


Fig. 16. Pupa of Aedes (0) fitchii (Felt and Young).

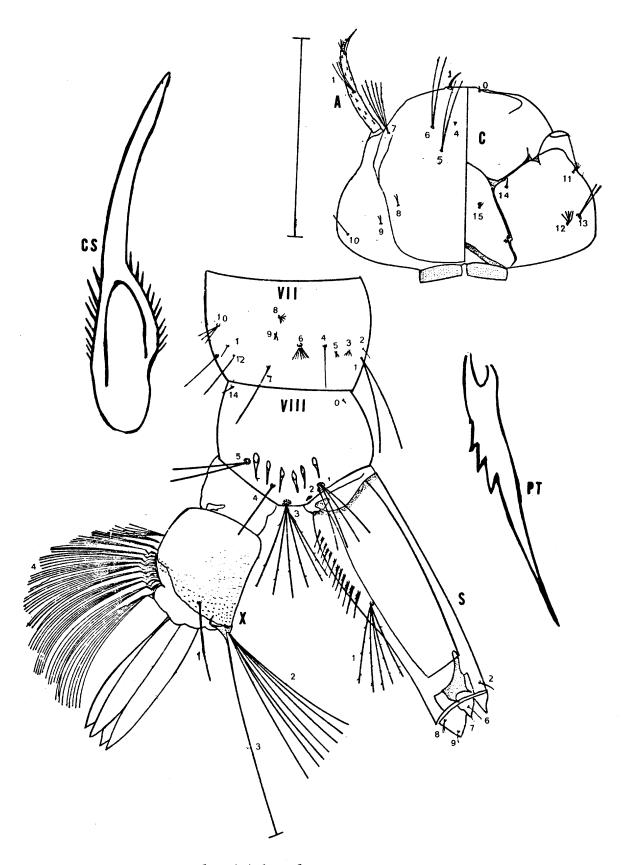


Fig. 17. Larva of Aedes (0) hexodontus Dyar.

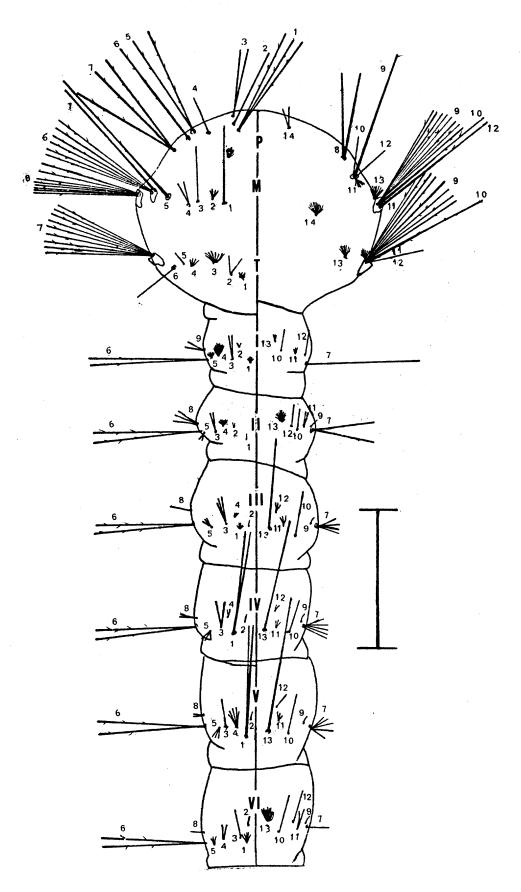


Fig. 18. Larva of Aedes (0) hexodontus Dyar.

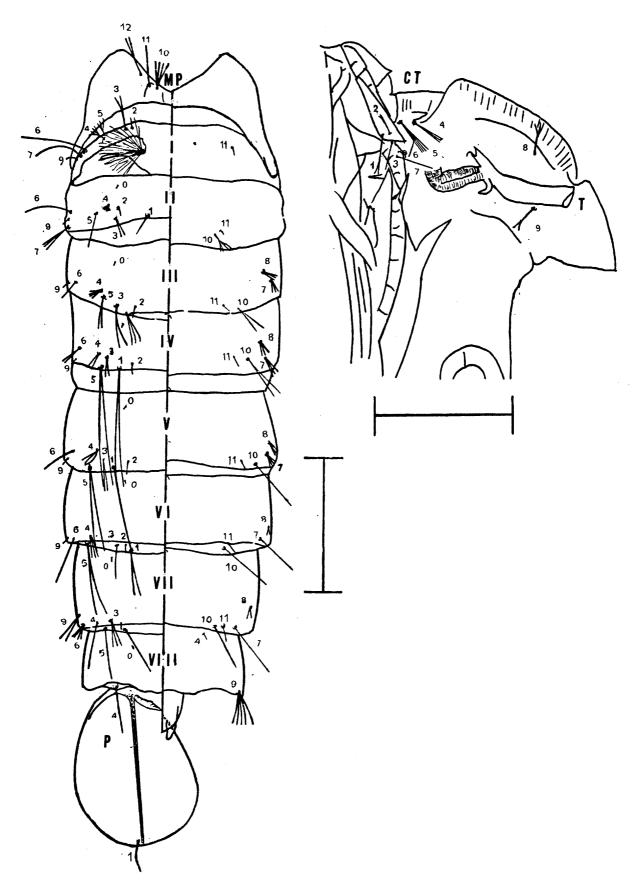


Fig. 19. Pupa of Aedes (0) hexodontus Dyar.

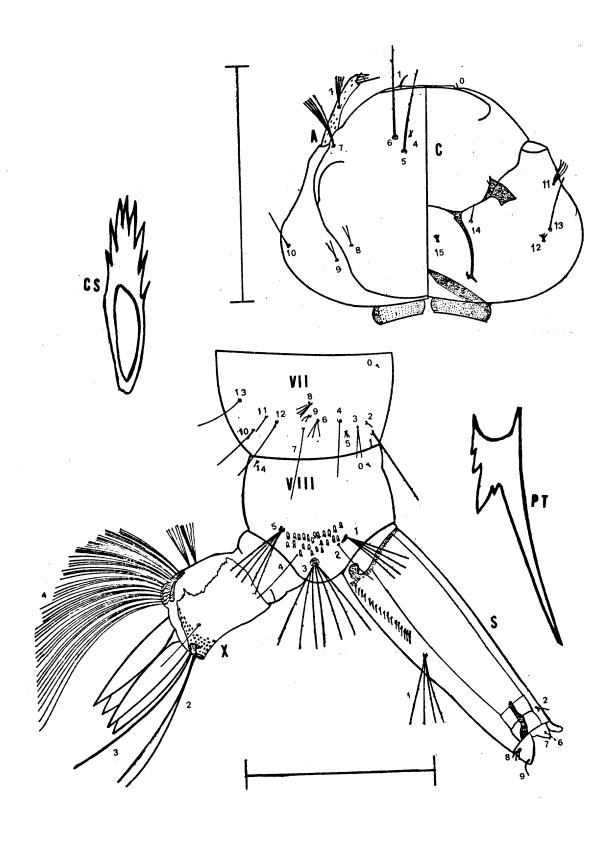


Fig. 20. Larva of Aedes (0) implicatus Vockeroth.

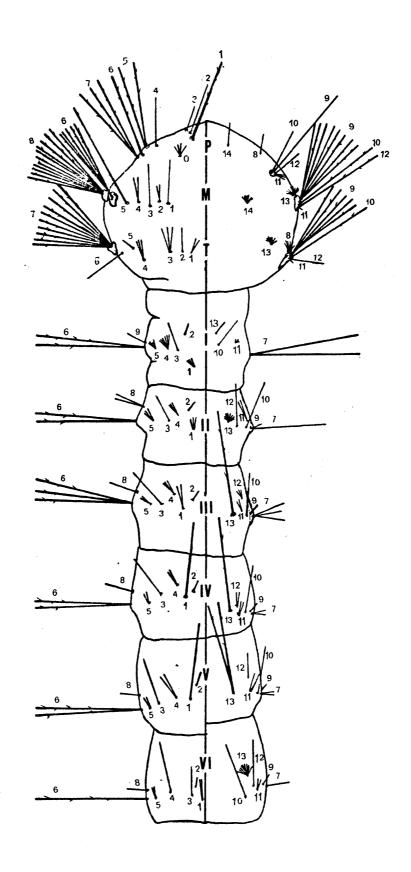


Fig. 21. Larva of Aedes (0) implicatus Vockeroth.

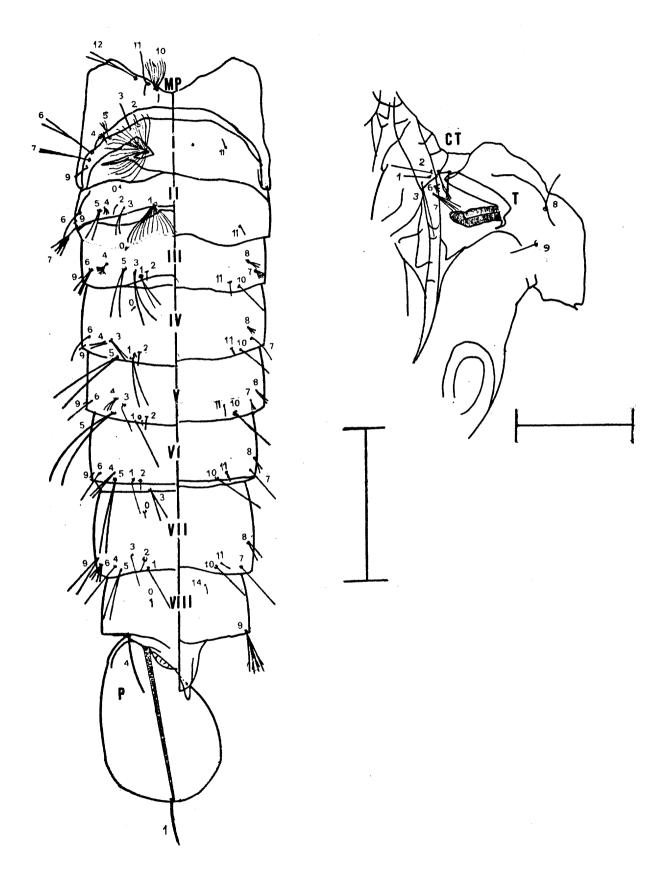


Fig. 22. Pupa of Aedes (0) implicatus Vockeroth.

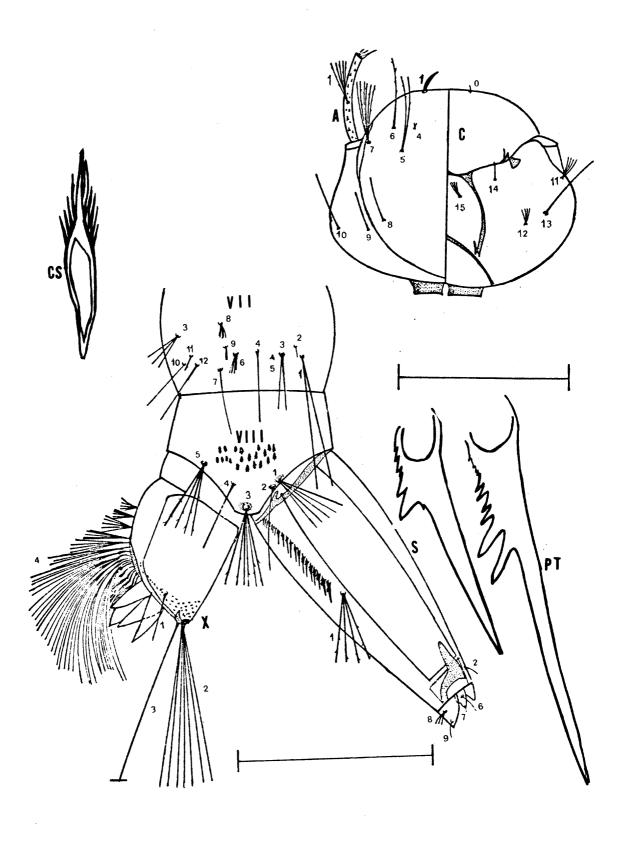


Fig. 23. Larva of Aedes (0) increpitus Dyar.

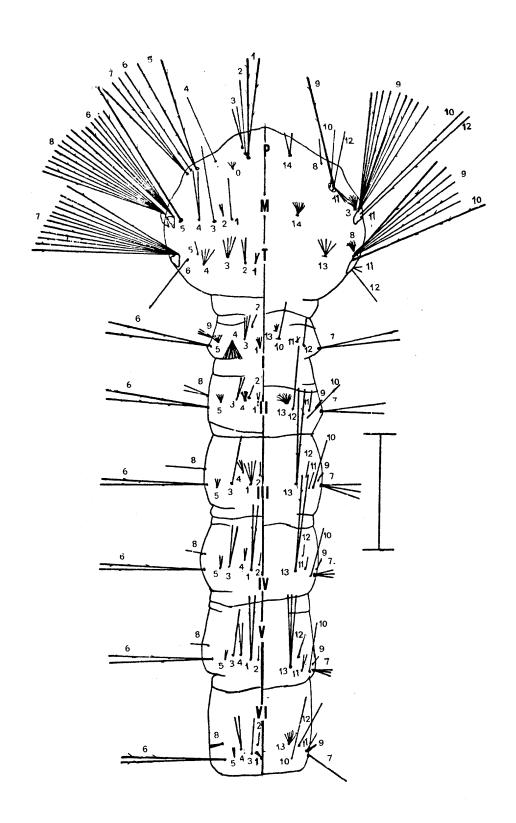


Fig. 24. Larva of Aedes (0) increpitus Dyar.

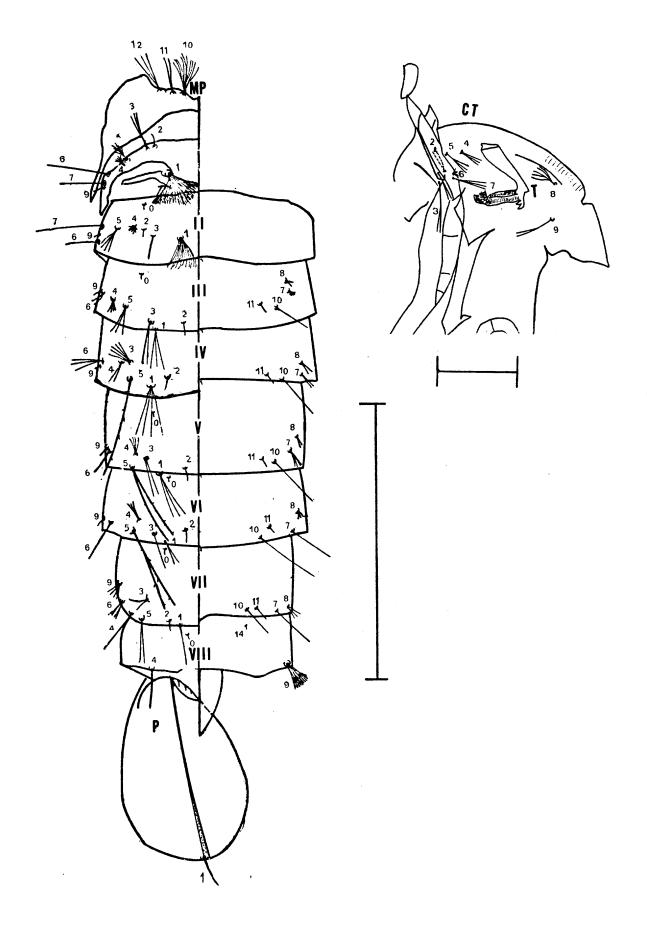


Fig. 25. Pupa of Aedes (0) increpitus Dyar.

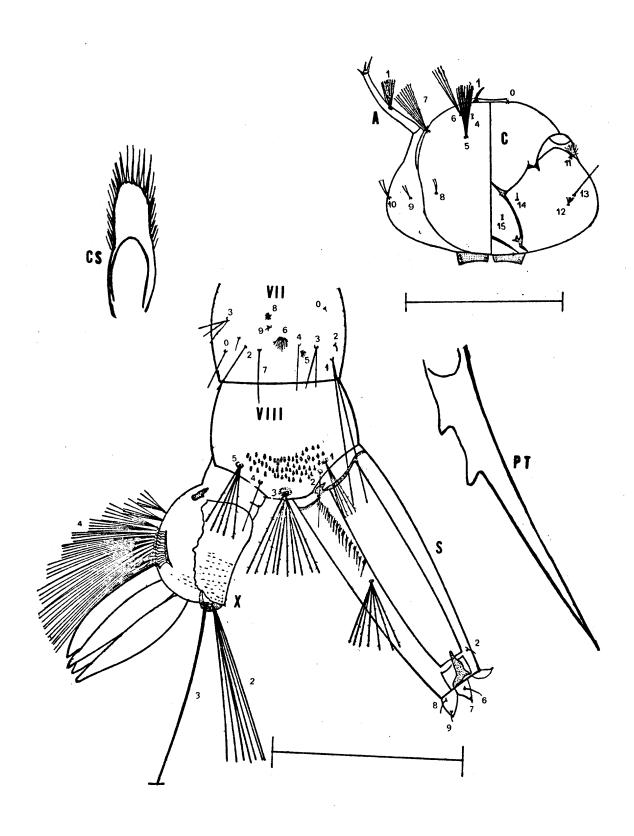


Fig. 26. Larva of Aedes (0) pullatus (Coquillett).

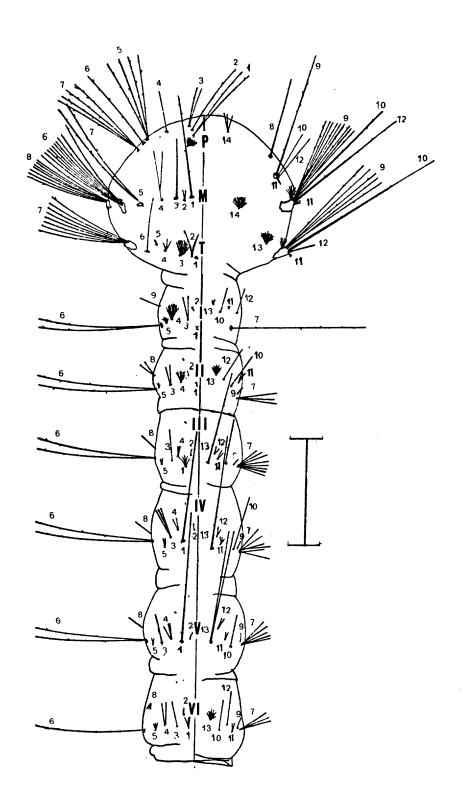


Fig. 27. Larva of Aedes (0) pullatus (Coquillett).

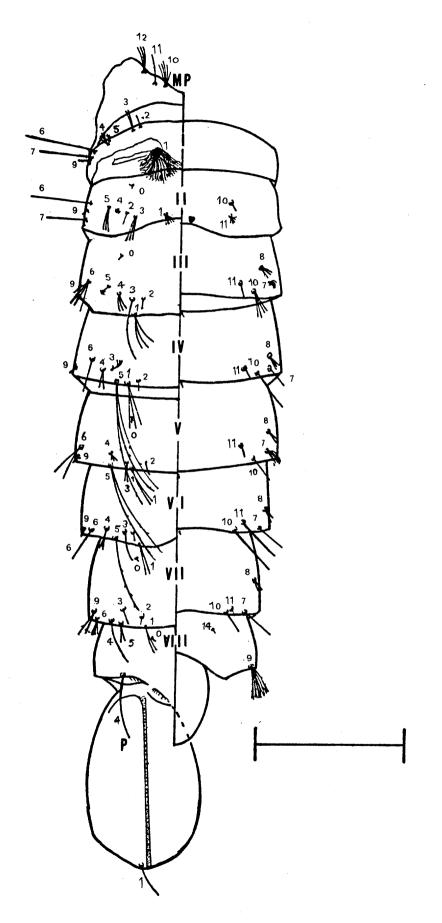


Fig. 28. Pupa of Aedes (0) pullatus (Coquillett).

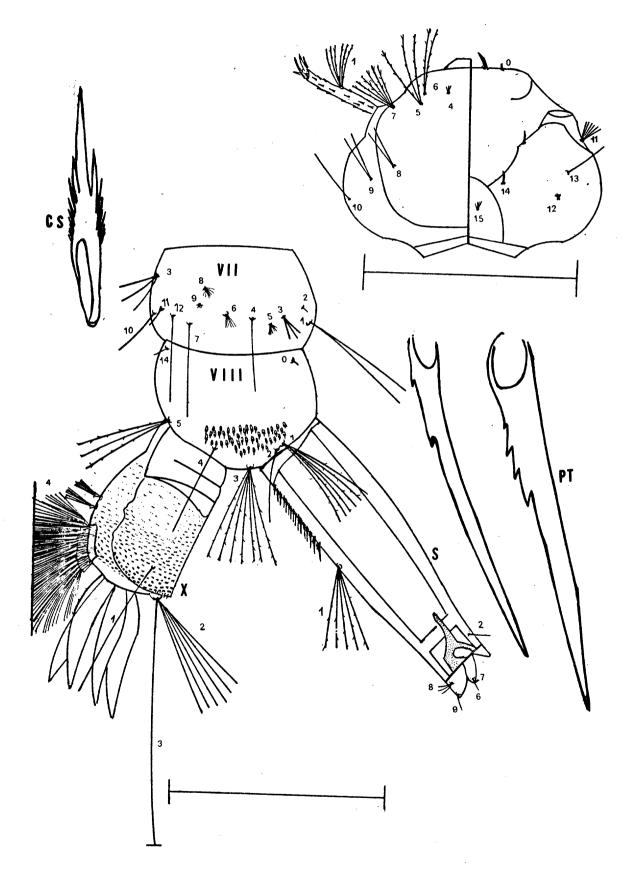


Fig. 29. Larva of Aedes (0) schizopinax Dyar.

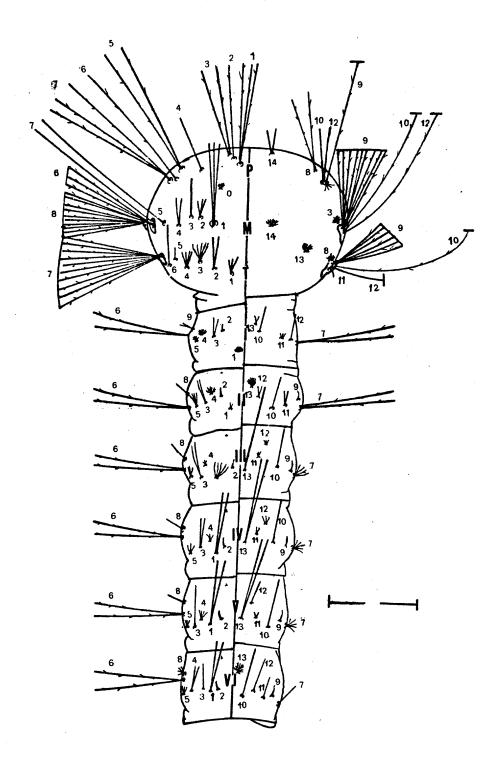


Fig. 30. Larva of Aedes (0) schizopinax Dyar.

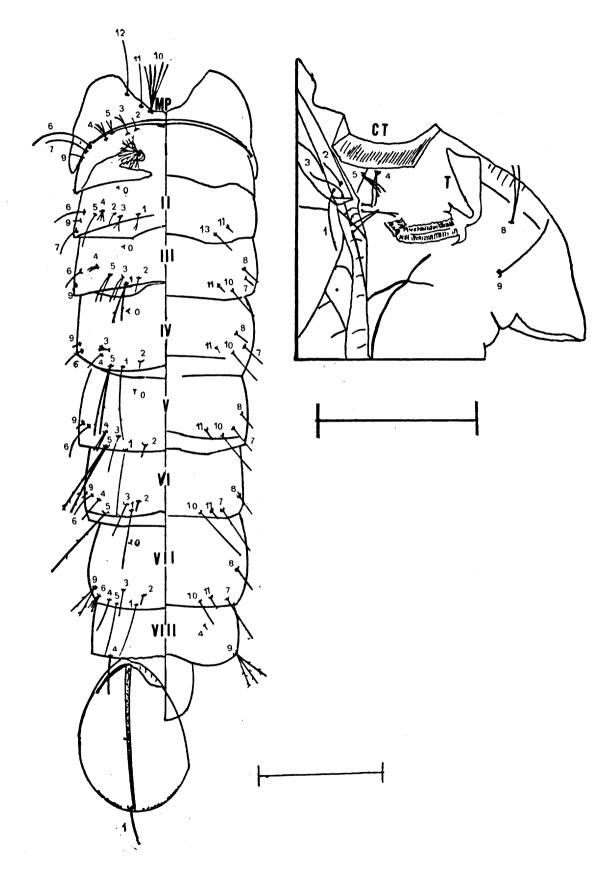


Fig. 31. Pupa of Aedes (0) schizopinax Dyar.

Table 1. Insect and locality code for data imput.

Table 1. Theect and locality code for data	Imput.
Insect	#
Aedes cataphylla Dyar	1
Aedes communis (De Geer) or Aedes nevadensis Chapman and Barr	2
Aedes fitchii (Felt and Young)	3
Aedes hexodontus Dyar	4
Aedes implicatus Vockeroth	5
Aedes pullatus (Coquillett)	6
Aedes schizopinax Dyar	7
Locality	#
Northern New Mexico	1
Southwestern New Mexico	2
North central Arizona	3
Northeastern Arizona	4
Southeastern Arizona	5
California	6
Nevada	7
Oregon	8
Utah	9

Table 2. Card layout for data imput.

Card #1

			
Column	Data	Column	Data
1	Insect	42-43	2-M
2- 3	Locality	44-45	3-M
4- 5	Sample	46-47	4-M
6- 7	4-C	48-49	1-T
8- 9	5-C	50-51	2 - T
10-11	6-C	52-53	3-T
12-13	7-C	54-55	4-T
14-15	8-C	56-57	3-I
16-17	9-C	58-59	6-I
18-19	10-C	60-61	3-11
20-21	1-A	62-63	6-11
22-23	1-P	64-65	1-111
24-25	2-P	66-67	3-111
26-27	3-P	68-69	6-111
28-29	4-P	70-71	1-17
30-31	5-P	72-73	3-IV
32-33	6-P	74-75	6-IV
34-35	7-P	76-77	1-V
36-37	8-P	78-79	3-V
38-39	14-P	80	Punch 1
40-41	1 – M		

Table 3. Card layout for data imput.

Card #2

Column	Data	Column	Data
1	Insect	22-23	2-VIII
2- 3	Locality	24-25	3-VIII
4- 5	Sample	26-27	4-VIII
6- 7	6-V	28-29	5-VIII
8- 9	1-VI	30-31	Pectin
10-11	3-VI	32-33	1-5
12-13	6-VI	34-35	8-5
14-15	1-VII	36-37	1-X
16-17	3-VII	38-39	4-X
18-19	Comb	80	Punch 2
20-21	1-VIII		

Table 4. Larval Chaetotaxy locality comparison for Aedes $cataphylla \ {\tt Dyar}$

	N. N.M.	N.C. Arix.	S. E. Ariz.	Calif.	Ut.
N. N.M.	X	3	9	7	9
N.C. Ariz.		X	6	8	8
S.E. Ariz.			X	10	11
Calif.				X	11
Ut.					X

Table 5. Larval Chaetotaxy locality comparison for Aedes

communis (De Geer) and Aedes nevadensis Chapman

and Barr.

	N. N.M.	Calif.	Nev.	Ut.
N. N.M.	x	7	8	5
Calif.		X	10	4
Nev.			X	6
Ut.				X

rval	Chaeto	taxy locality	comparison	Table 6. Larval Chaetotaxy locality comparison for Aedes fitchii (Felt and Young).	hii (Felt	and Y	oung).
N.	N. N.M.	N.C. Ariz.	N.E. Ariz.	S.E. Ariz. Calif.	Calif.	Ut.	Oregon
	×	16	16	12	11	12	15
		×	14	11	10	10	14
			×	12	80	6	14
				×	5	7	11
					×	6	6
						×	10
							×

Table 7. Larval Chaetotaxy locality comparison for Aedes hexodontus Dyar.

	N. N.M.	Calif.	Nev.	Ut.
N. N.M.	X	8	9	6
Calif.		X	8	8
Nev.			X	8
Ut.				X
				

Table 8. Larval Chaetotaxy locality comparison for Aedes implicatus Vockeroth

14. 14.111.	S.W. N.M.	Ut.
X	1	2
	X	2
		X
	X	x 1

Table 9. Larval Chaetotaxy locality comparison for Aedes $pullatus. \eqno(Coq.)$

	N. N.M.	S.E. Ariz.	Calif.	Nev.	Üt.
N. N.M.	X	9	12	13	15
S.E. Ariz.		X	8	10	13
Calif.			X	10	14
Nev.				X	13
Ut.					X

Table 10. Larval Chaetotaxy locality comparison for Aedes schizopinax Dyar.

	N. N.M.	Calif.	Nev.	Ut.
N. N.M.	X	5	9	9
Calif.		X	11	10
Wev.			X	14
Jt.				X

Table 11. % of characters examined by species with (1) significant variation between localities and (2) without variation within or between groups.

	% characters examined with significant variation between localities	% characters examined without variation within or between groups
Ae. cataphylla	16.67	11.11
Ae. communis & Ae. nevadensis	11.11	5.56
Ae. fitchii	20.37	5.56
Ae. hexadontus	20.37	3.70
Ae. implicatus	5.56	22.22
Ae. pullatus	22.22	7.41
Ae. schizopinax	20.37	1.85

Table 12. Character variability of species analyzed. (V = Varies significantly between localities studied; S = intralocality stability; + = intralocality variation.)

	· · · · · · · · · · · · · · · · · · ·						
Character	cat.	comm.	fit.	hex.	imp1.	pull.	schizo.
4-C	+	+	+	+	+	+	٧
5-C	+	+	٧	٧	+	+	+
6-C	S	+	+	+	S	V	+
7-C	+	+	- V	+	+	+	+
8-C	+	٧	+	٧	+	+	+
9-C	+	+	+	V	+	+	+
10-C	+	+	+	+	+	+	+
1-A	+	+	٧	+	+	٧	+
1-P	+	V	+	+	S	+	+
2-P	+	+	+	+	S	S	+
3-P	+	+	+	+	+	+	+
4-P	+	S	S	+	+	+	+
5-P	+	+	٧	+	+	٧	+
6-P	S	S	S	4-	S	S	+
7-P	+	+	+	4-	+	٧	٧
8-P	+	+	+	٧	+	+	+
14-P	٧	+	+	+	+	+	+
1-M	+	+	+	+	S	+	٧
2-M	٧	٧	٧	+	V	+	+
3-M	S	S	+	+	Š	+	+
4-M	+	+	+	٧	+	+	+
1-T	٧	+	+	٧	+	٧	+
2-T	٧	+	+	+	+	+	٧
3-T	+	٧	V	+	+	У	+
4-T	+	+	٧	+	+	٧	٧
3-I	+	+	+	٧	+	٧	+
6-I	+	+	+	4	+	+	+
3-II	+	٧	+	+	S	+	+
6-II	+	+	+	+	+	+	+
1-III	+	٧	+	٧	+	٧	+
3-111	+	+	+	+	S	+	+
6-111	+	+	+	+	+	+	+
1-IV	٧	+	٧	+	÷	+	+
3-IV	٧	+	+	+	+	+	+
6-IV	+	+	+	+	+	+	٧
1-V	+	+	+	+	+	S	V
3-V	+	+	+	+	+	+	+
6-V	S	+	+	+	+ S	+	+
1-VI	٧	+	+	V	+	+	٧
3-VI	+	+	+	+	+ S	+	+
6-VI	+	+	+	+	+	+	+
1-VII	+	+	+	+	V	+	٧
3-VII	+	+	+	+	+	+	+

Table 12. (continued)

Character	cat.	comm.	fit.	hex.	imp1.	pull.	schizo
comb	+	٧	+	+	+	٧	+
1-VIII	+	V	÷	+	+	+	+
2-VIII	S	+	+	+	S	+	+
3-VIII	+	+	+	+	+	+	+
4-VIII	+	+	\$	S	S	+	S
5-VIII	+	+	+	+	+	٧	٧
Pectin	V	+	٧	+	+	+	٧
1-5	٧	+	+	+	+	٧	+
8-\$	+	+	٧	٧	+	+	+
1-X	S	+	+	S	+	S	+
4-X	+	+	٧	٧	٧	+	+

Table 13. ANOVA F probability and Bartlett-Box F values for characters with significant intralocality variation

Species	Character	ANOVA F Prob.	Bartlett-Box F
Ae. cataphylla	14-P 2-M 1-T 2-T 1-IV 3-IV 1-VI Pectin 1-S	0.031 0.014 0.002 0.000 0.005 0.019 0.005 0.032 0.002	0.481 0.277 0.600 0.341 0.384 0.209 0.684 0.316 0.136
Ae. communis & nevadensis	3-C -P 2-M 3-T 3-II 1-III Comb. 1-VIII	0.001 0.028 0.040 0.033 0.020 0.040 0.000	0.113 0.688 0.148 0.458 0.603 0.202 0.688 0.641
Ae. fitchii	5-C 7-C 1-A 5-P 2-M 3-T 4-T 1-IV Pectin 8-S 4-X	0.003 0.001 0.023 0.005 0.012 0.001 0.008 0.027 0.001 0.000	0.362 0.295 0.687 0.651 0.507 0.488 0.418 0.476 0.666 0.663
Ae. nexodontus	5-C 8-C 9-C 8-P 4-M 1-T 3-I 1-III 1-VI 8-S 4-X	0.002 0.007 0.009 0.000 0.014 0.021 0.013 0.002 0.005 0.004	0.341 0.122 0.190 0.551 0.163 0.195 0.181 0.660 0.191 0.680 0.609

Table 13. (continued)

Species	Character	ANOVA F Prob.	Bartlett-Box F
Ae. implicatus	2-M	0.049	0.240
	1-VII	0.007	0.475
	4-X	0.026	0.469
Ae. pullatus	6-C	0.010	0.122
	1-A	0.003	0.500
	5-P	0.054	0.277
	7-P	0.015	0.438
	1-T	0.005	0.667
	3-T	0.023	0.268
	4-T	0.019	0.149
	3-I	0.003	0.534
	1-III	0.001	0.320
	Comb	0.000	0.188
	5-VIII	0.005	0.644
	1-S	0.004	0.590
Ae. schizopinax	5-C 7-P 1-M 2-T 4-T 6-IV 1-V 1-VI 1-VII 5-VIII	0.007 0.004 0.022 0.002 0.047 0.028 0.035 0.000 0.001 0.025 0.038	0.132 0.534 0.551 0.500 0.178 0.355 0.605 0.274 0.243 0.255 0.546

Table 14. Ranks and rank order correlation coefficients.

Species abundance and habitat diversity

Species	Abundance	Ranks Diversity of habitat
Ae. pullatus	1	1
Ae. cataphylla	2	2
Ae. fitchii	3	4.5
Ae. implicatus	4	4.5
le. hexodontus	5	6.5
le. communis	6	3
le. schizopinax	7	6.5
		rho = .750

Table 15. Ranks and rank order correlation coefficients. Amount of significant intralocality variation and diversity of habitat.

	Ranks Amount of significant	
Species	intralocality variation	Diversity of habitat
Ae. pullatus	1	1
Ae. fitchii	3	4.5
Ae. hexodontus	3	6.5
Ae. schizopinax	3	6.5
Ae. cataphylla	5	2.
Ae. communis nevadensis	6	3.
Ae. implicatus	7	4.5
		rho = .200

Table 16. Ranks and rank order correlation coefficients.

Amount of significant intralocality variation and larval self-association.

	Ranks	
Species	Amount of significant intralocality variation	Abundance
Ae. pullatus	1	1
Ae. fitchii	3	3
Ae. hexodontus	3	5
Ae. schixopinax	3	7
Ae. cataphylla	5	2
Ae. communis nevadensis	6	6
Ae. implicatus	7	4
		rho = .32

Table 17. Ranks and rank order correlation coefficients. Amount of significant intralocality variation and larval self-association.

		Ranks			
		Amount of significant			
Spe	cies	intralocality variation	Larval self-association		
Ae.	pullatus	1	1		
Ae.	fitchii	3	3		
Ae.	hexodontus	3	4		
Ae.	schizopinax	3	2		
Ae.	cataphylla	5	5		
Ae.	communis nevadensis	6	7		
Ae.	implicatus	7	6		
			rho = .929		

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