HYBRIDIZATION OF AEDES (PROTOMACLEAYA) ZOOSOPHUS WITH AE. (PRO.) TRISERIATUS GROUP SPECIES: HYBRID MORPHOLOGY

DAVID B. TAYLOR1

Department of Biology, University of Notre Dame, Notre Dame, IN 46556

ABSTRACT. Morphology of hybrids between Aedes (Protomacleaya) zoosophus and Ae. (Pro.) triseriatus group species is described. Adult females of hybrids key to Ae. zoosophus. Hybrids are differentiated from Ae. zoosophus by the dark longitudinal medial or submedial lines on the thorax and by the reduced width of the light tarsal and abdominal bands. The transverse band of light scales on the anterior scutum is complete in Ae. hendersoni / Ae. zoosophus hybrids and incomplete in Ae. triseriatus / Ae. zoosophus hybrids. Aedes brelandi / Ae. zoosophus hybrids are similar to Ae. hendersoni / Ae. zoosophus hybrids. However, due to the allopatric distributions of Ae. brelandi and Ae. zoosophus, such hybrids are not expected.

INTRODUCTION

The aedine subgenus Protomacleaya is composed of approximately 40 species of container breeding mosquitoes distributed throughout North, Central and South America. Distribution of Protomacleaya is primarily neotropical, but two species groups, Triseriatus and Zoosophus, with four species are restricted to the United States and adjacent regions of Mexico (Zavortink 1972). The Triseriatus group has three species, Aedes brelandi Zavortink, Ae. hendersoni Cockerell, and Ae. triseriatus (Say) while the Zoosophus group is monotypic. All four species occur in the southcentral U.S. and three, Ae. hendersoni, Ae. triseriatus, and Ae. zoosophus Dyar and Knab occur sympatrically. In central Texas, the three species frequently occur in the same wood lots and larvae can even be found inhabiting the same tree holes (Zavortink 1972; D. B. Taylor and J. Long, unpublished data). Though species of the Triseriatus group have been studied extensively, little is known of the biology or phylogenetic relationships of Ae. zoosophus. Zavortink (1972) summarizes our knowledge of this species in the following statement.

Aedes zoosophus differs so conspicuously from other species of Protomacleaya, particularly in or-

namentation of the adult and features of the larva, that I am placing it into a monotypic group. Since it possesses a combination of primitive characters, such as the undifferentiated genitalia of the male and the well developed ventral brush and anal saddle of the larva, and derived characters, such as the unusual ornamentation of the adult and the absence of hair 12-I in the larva, zoosophus is probably an early segregate of Protomacleaya.

Although the coexistence of these three species provides ample opportunity for natural hybridization, no Ae. zoosophus / Triseriatus group hybrids have been reported. Taylor (1982)² reported successful hybridization of Ae. zoosophus with each of the three species in the Triseriatus group. This paper presents morphological descriptions of the hybrids in order that field workers may recognize hybrid individuals.

MATERIALS AND METHODS

The strains of mosquitoes used for this study are presented in Table 1. All of the strains were maintained in the Vector Biology Laboratory, University of Notre Dame, Notre Dame, Indiana. Adults and larvae were maintained at 25° C with a photoperiod 16:8 (L:D). Aedes brelandi, Ae. hendersoni and Ae. zoosophus

Table 1. Strains of mosquitoes used in tests.

Strain	Species	Date collected	Location
CHISOS	Ae. brelandi	June 1978	Chisos Basin, Big Bend National Park, Brewster County, TX
SOCOL	Ae. hendersoni	1976	Pueblo County, CO
WALTON	Ae. triseriatus	June 1969	Izaac Walton Preserve, St. Joseph County, IN
Z 00	Ae. zoosophus	May 1979	Burleson County, TX

¹ Current address: USDA-ARS, Screwworm Research, Apartado 544, Tuxtla Gutierrez, Chiapas, Mexico.

² Taylor, D. B. 1982. Speciation in the *Aedes triseriatus* species complex. Ph.D. Dissertation. University of Notre Dame, Notre Dame, IN.

were maintained by induced copulation (McDaniel and Horsfall 1957, Taylor and Craig 1985) while Ae. triseriatus was maintained in free mating colonies.

The rearing and hybridization techniques used for this study were the same as those utilized by Taylor and Craig (1985). Reciprocal interspecific crosses were made by induced copulation. Approximately 100 females were mated for each cross. Following oviposition, eggs from the 50 most fecund females were hatched and reared to adults.

Larval characters were examined on larval exuviae preserved in 70% alcohol and on whole specimens mounted on microscopic slides in Euparal. Adult characters were examined on acetone preserved (Truman 1968) pinned specimens. The terminology of Harbach and Knight (1980) was used for morphological descriptions.

RESULTS

Interspecific crosses between Ae. zoosophus and species of the Triseriatus group exhibited a high degree of fertility. Only one of the six crosses, Ae. zoosophus 99 × Ae. brelandi & &, failed to produce adults. Both male and female Ae. brelandi / Ae. zoosophus and Ae. hendersoni / Ae. zoosophus hybrids were intersex (see Truman and Craig 1968 and Taylor 1987 for description of intersex syndrome). Male Ae. triseriatus / Ae. zoosophus hybrids from both reciprocal crosses were intersex whereas female hybrids were morphologically normal.

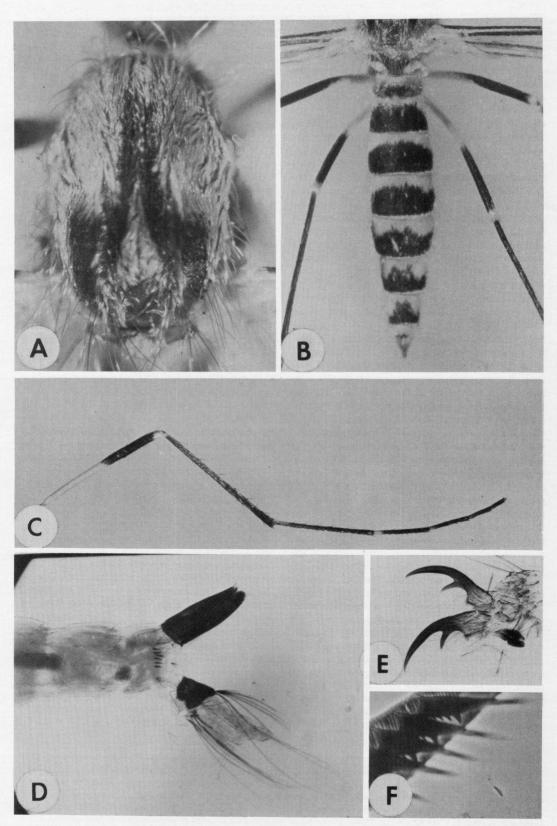
Hybrids between Triseriatus group species and Ae. zoosophus were morphologically intermediate to the parental species (see Zavortink 1972 for descriptions of the parental species). Progeny of reciprocal crosses were similar except where noted otherwise. Aedes hendersoni / Ae. zoosophus hybrid larvae were light in color. Anal papillae were intermediate in length (anal papilla-saddle index (APSI) 2.0), rounded at the tips, and subequal in length (Fig. 1). The saddle extended 0.6 to 0.7 the distance down the lateral surface of segment X. The indentation on the ventral margin of the saddle was 1.0 to 2.0 times as deep as wide or rarely closed on the ventral margin forming a hole in the lateral surface of the saddle. Seta 1-X usually had 4

margin of the saddle, conspicuously dorsad of the ventral edge. The ventral brush had 6 or 7 pairs of setae. Seta 1-S had 2 or 3 branches. The siphon acus was variable, attached or detached. but always closely associated with the base of the siphon. Pecten spines were intermediate in length (Pecten index (length / basal width) (PI) 4.0) with small basal teeth. The adult female thorax resembled most closely that of Ae. 200sophus. Light scales of the scutal fossa extended mesad of the anterior dorsocentral setae. The cream colored acrostichal scale line was broad and complete. Anterior dorsocentral scales were light. Median scutal fossal scales were buff-colored. Mesonotal setae were predominately light and acrostichal setae were restricted to the anterior promontory. The basolateral white spots of the abdominal terga were connected dorsally by buff basal bands (0.2 to 0.4 the width of the segment). Legs were black with light markings on the basal 0.5 of the femur, mid- and hindknee spots, and the base of the tarsal segments. Tarsomeres 1-3 of all legs had basal white bands. Frequently, bands were also present on segment 4 of the hindlegs. Bands were 0.2 to 0.3 the length of their respective tarsomere of tarsus III. Foreungues resembled those of Ae. zoosophus but with a more abrupt bend at the base of the basal tooth. The basal tooth was longer and thinner than that of Ae. zoosophus. Female palpi were longer than normal with palpomere 3 diverging laterally from the midline and palpomere 4 converging to give the appearance of being bowed outward. Antennae were slightly plumose. These characteristics were due to masculinization of the female hybrids. Male hybrids were intersex with reduced palpi, and incompletely rotated genitalia. Male antennae were less plumose than normal. When the paternal species was Ae. zoosophus, male and female hybrids were distinct and easily differentiated. However, when the paternal species was Ae. hendersoni, sexually dimorphic structures formed a continuum, making examination of the gonads necessary for differentiating the sexes.

branches and was inserted on the posterior

Aedes brelandi / Ae. zoosophus hybrids were morphologically similar to Ae. hendersoni / Ae. zoosophus hybrids with the following exceptions. Anal papillae were longer (APSI 2.4) but still intermediate to the parental species. In

Fig. 1. Morphology of Ae. hendersoni/Ae. zoosophus female hybrids. A) Thorax (SOCOL \times ZOO (99×60), light scales of fossa extend mesad of anterior dorsocentral setae, acrostichal and outer dorsocentral light scale lines complete, anterior transverse band of light scales complete; B) Abdomen (SOCOL \times ZOO), basolateral light spots connected dorsally by broad basal band of buff-colored scales; C) Hindleg (ZOO \times SOCOL), dark with light scales on basal 0.5 of femur, knee spots, and basal 0.1 to 0.2 of tarsomeres; D) Posterior segments of larva (SOCOL \times ZOO), anal papillae short and rounded, dorsal papillae 1.3 times



longer than ventral, saddle extends 0.7 distance down lateral surface of segment X, deep notch present on ventral margin of saddle, set a 1-X inserted on posterior margin of saddle and 4-branched (only 2 branches visible), ventral brush with 6 pairs of setae; E) Foreunguis (ZOO \times SOCOL), slight bend at base of basal tooth, basal tooth short but slender; F) Pecten spines (ZOO \times SOCOL), stout with several small basal teeth.

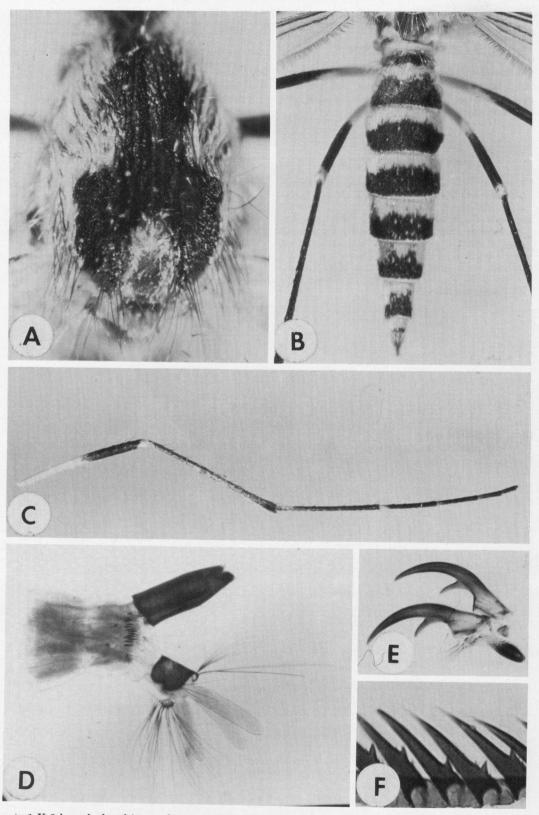
adult females, mesonotal setae were predominately dark and acrostichal setae were present. Basal bands of abdominal terga were narrower. Basal tarsal bands were present on tarsomeres 1-3 of all legs. On the hindlegs, the tarsal bands were 0.15 the length of tarsomere 1 and 0.25 the length of tarsomeres 2 and 3. Foreungues were similar to those of Ae. zoosophus with some indication of masculinization. Female and male hybrids were all intersexes. Female palpi were 0.5 the length of the proboscis and the antennae were slightly plumose. Male genitalia were incompletely rotated, palpi were short, and antennae were less plumose than normal. Morphology of the sexually dimorphic structures was continuous, making differentiation of male and female hybrids difficult without examination of the gonads.

Aedes triseriatus / Ae. zoosophus hybrid larvae were light-colored. Anal papillae were short (APSI 2.2), rounded at the tips and unequal in length. Dorsal papillae were 1.3 times longer than the ventral papillae (Fig. 2). The saddle extended 0.7 the distance down the lateral surface of segment X. The indentation on the ventral margin of the saddle was 1.0 to 2.0 times as deep as wide or rarely closed on the ventral margin forming a hole in the lateral surface of the saddle. Seta 1-X was 3-7 branched, usually 4-6, and inserted on the posterior margin of the saddle. The ventral brush had 7 pairs of setae. Seta 1-S had 2 or rarely 3 branches. The siphon acus was usually attached to the base of the siphon. Pecten spines were moderately long (PI 5.0), with several small basal teeth and one large distal tooth. The adult female thoracic pattern was most similar to that of Ae. triseriatus. Light-colored lateral scales did not extend mesad of the dorsocentral setae. The border of light and dark scales curved laterally. Light acrostichal and dorsocentral scales were absent. The transverse band of light scales on the anterior scutum was incomplete. Median scutal fossal scales were buff-colored and narrow. Mesonotal setae were intermixed light and dark-colored. Dorsocentral setae were reduced in number. Acrostichal setae were present and often formed a complete row. Basolateral abdominal spots on terga were connected dorsally by hasal bands which were buff-colored and varied in width from nearly absent to 0.5 the length of the segment. Legs were black with light scales on the basal 0.5 of the femur, midand hindknee spots and base of the tarsi. Tarsal bands were present on tarsomeres 1–3, occasionally on 4, of all legs. Bands on the hindtarsi were 0.15 to 0.3 the length of the segment. Foreungues were similar to those of Ae. triseriatus. Male hybrids were intersex, irrespective of the paternal species. Genitalia were incompletely rotated, palpi short, and antennae less plumose than normal. Female hybrids were morphologically normal.

DISCUSSION

This study demonstrated that species of the Triseriatus group can hybridize with Ae. 200sophus and produce viable adult hybrids. Given the morphological distinctiveness of the hybrids, and that none have been reported in the literature, effective precopulatory reproductive isolating mechanisms must maintain the integrity of these species. However, the absence of such reports in the literature does not preclude the existence of natural hybrids. The gross morphological differences existing between the Triseriatus group and Zoosophus group species make field workers hesitant to postulate hybridization as the origin of unusual specimens. Laboratory demonstration that such hybridization is possible, and the morphological descriptions presented herein should aid in the classification of hybrid individuals. Both hendersoni / Ae. zoosophus and Ae. triseriatus / Ae. zoosophus hybrids key to Ae. zoosophus, in the keys of Carpenter and LaCasse (1955) and Darsie and Ward (1981). Hybrids can be distinguished from Ae. zoosophus by the dark longitudinal medial or submedial lines on the thorax and by the reduced width of the tarsal and abdominal bands. The transverse band of light-colored scales on the anterior scutum is complete in Ae. hendersoni / Ae. zoosophus hybrids and incomplete in Ae. triseriatus / Ae. zoosophus hybrids. Ae. brelandi / Ae. zoosophus hybrids are similar to Ae. hendersoni / Ae. zoosophus hybrids. However, due to the allopatric distributions of Ae. brelandi and Ae. zoosophus, hybrids between these two species are not expected to occur naturally.

Fig. 2. Morphology of Ae. triseriatus/Ae. zoosophus female hybrids. A) Thorax (ZOO \times WALTON ($\mathfrak{PP} \times \mathfrak{FF}$), light scales of fossa do not extend mesad of anterior dorsocentral setae. Anterior transverse band of light-colored scales incomplete; B) Abdomen (ZOO \times WALTON), white basolateral spots connected dorsally by basal bands of buff-colored scales; C) Hindleg (ZOO \times WALTON), dark with light scales on basal 0.5 of femur, knee spots and basal 0.1 to 0.2 of tarsomeres; D) Posterior segments of larva (WALTON \times ZOO), anal papillae short and rounded on ends, dorsal papillae 1.3 times longer than ventral, saddle extends 0.7 distance down lateral surface of segment X, distinct notch present on ventral margin of saddle,



seta 1-X 3-branched and inserted on ventral margin of saddle, ventral brush with 7 pairs of setae; E) Foreunguis (ZOO \times WALTON), long with gradual curve, basal tooth small and slender; F) Pecten spines (WALTON \times ZOO), moderately long with several small basal teeth, most distal tooth larger than more basal.

ACKNOWLEDGMENTS

I thank J. Long for his assistance in collecting Ae. brelandi and Ae. zoosophus. This research was supported by National Institutes of Health research grant no. A-02753.

REFERENCES CITED

- Carpenter, S. J. and W. J. LaCasse. 1955. Mosquitoes of North America. Univ. Calif. Press, Los Angeles. 360 pp.
- Darsie, R. F., Jr., and R. A. Ward. 1981. Identification and geographical distribution of the mosquitoes of North America, north of Mexico. Mosq. Syst. Suppl. 1, 313 pp.
- Harbach, R. E. and K. L. Knight. 1980. Taxonomists' glossary of mosquito anatomy. Plexus Publ. Co., Marlton, NJ. 415 pp.

- McDaniel, I. N. and W. R. Horsfall. 1957. Induced copulation of aedine mosquitoes. Science 125:745.
- Taylor, D. B. 1987. Genetic compatibility of Aedes (Protomacleaya) triseriatus with A. (P.) brelandi and A. (P.) hendersoni (Diptera: Culicidae). Ann. Entomol. Soc. Am. 80:109-117.
- Taylor, D. B. and G. B. Craig. 1985. Unidirectional reproductive incompatibility between Aedes (Protomacleaya) brelandi and A. (P.) hendersoni (Diptera: Culicidae). Ann. Entomol. Soc. Am. 78: 769-774.
- Truman, J. W. 1968. Acetone treatment for preservation of adult and larval mosquitoes. Ann. Entomol. Soc. Am. 61:779-780.
- Truman, J. W. and G. B. Craig. 1968. Hybridization between Aedes hendersoni and Aedes triseriatus. Ann. Entomol. Soc. Am. 61:1020-1025.
- Zavortink, T. J. 1972. Mosquito studies (Diptera: Culicidae). XXVIII. The new world species formerly placed in *Aedes (Finlaya)*. Contrib. Am. Entomol. Inst. (Ann Arbor) 8(3):1-206.