ARTICLES

The Distribution and Evolution of the Culex Mosquitoes of the Subgenus Neoculex in the New World

Jay H. Linam
Department of Biology
Southern Colorado State College
Pueblo, Colorado

and

Lewis T. Nielsen
Department of Biology
University of Utah
Salt Lake City, Utah

Introduction

The subgenus Neoculex in the New World was a source of taxonomic confusion until Bohart (1948) defined the North American species belonging to this subgenus and presented keys to adult females, adult males, male genitalia, and fourth instar larvae.

Previous to Bohart's work species of the subgenus Neoculex were confused not only among themselves but with species of the subgenus Culex. Culex territans Walker was confused commonly with Culex restuans Theobald. A paper by Clarke (1940) contained this statement: "Adults were determined as Culex territans, having white dots on the mesonotum." There seems little doubt that he was referring to adults of restuans as the white dots on the mesonotum are usually indefinite or lacking in territans, and quite pronounced in restuans (sometimes referred to as "The white spotted Culex"). This belief is further strengthened by a discussion of the biting habits of the species in question. Clark stated that the species would bite humans. Culex restuans feeds on humans quite readily while members of the Neoculex apparently will only rarely attempt to bite warm blooded animals. In nature they have been observed to feed on cold blooded vertebrates, generally frogs (Shannon, 1915; Horsefall, 1955). In the laboratory Herman (1938) succeeded in inducing a female to feed upon a canary. Matheson (1944) was not able to induce a female to bite him.

Culex territans also has been confused with Culex apicalis Adams, another Neoculex species. In fact, apicalis Adams was for a time considered to be a synonym of territans, and one cannot always tell which species was actually involved in the older literature concerning these species. Culex apicalis apparently is restricted to Mexico and the southwestern United States and California and all references to this species in northern, eastern or southern states and Canada almost certainly pertain to territans.

Culex (Neoculex) territans Walker

This species has the widest distribution of any Neoculex species occurring in the Nearctic region. It occurs throughout most of the United States including Alaska (Gjullin, et al., 1961). In the western United States, Arizona and New Mexico are the only states from which it has not yet been reported.

The larvae of territans are most generally found in permanent marshes and ponds containing fresh water. The predominant vegetation in these situations is usually composed of species of Typha, Scirpus, Carex, Lemna, and grasses. There are infrequent records of the occurrence of territans in such areas as log ponds (Nielsen and Linam, 1963; McHugh, et al., 1964), pastures and road side ditches (Smith, 1962), grassy edges of an irrigation reservoir (Baker, 1961). Natvig (1948) records their presence in rock pockets in Europe.

Though active the year around in the southeastern states, in the Rocky Mountain States the females pass the winter in hibernation. They are reported by Berg and Lang (1948) to be capable of withstanding winter temperatures in natural sites of -18° F without injury.

Adults are attracted to light. Smith (1962) reported collecting territans in light traps in the Milk River Valley of Montana. McCreary and Stearns (1937) have taken them in light traps in Delaware and the Communicable Disease Center of the Public Health Service reported, (Anonymous, 1951), that 147 light traps operated on 11,178 nights in Missouri River Basin states during a period from 1938-1950 collected 1,338 specimens or 0.2% of the total catch. For discussions of seasonal variations one should consult the paper of Michener (1945). Frohne and Frohne (1954) discuss the swarming of this species.

Culex (Neoculex) boharti Brookman and Reeves

This species was originally described by Bohart (1948) as Culex reevesi. Brookman and Reeves (1950) reported that the name reevesi had been priorily assigned to another Neoculex species from California. They, therefore, designated Culex boharti Brookman and Reeves n.n. for Culex reevesi Bohart.

Culex boharti has been reported from California (Freeborn and Bohart, 1951) and Nevada (Richards, et al., 1956; Chapman, 1966). We now report the following new collection records of this species: IDAHO: Valley Co.: McCall, VII-28-60 (F. C. Harmston). WASHINGTON: Jefferson Co.: 9 mi. below Graves Creek Camp on North Fork Road and 10 mi. below Graves Creek Camp on North Fork Road, VII-20-60 (F. C. Harmston). OREGON: Union Co.: Hilgard Park, Hilgard Jct., VIII-19-62, VIII-10-68 (L. T. Nielsen, J. H. Linam, and J. H. Arnell).

Bohart (1948) stated that the larvae generally occur in partially shaded streambed pools and along creek margins. Our larval collections

are all from streambed habitats, also partially shaded and with an abundance of vegetation surrounding them. There was considerable algal growth in the water at the Oregon site.

Culex (Neoculex) apicalis Adams

Culex apicalis Adams appears to be restricted to the southwestern United States and Mexico. In the United States it is known to occur in Arizona (Bohart, 1948), California (Bohart, 1948), Nevada (Chapman, 1961), New Mexico (Ferguson and McNeel, 1954), Texas (Breland, 1956), and Utah (Linam and Nielsen, 1966). The records of its occurrence in Idaho (Harmston and Rees, 1946), Montana (Dyar, 1929; Mail, 1934), Colorado (Lasky, 1946; Harmston, 1949), and Wyoming (Rees and Harmston, 1948), almost certainly pertain to territans. To the distribution of this species in Utah as listed by Linam and Nielsen (1966) should be added: Garfield Co.: 10 mi. east of Boulder, V-20-66, L. T. Nielsen and J. H. Arnell). Palacios (1952) reported apicalis from several localities in southern Mexico.

Although the species has been found in a variety of habitats it favors fresh water pools in streambeds and springs which are at least partially shaded and contain conspicuous algal growth.

In Zion National Park, Utah, it has been collected in large numbers in small to large sandstone rock holes filled by precipitation runoff. These rock holes are found along drainage lines and are often a foot or more in depth and may retain water for several weeks. We also have collected larvae in a closed cistern in which the water was over six feet in depth. Additional notes on distribution, biology and overwintering habits are discussed by Linam and Nielsen (1966).

Culex (Neoculex) reevesi Wirth

Collections of this species have been restricted to the coastal areas of southern California and Baja California, Mexico. The most complete discussion of the distribution of this species as well as the most comprehensive description of the various stages is contained in the paper by Brookman and Reeves (1953). This paper and Galindo (1943) contain limited information on the bionomics of this species; larvae apparently favor habitats associated with streams.

Culex (Neoculex) arizonensis Bohart

This species was described by Bohart (1948) from Arizona. It has also been reported from Mexico (Palacios, 1952). Collections have been from shaded streambed pools.

Culex (Neoculex) derivator Dyar and Knab

This species is known only from Mexico and Central America (Stone, et al., 1959). Like most of the Neoculex species of the Americas this species favors streambed pools, all reported larval collections being from this habitat.

Discussion

The subgenus Neoculex represents a group which undoubtedly originated in and evolved principally in the Old World. Stone, et al. (1959) and Stone (1961; 1963; 1967; 1970) listed the world total of known Neoculex at 70 species, 2 subspecies and one variety. Of this total only 6 species are known to occur in the New World.

We support the proposition made by Ross (1964) that all of the American Neoculex species except territans originated in the New World having evolved from an ancestor which arrived from Asia across the Bering Sea and colonized the western Americas, eventually giving rise to a cluster of endemic species (apicalis, arizonensis, boharti, and reevesi). We believe that the Central American species, Culex derivator, also belongs with this cluster.

Culex territans is believed to have arrived in the Americas at a later period and became widely distributed across Canada and most of the United States. This species is wide spread over the holarctic region and seems to be the most plastic and adaptable Neoculex species. Not only does it have the widest altitudinal and longitudinal distribution but it also occurs in the greatest variety of larval habitats. It may be very close to the ancestral form of the other New World Neoculex. Ross (1964) indicated that territans evolved in Eurasia and moved into North America from the north. Although based on published records there is a distributional gap extending from western USSR to Alaska, the species probably occurs across Siberia and China. Two species of Neoculex have been reported from Japan (LaCasse and Yamaguti, 1955). One of these, Culex rubensis, occurs in both Japan and Korea. It appears to be indistinguishable in the adult female and male terminalia from territans, and differs only slightly from that species in the larval stage. It may well be only a variety or possibly a subspecies of territans. This pattern of distribution indicates that this species became widespread in the Old World and eventually migrated to North America during some past period when a favorable migratory route existed. The ancestor of the closely related group of western endemic species, unlike territans, was probably restricted to pools associated with springs and streams or those formed along drainage routes; all of the species believed derived from the ancestral form appear to be virtually restricted to this type of habitat.

Ross (1964) indicated that at least 30,000 years of isolation are needed to evolve an insect population into a species distinct from the parental form. Fossil evidences of the Culicidae are uncommon but there are records of fossil Culex from Eocene rocks of Colorado, Utah and Wyoming. This epoch lasted some 20 million years and began some 65 million years ago. Lands were lower and climates warmer and the forerunners of most living genera of mammals were present. It seems that conditions should have been excellent for the widespread distribution of mosquitoes. The rise of mountains during the Pliocene and the glaciation of the Pleistocene must certainly have contributed some isolating barriers among existing mosquito populations. Some of these isolated populations were probably the beginnings of the western endemic Neoculex species.

On such scant evidence as is available, one may conjecture tha the Culex mosquitoes began colonizing North America as early as 50-70 million years ago.

Culex apicalis is widely distributed throughout Mexico and the southwestern states, occurring across western Texas, New Mexico and Arizona. It is common over most of California at elevations below 5000 ft. It has also been collected in extreme west central Nevada, where it appears to be highly localized. On the basis of its present distribution it seems likely that apicalis had its origin in some inland locality, perhaps somewhere in the area encompassing southern California, western Arizona and northwestern Mexico. If this assumption is correct the species has moved east into New Mexico and west Texas and has become widely dispersed in Mexico. Inland the most northeasterly records of apicalis are from southern Utah, an area of low elevation and warm climate. This species probably moved into Utah from Arizona, using the Colorado and Virgin Rivers and their tributaries as migratory routes. At some past time, perhaps the Altithermal period, it may have occupied a more northerly range and has since retreated southward as the climate cooled. On the basis of Cottam's, et al., (1959) interpretation of the postpluvial climate in Utah it would seem that climatic conditions would have allowed this species to extend its range into northern Utah though there may have been factors other than climate that would have prevented this. If apicalis did occupy a more northerly range, we feel that it is possible that it may even have been extirpated from Utah at a later, cooler period and has since re-entered the southern portions of this state by the migratory routes mentioned above.

The distribution of Culex boharti, while still poorly known, seems to indicate this species to be more widespread than previously realized. This species may have developed from the ancestral form during a warmer period when much of the western United States was inhabitable by it. Subsequent climatic changes probably left disjunct populations scattered from the Olympic Peninsula in Washington southwards through Idaho, Nevada and California. At first we assumed the occurrence of boharti in the Pacific Northwest represented a northern extension of its range. Linam (1965) noted that boharti was known only from California (Bohart, 1948) but that if Ross' (1964) postulation of an ancestor from Asia for the western endemic Neoculex species was correct then it seems quite possible that populations at the southern limits of the range of boharti had been encountered first and that continued collecting would reveal its presence throughout the northwest portions as well as elsewhere in the western United States. Subsequent reports (Chapman, 1966) and collections by us proved this to be the case. We believe this species evolved from an isolated population in the northwestern United States and moved south into southern California and southeast into Nevada eventually becoming sympatric with apicalis and reevesi.

Culex arizonensis appears to occupy an area between central Arizona and southern Mexico. Palacios' (1952) paper would indicate that this

species is widely distributed in southern Mexico. We believe it likely that arizonensis originated in central or southern Mexico and that the Arizona type locality probably represents the northern most extension of its range. The species is now sympatric with apicalis over much of its known distribution.

Culex reevesi has the most restricted distribution of any species in the group. Validated records are from Monterey, California, south to a coastal point 65 kilometers south of Tijuana in Baja California (Brookman and Reeves, 1953). The mosquito fauna of Baja California is very poorly known except at the extreme southern and northern portions and we believe reevesi will eventually be found throughout the coastal regions of this peninsula. We consider it a strong possibility that reevesi evolved from an isolated population in Baja California, eventually moving north into California where it became sympatric with apicalis and boharti.

Culex derivator is the southernmost representative of the Neoculex in the New World and the only known tropical species in the complex. Its known range from Cordoba in southern Mexico to Panama would indicate its origin from a population of the ancestral species which penetrated far south and became adapted to a tropical environment.

Although we consider it unlikely that other Neoculex species will be found in North America there are extensive areas in northern Mexico and portions of Central America where the mosquito fauna is very poorly known. Collecting in these areas should further clarify the representation of the Neoculex complex in the New World.

Note: We recently have been notified by T. J. Zavortink, Department of Zoology, University of California at Los Angeles that the Project For a Systematic Study of the Mosquitoes of Middle America under the direction of J. N. Belkin has in possession three undescribed Neoculex species from Central America.

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