DISTRIBUTION PATTERNS OF NORTH AND CENTRAL AMERICAN MAYFLIES (EPHEMEROPTERA)

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ABSTRACT

Collection records of North and Central American mayflies were plotted on maps, based on published records, and the distributional limits of species were found to form 24 distinct distribution patterns within 5 larger subdivisions. The Arctic subdivision includes 15 species that occur only above 58° north, and includes two patterns, the Palearctic (Europe) and the Nearctic (North America). The North American subdivision includes 14 species in two patterns that occur almost from coast to coast. The Western North American Subdivision includes 209 species in 9 patterns whose distributional limits are west of the east slope of the MacKenzie, Rocky, and Sierra Madre Occidental Mountains to Jalisco (21° N). The Eastern North American Subdivision includes 373 species in 10 patterns east of the western mountains to Veracruz (21° N). The Mesoamerican Subdivision includes 99 species in 2 patterns, and the distributional limits of most species are from Panama to Jalisco and Veracruz, Mexico. Species occur in only one pattern and one subdivision, except for those that are widely distributed or holarctic, and patterns are composed of only boreal species, or of boreal and austral species, but none are composed solely of austral species.

INTRODUCTION

In a previous study of mayfly distribution in North America, Berner (1959) placed the species in eight large subdivisions, 5 in the United States and 3 in Canada, which were demarcated by state lines and provincial boundaries. He stated that the divisions were chosen arbitrarily as a matter of convenience, however, Edmunds, Jensen and Berner (1976) chose to follow this same artificial system. They used Berner's subdivisions and further separated Alaska from the Yukon Territory, divided Mexico into north and south by the Tropic of Cancer, and separated Mexico from Central America by the Mexican/Guatemalan border. Flannagan and Flannagan (1982) charted the distribution of the mayflies, stoneflies and caddisflies of Manitoba, and proposed 11 subdivisions, 3 in the United States and the others in Canada and Alaska, based on water drainage systems.

The results of the present study are based on the published collection records from all of North and Central America. The locality record of species were plotted on maps with dots, and the distributional limits of those that were found to occupy the same, or nearly the same, geographical region were included together as a pattern (see the Western United States Distribution Pattern, Map III). The geographical limits of the patterns are based on the species with the widest latitudinal and/or longitudinal distributions (Map III), and each species occurs in only one pattern, except for those that are widely distributed, and those that are Holarctic.

SUBDIVISIONS

The geographical limits of the North and Central American distribution patterns suggest that mayflies be included in 5 subdivisions, the Arctic, the North American, the Western North American, the Eastern North American, and the Mesoamerican.

The Arctic Subdivision includes at least 15 species that occur only above 58°N latitude and are either Holarctic, Palaearctic (occur only in Eurasia) or Nearctic (occur only in North America).

The Western North American Subdivision (Map 1) includes 209 species that are distributed in nine patterns, and the Eastern North American
Subdivision (Map I) includes 373 species that are distributed in 10. The eastern distributional limits of most western species, and the western limits of most eastern species are together in a rather narrow geographical area along the eastern slope of the MacKenzie Mountains in the Northwest Territories, the eastern slope of the Rocky Mountains in southern Canada and the United States, and the eastern slope of the Sierra Madre Occidental in Mexico (Map I). The most southern distributional limits of Western North American species are in western Mexico in the state of Jalisco (21°N), and the most southern distributional limits of the Eastern North American species are in eastern Mexico in the state of Veracruz, also at 21°N. The narrow geographical region from Jali-
sco to Veracruz, along the northern slope of the Sierra Madre del Sur, is also the northern limit of distribution of Mesoamerican species that are endemic to southern Mexico and Central America. The Mesoamerican Subdivision (Map I) includes 99 species that are distributed in two patterns.

The North American Subdivision includes 14 species that are so widely distributed in the United States and Canada that their eastern and western affinities are uncertain.

DISTRIBUTION PATTERNS

North and Central American mayflies include Neotropical and Nearctic elements, and it is
sometimes difficult to determine whether a genus originated from the north or the south. The origins of *Caenis, Hexagenia* and some baetid genera cannot be stated with certainty, and these taxa are herein considered to be of boreal origin as a matter of convenience. The distribution patterns were found to include species of both austral and boreal origin, and of species only of boreal origin, but no patterns were comprised solely of species from genera of austral origin. There are presently 705 described species in North and Central America and only 30 (less than 0.5%) do not fit neatly within the geographical limits of a pattern. Seven species do not have a distributional pattern that is consistent with that of any other species, and they cannot be included in a pattern. An additional 23
species are distributed in a pattern, but they are also known, or reported by at least one record, outside the pattern in which they are distributed. Interestingly, 18 of the 23 collection records are in two localities, one in Saskatchewan, in Canada, and the other in Arkansas, in the southern United States.

The 12 species that occur outside their pattern of distribution in Saskatchewan are all western species, and they cannot be considered to constitute a separate pattern as they are primarily distributed in 4 different patterns. Four of the species are distributed in the widespread Western North American Pattern (Map II), 6 are distributed in the Northwest Pattern (Map IV), and one species each is distributed in the Rocky Mountain (Map VI), and in the Northwest and Rocky Mountain (Map VIII) patterns. The 6 species that occur in the Ozark Plateau, in Arkansas, are all primarily distributed in the Appalachian Pattern (Map III), and these species could, and maybe should, be considered to constitute a distinct pattern.

The species that are known to occur outside their pattern of distribution are all named in the discussion under the pattern in which they are distributed, and those species whose known distribution is not consistent with that of any species are discussed at the end of the paper.

Species that are known from only one or two localities are included in the distribution pattern that appears to reflect their true distribution. For example, *Ameletus celer* McDunnough is known only from its type locality in the Rocky Mountains of Alberta, and *Ameletus connectina* McDunnough is known only from its type locality in the Coast Ranges of British Columbia. Both species are considered to be distributed in the Northwest Pattern, instead of the Rocky Mountain for the former and the Coast Ranges for the latter. Another example, *Ameletus falsus* McDunnough, is known from two localities in the Rocky Mountains of Arizona, but I consider it to be distributed in the Southwest pattern.

A. ARCTIC SUBDIVISION

The Nearctic Pattern is based on the known distribution of four species of *Baetis*, *B. foemina* McDunnough, *B. hudsonicus* Ide, *B. macani* Kimmins, and *Baetis lapponicus* (Bengtsson), and the latter two are holarctic.

B. NORTH AMERICAN SUBDIVISION

The Pancontinental Pattern includes 10 boreal species that are amongst the most widely distributed in the world. They occur, essentially, from coast to coast, and from northern Canada to the southern United States. One species *Hexagenia limbata* Serville, has been reported from as far south as Jalisco, Mexico. All species occur west of the 115th meridian, and east of the 73rd, and from 66°N to at least 30°N.

The Widespread North American Pattern includes 4 boreal species, *Baetis quilleri* Dods, *Ephoron album* (Say) *Heptagenia elegantula* (Eaton) and *Pseudonar centralis* McDunnough, which are widely distributed in North America. Their limits of distribution are from the Pacific Coast (122°W) to Ohio (84°W), and from Saskatchewan (52°N) to Florida, Arizona, New Mexico and Texas (30°N). The latitudinal and longitudinal limits of distribution of these are much narrower than pancontinental species, and their distributions are disjunct. When two or more species have similar distributions and distributional limits, they should share the same pattern of distribution.

C. WESTERN NORTH AMERICAN SUBDIVISION

The Widespread Western North American Distribution Pattern (Map II) is based on the distribution and distributional limits of 6 boreal and one austral species that are widely distributed in Western North America from the Northwest Territories (68°N) to southern California (34°N), and Arizona and New Mexico (31°N). Species
are absent from the western deserts in southern Oregon, most of Nevada, southwestern Utah, southeastern California, and western Arizona. Three boreal species, *Drunella grandis* (Eaton), *Ephemerella inermis* Eaton, and *Iron longimanus* (Eaton), and the austral *Tricorythodes minutus* Traver, have been collected in Saskatchewan, and *E. inermis* has also been collected in western South Dakota.

The Western United States Distribution Pattern (Map III) is based on the distribution of 9 boreal species. The distributional limits are primarily in the United States, with a range from southern Alberta and British Columbia Canada, (52°N), to Sonora, Mexico (30°N). Species are generally absent from the western deserts of Nevada, western Utah and Arizona, and southern California. In this pattern I have superimposed
the distributions of 6 species in an attempt to illustrate how species with similar patterns were included in the same pattern, and how distributional limits of patterns were established.

The Northwest Distribution Pattern (Map IV) is based on the distribution and distribution limits of 71 species of which only two are austral. The Northwest, in this context, is the area from southern Oregon (42°N) to northern Utah and Colorado (40°N) to the Northwest Territories (68°N). *Ameletus oregonensis* McDunnough, *Analetris eximia* Edmunds, *Anepeorus rusticans* McDunnough, *Choroterpes albiannulata* McDunnough, *Isonychia campestris* McDunnough and the Austral *Lachlania saskatchewanensis* Ide also occur in Saskatchewan.
The Southwest Distribution Pattern (Map IV) is based on the distribution and distributional limits of 40 endemic species, 25 of which are boreal. The Southwest, in this context, is the area including southern California, southwestern Utah (37°N), southwestern Texas (104°W), and western Mexico from along the eastern slope of the Sierra Madre Occidentals to Jalisco (21°N).

*Homoeoneuria allenii* Pescador and Peters also occurs in eastern Utah.

The Coast Ranges Distribution Pattern (Map V) is based on the distribution of 46 species, of which 44 are boreal. The distributional limits of the species are in the Pacific Coast Mountain Ranges from British Columbia (51°N) to southern California (34°N).
The Rocky Mountain distribution Pattern (Map VI) is based on the distribution of 10 boreal and one austral species distributed in the inland mountains of western North America from the Mackenzies (68°N) to the southern Rockies in southern Arizona and New Mexico. The boreal *Heptagenia solitaria* McDunnough also occurs in Saskatchewan.

The Northwest and Coast Ranges Distribution Pattern (Map VII) is based on the distributional limits of 11 boreal species which occur in the Northwest from Alberta and British Columbia (52°N) to Wyoming, including Idaho, Washington and Oregon, and in the Coast Ranges of California to Baja California, Mexico (26°N).

The Northwest and Rocky Mountain Distri-
bution Pattern (Map VIII) is based on the distributional limits of 7 boreal and one austral species. Their distributional limits in the northwest are from the Northwest Territories (68°N) to northern California, and they occur in the southern Rocky Mountains and the Sierra Madre Occidentals to Chihuahua, Mexico (28°N). The austral *Traverella albertana* (McDunnough) also occurs in Saskatchewan.

The Disjunct Western Distribution Pattern (Map IX) is based on the distribution of 5 boreal and one austral species that are distributed on the Pacific Coast, west of the Great Basin, and the Mojave and Sonoran Deserts, and they have disjunct populations that are distributed in the Rocky Mountains east of the deserts. The distri-
butional limits of the coastal populations are from central Washington (46° N) to southern Baja California (27° N), and the limits of distribution of the inland populations are from southern Alberta (49° N) to Arizona and New Mexico (31° N).

D. MESOAMERICAN SUBDIVISION

The Widespread Mesoamerican distribution pattern (Map V) includes species that occur in Mesoamerica, and that also occur in eastern and/or western North America to the southern United States. Seven species of austral origin have dispersed northward to Texas (31° N) and to Arizona and New Mexico (35° N) and their limits of distribution are in Panama (9° N). Two other species, *Isonychia manca* (Eaton) and *Choroterpes inornata* Eaton, have a boreal origin, and, presumably, have dispersed southward into Mesoamerica. The former species occurs from Texas to Honduras (14° N), and has been reported from Kansas, and the latter occurs from southern Colorado (37° N) to Oaxaca, Mexico (17° N).

The Mesoamerican Distribution Pattern (Map I) has the same geographical limits as the subdivision, Panama (9° N) to Jalisco and Veracruz (21° N). Ninety species are endemic to Mesoamerica, except for *Hexagenia albivitta* (Walker) which has been reported from Brazil (12° S).

E. EASTERN NORTH AMERICAN SUBDIVISION

The Widespread Eastern Distribution Pattern (Map II) is based on the distribution and distributional limits of 29 boreal species that are widely distributed in Eastern North America from the Arctic Circle (68° N) to Florida (29° N) and Texas. The species are distributed in all of the subdivision, except for southern Texas and northeastern Mexico.

The Appalachian Distribution Pattern (Map III) is based on the distribution of 41 species, of which only one is austral, and whose distributional limits are in the Appalachian Mountains and along the eastern seaboard from New Brunswick (48° N) to Georgia, Florida and Mississippi (30° N). Six species *Attenella attenuata* (McDunnough), *Habrophlebioides americana* (Banks), *Paraleptophlebia gutata* (McDunnough), *Pseudocloeon carolina* (Banks), *P. cingulatum* McDunnough and *P. dubium* (Walsh) also occur on the Ozark Plateau, in Arkansas (34° N, 93° W).

The Eastern United States Distribution Pattern (Map IV) is based on the distribution of 30 boreal species that occur primarily in the United States, with their northern distributional limits along the Canadian border. The species are distributed from eastern Texas to South Dakota (100° W), southern Ontario, Quebec and Nova Scotia (46° N, 60° W), and on the eastern seaboard to northern Florida (30° N).

The Midwest distribution Pattern (Map V) is based on the distribution of 37 species, of which only 3 are austral. The latitudinal limits of the Midwest species are much narrower than those in the Eastern United States Pattern, ranging from eastern Texas (94° W) to eastern Minnesota, southern Ontario and Quebec, to New York and the Appalachian Mountains to Florida (27° N).

The Northeast Distribution Pattern (Map VI) is based on the distribution of 71 boreal species. The northeast, in this context, is eastern North America from Hudson Bay (58° N) to Nova Scotia (60° W), and the eastern seaboard to Virginia and Kentucky, and Missouri (37° N), and Minnesota and eastern Manitoba (100° W).

The South-Central and Gulf Coast Distribution Pattern (Map VI) is based on the distribution of 25 species of which 15 are austral. The distributional limits of the species are from Kansas (39° N) to Louisiana (92° W), the gulf coast to Veracruz, Mexico (21° N), and in most of the area along the Rio Grande in Texas (104° W).

The Central Distribution Pattern (Map VII) includes 7 boreal and 2 austral species whose distributional limits are from Hudson Bay (62° N) to western Florida (30° N, 86° W), and central Texas to Saskatchewan (106° W). *Stenonema terminalum* (Walker) has been reported also from North Carolina.
The Northeast and Appalachian Distribution Pattern (Map VIII) is based on the distributional limits of 16 species, of which only 2 are austral, that are distributed from central Ontario (51°N) to Minnesota (93°W) and Nova Scotia (60°W), and in the Appalachian Mountains to northern Florida (30°N).

The Southeast Distribution Pattern (Map IX) is based on the distribution of 89 boreal and 4 austral species. The Southeast, in this context, includes eastern North America from Louisiana (92°W) to West Virginia and Virginia (38°N) to the Atlantic Ocean and the Gulf of Mexico. All species are endemic, except Baetis ephippatus Traver which also occurs as far north as Indiana.

The North-central Distribution Pattern (Map IX) is based on the distribution of 20 species, all but one of which are boreal. The limits of distribution of the species are generally along the US/Canadian border from western Alberta (52°N, 120°W) to Illinois, Indiana and Michigan (37°N, 86°W). Rhithrogena pellucida Daggy has been reported from central Alabama.

OTHER SPECIES

The following species do not fit a pattern of distribution that is expressed by any other species. In some cases, the validity of the identification is questionable, and in all of them the known distribution is based on only a few records.

Baetodes edmundsi Koss is known from only three collection localities, one each in Arizona, New Mexico and central Texas. Two records are in the Southwest Pattern and the other is in the South-central and Gulf Coast Pattern. Leptohyphes dolani Allen is known from only two localities, one in southern Texas and the other in the Savannah River separating Georgia and South Carolina.

One is in the Southeast Pattern and the other is in the South-central and Gulf Coast Pattern. Tricorythodes edmundsi Allen occurs in northern Utah, in the Northwest Pattern, and in eastern Mexico, in the South-central and Gulf Coast Pattern. The identification of all of the above-mentioned species is certain, and future collection studies will probably serve to clearly establish their limits of distribution.

The taxonomy of Callibaetis is poorly known, as it is difficult to identify described adults, and the nympha stage of only a very few species is described. It is therefore suspected that the following records are based on misidentifications. Callibaetis americanus Banks has been reported from Colorado, Montana and New Hampshire; C. montanus Eaton has been reported from Central America, central California and Kansas; C. pacificus Seemann has been reported from southern California, Arizona and Oklahoma; and C. pictus (Eaton) has been reported from California, Texas and southern Mexico.

REFERENCES