The Distribution of Snowpool *Aedes* Mosquitoes in the Southwestern States of Arizona and New Mexico with Notes on Biology and Past Dispersal Patterns

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ABSTRACT The distribution of mountain *Aedes* mosquitoes in Arizona and New Mexico is presented, distribution elsewhere reviewed, and ecological notes made with reference to accounts in the literature. Present patterns of distribution are interpreted in terms of historical events.

Introduction

In the foothills and mountains of Arizona and New Mexico, cold adapted *Aedes* mosquitoes of the subgenus *Ochlerotatus* Lynch Arribalzaga reach their known southern distributional limits. The larvae of these species develop in pools either directly resulting from spring snow melt or indirectly from snow melt by runoff or stream overflow. Such mosquitoes are usually common in the colder parts of the northern hemisphere, and as they extend south along mountain chains, most become progressively restricted to higher elevations. In the Southwest, with the exception of *Aedes increpitus*, they do not occur at elevations below 2,134 m (7,000 ft). All are univoltine and overwinter in an egg stage with an obligatory diapause. *Aedes cinereus*, the sole representative of the subgenus *Aedes* in the Nearctic, also occurs with great frequency in snowpools over much of its range.

The present study was undertaken to determine the occurrence and distribution of snowpool *Aedes* mosquitoes in the American Southwest, to interpret present southwestern distribution in terms of historical events, and to obtain ecological and biological observations of these species at the southernmost extension of their ranges in North America.

The species presently known to occur in the American Southwest are: *Ae. cataphylla Dyar, Ae. cinereus Meigen, Ae. communis* (De Geer), *Ae. excrucians* (Walker), *Ae. fitchii* (Felt and Young), *Ae. hexodontus* Dyar, *Ae. implicatus* Vockeroth, *Ae. increpitus* Dyar, *Ae. pullatus* (Coquillett), and *Ae. schizopinax* Dyar. Three of the above, *implicatus, increpitus,* and *schizopinax* are known only from the Nearctic; the remaining are *Holarctic*.

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Until recently there existed only a few scattered records of snowpool *Aedes* species in the Southwest. As a consequence of this meager knowledge, the southern boundaries of distribution could not be assessed. Our efforts of the past few years have resulted in an increase of from 4 to 10 in the number of mountain *Aedes* species known to occur in the area as well as increased understanding of the distribution of all mosquitoes that occur in the Arizona-New Mexico mountains. In the course of establishing distribution, we have obtained sufficient material with which to undertake a detailed statistical examination of larval chaetotaxy in an effort to determine affinities of one population to another and aid deduction of dispersal routes into the Southwest. This analysis will be presented in a subsequent paper.

The present distribution of these species in the Southwest suggests that colder temperatures during Pleistocene glaciation allowed them to move southward. They were left as relict populations on mountain top islands after the glaciers receded and temperatures warmed. In an attempt to understand distribution as a consequence of past dispersal, some of the numerous publications of past climatic history of the area during the Pleistocene have been reviewed. Frey (1965) stated, "Present distributions of organisms gives us information regarding only the most recent phase of colonization." The logic of the approach of considering the Pleistocene before working backward in the interpretation of the distribution of snowpool *Aedes* is strengthened by the numerous studies that have demonstrated that climatic change associated with the Pleistocene was not confined to the border of the major ice sheets but extended to the southwestern United States as well.

General Methods

Information on the southwestern distribution of snowpool *Aedes* was extremely meager prior to the commencement of this study. As a consequence, most of the distributional data and all material examined was personally collected by the authors. Collections were made from March 1967 through July 1976. Standard techniques were employed in the collecting, preservation, and mounting of material.

When possible, larvae were obtained in order to have associated series of larval, pupal and adult stages. Larvae were reared by placing them in an incubator cycled at 12 hours of light at 23 C and 12 hours of dark at 10 C, feeding with a small amount of Tetra Biomin 66 Tubenfutter and replacing a portion of the larval water with fresh distilled water daily. Most sites were sampled on more than one occasion and a large series of larval material was obtained for most species. Adults with associated exuviae were also obtained in many cases.

Likely habitats in potential sites were intensively sampled using a standard 1 pint enamel dipper. Adult females attracted to the authors were collected with a chloroform killing tube.

The bulk of the study material has been deposited in the University of Utah collection.

Distribution

Investigations of the southern boundaries of snowpool *Aedes* distribution is beset with a number of technical problems. Such obstacles include: the difficulty of determining optimum collecting time since climatic conditions in a given area vary greatly from year to year; the fact that in only about four months of the year (March-June) can larval collections be made; the fact that snow runoff may impede access to collecting sites by making dirt roads impassable; the necessity for repeated collection in a given area since lower elevations may be collectable weeks before higher elevations can be profitably investigated; the necessity for sampling sites on more than one occasion since some larvae such as *Ae. cinereus* may not be found in a pool as early as those of other species, and uncommon species may show up only after repeated sampling; the fact that mountainous areas likely to support snowpool *Aedes* are often without roads and thus must be investigated by long hikes or on horseback; and finally, the determination of the distribution of relict populations is made difficult by the fact that considerable time and effort is required in checking apparently suitable areas which give negative results.

Additional distributional records: Previous records and literature citation of snowpool mosquito distribution in the mountains of Arizona and New Mexico may be found in the publications of Nielsen, Wolff and Linam (1973) and Wolff, Nielsen, and Linam (1974). Areas found negative are also reported in the latter publication. Additional unpublished larval distributional records follow:

New Mexico

Ae. cataphylla Dyar. Colfax Co.: Black Lakes, v-25-75, 2,600 m (8,530 ft); Rio Arriba Co.: Tres Lagunitas, vi-5-76, 2,896 m (9,500 ft); Taos Co.: 9.66 km (6 miles) south of Red River along the East Fork, v-21-74, 2,880 m (9,450 ft); Hwy 64 1.61 km (1 mile) west of La Jara Canyon v-21-74, 2,560 m (8,400 ft).

Ae. cinereus Meigen. Rio Arriba Co.: Trout Lakes, v-15-74, 2,816 m (9,240 ft).

Ae. communis (De Geer). Rio Arriba Co.: Tres Lagunitas, vi-5-76, 2,896m (9,500 ft); Santa Fe Co.: Pecos Wilderness at Lake Katherine, vi-27-76, 3,579 m (11,742 ft).

Ae. excrucians (Walker). Rio Arriba Co.: Trout Lakes, v-15-74, 2,816 m (2,250 ft); Tres Lagunitas, vi-5-76, 2,896 m (9,500 ft); Taos Co.: 9.66 km (6 miles south of Red River along East Fork, v-21-74, 2,880 m (9,450 ft).

Ae. fitchii (Felt and Young). Colfax Co.; v-25-75, 2,600 m (8,530 ft); Rio Arriba Co.; Tres Lagunitas, vi-5-76, 2,896 m (9,500 ft); Taos Co.: 9.66 km (6 miles) south of Red River along the East Fork, v-21-74, 2,880 m (9,450 ft).

Ae. hexodontus Dyar. Rio Arriba Co.: Tres Lagunitas, vi-5-76, 2,896 m (9,500 ft); Taos Co.: 9.66 km (6 miles) south of Red River along the East Fork, v-21-74, 2,880 m (9,450 ft).

Ae. implicatus Vockeroth. Taos Co.: Hwy 64, 1.61 km (1 mile) west of La Jara Canyon, v-21-74, 2,560 m (8,400 ft).

Ae. increpitus Dyar. Rio Arriba Co.: Trout Lakes, v-15-74, 2,896 m (9,240 ft); Taos Co.: 9.66 km (6 miles) south of Red River along the East Fork, v-21-74, 2,880 m (9,450 ft).

Ae. pullatus (Coquillett). San Miguel Co.: Pecos Wilderness along Willow Creek, 3.22-4.02 km (2-2.5 miles) east of Hwy 63, v-19-74, 2,530-2,560 m (8,300-8,400 ft); Pecos Wilderness near junction of Pecos River and Willow Creek, v-19-74, 2,560 m (8,400 ft); Pecos Canyon; 16.09 km (10 miles) north of Pecos, iv-21-73, 2,286 m (7,500 ft); Santa Fe Co.: Pecos Wilderness at Lake Katherine, vi-27-76, 3,579 m (11,742 ft); Taos Co.: 9.66 km (6 miles) south of Red River along the East Fork, v-21-74, 2,880 m 9,450 ft); Wheeler Peak Wilderness, Bull of Woods area near junction of rd. 58 and 58 A, v-21-74, 3,109 m (10,200 ft); Hwy. 64, 1.61 km (1 miles) west of La Jara Canyon, v-21-74, 2,560 m (8,400 ft); Latir Lakes, vii-17-76, 3,353 m (11,000 ft) and 3,548 m (11,640 ft).

Ae. schizopinax Dyar. Colfax Co., Moreno Valley near Angle Fire Sky Basin at junction of Hwy. 6 and 38, v-21-74, 2,560 m (8,400 ft); Upper Black Lakes, v-25-75, 2,591 m (8,500 ft); 1.61 km (1 mile) north of Eagle Nest Lake, v-21-74, 2,591 m (8,500 ft); Rio Arriba Co.: Trout Lakes, v-15-74, 2,816 m (9,240 ft); Taos Co.: Hwy 38 at and east side of Carson National Forest, v-21-74, 2,987 m (9,800 ft).

Arizona

Ae. cataphylla Dyar. Greenlee Co.: Hannagan Recreational area, iv-25-74, 2,804 m (9,200 ft).

Ae. fitchii (Felt and Young). Greenlee Co.: Hannagan Recreational area, iv-25-74, 2,804 m (9,200 ft); Horseshoe Cienega, iv-25-74, 2,774 m (9,100 ft); Apache Co.: Numerous small lakes which dot crest of Chuska Mountains, iv-26-74, 2,743 m (9,000 ft).

Ae. implicatus Vockeroth. Greenlee Co.: Hannagan Recreational area, iv-25-74, 2,804 m (9,200 ft); 8.05 km (5 miles) south of Hannagan Recreational area at K. P. Cienega campground.

Ae. pullatus (Coquillett). Greenlee Co.; Hannagan Recreational area, iv-25-74, 2,804 m (9,200 ft).

Prior to the above new distributional record *Ae. cinereus* was known in New Mexico only from Chama near the Colorado border (Wolff, Nielsen and Linam 1974). Other larvae associated with the *cinereus* were *schizopinax*, *increpitus*, *excrucians*, and the chaoborine *Mochlonyx velutinus*. *Ae. communis* at Lake Katherine was found in a partially shaded snow melt pool surrounded by large boulders. The area is thinly forested with spruce trees. *Ae. fitchii* is probably common through the Chuska Mountains which extend from northeastern Arizona into northwestern New Mexico. The *schizopinax* larval distribution records were from temporary pools in montane forest. A large amount of organic matter was noted in 3 of the 4 pools sampled.

Species Accounts

Aedes (Ochlerotatus) cataphylla Dyar

Distribution

Palearctic: Northern and Central Europe, Denmark, Fennoscandia, Siberia (Natvig 1948), China (Stone 1961).

Nearctic: Western cordillera from Alaska through Cascades into the Sierra Nevada, Virgin and Toiyabe Ranges of Nevada. Along the Rocky Mountains south into the Mogollon Mountains of southern New Mexico. In northern New Mexico widespread in the San Juan and Sangre de Cristo and higher mountain valleys. In Arizona widespread and common along the Kaibab Plateau, Mogollon Rim and White Mountains.

Biology

This species most often occurs in open grassy mountain meadows where it may appear several weeks before other associated mountain *Aedes*. In the Southwest it is most commonly associated with *fitchii*, *implicatus*, and *pullatus*. *Ae. cataphylla* has frequently been collected in the Southwest from overflow pools along rivers where it is associated with *implicatus* and *pullatus* and it has been noted that when *implicatus* and *cataphylla* are the species associated, one or the other usually is much more abundant. In northern Arizona it was observed that *cataphylla* has frequently invaded borrow pits along highways. Southwest collections were made from montane pools from March 18 to June 22, between 2,396 m (7,860 ft) and 3,353 m (11,000 ft) in the yellow pine to spruce fir associations.

Aedes (Aedes) cinereus Meigen

Distribution

Palearctic: Throughout the Eurasiatic continent from the Atlantic to the Pacific (Natvig 1948).

Nearctic: Throughout most of North America from the Atlantic to the Pacific. Occurs in northern New Mexico, but has not been collected in Arizona.

Biology

In Utah, this species occurs between 1,280 m (4,200 ft) and 1,981 m (6,500 ft) in the lower mountain valleys (Nielsen and Rees 1961). It is present in Nevada in the foothills and valleys but is not regarded as a snow-pool species by Chapman (1961). New Mexico records are from Rio Arriba County at Chama at 2,396 m (7,860 ft) and from the San Juan Mountains, Trout Lakes Area at 2,816 m (9,240 ft). Larvae of *cinereus* were noted to be in an earlier stage of development than all other associated *Aedes* except *schizopinax*. Larval collections were made from May 15 to June 11. The species is apparently univoltine in all the mountainous areas of the western United States.

Aedes (Ochlerotatus) communis (De Geer) Sens. Str.

Ellis and Brust (1973) recognized three sibling species in the *Aedes communis* sens. lat. complex: *Ae. communis* (De Geer) sens. str., *Ae. churchillensis* Ellis and Brust, an autogenous form which they described from western Canada, and *Ae. nevadensis*, first described as a subspecies by Chapman and Barr (1964) which they raised to species status. They included keys to separate the larvae and imagos. Both *Ae. communis* (De Geer) sens. str. and

Ae. nevadensis Chapman and Barr are known from the Rocky Mountains of western United States. New Mexico material, like that of Colorado, appears to be *Ae. communis* sens. str. Further studies to clarify the systematics and distribution of the *communis* complex on a world wide basis are needed.

Distribution of *Aedes communis* sens. lat.

Palearctic: Great Britain, northern Europe, Denmark, Fennoscandia, Syria, U.S.S.R. (Natvig 1948), Turkey (Parrish 1959), China (Stone 1961).

Nearctic: Alaska and all Canadian provinces, eastern United States south to New Jersey and Pennsylvania. Western cordillera through the Cascades, Blue Mountains of Oregon, Sierra Nevada and Ruby Mountains of Nevada. In all the states of the Rocky Mountain region, from Montana into northern New Mexico. The species has not been found in Arizona despite intensive searching in what appear to be suitable habitats.

Biology of *Aedes communis* sens. str.

Ae. communis is a dominant forest mosquito of the coniferous zone in the northern hemisphere. This species to a limited degree also invades arctic and alpine tundra regions. As the range extends south, the species distributes itself along mountain chains at increasing elevations. In Colorado, the species has not been collected below 2,134 m (7,000 ft), and is found in montane and subalpine forests up to 3,658 m (12,000 ft). In northern New Mexico larvae have been collected only above 2,816 m (9,240 ft).

In the Rocky Mountains larvae of *communis* occupy a wide range of habitats but are usually found in pools located beneath spruce, pine, fir, willows or alders, thus indicating a preference for shaded or partially shaded situations. This also appears to be the case in California (Carpenter 1962), and in Colorado (Harmston and Lawson 1967). Larvae were found in deep pools both in deciduous and evergreen forests in northern New Jersey and Pennsylvania (Carpenter and La Casse 1955). *Ae. communis* larvae were collected in a deep shaded forest pool in northern New Mexico in 1973 and 1974. A few specimens were taken in more open, partially shaded pools but larvae were never abundant in these situations. In 1976, this species was collected in the Pecos Wilderness at Lake Katherine near Santa Fe at 3,579 m (11,742 ft) from a partially shaded pool surrounded by boulders. This record represents the known southernmost extension of *Ae. communis* in the American Southwest.

Aedes (Ochlerotatus) excrucians (Walker)

Distribution

Palearctic: Europe, USSR, Siberia, Mongolia, Northwest China (Gutsevich, et al. 1974), Hokkaido, Japan (La Casse and Yamaguti 1950).

Nearctic: From the Northwest Territories across Canada to Maryland in eastern North America; western cordillera from Alaska to the Cascades and montane regions of Washington and Oregon. Rocky Mountains to Sangre de Cristo and San Juan Mountains of northern New Mexico. Not known from Arizona.

Biology

In Utah and Colorado this species appears to be restricted to elevations above 2,438 m (8,000 ft). In northern New Mexico we collected *excrucians* from two localities, both above 2,743 m (9,000 ft) in coniferous forest habitat. Larvae were taken from open, deeper, semi-permanent pools usually with emergent vegetation and were associated with *cataphylla, fitchii* and *chaoborines*.

Aedes (Ochlerotatus) fitchii (Felt and Young)

Distribution

Palearctic: Gutsevich, et al. (1974) have recently reported the occurrence of this species in the U.S.S.R.

Nearctic: Alaska, Canada, northern contiguous United States as far south as Maryland in the east. Western cordillera through Cascades into the Sierra Nevada and Ruby Mountains of Nevada. Along the Rocky Mountains southward into Arizona and New Mexico. In northern Arizona widely distributed and common along the Kaibab Plateau, and in the Chuska Mountains. In southwestern Arizona distributed along the Mogollon Rim and in the White Mountains with southernmost extension in the Hannagan Recreational Area of Greenlee County. Common in northern New Mexico in Jemez, Sangre de Cristo and San Juan Mountains and the higher mountain valleys.

Biology

Aedes fitchii has the widest altitudinal range of any mosquito species in the Rocky Mountain region of the western United States, having been collected at elevations from 1,067 - 3,048 m (3,500 ft to over 10,000 ft). Occurrence has been noted from a wide variety of habitats but the species shows a distinct preference for open, deeper, semi-permanent pools with emergent vegetation where it often is found associated with species in the *excrucians* complex. Larvae of *fitchii* have been found in such pools in the Southwest and in roadside borrow pits. Larvae are frequently associated with *cataphylla* but develop more slowly. In the Southwest, larvae have been collected from April 30 to June 12 in montane pools in yellow pine and spruce fir forests. Biting females were collected in the Trout Lakes area of Rio Arriba County, in northern New Mexico on viii-28-73 at 2,835 m (9,300 ft).

Aedes (Ochlerotatus) hexodontus Dyar

Distribution

Palearctic: Sweden (Vockeroth 1954), Fennoscandia (Dahl 1974), USSR (Gutsevich, et al. 1974). Although this species was reported from Japan by Suzuki (1959), the figures and ecological data presented suggest a member of the *punctor* subgroup other than *hexodontus*. The distribution of this species in the Palearctic is not well known due to past taxonomic confusion with *punctor*.

Nearctic: Alaska across the tundra to eastern Canada where it occurs as far south as Labrador. Western cordillera from Alaska to the Cascade of Washington and Oregon, the Sierra Nevada range of California and the Ruby Mountains of Nevada. Rocky Mountains to northern New Mexico where it is widely distributed in Jemez, San Juan, and the Sangre de Cristo Ranges. Southernmost extension in Pecos Wilderness of North Central New Mexico.

Biology

Ae. hexodontus is primarily an arctic tundra species which becomes restricted to the higher elevations as it extends south. In New Mexico larvae have been found in variety of unshaded pools. These include snow pools of variable size in large meadows as well as small pools along pond or lake margins. *Ae. hexodontus* in New Mexico was associated most often with *pullatus*. Collections were made from April 30 to June 24 between 2,804 - 3,353 m (9,200 and 11,000 ft).

Aedes (Ochlerotatus) implicatus Vockeroth

Distribution

Palearctic: This species has not been reported from the Old World. Nielsen (1955) has pointed out the great similarity of *implicatus* with the European *Aedes leucomelas* (Meigen) and suggested that the two species may prove to be identical.

Nearctic: Widely distributed in boreal regions of Alaska, Canada, and the United States. Throughout the eastern states as far south as Ohio and New Jersey. In the western States the species extends through the Rocky Mountain states and into Arizona and New Mexico. In Arizona, *implicatus* is widely distributed along the Mogollon Rim and in the White Mountains. In New Mexico, the species is widely distributed in the north and is common in the San Juan Mountains. Collections have also been made from the Jemez, Mogollon, and Sangre de Cristo Ranges. *Ae. implicatus* is more commonly found in the montane zone but may invade subalpine habitats. As its range extends south in the Rocky Mountains, it continues to favor the montane zone, but occurs with considerable frequency in snow melt and stream overflow pools in mountain valleys, and wherever it occurs, the pools are almost invariably associated with willows. In the Southwest, larvae have been collected from March 3 to June 9 from 2,377 - 3,048 m (7,800 to 10,000 ft). Larvae were usually found in willow-shaded, stream overflow pools often associated with *cataphylla* and *pullatus*.

Aedes (Ochlerotatus) increpitus Dyar

Distribution

Nearctic: Western cordillera from southwestern Canada through Cascades into the Sierra Nevada Range of California and the Ruby Mountains of Nevada. Common throughout the Rocky Mountain states and into Arizona and New Mexico. In Arizona known only from Greer along the Mogollon Rim at 2,591 m (8,500 ft). In northern New Mexico widely distributed in mountains and mountain valleys.

Biology

Ae. increpitus has a wide altitudinal range. In the northern part of its range in the western United States it is most often found in streamside pools in mountain valleys, usually at elevations between 1,219 - 2,438 m (4,000 to 8,000 ft). Larvae have been collected in the northwestern United States from sea level to about 1,829 m (6,000 ft) (Gjullin and Eddy 1972). In Nevada, Chapman (1961) reported collections from 1,311 m (4,300 ft) to 2,499 m (8,200 ft). As its range extends southward, *Ae. increpitus* occurs more frequently in snowpools at 2,438 - 3,048 m (8,000 to 10,000 ft). At Greer, Arizona and commonly in northern New Mexico larvae also have been collected from willow-shaded stream overflow pools. In New Mexico this species is common in the Espanola area at 1,707 m (5,600 ft) but has not been collected at lower elevations in this State. Larvae have been collected March 7 to June 12 between 1,707 m (5,600 ft) and 2,835 m (9,300 ft) in pools in piñon-juniper woodland to coniferous forest. Biting females were taken in northern New Mexico, at Trout Lakes in Rio Arriba County on viii-28-73 at 2,835 m (9,300 ft).

Aedes (Ochlerotatus) pullatus (Coquillett)

Distribution

Palearctic: Widespread throughout northern Palearctic region (Natvig 1948; Gutsevich et al., 1974; Ch'in and Su 1960; Barraud 1934; Mani 1968).

Nearctic: Eastern Canada, Labrador, Baffin Island, and northern Quebec (Jenkins and Knight 1950). Eastern United States in restricted localities in northern Michigan (Irwin 1941, 1942). Western cordillera from Alaska south through the Cascades into the Sierra Nevada Range of California and the Ruby Mountains of Nevada. Rocky Mountains south as far as the White Mountains of southeastern Arizona. In northern New Mexico widely distributed in the Jemez, San Juan, and Sangre de Cristo Ranges.

Biology

In the western United States larvae have been collected from such diverse habitats as small, shaded forest pools and sunlit mountain meadows, from pools rich in organic matter to bare rock pools, and from deep semi-permanent pools to transient situations. In the Rocky Mountains *pullatus* shows great altitudinal range. Nielsen (1955) verified a record of an adult male taken at Mantua, Utah at 1,577 m (5,175 ft) and larvae taken at Loveland Pass Colorado at 3,655 m (11,992 ft). Carpenter (1968) reported that in the Sierras of California, *pullatus* reaches its greatest abundance at elevations between 2,896 - 3,658 m (9,500 and 12,000 ft). This species has been collected in the Southwest between 2,195 - 3,048 m (7,200 and 10,000 ft), from March 23 to June 23 from snow pools, overflow pools along mountain streams, and from rock pools in the Santa Fe Ski Basin area. Larvae have also been collected in Arizona and New Mexico in flooded depressions left by fallen trees, a habitat in which other montane *Aedes* are less commonly found. Observations made by Nielsen (1955) at several localities in the Rocky Mountains indicates that larvae do not appear until maximum daily water temperature exceeds 50 F. This may account for the late appearance in relation to associated species that appear to have lower temperature requirement. Biting females were collected at Trout Lakes, Rio Arriba County on viii-28-73 at 2,804 m (9,200 ft).

Aedes (Ochlerotatus) schizopinax Dyar

Distribution

Nearctic: Foothills of Fremont Mountains of Oregon, Sierra Nevada and the Toiyabe, Schell Creek and Ruby Mountain Ranges of Nevada. Rocky Mountains from Montana to the Sangre de Cristo and San Juan Ranges of northern New Mexico. Not know from Arizona.

Biology

In the northern part of its range, this species occurs primarily in the foothills below 2,134 m (7,000 ft). Although generally considered a rare species, larvae were collected abundantly in 1974 in the Moreno Valley of the Sangre de Cristo Mountains of northern New Mexico. Little is known of adult habits. Females are not known to bite man and when the Moreno Valley area was revisited three weeks after larvae were collected, we were unable to collect or observe any adult activity. Selection of oviposition sites rich in organic matter and lack of observed biting suggest either autogenous development of the eggs or a preferred host other than man. Larvae were collected in New Mexico from May 15 to May 21, 2,560 - 2,835 m (8,400 to 9,300 ft) in snow melt pools unusually rich in organic matter.

Synopsis of Southwestern Distribution of Snowpool *Aedes*

Arizona:

Ae cataphylla and *fitchii* are known from the Kaibab Plateau, *fitchii* in the Chuska Mountains, and *cataphylla, fitchii, implicatus, increpitus,* and *pullatus* from the Mogollon Rim and White Mountains in the southeast.

New Mexico:

The Sangre de Cristo and San Juan Mountains have yielded *communis cataphylla, excrucians, fitchii, hexodontus, implicatus, increpitus, pullatus* and *schizopinax. Ae. cinereus* has been taken in the San Juan Mountains. From the Jemez Mountains *fitchii, hexodontus, implicatus, increpitus,* and *pullatus* are known. *Ae. cataphylla* and *implicatus* have been collected in the Mogollon Mountains.

Table 1 presents the snowpool mosquito distribution by mountain range. Table 2 gives the number of collections containing each species by elevation. Only *increpitus* was taken below 2,134 m (7,000 ft). Most of the collections were made between 2,286 - 3,048 m (7,500 and 10,000 ft). Four species: *communis, cataphylla, hexodontus* and *pullatus* were taken above 3,048 m (10, 000 ft). *Ae. pullatus* was present in about 45% of the collections made and was by far the most common snowpool mosquito taken in the Southwest. *Ae. cataphylla, fitchii* and *implicatus* were next most common being taken in 29% 25%, and 20% of the collections respectively. Figures 1-3, present the southwestern distribution of species on a county outline map. Each dot represents a locality where one or more collections were made.

The distributional pattern of the mountain *Aedes* in the southwestern United States suggests that the movement south of the majority of species occurred from the Sangre de Cristo Mountains of the Colorado Rocky Mountain mass 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. From the San Juan Mountains they penetrated the Jemez Mountains that make up the southwestern corner of the main Colorado Rocky Mountain mass. Penetration continued along the Rocky Mountain chain into the Gila Wilderness of southwestern New Mexico with establishment in the White Mountains and along the Mogollon Rim of southeastern Arizona. Snowpool mosquitoes are not known from the Coconino Plateau of Arizona where suitable habitat is scarce. Populations on the Kaibab Plateau of northern Arizona almost certainly invaded from southern Utah. The *fitchii* populations in the isolated Chuska Mountains of Arizona may have arrived either from southern Colorado, Utah or northern New Mexico. Table 3 gives the larval associations for mosquitoes collected in the mountains and mountain valleys of the Southwest from 1967 to 1976. Indicated are the number of times a species was associated with others. Self association indicates that a species was found alone. Most snowpool species were found to be associated with a number of other mountain mosquitoes.

Fig. 4 gives the range in elevation of larval habitats from 1967 to 1976. *Ae. communis, excrucians,* and *hexodontus* were exclusively found at elevations above 2,743 m (9,000 ft). All other species in the group showed a much wider altitudinal range occurring in mountain valleys as well as at higher elevations. Our observation of both *cataphylla* and *pullatus* below 2,438 m (8,000 ft), differs from that of Jenkins (1958) who stated, "In North America these mosquitoes, together with arctic and certain subarctic species, occur at or near sea level in the northern areas. Further south they are restricted to near timberline in the higher elevations. . . ."

Fig. 5 gives the seasonal occurrence of mosquito larvae in the mountains of Arizona and New Mexico from 1967 to 1976. *Ae. cataphylla, implicatus,* and *increpitus* are each known to hatch early and their appearance in early March is not unexpected. The early recorded presence of *pullatus,* however, a species which normally is slower in development than associated showpool *Aedes,* is due to records at or below 2,286 m (7,500 ft).

Interpretation of Present Snowpool *Aedes* Distribution In Arizona and New Mexico Based on Evidence of Climatic Change in the American Southwest

Available information from fossil, geological, and pollen analyses indicated a full-glacial climate in the Southwest about 20,000 years ago which was both wetter and colder than at present. The most recent or Wisconsin Pleistocene glaciation in the Southern Rocky Mountains consisted of several distinct substages during which ice advanced and retreated. Small glaciers are known to have been in New Mexico in the Sangre de Cristo (Ray 1940), San Juan (Smith 1936), and Sacramento Mountains where Sierra Blanca was found to be the southern most glaciated peak in the United States (Smith and Ray 1941). The assumption has been made (Ray 1940) that this glaciation in the Southern Rocky Mountains could be attributed to a reduction in mean annual temperature with consequent reduction in rate of evaporation producing a wetter climate. It was further speculated that probably only a few degrees reduction in the summer temperature could cause this glaciation.

Leopold (1951) concluded that during the Pleistocene in New Mexico the coldest month was probably not much colder than at present but that there was a much greater lowering of summer temperature and that the late Pleistocene Lake Estancia in the closed basin of Estancia, N. M., required both increased precipitation and lower temperature. Antevs (1954) concluded that glacial and pluvial culminations were contemporaneous in the Southwest and that the Cary (Wisconsin 11) snow-line depression was about 1,219 m (4,000 ft) lower than at present. Antevs further concluded that the Cary glaciation in New Mexico was the product of both lower temperature and heavier snowfall with temperature of paramount importance but with snowfall increasing in importance southward. Bent and Wright (1963) on the basis of present and full glacial pollen analyses from the Chuska Mountains, an isolated range extending from Arizona into northwestern New Mexico, inferred a depression of the tree line during the Pleistocene of at least 762 m (2,500 ft).

The dry playa lake, now dominated by Juniper grassland in Catron Co., N. M., at 2,134 m (7,000 ft), known as the San Augustin Plains was studied for surface and fossil pollens by Clisby and Sears (1956). A full glacial spectrum (23,070 ± 650 years before present) of mainly pine and spruce is interpreted by Martin (1964) from this and unpublished data as evidence for a boreal forest 20,000 years ago. Martin (1964) has also discussed pollen studies indicating an invasion of the Llano Estacado of Texas-New Mexico by pine parkland requiring at least 1,000 m (3,275 ft) vertical vegetation shift.

The altithermal, a post-glacial period in which temperatures were warmer than they are today, extended from about 9,500 to 2,000 years ago (Deevey and Flint 1957). The pollen record, however, affords, as of yet, no clear indication that southern Arizona and New Mexico were much hotter and dryer in the past than at present (Martin and Mehringer 1965). Murray (1957), however, analyzed the Burnet Cave Pleistocene fauna in New Mexico and interpreted the presence of desert species in association with animals representing a colder climate as evidence of an altithermal period when the desert species could have appeared and boreal ones would have been eliminated.

Martin (1964) has reconstructed a full-glacial vegetation map of the Southwest on the basis of pollen-spectra believed to be of full-glacial age. The greatest area was thought to consist of yellow pine parkland. An extensive spruce-fir-pine forest was largely contiguous in both states; alpine areas were interspersed within the boreal matrix.

We have superimposed Martin's reconstruction over a county outline map of Arizona and New Mexico showing sites from which snowpool *Aedes* have been collected. The resulting map (Fig. 6) indicates that with the exception of the Kaibab Plateau, which was presumable continuous with boreal forest to the north, all areas presently known to harbor snowpool mosquitoes in Arizona and New Mexico were formerly connected by a vast boreal forest. Thus, during the glacial periods of the Pleistocene, a lowering of the timberline by 1,219 m (4,000 ft) would have allowed direct connection between the present disjunct Jemez, Mogollon, White and Chuska Mountains, and permitted the movement of the northern *Aedes* species into these areas.

It is our belief that snowpool *Aedes* were actively extending their ranges in Arizona and New Mexico within the last 10,000-20,000 years and at that time probably were found throughout the boreal forest that extended into these areas.

The warmer or interglacial periods which began approximately 10,000 years ago and lasted for some 7,000 years would have then forced the mosquitoes to move to higher elevations into available suitable habitat where they exist today as isolated relict populations. This interpretation is supported by the fact that several isolated mountain ranges exist in southeastern Arizona: the Pinalenos, Galluros, Santa Catalinas, Santa Ritas, Huachucas and Chiricahuas, which are negative for snowpool *Aedes* so far as we are aware.

All of these ranges contained spruce, fir and pine forests during the Pleistocene (Fig. 6) but were separated by low lying deserts from the main boreal forests to the north. Three of these ranges, the Pinalenos, Santa Catalinas and the Chiricahuas still contain apparently suitable habitat for

larval production. It is our belief that these areas were never populated due to their isolation from the northern route of migration.

Present snowpool *Aedes* distribution reflects accurately the remaining areas where suitable habitat still exists. Fig. 7 shows the present distribution of spruce-fir pine forests in the Southwest to which the majority of species are restricted. In the western United States only *cinereus, fitchii* and *increpitus* are known to occur with frequency at elevations below those which support boreal forests and even these species are much more abundant in forested areas in Arizona and New Mexico (Fig. 1). These three species may still be capable of extending their ranges in the southwestern mountains and valleys. Three other species, *cataphylla, implicatus* and *schizopinax* (Fig. 2) will readily invade open areas, including man-made borrow pits along roads. However, in the Southwest they have never been collected below 2,286 m (7,500 ft). and occur with greatest frequency above 2591 m (8,500 ft) in temporary snow melt pools in high mountain meadows associated with spruce-fir or yellow pine forests. This type of habitat is the most common found in the southwestern mountains and probably accounts for the fact that *cataphylla* and *implicatus* represented more than 50% of the species collections during this study. The rarity of *schizopinax* is probably due to its restriction to very shallow pools which are extremely rich in organic content. We did not find this to be a common type of mountain *Aedes* habitat.

Three species, *communis, excrucians* and *hexodontus* were restricted to the mountains of northern New Mexico (Fig. 3) at elevations over 2,743 m (9,000 ft). Despite intensive searching we were unable to find these species in Arizona or the more southern mountains of southwestern New Mexico, although suitable habitat appeared to be present. In the White Mountains and Hannagan Meadow areas of Arizona *hexodontus*-type habitat was common, but supported populations of *cataphylla, implicatus* and *fitchii; communis*-type habitat was supporting *implicatus* and *pullatus; excrucians*-type habitat contained *cataphylla* and *fitchii*.

It is interesting to speculate as to whether *communis, excrucians* and *hexodontus* were late comers and migrated no further south than their present distribution or whether they formerly occupied a more extensive southern distribution. The latter explanation appears more likely. All three species are widely distributed throughout both the Nearctic and Palearctic regions. Ecological data appear to indicate that they require the colder climes of the higher elevations in the montane and subalpine zones; *hexodontus* particularly seems to favor tundra-type habitats over much of its range. We prefer to accept the hypothesis that these three species became widely distributed in the southwestern mountains, where much suitable habitat existed, but were extirpated from all but the extreme northern area during the altithermal periods. Only *hexodontus* appears to remain relatively well established in northern New Mexico; *communis* and *excrucians* are rare and appear to have only a tenuous foothold in this area. The possibility still exists that any one of these species may still occur further south. The extensive Gila Wilderness area in southwestern New Mexico has been largely unexplored; most of the area being accessible only by foot trails. Thus far, this area has yielded only *cataphylla* and *implicatus*, but suitable habitat for other snowpool *Aedes* undoubtedly exists there.

The most abundant and successful species in the southwestern mountains is *pullatus* (Fig. 3) which accounted for nearly half of the total collections (49). The success of *pullatus* is undoubtedly due to its wide ecological and altitudinal tolerance. The species was taken at elevations from 2,134 m (7,000 ft) to over 3,353 m (11,000 ft) and occurred in virtually every type of habitat found. The ability of this species to invade new habitat is remarkable; man-made excavations such as those occurring in the construction of ski lifts, ditches, outside toilets and natural depressions such as those left from the roots of a fallen evergreen are quickly utilized. We observed one instance in which campers had dug a small depression in the soil to put out a campfire; the following year this depression contained *pullatus* larvae. Of all the snowpool *Aedes*, *pullatus* is the species most likely to retain its widespread abundance in the southwest mountains.

The southernmost area which appeared promising for mountain *Aedes* presence was the Sacramento Range in Otero County, New Mexico where the southernmost glaciated peak occurs. This range was connected to the main boreal forest by a narrow neck extending south through the central part of the state (Fig. 6). We were able to find some restricted habitat which looked favorable for *Aedes* larvae at an elevation above 2,438 m (8,000 ft). In one locality, *Culiseta incidens* larvae were present. In all others, no larvae were found. These mountains do not appear to support snowpool *Aedes* at present.

Acknowledgments

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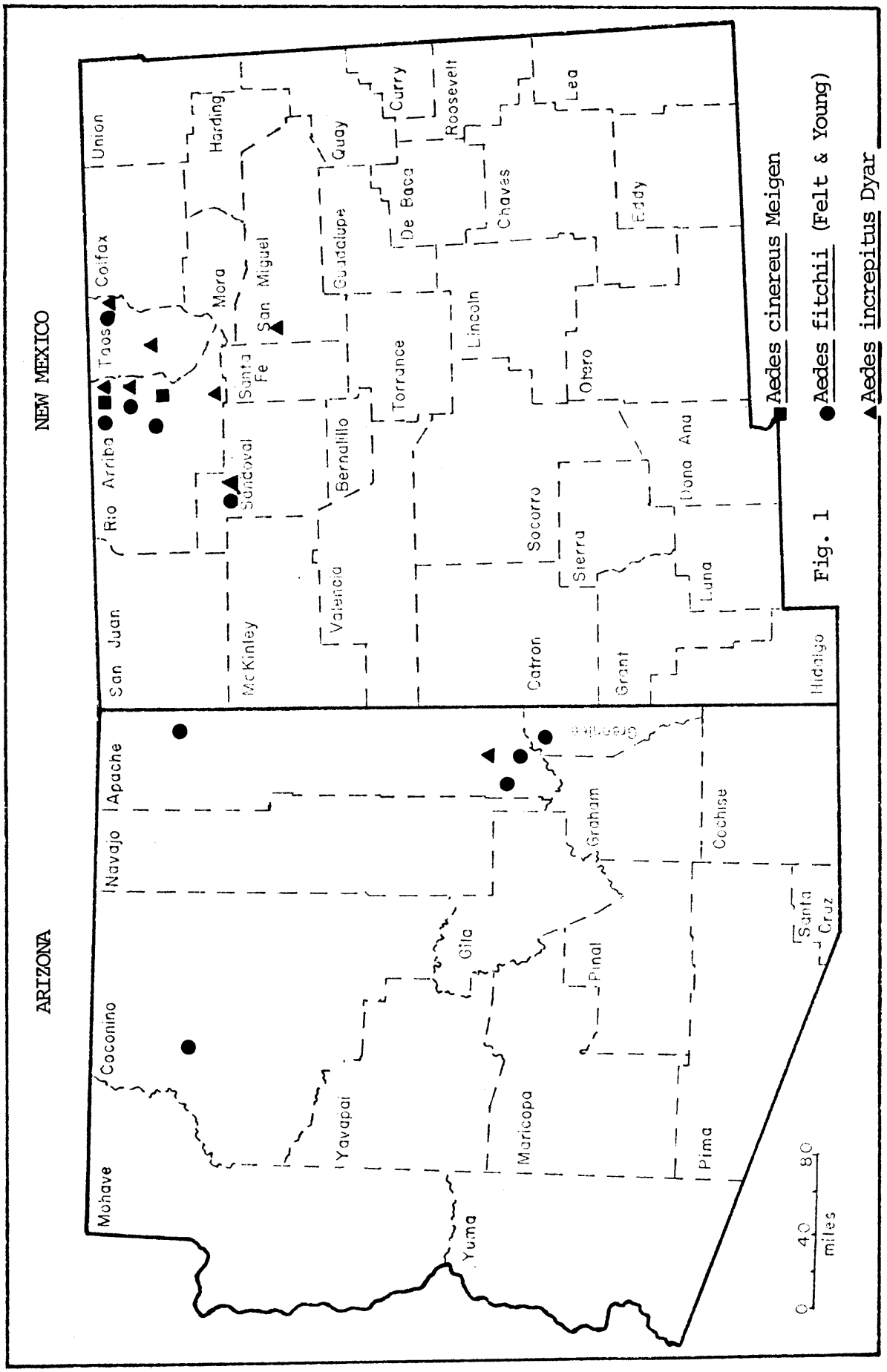
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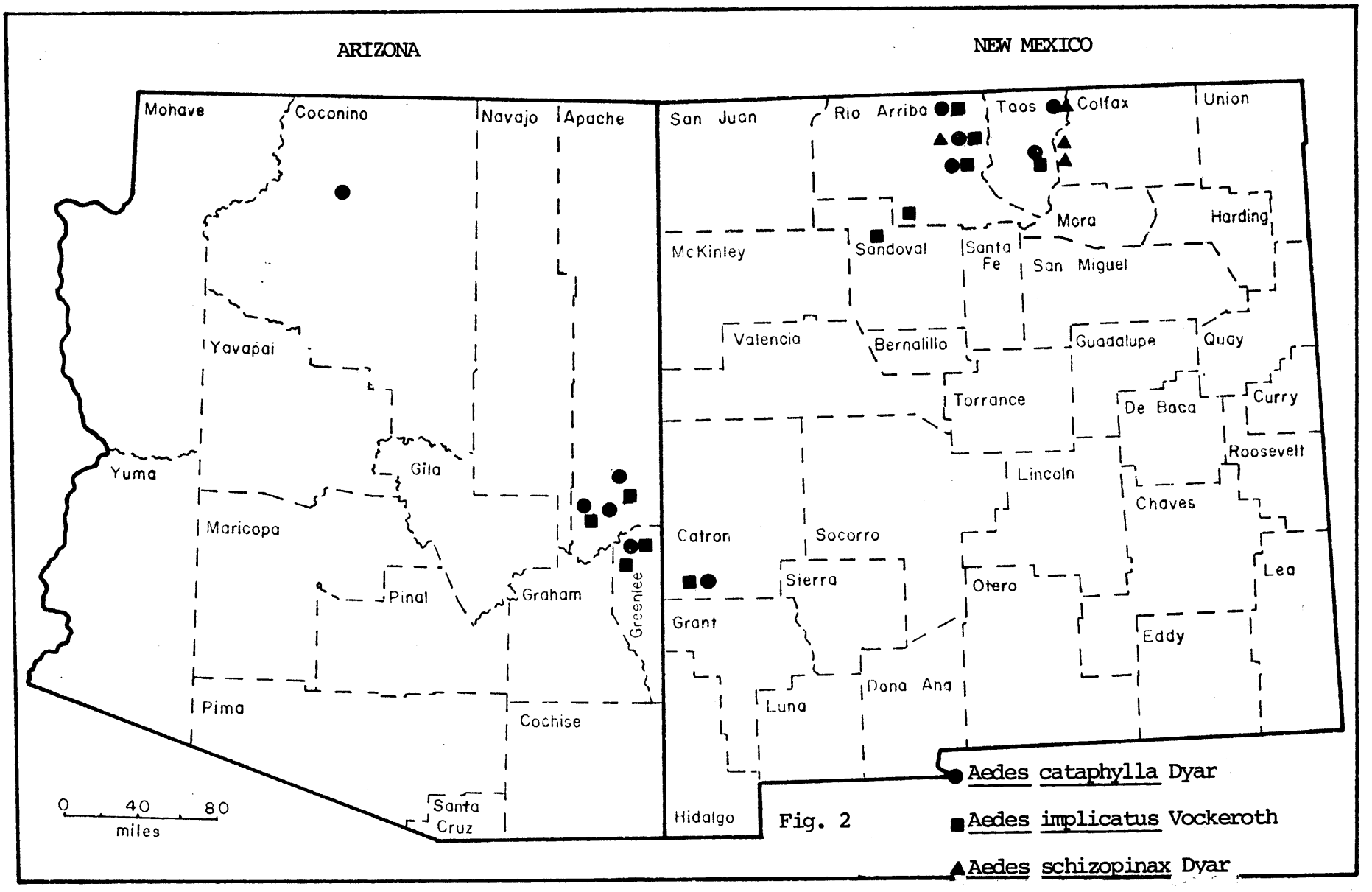
Fig. 1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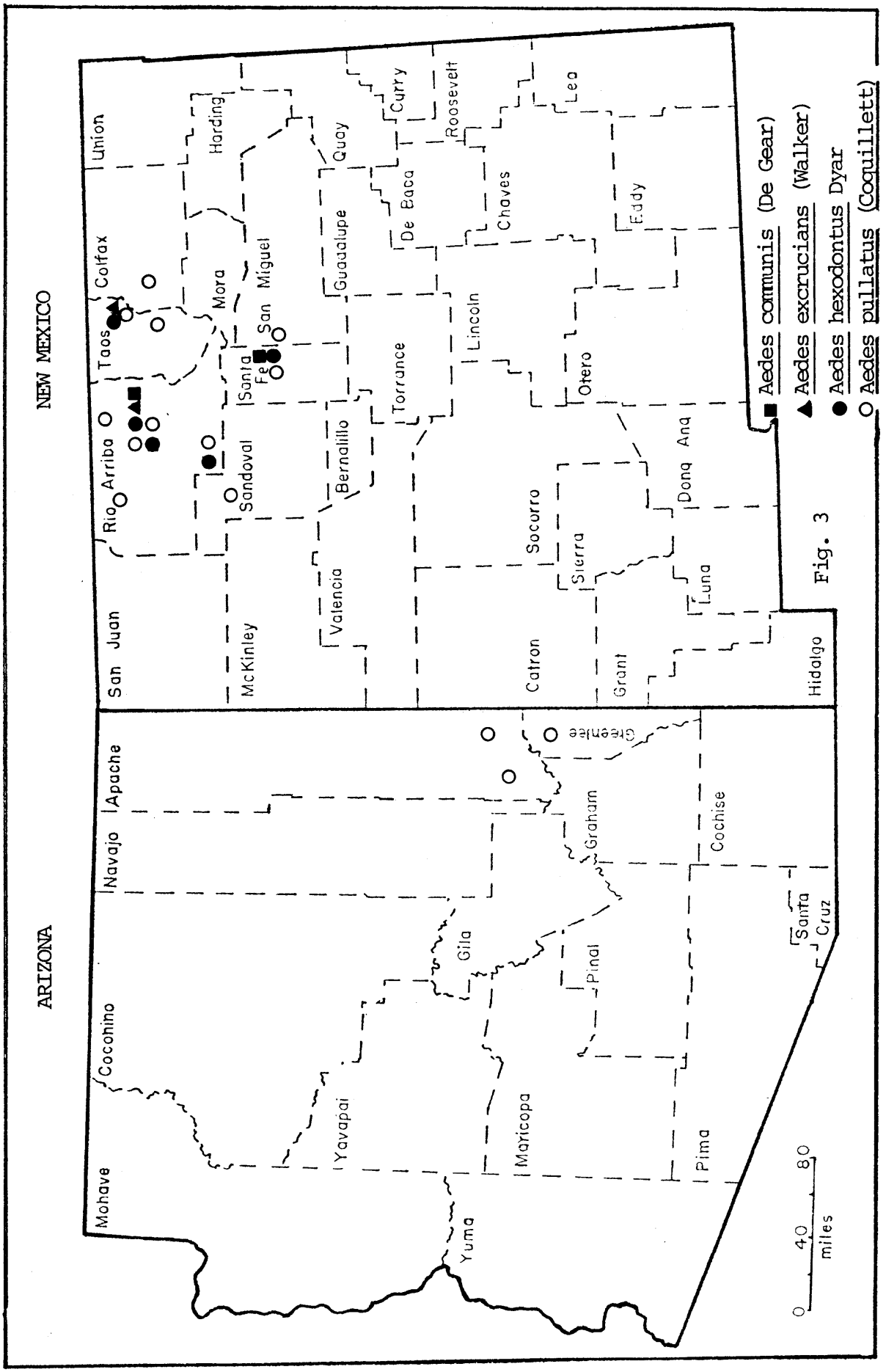
Aedes implicatus Vockeroth
Aedes schizopinax Dyar

Fig. 2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Aedes excrucians (Walker)
Aedes hexodontus Dyar
Aedes pullatus (Coquillett)

Fig. 3

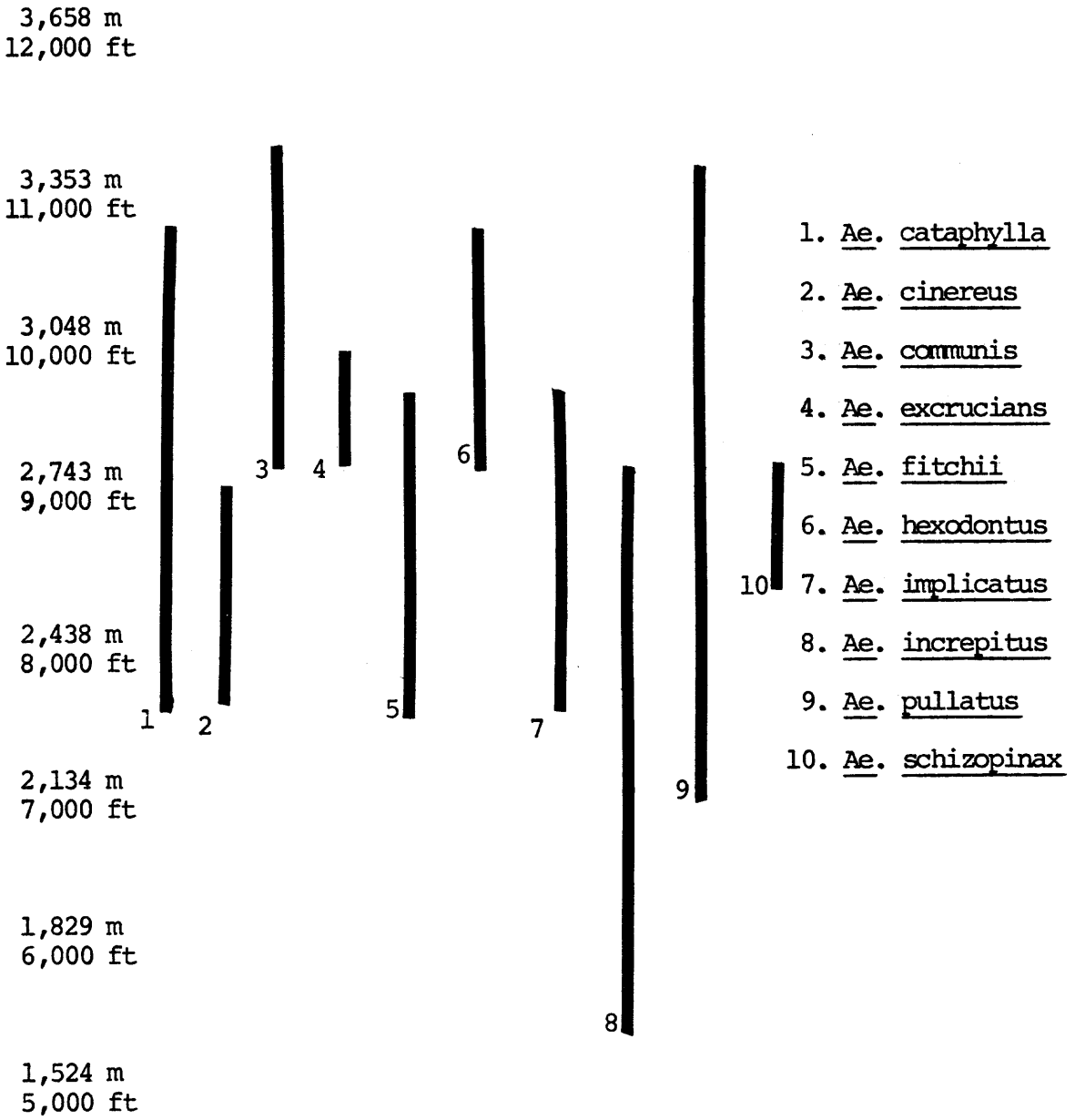

Fig. 4. - RANGE IN ELEVATION OF LARVAL HABITATS OF ARIZONA-NEW MEXICO MOUNTAIN AEDES MOSQUITOES. 1967-76.

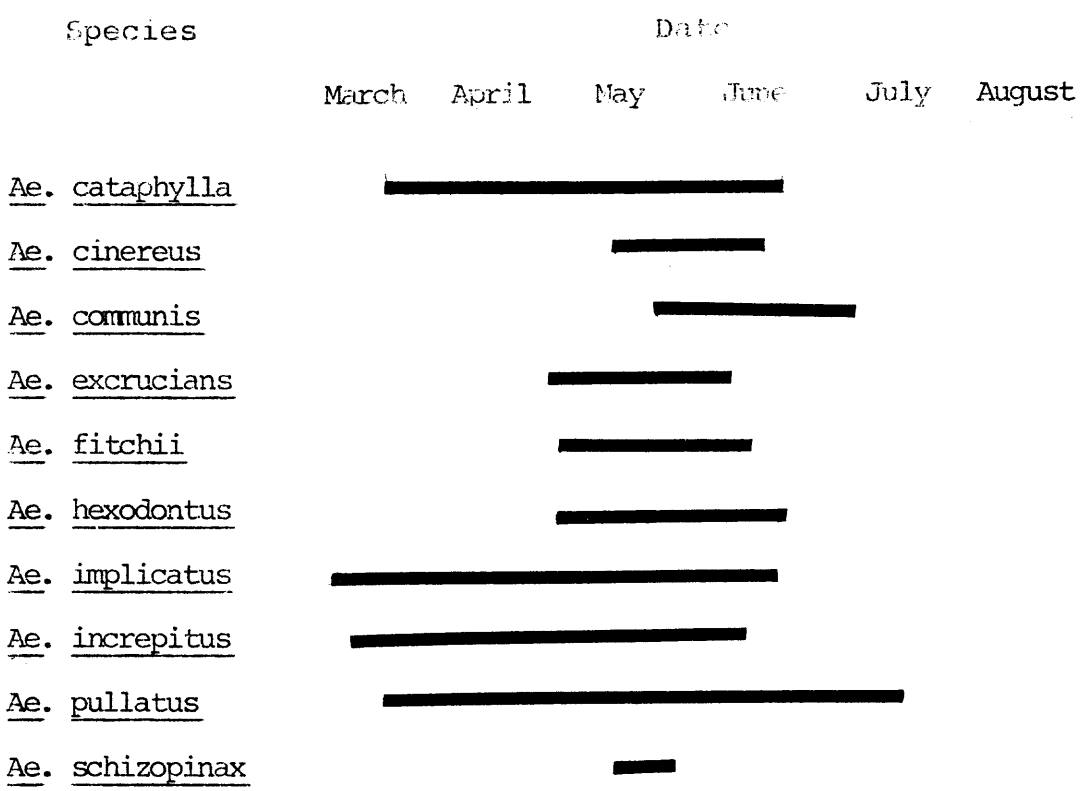

Fig. 5. SEASONAL OCCURRENCE OF AEDES MOSQUITO LARVAE IN THE MOUNTAINS OF ARIZONA AND NEW MEXICO, 1967-76.

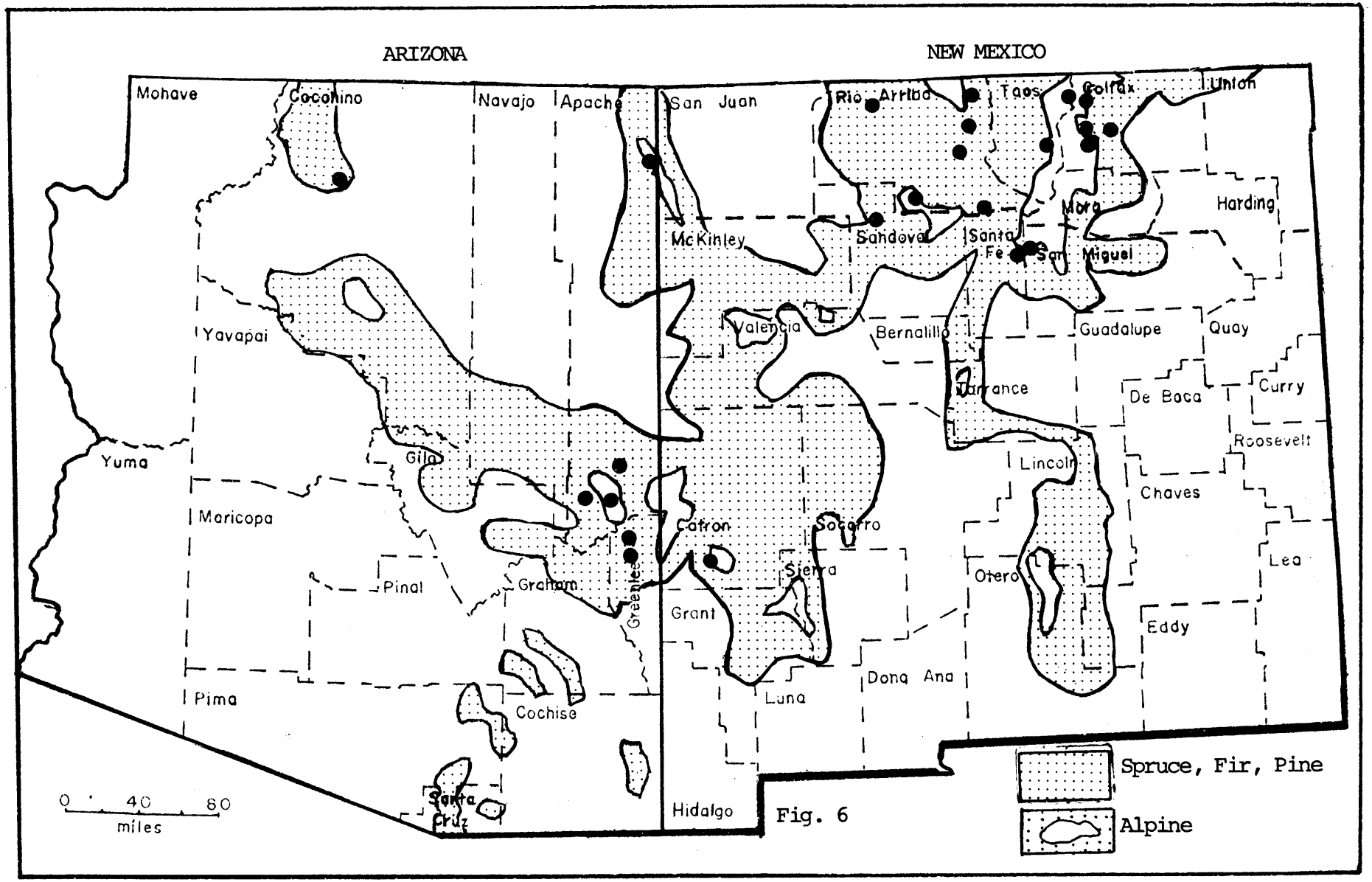

Fig. 6

Present Snowpool Aedes Distribution and reconstruction of Full-glacial Vegetation.
(Vegetation in adapted form from Martin 1964.)

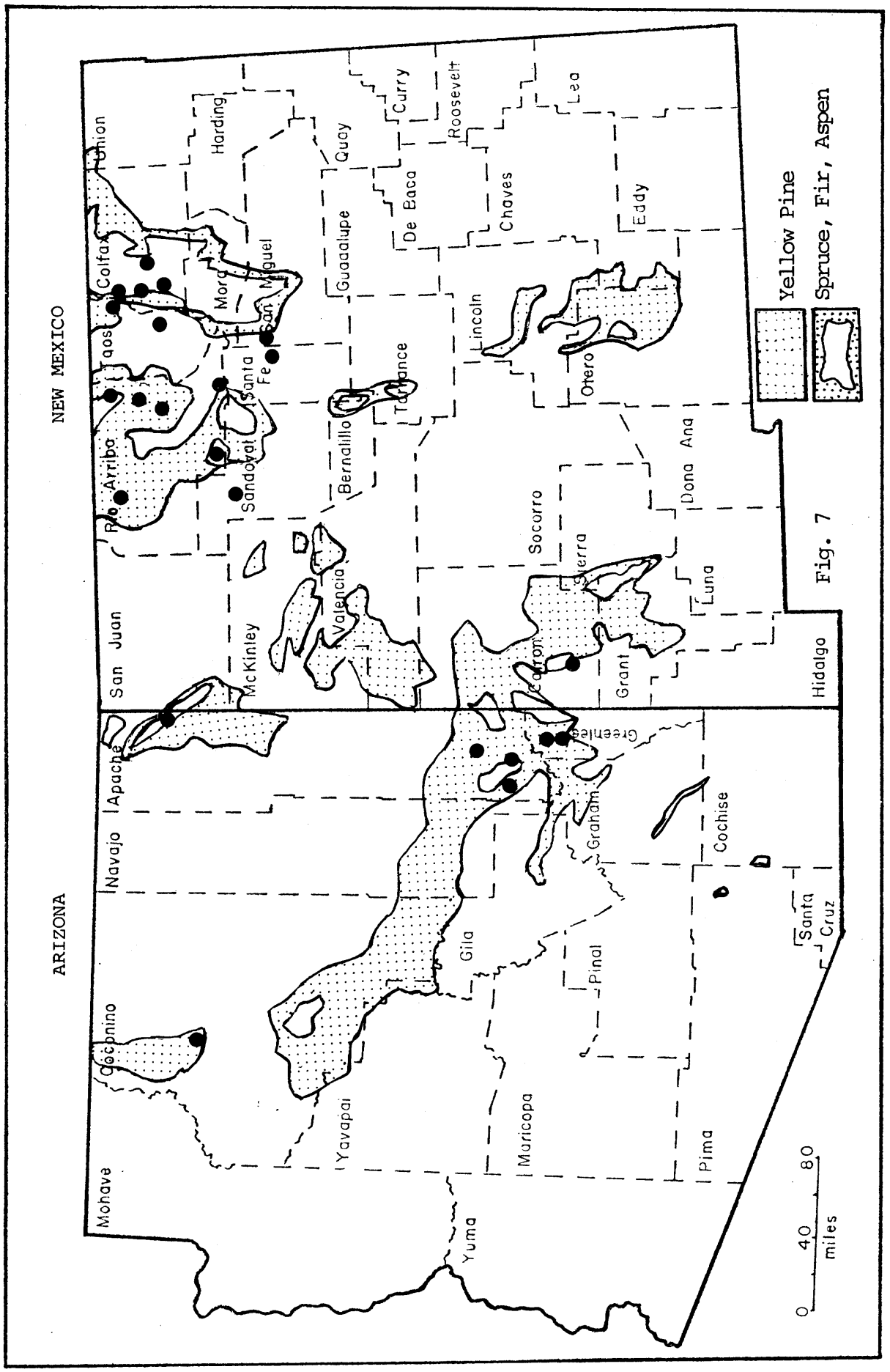

Fig. 7

Present Snowpool Aedes Distribution and Modern Distribution of Ponderosa Pine Parkland and Boreal Forest of Spruce-Fir Aspen, (Vegetation in adapted form from Martin 1964).

Species	Arizona			New Mexico			
	Chuska	Kaibab Plateau	Mogollon Rim & White	Jemez	Mogollon	Sangre de Cristo	San Juan
Ae. cataphylla		X	X		X	X	X
Ae. cinereus							X
Ae. communis						X	X
Ae. excrucians						X	X
Ae. fitchii	X	X	X	X		X	X
Ae. hexodontus				X		X	X
Ae. implicatus			X	X	X	X	X
Ae. increpitus			X	X		X	X
Ae. pullatus			X	X		X	X
Ae. schizopinax						X	X

Table 1 - Arizona-New Mexico Distribution of Mountain Mosquitoes by Mountain Range.

Elevation	No. of Collections	No. Collections Containing Each Species									
		Ae. cataphylla	Ae. cinereus	Ae. communis	Ae. excrucians	Ae. fitchii	Ae. hexodontus	Ae. implicatus	Ae. increpitus	Ae. pullatus	Ae. schizopinax
1,676 - 1,829 m 5,500 - 6,000 ft	5								5		
1,829 - 1,981 m 6,000 - 6,500 ft											
1,981 - 2,134 m 6,500 - 7,000 ft	1								1		
2,134 - 2,286 m 7,000 - 7,500 ft	2									2	
2,286 - 2,438 m 7,500 - 8,000 ft	14	1	2			2		6	7	7	
2,438 - 2,591 m 8,000 - 8,500 ft	15	6				4		4	1	5	2
2,591 - 2,743 m 8,500 - 9,000 ft	8	2				6		1		1	1
2,743 - 2,896 m 9,000 - 9,500 ft	33	16	1	4	6	9	2	9	4	15	2
2,896 - 3,048 m 9,500 -10,000 ft	23	6		2	7	6	10	2		11	1
3,048 - 3,200 m 10,000 -10,500 ft	1									1	
3,200 - 3,353 m 10,500 -11,000 ft	5	1					2			4	
3,353 - 3,505 m 11,000 -11,500 ft											
3,505 - 3,658 m 11,500 -12,000 ft	3			1						3	
Totals	110	32	3	7	13	27	14	22	18	49	6

Table 2. - Elevation of Aedes Collected, 1967-76.

	Ae. cataphylla	Ae. cinereus	Ae. communis	Ae. excrucians	Ae. fitchii	Ae. hexodontus	Ae. implicatus	Ae. increpitus	Ae. pullatus	Ae. schizopinax	Cu. tarsalis	Ch. americanus	Cs. incidens	Cs. inornata	Eu. underwoodi	Mo. velutinus
Aedes cataphylla	8		2	4	11	8	10	3	10							2
Ae. cinereus				1			1	1	2	1			1	1		1
Ae. communis				2	2	2	1	1	5	1					2	3
Ae. excrucians				2	5	5		3	3	2		1				2
Ae. fitchii					11	3	1	4	3	1			2	1		
Ae. hexodontus						4	2	1	5							1
Ae. implicatus							3	4	13				1	1		1
Ae. increpitus								8	6	2			2	2		
Ae. pullatus									19	1			5	2	2	4
Ae. schizopinax										2				1		1
Culex tarsalis												1		1		
Chaoborus americanus														2		
Culiseta incidens													7	2		
Cs. inornata														1		
Eucorethra underwoodi																
Mochlonyx velutinus																

Table 3. - Larval Associations for Mosquitoes Collected in the Mountains and Mountain Valleys of the American Southwest, 1967-76.

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