THE DISTRIBUTION OF SOUTHWEST NORTH AMERICAN MAYFLY GENERA (EPHEMEROPTERA) IN THE MEXICAN TRANSITION ZONE

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ABSTRACT

Halffter (1976), in an attempt to explain the origin and dispersal of Neotropical insects in North America, developed a theory of reference models, with which the distribution of a given group can be compared. He characterized dispersal in the Mexican Transition Zone (the southern U.S., Mexico and most of Central America), and grouped patterns by origin as follows: the boreal Paleo-american and Nearctic Patterns, and the austral Ancient South American and Typical Neotropical Patterns, and stated that some groups fit these patterns poorly or not at all. Southwest genera are ideal subjects to test the fit of mayflies to these models, and it is concluded that they fit three of the four models very well. Genera of recent boreal origin do not fit the Nearctic Pattern criteria, except for three species, but fit their own unique pattern with their own criteria. Those that fit the Paleo-american Pattern have disjunct distributions in Mesoamerica and North America north of Mexico; those that fit the Ancient South American Pattern have a nearly equal number of species in South America, Mesoamerica and North America; and those that fit the Typical Neotropical Pattern have more species in South America, fewer in Mesoamerica and still fewer in North America.

INTRODUCTION

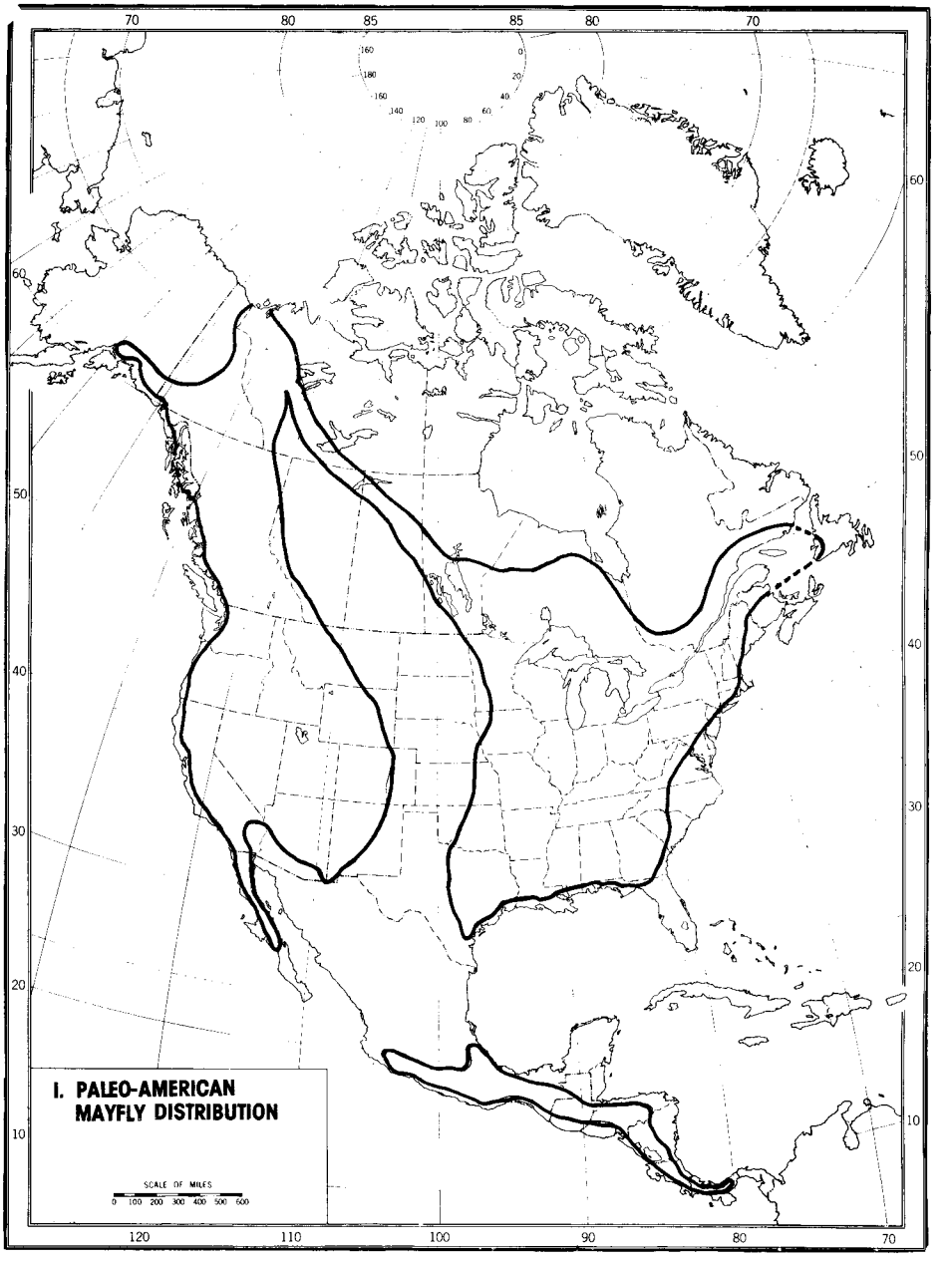
From the standpoint of systematics, the Ephemeroptera of the Southwest of North America are well understood with a sound knowledge of the taxonomy of the fauna and its composition, and an understanding of the patterns of distribution of the North and Central American species. The fauna is diverse and referable to 7 families, 29 genera and 80 species, of which 37 (46 percent) are endemic to this geographical area.

Halffter (1976), in an attempt to explain the origin of the present Neotropical insect fauna and its expansion in North America, developed a theory of reference concepts, or models, with which the actual distribution of a given group of insects can be compared. He characterized dispersal patterns that insects assume in what he called the Mexican Transition Zone (MTZ). He defined the zone as a complex and varied overlapping area of Neotropical and Nearctic faunas which includes the southern United States. Mexico, and most of Central America. He grouped the dispersal patterns according to origin as follows:

1. the boreal paleo-american pattern;
2. the boreal nearctic pattern;
3. the austral ancient south american pattern;
4. and the austral typical neotropical pattern.

Halffter stated that the distributions of some insect groups fit poorly, or not at all, into these patterns, but that these were a minority of the entomofauna. The mayfly genera whose species

I.C. Campbell (ed.) Mayflies and Stoneflies, 169–180.



Map I. Paleo-American mayfly distribution.

make up the Southwest Distribution Pattern have been thoroughly examined during extensive field work over the last 20 years, and they appear to be ideal subjects to test the fit of mayflies into these models. The Southwest is within the geographical limits of the MTZ, and the fauna is composed of Neotropical and Nearctic elements.

Fifteen of the Southwest genera are considered to be boreal and 8 austral. The taxonomy and origin of *Baetis* Leach, *Callibaetis* Eaton, *Centroptilum* Eaton and *Caenis* Stephens are not well understood in the MTZ, especially tropical Mexico and Central America, so they are not included in this study.

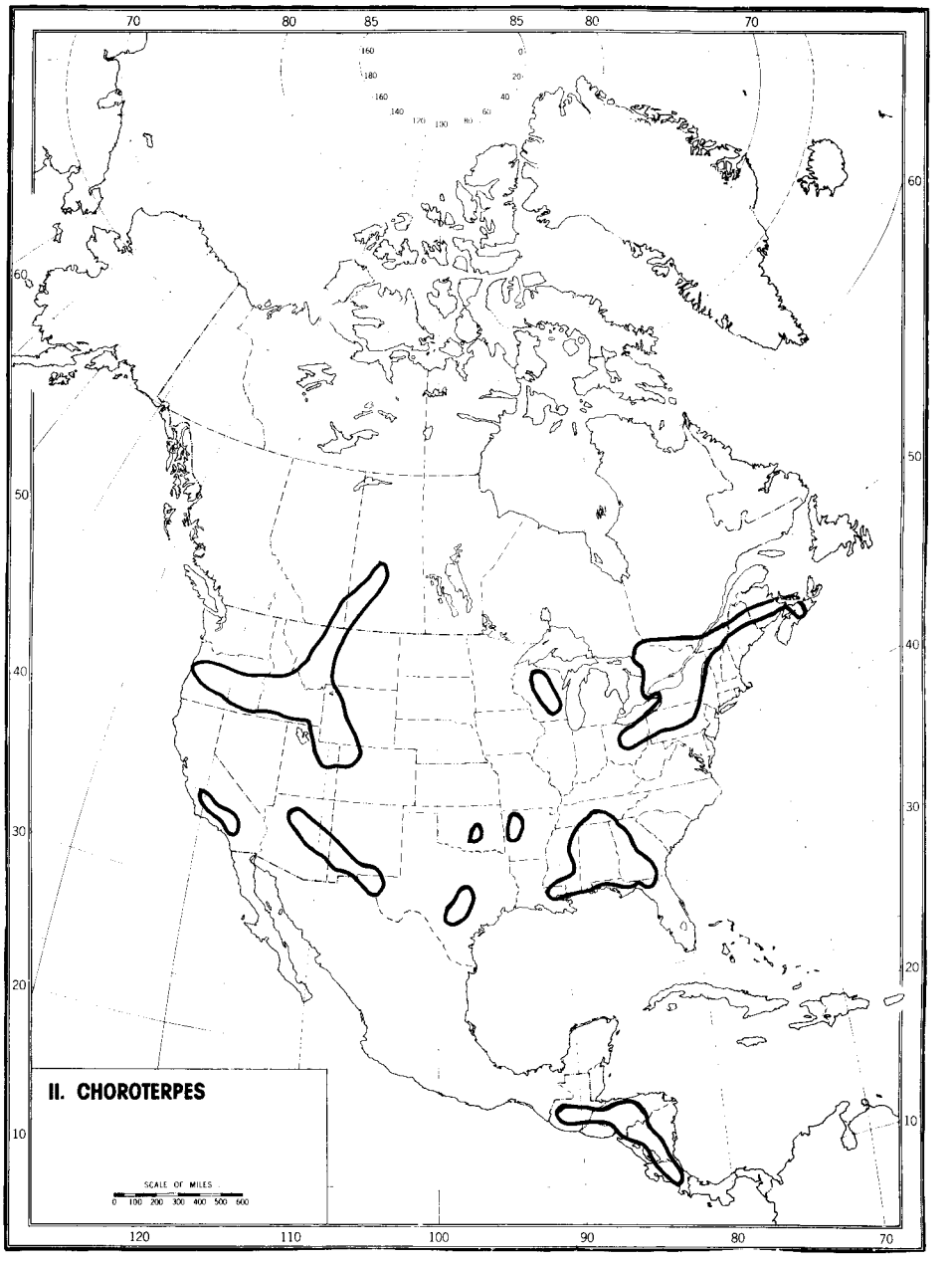
THE PALEO-AMERICAN DISPERSAL PATTERN

This (Map I) includes groups with Old World origins that have had an ancient penetration from the north, and they have a greater richness and diversity in the Old World than in America. In some cases, it is diffcult to determine whether the group originated in America or the Old World. Prior to the Miocene, before desertization in western North America, these groups occupied the Mexican Plateau. In the MTZ, the insects are not necessarily limited to the mountains, and they may extend to South America and the Antilles.

Choroterpes Eaton, *Iron* Eaton, *Heptagenia* Walsh, and *Rhithrogena* Eaton appear to meet the criteria of this dispersal pattern. They all are widely distributed in the world, and they are widely distributed in North and Central America. The distributional range in the new World is from the Arctic Zone (60° + N) to the Upper Tropical Zone (0°–10°N) (see Allen 1980). The known distribution of the species, and the number of described species in the Old World compared to the New, suggests that *Choroterpes, Heptagenia,* and *Rhithrogena* originated in the Old World, and the origin of *Iron* may have been in America. Their penetration into the MTZ appears to have been a long time ago as they each have southern Mexican and/or Central American populations which are now geographically isolated from populations in North America north of Mexico.

Iron is widely distributed in North and Central America from the Northwest Territories, in northern Canada, to Panama, and six species have penetrated into the MTZ. *Iron margarita* (Edmunds and Allen) is endemic to the Southwest, and occurs from central Arizona (*ca.* 35°N) to Baja California (26°03'N), and *I. albertae* (McDunnough), *I. deceptivus* (McDunnough), and *I. longimanus* Eaton are widely distributed in western North America and reach their southern distributional limits in southern California, Arizona and New Mexico. *Iron metlacensis* (Traver) and *I. packeri* (Allen and Cohen), form the Mesoamerican element of the genus and they occur in the MTZ from Moralia, Mexico (19°40' N) to Costa Rica (9°28'N). *Heptagenia* is distributed in North and Central America from central Saskatchewan to Veracruz, Mexico, and four species occur in the MTZ. Three, *H. elegantula* Eaton, *H. simplicioides* (McDunnough), and *H. solitaria* (McDunnough) are widely distributed in western North America to southern California, Arizona and New Mexico. *Heptagenia bella* Allen and Cohen represents the Mesoamerican population in the MTZ, and it occurs only in Veracruz, Mexico (19°N). *Rhithrogena* is distributed in North and Central America from the Northwest Territories to Guatemala, and six species have penetrated the MTZ. *Rhithrogena hageni* Eaton, *R. morrisoni* (Banks), and *R. undulata* (Banks) are widely distributed in western North America to southern California, Arizona and New Mexico; *R. plana* Allen and Chao and *R. vitta* Allen and Chao are endemic to the Southwest, in Arizona (34°–35°N); and *R. notialis* Allen and Cohen represents the Mesoamerican population and is known from Michoacan, Mexico (19°14'N) to Guatemala (14°40'N). The pattern of distribution of these genera (Map I) are distinguished from that of the other genera as they have a Mesoamerican population, an Eastern North American population, and a Western North American population, which are disjunct except for some species in the Northwest Territories. Eastern and western North American species occur together in the Mackenzie River. Species also occur in all of the western deserts except the Chihuahuan.

Choroterpes is distributed in North and Central America from central Saskatchewan and Nova Scotia to Costa Rica, and nine species have penetrated the MTZ. *Choroterpes terratoma* Seemann occurs as far south as the Southwest in southern California; *C. kossi* Allen is endemic to the Southwest, in Arizona (35°18'N), New Mexico and western Texas (31°30'N); and *C. crocatus* Allen and *C. nanita* Traver are known from the MTZ in Texas. *Choroterpes atramentum* Traver, *C. nervosa* Eaton, and *C. vinculum* Traver form the southern element of the genus in the MTZ and they occur only in Central America from Guatemala (14°38' N) to Costa Rica (9°39'N). The other two species, *C. inornata* Eaton and *C. mexi-*

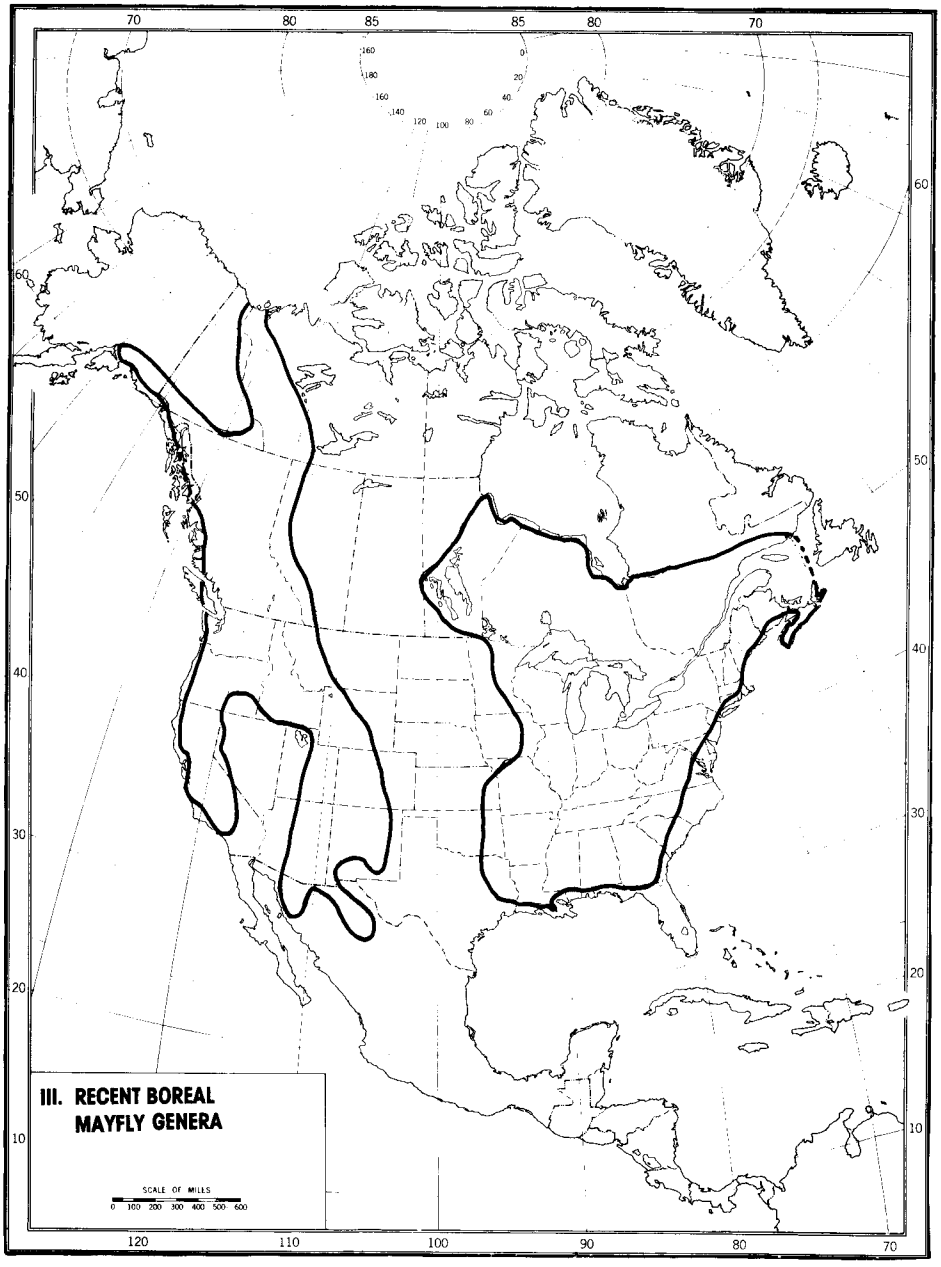


Map II. Choroterpes.

cana Allen, have continuous distributions in the MTZ and are discussed in the following model. The *Choroterpes* that appear to fit this dispersal model, and whose pattern of distribution is generally the same as the heptageniid genera discussed above, occur in what appear to be relict populations in Mesoamerica, and in eastern and western North America (Map II).

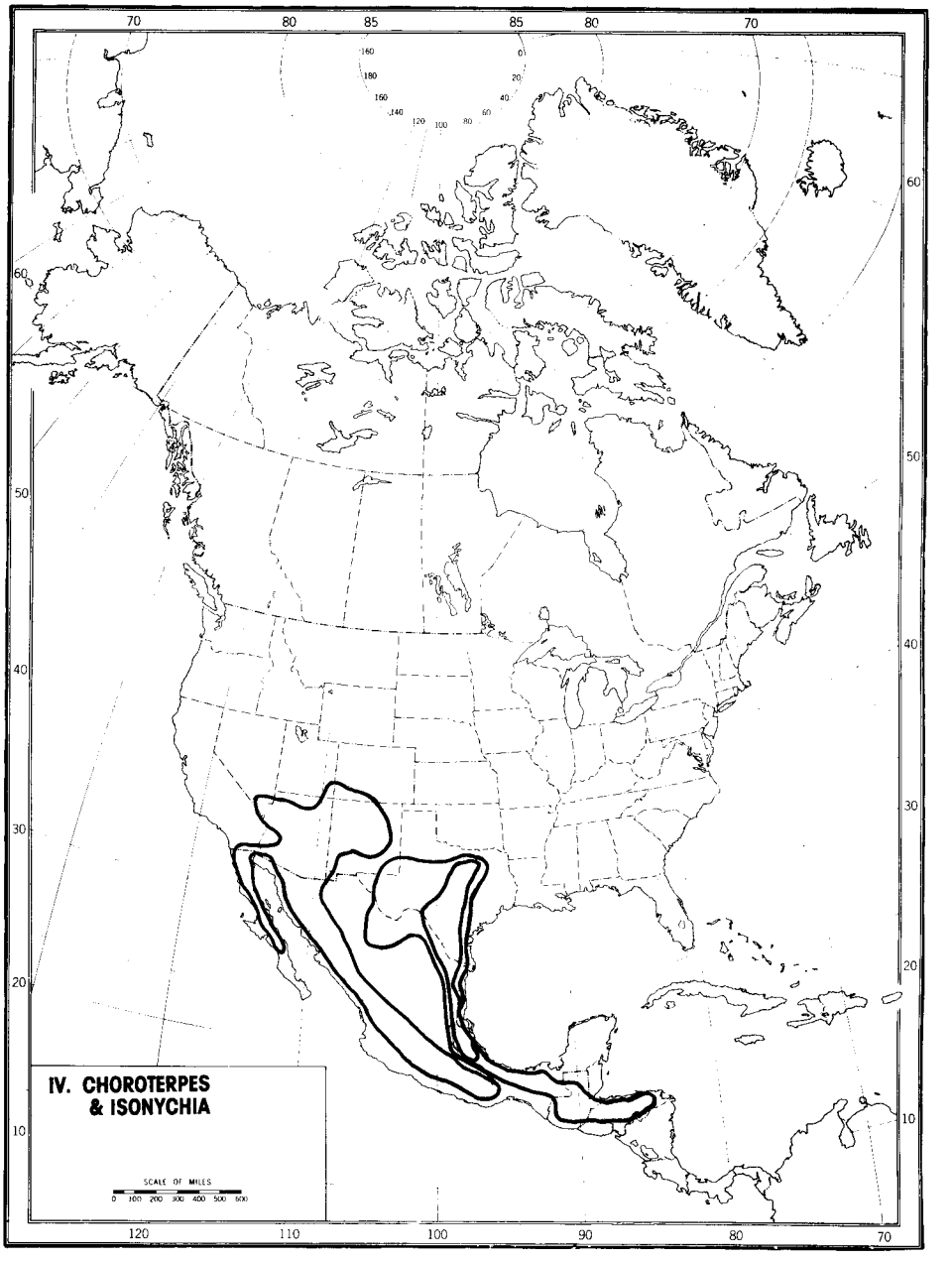
THE NEARCTIC DISPERSAL PATTERN

This pattern is expressed by species of Holarctic and Nearctic genera of recent penetration (Pliocene-Pleistocene) into the MTZ. Inside the zone they are restricted almost exclusively to the mountain systems of Mexico and northern Central America, and the barrier that limits dispersal seems to be the low tropical plains around Lake Nicaragua.



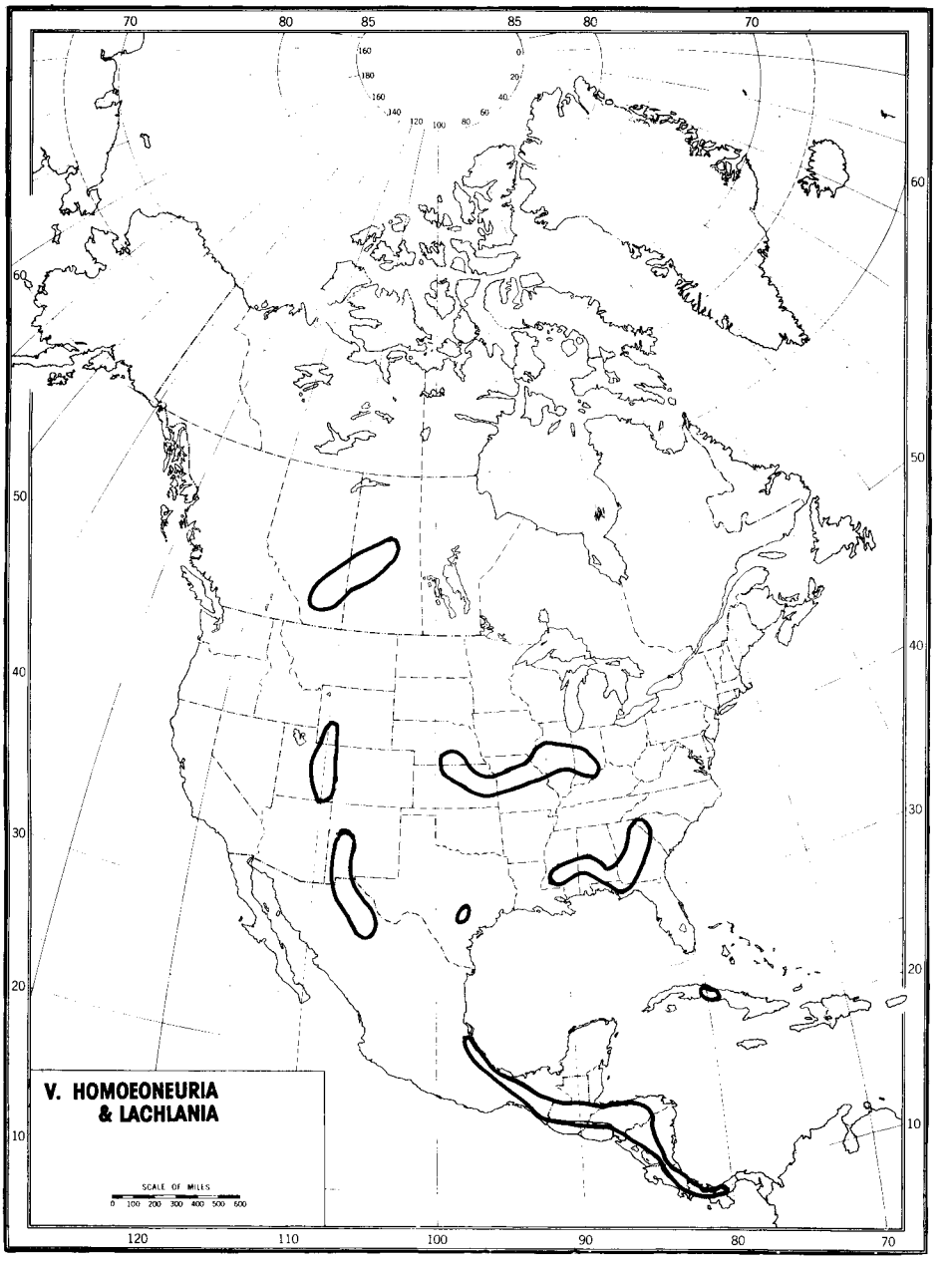
Map III. Recent boreal mayfly genera.

Species of eight genera are presumed to have had a boreal origin, and to have had a recent penetration into the MTZ, but only three of their species fit the distributional criteria of the model. The remaining species apparently do not fit the model as they do not really penetrate the MTZ. The distributional limits inside the zone, are the mountain systems of Southern Californa, Arizona, New Mexico, and Northern Mexico, and the barrers that limit dispersal appear to be the warm Mexican coastal streams in northern and central Mexico. All of the genera are holarctic. *Ameletus falsus* (McDunnough) *Cinygmula par* Eaton, *Drunella doddsi* Needham, *D. flavilinea* (McDunnough), *D. grandis* (Eaton), *D. pelosa* (Mayo), *D. spinifera* (Needham), *Ephemerella inermis Eaton, E. maculata* Traver, *E. mollitia* Seemann, *Paraleptophlebia memorialis* Eaton, *Ser-*



Map IV. Choroterpes & Isonychia.

ratella micheneri (Traver), *S. teresa* (Traver), *S. tibialis* (McDunnough), and *Siphlonurus occidentalis* Eaton are all distributed in western North America to the Southwest, but to only the very northern limits of the MTZ. *Ephemerella altana* Allen (35°34'–33°51'N) and *Isonychia intermedia* Eaton (35°12'–28°40'N) are endemic to the Southwest. These genera appear to share a common dispersal model in North America (Map 3) as they occur from the Arctic Zone to the Middle North Temperate Zone (30°–40°N). Their pattern of distribution is characterized by disjunct eastern and western North American populations whose most southern distributional limits are in the gulf states in the east, and in Sonora, Mexico and southern California in the west. In western North America, species are present in only the marginal regions of the southern deserts, and in



Map V. Homoeoneuria & Lachlania.

only the mountainous parts of the Great Basin.

Three species, from genera of presumed ancient penetration into the MTZ, have a continuous distribution from the southern United States through the MTZ to southern Mexico and/or Central America (Map IV), and they appear to fit the distributional criteria of this model. *Isonychia manca* Eaton is distributed from Texas (31°47'N) to Guatemala and Honduras (14°05'N); *Choroterpes mexicanus* Allen is known from Texas (32°45'N) to Veracruz, Mexico (20°34'N); and *C. inornata* Eaton has a continuous distribution in the MTZ in western Northern America from southern Colorado (37°16'N) to Oaxaca, Mexico (17°05'N).

THE ANCIENT SOUTH AMERICAN DISPERSAL PATTERN

This pattern (Map V)) includes insects that originated from South American immigrants which arrived between the late Mesozoic and the Miocene. Penetration in the United States was deep and important, and in some groups, the elements contribute a very important part of all genera east of the 100th meridian.

Species of *Dactylobaetis* Traver and Edmunds, *Homoeoneuria* Eaton, *Lachlania* Hagen, *Traverella* Edmunds, and *Tricorythodes* Eaton, have penetrated deeply into North America and all occur above 41°N. The distributional limits in North and Central America are from Panama in the Upper Tropical Zone to the Northwest Territories in the Arctic Zone.

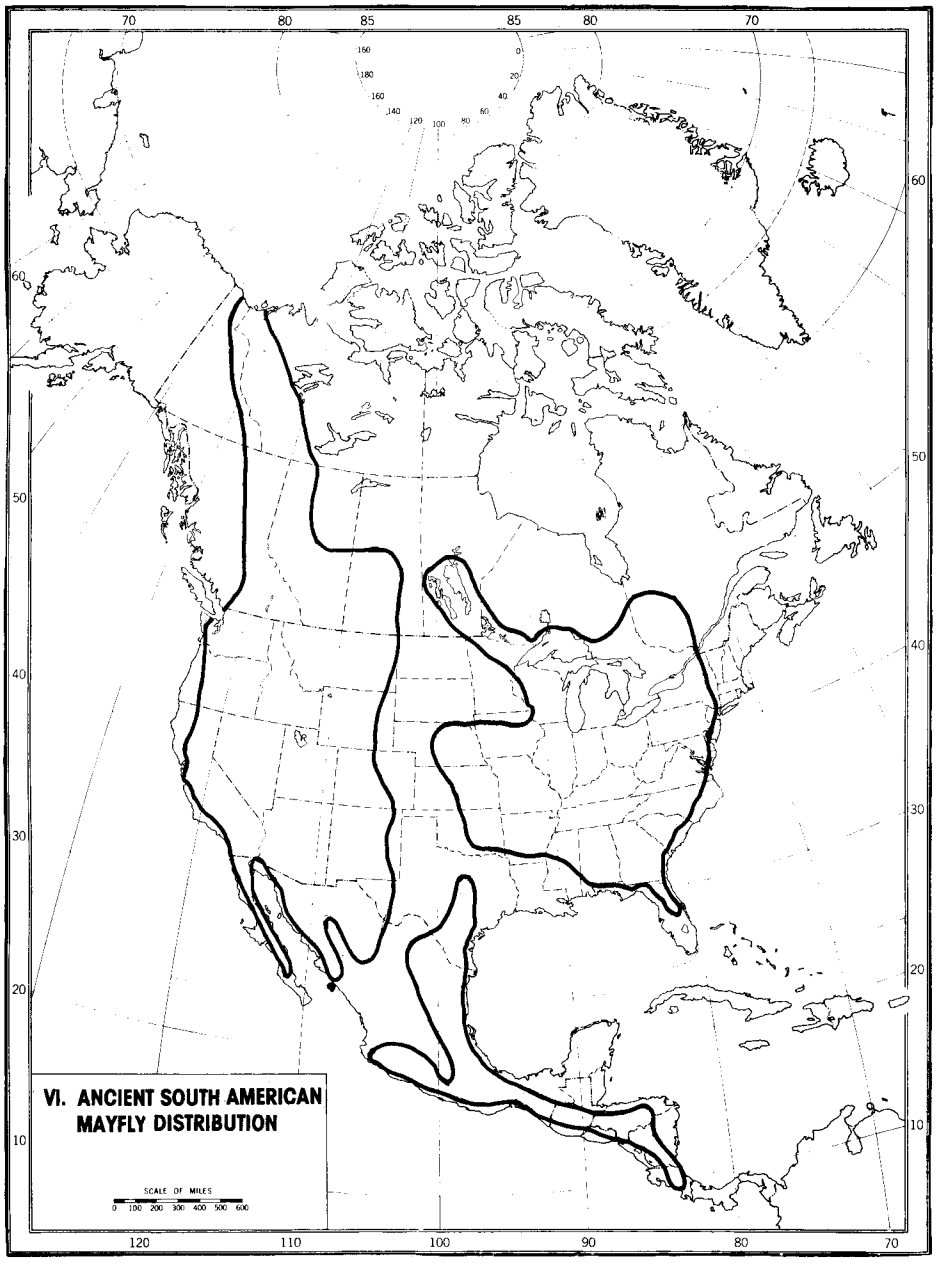
Dactylobaetis is known from five described species in South America, six in Mesoamerica, and five in North America north of Mesoamerica, and all are distributed west of the 100th meridian. The northern distributional limit of the genus is in Idaho (44°N). *Dactylobaetis navis* Allen and Chao, *D. salinus* Allen and Chao, and *D. trivialis* Allen and Chao, are endemic to the Southwest, in Arizona and New Mexico (32°42'–36°46'N), *Dactylobaetis mexicanus* Traver and Edmunds is known in the MTZ from Tamaulipas, Mexico (23°43'N) to Texas (32°45'N), and the six Mesoamerican species are distributed from Honduras (14°05'N) to Veracruz, Mexico (19°15'N).

Homoeoneuria has only one described species in South America, one in Mesoamerica, and four in North America north of Mesoamerica. One species occurs west of the 100th meridian, and three occur in the east. The northern distributional limit of the genus is Illinois and Indiana (41°N). *Homoeoneuria alleni* Pescador and Peters, is distributed in the MTZ from Chihuahua, Mexico (28°40'N) to southern Utah (37°06'N), and *H. salviniae* Eaton is distributed in Mesoamerica, from Guatemala (14°38'N) to Chiapas, Mexico (16°40' N). *Lachlania* is composed of 12 species, five from South America, one from Cuba, four from Mesoamerica, and two from North America north of Mesoamerica. The most northern distributional limit of the genus is in Saskatchewan (52°N), and in the United States and Canada the genus occurs only west of the 100th meridian. *Lachlania dencyanna* Koss is endemic to the Southwest, and occurs from New Mexico (32°47'N) to Chihuahua, Mexico (28°45'N), and *L. fusca* (Navas) and *L. lucida* Eaton are distributed in Mesoamerica, from Panama (9°14'N) to Veracruz, Mexico (20°22'N). The pattern of distribution of *Homoeoneuria* and *Lachlania* in North and Central America (Map VI) is similar to that of the boreal *Choroterpes* as it is made up of isolated disjunct populations.

Traverella is composed of five species in South America, three in Mesoamerica, and four in North America north of Mesoamerica. Two species occur east of the 100th meridian, and two occur west. *Traverella albertana* (McDunnough) is known from Alberta (52°45'N) to Arizona, and *T. castanea* Kilgore & Allen is endemic to the Southwest, in Arizona and New Mexico (32°36'–35°41'N). *Traverella presidiana* Traver occurs in the MTZ from Tamaulipas, Mexico (23°47'N) to Texas (31°49'N), *Traverella* sp. "A" Allen is known from Guatemala (14°40'N) to Jalisco, Mexico (20°33'N), and *Traverella sp.* "C" Allen occurs from Honduras (14°07'N) to Nuevo Leon, Mexico (25°42'N).

Tricorythodes is a moderately large genus with nine species in South America, six in Mesoamerica, and 13 in North America north of mesoamerica. Eight species occur east of the 100th meridian, and five are distributed west. *Tricorythodes minutus* Traver occurs from southern California, Arizona and New Mexico to the Northwest Territories (68°14'N). *Tricorythodes dimorphus* Allen, *T. condylus* Allen, *T. corpulentus* Kilgore and Allen and *T. explicatus* Eaton are endemic to the Southwest, and known from Sinaloa, Mexico (24°50'N) to southern California, Arizona and New Mexico (34°07'N). The six Mesoamerican species are known only from southern Mexico.

The pattern of distribution of all the genera that fit this model are similar to those that fit the Paleoamerican pattern as they have disjunct Mesoamerican, western North American, and eastern North American populations. They differ, howev-

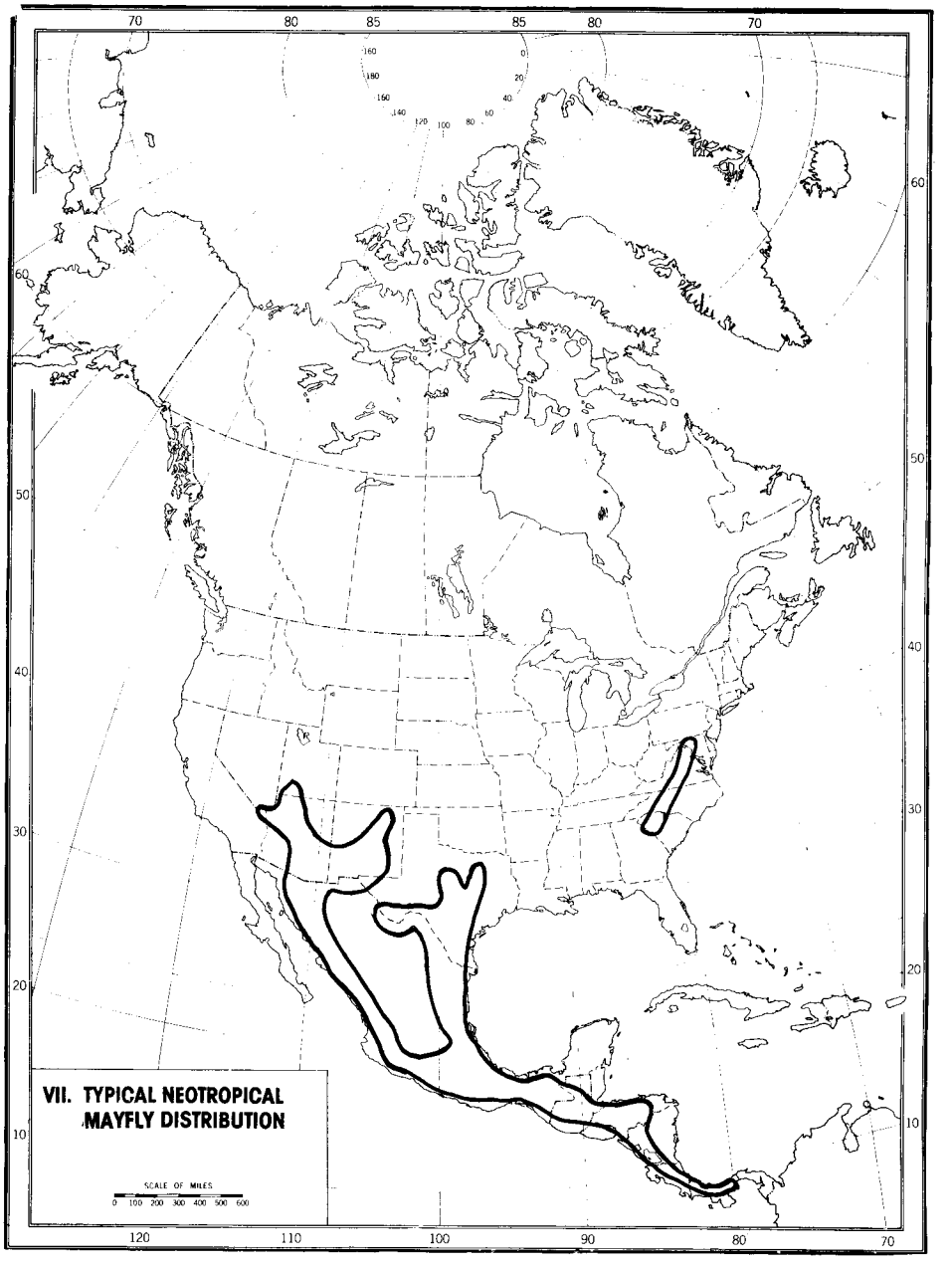


Map VI. Ancient South American mayfly distribution.

er, as some Mesoamerican species occur as far north as the United States, and western North American species occur in all of the western deserts to Baja California, Sonora, and Sinaloa (Map V).

THE TYPICAL NEOTROPICAL DISPERSAL PATTERN

This pattern (Map VII) includes insects that have had a recent penetration into the MTZ from South America (beginning at the end of the Pliocene). Northern expansion took place after the elevation of the Mexican Plateau. Their dispersal has been limited by the Sonoran Desert



Map VII. Typical neotropical mayfly distribution.

with a narrow penetration into the United States. On the other hand, the gulf coastal plain has been favorable for penetration towards the north.

The present distribution of *Baetodes* Traver and Edmunds, *Leptohyphes* Eaton,and *Thraulodes* Ulmer suggest that they have had a recent penetration into the MTZ. All have a limited distribution into the United States to only southern Utah (37°N). All have a continuous distribution in the maritime corridor on the Mexican gulf coast from southern Mexico to Texas, and species occur on the Pacific coastal plain from southern Mexico to Arizona and New Mexico (Map VII).

Twelve species of *Baetodes* are known from South America, 13 from Mesoamerica, and only two from North America north of Mexico. The North American species, *B. arizonicus* Koss is endemic to the Southwest (35°12'N), and *B. ed-*

mundsi Koss occurs in Arizona and in Texas (29°45'N). The Mesoamerican species occur from Panama (8°N) to Neuvo Leon and Tamaulipas, Mexico (25°N).

Leptohyphes is a large genus with 34 species in South America, 22 in Mesoamerica, and 10 in North America north of Mesoamerica. The northern limits of the genus is in southern Utah (37°N). *Leptohyphes apache* Allen, *L. miris* Allen, *L. quercus* Kilgore and Allen, are endemic to the Southwest. Two species have a wide latitudinal distribution in the MTZ, and are known from Central America to the Southwest. *Leptohyphes ferruginus* Allen is known from Honduras (14°03'N), Veracruz and Sonora, Mexico, to Arizona (33°32'). *Leptohyphes packeri* Allen occurs from Honduras (14°05'N) and Guatemala, on the Mexican gulf coast in Veracruz and Tamaulipas, in Neuvo Leon, and to Texas (34°30'N). It also has a continuous distribution on the west coast of Mexico from Chiapas (16°45'N) to Sonora, and to Arizona (34°50'N). *Leptohyphes michaeli* Allen, *L. pilosus* Allen, *L. paraguttatus* Allen, and *L. sabinas* Traver, occur in the MTZ from eastern Mexico to Texas.

Nineteen species of *Thraulodes* are described from South America, sixteen are known from Mesoamerica, and seven occur in North America north of Mesoamerica. *Thraulodes brunneus* Koss, *T. salinus* Kilgore and Allen, and *T. speciosus*-Traver are endemic to the Southwest, in Arizona and New Mexico. *Thraulodes arizonicus* McDunnough has a wide latitudinal distribution in the MTZ and is known from Honduras (14°05'N) to Veracruz and up the Mexican gulf coast to Tamaulipas and Neuvo Leon (26°33'N). This species also occurs on the west coast of Mexico from Chiapas (16°39'N) to Sonora and Chihuahua and Arizona (35°12'N). *Thraulodes gonzalesi* Traver and Edmunds is distributed in the MTZ from Tamaulipas, Mexico (23°43'N) to Texas (32°27'N), *T. lunatus* Traver and Edmunds is known from Tamaulipas and Neuvo Leon, and *Thraulodes* sp. "B" Allen is known from Chiapas to Nuevo Leon. The pattern of distribution of the species in these genera is continuous from Panama to the southern United States, and the northward dispersal appears to be limited by the western deserts (Map VII).

Caudatella Edmunds, *Ironodes* Traver, and *Nixe* Flowers evolved in North America and one species of each genus occurs in the Southwest and the MTZ. *Nixe (Akkarion),* and the other two genera are restricted to western North America and *Nixe (Nixe)* occurs only in eastern North America. *Caudatella heterocaudata* McDunnough, *Ironodes nitidus* (Eaton) and *Nixe rosea* Traver are in southern California; and *Nixe salvini* Kimmins is endemic to the Southwest, and is known only from northern Sonora, Mexico.

Stenonema Traver also evolved in North America, and although the genus does not occur in the Southwest, *S. mexicana* (Ulmer) is known in the MTZ from Tabasco, Mexico (18°01' N) to Panama (9°21' N).

CONCLUSION

I conclude that: (1) the distribution of the Southwest mayfly genera in the MTZ appears to fit very well in three of the four reference models; (2) the patterns of distribution of all of the genera that fit in each dispersal model are unique and distinctive; (3) the genera that were compared to the Paleo-american fit very well; (4) in *Choroterpes,* most of the North and Central American species fit the Paleo-american model, but two *C. mexicanus* and *C. inornata,* along with *Isonychia manca,* fit the Nearctic model; (5) *Ameletus* Eaton, *Drunella* Needham, *Ephemerella* Walsh, *Isonychia* Eaton, *Paraleptophlebia* Lestage, *Serratella* Edmunds, and *Siphlonurus* Eaton do not fit the distributional critera of the Nearctic model, but appear to have their own dispersal model in North America; (6) genera that were compared to the Ancient South American model fit well, and are characterized by having, essentially an equal distribution of species in the Americas with a total 25 species in South America, 19 in Mesoamerica, and 28 in North America, north of Mesoamerica; and (7) the genera that were compared to the Typical Neotropical model fit the criteria well, and are characterized by having an unequal distribution of

species in the Americas with a total of 65 South American species, 48 Mesoamerican, and only 17 North American.

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