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EPHEMEROPTERA

W. P. McCafferty[1] & C. R. Lugo-Ortiz[1]

RESUMEN. El orden paleóptero de insectos acuáticos Ephemeroptera, comprende alrededor de 2 500 especies distribuidas en todo el mundo. El grupo se remonta al Paleozoico, con grupos extintos prevalecientes en el Mesozoico y grupos recientes evolucionados para el Cenozoico. Las especies existentes están separadas en dos subórdenes, Pisciforma (cinco familias en México, con larvas pisciformes y de cabeza achatada) y Rectracheata (seis familias en México, con larvas más diversas con sistemas traqueales avanzados). La fauna mexicana de efemerópteros contiene actualmente 116 especies en 35 géneros, predominan las familias Baetidae, Leptophlebiidae y Leptohyphidae y los géneros *Baetodes, Callibaetis, Camelobaetidius, Leptohyphes, Thraulodes* y *Tricorythodes*.

Aproximadamente 50% de las especies mexicanas han sido descubiertas a partir de 1976, pero en ocho estados no han sido reportados efemerópteros. La colecta y correlación de etapas larvarias y adultas es crítica para adelantar el conocimiento de la biodiversidad en México. Las especies mexicanas representan 17% de las conocidas en América del Norte, 11% de las conocidas en el Hemisferio Occidental y 5% de las conocidas en el mundo.

Veracruz posee la fauna más rica de efemerópteros dentro de México, con 33 especies reportadas, incluyendo siete de las 30 especies endémicas. 63 especies son conocidas de no más de un estado. México comparte 56 especies con EU y 37 especies con regiones al sur de México. 17 géneros mexicanos tienen afinidades neotropicales y 13 tienen afinidades neárticas. Las influencias neotropicales en México, sin embargo, son mejor expresadas por las 84 especies o más que pertenecen a linajes neotropicales y las 25 que pertenecen a linajes neárticos. Las afinidades de tres géneros son dudosas, pero *Caenis, Hexagenia* y posiblemente *Callibaetis* están compuestas de linajes neárticos y neotropicales en México. Se provee una lista de cotejo para México que incluye una clasificación filogenética superior, indicación de endémicos, estados en los cuales las especies han sido reportadas y etapas primarias de vida de las cuales éstas son conocidas.

INTRODUCTION

Mayflies, those insects belonging to the order Ephemeroptera, constitute an important group of freshwater macroinvertebrates known from throughout the world, excluding remote oceanic islands and extreme polar regions. Although difficult to estimate at this time, there are probably well over 2 500 extant species worldwide, with approximately 2 250 having been described at this time (McCafferty *et al.*, 1990). Catalogues of species for most world regions do not exist; however, a recent catalogue of generic names that have been applied to Ephemeroptera lists some 231 names currently in use (Hubbard, 1990). 35 genera are currently known from Mexico.

North-temperate regions around the world appear particularly rich in numbers of mayfly species, but we expect the majority of new species to be discovered from the tropics, especially in the Oriental and Neotropical regions. By way of comparison, McCafferty *et al.*, 1993, inventoried 97 species of mayflies in the USA state of Colorado. At this point in time we cannot account for only 116 species in all of Mexico. Although the two areas have similar topo-

[1]Department of Entomology, Purdue University, West Lafayette, Indiana 47907, USA.

graphies, Colorado is considerably smaller than Mexico in land mass, and it is relatively well known with respect to its mayfly fauna due to the aquatic research conducted there for nearly a century. Mexico, on the other hand, remains relatively poorly known, and we expect many more mayflies to be discovered there.

The phylogeny and supergeneric classification of the Ephemeroptera was most recently treated by McCafferty (1991) and modified by McCafferty & Wang (1994) wherein two major suborders within the order were recognized, the Pisciforma containing some 14 extant families worldwide having primitively formed minnowlike larvae or flatheaded larvae derived from such, and the Rectracheata containing some 13 extant families worldwide having more advanced tracheal systems, gills, wing related structures, and a myriad of larval body forms. A phylogram depicting the relative phyletic positions of the Mexican families is presented in figure 13.1. This can be compared with the phylogenetic higher classification of Mexican mayflies used in table 13.1, where current subordinal, infraordinal, and superfamilial classifications applicable to these families are indicated. Both suborders are well represented in Mexico, but only 11 families are represented there (many of the north-temperate psammophilous pisciform families, Amphinotic pisciform families, and certain pannote families of the Rectracheata being absent from Mexico). The families Baetidae (Pisciforma) and Leptophlebiidae and Leptohyphidae (Rectracheata) demonstrate the greatest species radiation in Mexico.

Mayflies date from the Carboniferous [see the most recent catalogue of fossil mayflies by Hubbard (1987)], however, Paleozoic mayflies are quite distinct from other mayflies. Many recent families had appeared by the Cretaceous (McCafferty, 1990) with primitive Pisciforma such as the Hexagenitidae best represented in the Lower Cretaceous, Jurassic, and Triassic. Virtually all modern families were present by the Tertiary. Several higher taxa of fossils, including the once dominant Hexagenitidae and

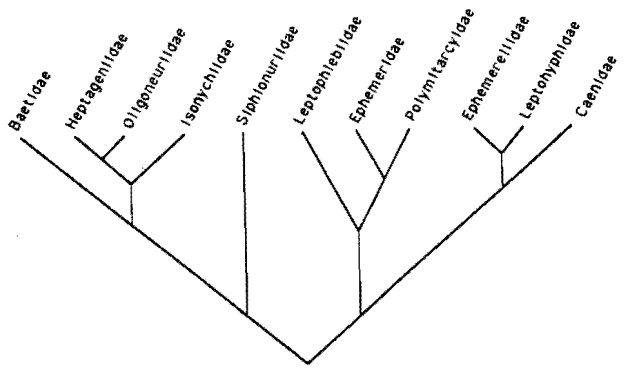

Fig. 13.1. Phylogeny of the extant Ephemeroptera families of Mexico (cf. Table 1 for applicable subordinal, infraordinal, and superfamily phylogenetic classification).

some other Pisciforma, did not survive the transitional period between the Mesozoic and Cenozoic. Apparently the order was severely decimated by mass extinction during this period, particularly in the Southern Hemisphere (McCafferty, 1990, 1991) as were numerous other organisms (cf. *e.g.* Raup, 1988). No mayfly fossils are known from Mexico.

Knowledge of the historical world biogeography of mayflies is well documented for some groups and regions and poorly known for others. Edmunds (1975), gave a classical biogeographic account of the Amphinotic pisciform mayflies, those ancient groups that clearly show vicariant relationships between Australia, New Zealand and Chile/Argentina, paralleling the continental breakup of Transantarctica. Other Gondwanan relationships among mayflies are not as clear, although there exist several Pantropical lineages, for example, among the Oligoneuriidae. McCafferty (1991) showed that several families not now in the Neotropics were present in Brazil during the Lower Cretaceous, suggesting a Pangaean distribution for many of the families presently more geographically restricted. As for Holarctic families, only the family Potamanthidae has been thoroughly examined with respect to applying a comprehensive species phylogeny to

Table 13.1. Mexican Ephemeroptera, with an indication of known regional distributions (abbreviated), known primary stages (bracketed A = adult, L = larva), and endemic species (asterisked).

Suborder Pisciforma
Siphlonuroidea
SIPHLONURIDAE
Siphlonurus occidentalis (Eaton) [A,L]: Chi, Son.
Heptagenioidea
ISONYCHIIDAE
Isonychia intermedia (Eaton) [A,L]: Chi.
Isonychia sicca (Walsh) [A,L]: NL, SLP, Son, Tab, Tam, Ver.
OLIGONEURIIDAE
Homoeoneuria alleni Pescador & Peters [L]: Chi.
Homoeoneuria salviniae Eaton [A,L]: Chp.
**Lachlania iops* Allen & Cohen [L]: Chp, SLP.
Lachlania powelli Edmunds [A,L]: Gue.
HEPTAGENIIDAE
Iron margarita (Edmunds & Allen) [A,L]: BaN, BaS.
Iron metlacensis (Traver) [A,L]: Mic, Mor, Oax, Ver.
Ironodes nitidus (Eaton) [A,L]: BaN.
**Nixe bella* (Allen & Cohen) [L]: Ver.
**Nixe salvini* (Kimmins) [A]: Son.
Rhithrogena morrisoni (Banks) [A,L]: BaN.
Rhithrogena notialis Allen & Cohen [L]: MDF, Mic, Oax, Ver.
Stenonema mexicanum integrum (McDunnough) [A,L]: Tam.
Stenonema mexicanum mexicanum (Ulmer) [A,L]: Tab.

Baetoidea
BAETIDAE
Acentrella insignificans (McDunnough) [A,L]: Chi, Son.
Acerpenna pletura Lugo-Ortiz & McCafferty [L]: Tam.
Baetis caelestis Allen & Murvosh: [L] BaN, BaS, Chi.
Baetis flavistriga McDunnough [A,L]: Chi.
Baetis magnus McCafferty & Waltz [A,L]: Chp, Chi, Dur, Méx, Mor, NL, Oax, SLP, Ver.
Baetis notos Allen & Murvosh [L]: Ver.
Baetis tricaudatus Dodds [A,L]: BaN.
Baetodes adustus Cohen & Allen [L]: Ver.
Baetodes caritus Cohen & Allen [L]: Chi, Gue, Mor, Ver.
Baetodes deficiens Cohen & Allen [L]: Gue, Jal, Mor, Son, Ver.
Baetodes edmundsi Koss [A,L]: Sin, Son.
**Baetodes fortinensis* Mayo [L]: Ver.
Baetodes fuscipes Cohen & Allen [L]: Sin, Son, Ver.
**Baetodes inermis* Cohen & Allen [L]: Gue, Mor, Oax, Jal, Tam.
**Baetodes longus* Mayo [L]: NL, Tam.
**Baetodes obesus* Mayo[L]: Ver.
Baetodes pallidus Cohen & Allen [L]: Chp, Jal.
**Baetodes pictus* Cohen & Allen [L]: Ver.
Baetodes tritus Cohen & Allen [A,L]: Chp, Jal, Mor, Tam, NL, Ver.
Callibaetis californicus Banks [A,L]: Méx, Mor, NL.
Callibaetis floridanus Banks [A,L]: Gue, Mor, NL.
Callibaetis montanus Eaton [A]: Méx, Son.
Callibaetis pictus (Eaton) [A]: BaS, Chp, Chi, Dur, Gue, Méx, MDF, Mor, Son, Ver.
Callibaetis punctilusus McCafferty & Provonsha [A]: Chp, NL.
Callibaetis ulmitus (Pictet) [A]: exact locale unknown.
**Camelobaetidius arriaga* (Traver & Edmunds) [A] Chp.
**Camelobaetidius chiapas* (Traver & Edmunds) [A]: Chp. BaS, Chp, Chi, Dur. Gue,

Table 13.1. Mexican Ephemeroptera, with an indication of known regional distributions (abbreviated), known primary stages (bracketed A = adult, L = larva), and endemic species (asterisked) (*Continues*).

**Camelobaetidius chiapas* (Traver & Edmunds): [A]: Chp
**Camelobaetidius jenseni* (Traver & Edmunds) [A]: Chp.
Camelobaetidius mexicanus (Traver & Edmunds) [A,L]: Chp, Gue, Jal, Mor, NL, Oax, Sin, Son, Tam, Ver.
Camelobaetidius musseri (Traver & Edmunds) [L]: Chp, Gue, Jal, Mor, NL, Oax, SLP, Ver.
**Camelobaetidius sinaloa* (Allen & Murvosh) [L]: Sin.
Camelobaetidius trivialis (Allen & Chao) [L]: Son.
Camelobaetidius warreni (Traver & Edmunds) [A,L]: BaS, Chp, Chi, Gue, Oax, Son.
Cloeodes excogitatus Waltz & McCafferty [L]: exact locale unknown.
**Cloeodes peninsulus* Waltz & McCafferty [L]: BaS.
**Fallceon eatoni* Kimmins [A]: Son.
Fallceon longifolius (Kluge) [A,L]: Hid.
Fallceon quilleri (Dodds) [A,L]: BaN, BaS, Chp, Chi, SLP, Sin, Son.
Moribaetis macaferti Waltz [L]: Chp, Oax, Ver.
Moribaetis salvini (Eaton) [A,L]: Ver.
Paracloeodes minutus (Daggy) [A,L]: BaS.

Suborder Rectracheata
Infraorder Lanceolata
Leptophlebioidea
LEPTOPHLEBIIDAE
Choroterpes inornata Eaton [A,L]: BaN, BaS, Chi, Oax, Sin, Son.
Farrodes texanus Davis [A,L]: Tam.
Hydrosmilodon primanus (Eaton) [A,L]: Tab, Ver.
Neochoroterpes oklahoma (Traver) [A,L]: Chp, Chi, Dur, NL, SLP, Tam, Ver, Zac.
**Neochoroterpes orientalis* Henry [A,L]: Que, Pue.
Paraleptophlebia memorialis (Eaton) [A,L]: BaN.
Thraulodes brunneus Koss [A,L]: BaN, BaS, Chi, Dur, Gue, Jal, Mic, Méx, Mor, Oax, Son, Ver.
**Thraulodes ephippiatus* Traver & Edmunds [A]: Chp.
Thraulodes gonzalesi Traver & Edmunds [A,L]: Chi, NL, Sin, Son, Tam.
Thraulodes hilaris (Eaton) [A]: Tab.
Thraulodes humeralis Navás [A]: exact locale unknown.
**Thraulodes lunatus* Traver & Edmunds [A,L]: Hid, NL, Tam, Zac.
Thraulodes mexicanus (Eaton) [A]: exact locale unknown.
Thraulodes packeri Traver & Edmunds [A,L]: Chp.
Thraulodes spangleri Traver & Edmunds [A]: Chp.
Thraulodes speciosus Traver [A,L]: Chi, Gue, Son.
Thraulodes zonalis Traver & Edmunds [A,L]: Chp.
Traverella albertana (McDunnough) [A,L]: Chi.
Traverella castanea Kilgore & Allen [L]: Chi, Sin, Son.
Traverella presidiana (Traver)[A,L]: NL, Tam.

Ephemeroidea
EPHEMERIDAE
Hexagenia albivitta (Walker) [A,L]: Ver.
Hexagenia bilineata (Say) [A,L]: SLP.
Hexagenia limbata (Serville) [A,L]: Jal, NL, SLP, Tam.
Hexagenia mexicana Eaton [A]: Oax, Ver.
POLYMITARCYIDAE
Campsurus cuspidatus Eaton [A]: SLP, Ver..

Table 13.1. Mexican Ephemeroptera, with an indication of known regional distributions (abbreviated), known primary stages (bracketed A = adult, L = larva), and endemic species (asterisked).

Campsurus decoloratus (Hagen) [A,L]: Tam.
Euthyplocia hecuba (Hagen) [A,L]: Chp, Ver.

Infraorder Pannota

EPHEMERELLIDAE

Drunella flavilinea (McDunnough) [A,L]: BaN
Ephemerella altana (allen) [A,L]: BaN
Serratella micheneri (Traver) [A,L]: BaN, BaS

LEPTOHYPHIDAE

**Leptohyphes alleni* Brusca [L]: Oax.
Leptohyphes apache Allen [L]: Chi.
**Leptohyphes berneri* Traver [A]: Ver.
Leptohyphes brunneus Allen & Brusca [L]: Chp, Jal, Mor.
Leptohyphes castaneus Allen [L]: Oax.
**Leptohyphes dicinctus* Allen & Brusca [L]: Gue.
Leptohyphes ferruginus Allen & Brusca [L]: Son, Ver.
Leptohyphes hispidus Allen & Brusca [L]: Chp, Ver.
Leptohyphes lestes Allen & Brusca [L]: Gue.
Leptohyphes michaeli Allen [L]: NL.
Leptohyphes mirus Allen [L]: Chi, Sin, Son.
Leptohyphes nigropunctus Traver [A]: Gue.
Leptohyphes packeri Allen [A,L]: Chi, Nay, NL, Oax, SLP, Sin, Son, Tam, Ver.
**Leptohyphes pilosus* Allen & Brusca [L]: Ver.
**Leptohyphes sabinas* Traver [A]: NL, Tam, Ver.
**Leptohyphes spiculatus* Allen & Brusca [L]: Mor.
**Leptohyphes tarsos* Allen & Murvosh [L]: Son.
**Leptohyphes zalope* Traver [A]: Gue.
**Tricorythodes angulatus* Traver [A]: exact locale unknown.
**Tricorythodes comus* Traver [A]:Gue.
Tricorythodes condylus Allen [A,L]: Chi, Son.
Tricorythodes dimorphus Allen [A,L]: Chi.
Tricorythodes edmundsi Allen [L]: Tam.
Tricorythodes explicatus (Eaton) [A,L]: BaN, BaS, Chi, Sin, Son.
**Tricorythodes mulaiki* Traver [A]: Gue.
**Tricorythodes notatus* Allen & Brusca [L]: Mor, Oax.
**Tricorythodes ulmeri* Allen & Brusca [L]: Mor.

CAENIDAE

Caenis anceps Traver [A,L]: Ver
Caenis bajaensis Allen & Murvosh [A,L]: BaS, Chp, Dur, Nay, Son.
Caenis latipennis Banks [A,L]: Chp, NL.

causal biogeography (Bae & McCafferty, 1991). The Potamanthidae perhaps typify a number of mayfly families that are essentially Holarctic with significant representation of lineages in the Orient, and with some of them demonstrating occasional incursions into Mesoamerica or the Afrotropics. McCafferty *et al.*, (1992), comprehensively treated the biogeography of the Mesoamerican mayflies, including many Mexican mayflies, with emphasis on the Panamerican genera and ascertaining their Neotropical or Nearctic origins.

This ancient paleopterous group of insects is the only extant group of insects to maintain a subimago (winged pre-adult stage) in post-embryonic development. This unique stage

has recently been shown to provide protective unwettable qualities (not present in adults) to the mayfly as it emerges from the relatively long-lived aquatic larval stage (Edmunds & McCafferty, 1988). Although the adult stage is foregone in the females of a few mayfly taxa, it evidently is required in all males, allowing the extreme metamorphosis and maturation from larvae not possible in the single molt to subimago (Edmunds & McCafferty, 1988). The genus *Campsurus* is the only representative in Mexico of these specialized groups that has eliminated the adult stage as females, although the related and similarly specialized genus *Tortopus* should certainly be found in Mexico (it occurs abundantly in Texas and Central America).

Besides their relatively ancestral position among extant insects, mayflies have historically attracted the attention of philosophers and poets because of their generally short-lived adult stage, which also is the basis of the stem word of the order ("ephemeral"). For the past couple of centuries, the group has also been of primary interest to fisherman in those parts of the world where salmonids are fished, and, in fact, mayflies were the first, and considered by many to still be the best, models for fishermen's artificial flies (McCafferty, 1981). In modern times, Ephemeroptera have become one of the primary indicators of water quality in running water environments, and along with Plecoptera and Trichoptera, form the basis of EPT (Ephemeroptera-Plecoptera-Trichoptera) rapid bioassessment systems of analysis (*e.g.* Lenat, 1988). Mayflies are among the most sensitive aquatic insects to alterations of water quality, and they are an integral part of any biotic indices based on benthic macroinvertebrates (*cf.* reviews in Rosenberg & Resh, 1993). It is in part for this reason that recent emphasis in taxonomy of the group has been placed on the larval, aquatic stage. In Mexico, species lists and identification keys to the larvae of mayflies will be of utmost importance in developing stream biomonitoring and conservation practices. Lugo-Ortiz & McCafferty, (in manuscript), are currently preparing a Spanish key to the Mexican and Central American genera. A first species list for Mexico is contained herein.

THE MEXICAN FAUNA

Taxonomy and History

Although the mayflies of Canada and the United States are relatively well known, the mayflies of Mexico have been sorely neglected until quite recently. The first mayfly described from Mexico was *Cloe undata* Pictet, (1845) [= *Callibaetis undatus* (Pictet)], a poorly known species of doubtful validity. The last accounting of the entire Mexican mayfly fauna was contained in generic tables provided by Edmunds *et al.*, (1976) wherein 63 nominal species were listed as being present in either "northern" or "southern" Mexico. Besides the several Mexican mayflies that were housed in European collections in the 19th Century and were described by the Honorable Reverend A.E. Eaton, (esp. Eaton, 1885, 1892), and those collected in the first part of the 20th Century and described by a few others (*e.g.*, Traver, 1958, 1959) the primary contributors of the species known from Mexico in 1976 were Traver & Edmunds (1967, 1968) for species of the genera *Thraulodes* and *Camelobaetidius*, respectively, Cohen & Allen (1972) for species of the genus *Baetodes*, and Allen & Brusca (1973) for species of the genera *Leptohyphes* and *Tricorythodes*.

Table 13.1 contains a list of 116 species and 35 genera of mayflies now known from Mexico. Families are arranged phylogenetically in the table, but genera and species are, of necessity, arranged alphabetically under each family. It can be seen from this that in less than 20 years the number of species known from Mexico has almost doubled. If one considers the number of new species from Mexico that are either in press or in preparation by Lugo-Ortiz & McCafferty, the number will have more than doubled. Primary contributions to this increase in information have included 1)

the revision oriented or genus-specific works by Allen & Brusca (1978) for *Thraulodes*, Cohen & Allen (1978) for *Baetodes*, Waltz & McCafferty (1985) for *Moribaetis*, Waltz & McCafferty (1987) for *Cloeodes*, Henry (1993) for *Neochoroterpes*, Lugo-Ortiz *et al.* (1994) and McCafferty & Lugo-Ortiz (1994) for *Fallceon*, and Lugo-Ortiz & McCafferty (1994b) for *Acerpenna*, and 2) the regional taxonomic works encompassing Mexico by Allen (1977, 1985), Allen & Cohen (1977), Allen & Murvosh (1983, 1987a, b, c), and Lugo-Ortiz & McCafferty (1994a).

The above mentioned works on Mexican mayflies are by no means exhaustive. Several Ephemeroptera specialists have contributed to our knowledge of Mexican mayflies in piecemeal fashion over the years. With the recent death of R.K. Allen, who devoted much of his career to collecting and studying Mexican mayflies, the number of active specialists with expertise on the Ephemeroptera of Mexico has been severely reduced. Essentially, the present authors of this chapter are the only specialists actively involved in studying all taxa of Mexican mayflies. Certain other specialists on specific mayfly families other than us are capable of offering expertise on Mexican fauna within their specialties. In addition to us, this would include primarily the North American workers W.L. Peters, for the Leptophlebiidae genera (B.C. Henry for *Neochoroterpes* species), A.V. Provonsha for *Caenis* species, and R.D. Waltz for the Baetidae genera and species. It will be important to train local Mexican entomologists in methods of collecting, rearing, and identifying mayflies in Mexico. Only in this way will the Mexican fauna ever become completely known and its biodiversity realized.

Life stages and their correlation

The two metamorphic life stages of mayflies that are of primary importance with respect to demonstrating morphological variation at the various taxonomic levels are the larval stage and the adult stage. The egg and subimago generally lack characteristics of broad taxonomic applicability, although eggs can be somewhat useful in certain taxa, and subimagos will show all wing venation characteristics that are diagnostic (generally restricted to higher taxa). We have indicated in table 13.1 which of the primary stages are known for the Mexican species. It can be seen from this that 53 Mexican species are known from both the larval and adult stages, 40 are known as larvae only, and 23 are known from adults only. This presents somewhat of a dilemma in identifying species because, when only unknown larvae or adults are collected, it can be difficult to know if they represent an undescribed stage of an otherwise described species, or represent a new species. For this reason, and because both stages can be of extreme importance in delineating species and their relationships, we cannot stress too much the importance of collectors in Mexico attempting to rear larvae to the adult stage whenever possible. Only in this way will needed stage correlations of known species be added to our taxonomic data, and will there be greater assurances of recognizing new or previously described species. Some species in Mexico that are known only from one of the primary stages will remain suspect until the other primary stage is known.

Rearing, with respect to mayflies, involves keeping the last instar aquatic larvae (with black wingpads) alive in adequate containers of water from their habitat (in shaded conditions with ambient temperatures and adequate substrate maintained) until the subimago emerges. The subimago, then, needs to be kept alive until it molts to the adult stage. This usually takes one or two days. The larval exuviae from the last instar along with other specimens of the same larvae need to be kept with the reared subimagos and then adults for correlative purposes. Additional details on rearing may be found in Edmunds *et al.*, (1976) and McCafferty (1981).

Generally, the male adult, rather that the female adult, possesses the most important, and sometimes only, species-specific charac-

teristics, or even generic characteristics in some instances. This is because male genitalia of most mayflies demonstrates many taxonomic characters; but also other secondary sexual characteristics of the male, such as foreleg segmentation and eye development, can be important. Fortunately, only three species of Mexican mayflies that are known as adults are known as female adults only. These include *Homoeoneuria salviniae*, *Callibaetis montanus*, and *C. undatus*. In the case of *C. montanus*, we have seen male adults of this species and will describe them in the near future, and in the case of *C. undatus*, it may prove to be a junior synonym of *C. pictus*. The larvae will be as important as the male adult in resolving the latter possibility since we have also seen the undescribed larvae of *C. pictus*. Reared male adults of *H. salviniae* would help confirm species validity (cf. Pescador & Peters, 1980) and also verify or nullify a larval association by Allen & Cohen (1977), that was not based on rearing but only on geographic proximity.

Regional distribution and endemism

Table 13.1 includes an indication of the Mexican regions (essentially Mexican states abbreviated, with Baja California Norte and Baja California Sur abbreviated as BaN and BaS, respectively, and Mexico, D.F. as MDF) where published records of the species now exist. Some of these records are in press at the time of this writing, (Lugo-Ortiz & McCafferty, 1994b, Lugo-Ortiz *et al.*, 1994); other records that we are aware of and that will be published in the near future are not indicated in table 13.1.

No mayflies have yet been reported from Aguascalientes, Campeche, Coahuila, Colima, Guanajuato, Quintana Roo, Tlaxcala, and Yucatan. Whereas the Yucatan Peninsula generally lacks sufficient running water habitats to support many mayflies, which might explain the absence of reported mayflies from Campeche, Quintana Roo, and Yucatan, we do expect that the mayfly fauna of these other states to be relatively rich, especially Guanajuato. Coahuila is mostly desert, but should support isolated populations similar in kind and numbers to other northern states. It is atypical for states bordering the USA in that it has not been sampled nearly as much as the others. States with reported mayflies follow in descending order of number of species represented: Veracruz (33 spp.); Chiapas, Chihuahua, and Sonora (each with 24 spp.); Nuevo Leon (17 spp.); Guerrero (16 spp.); Tamaulipas (15 spp.); Oaxaca (14 spp.); Baja California Norte (12 spp.); Sinaloa (11 spp.); Baja California Sur and Jalisco (each with nine spp.); San Luis Potosi (seven spp.); Durango (five spp.); Tabasco (four spp.); Mexico (three spp.); Hidalgo, Mexico, D.F., Michoacan, Nayarit, and Zacatecas (each with two spp.); and Puebla and Queretaro (each with one sp.). From this it becomes apparent that the interior of Mexico has been the most neglected by collectors. This is somewhat ironic because we expect the greatest diversity in those areas that are transitional between the Neotropics and Nearctic, having both lowland and highland running water habitats, and semi-tropical climatic conditions.

Only three species of mayflies are currently known from ten or more states in Mexico: *Callibaetis pictus*, *Camelobaetidius mexicanus*, and *Thraulodes brunneus*. These species also extend variously into southwestern USA, but are essentially Mexican. Another five species may be considered widespread in Mexico based on the relatively large number of states where they have been found. They include *Baetis magnus*, *Camelobaetidius musseri*, *Fallceon quilleri*, *Neochoroterpes oklahoma*, and *Leptohyphes packeri*. *Baetis magnus* extends northward as far as Nebraska and southward as far as Costa Rica, *C. musseri* extends through Central America, *F. quilleri* is found throughout much of North America, *N. oklahoma* extends into Colorado and Oklahoma, and *L. packeri* extends into the extreme southwestern USA. We find it interesting that essentially all of the relatively widespread species in Mexico are restricted to the three species-rich families in Mexico: Baetidae, Leptophlebiidae, and Leptohyphidae.

Sixty-three species, or close to half the Mexican species, are known from one state only. This includes most of the 30 species that are apparently endemic to Mexico (cf. asterisked species in table 13.1). Any assessment of mayfly endemism in Mexico at this time, however, could be premature mainly because 19 of the presumed endemic species belong to the genera *Baetodes*, *Camelobaetidius*, *Leptohyphes*, and *Tricorythodes*, all of whose species are in critical need of revision. Nonetheless, if one assumes that these species will all prove valid, then at this time it appears that the greatest degree of endemism is in Veracruz, where seven of the endemics occur. Guerrero has five endemics, and Chiapas four. The vast majority of endemism apparently occurs in the southern half of Mexico, where 20 of the endemic species are found.

Biogeography of Mexican mayflies

Undoubtedly, mayfly species have evolved in Mexico. Theoretically, these would include the endemics discussed above and indicated in table 13.1, and possibly any of those species with primary distributions in the country. In our opinion, the best candidates for this latter category would include the following species: *Iron metlacensis*, *Rhithrogena notialis*, *Baetis magnus*, *Baetodes fuscipes*, *Baetodes pallidus*, *Callibaetis montanus*, *Callibaetis pictus*, *Callibaetis punctilusus*, *Camelobaetidius mexicanus*, *Neochoroterpes oklahoma*, *Thraulodes brunneus*, *Thraulodes speciosus*, *Leptohyphes brunneus*, and *Leptohyphes packeri*.

Obviously all non-endemic species in Mexico have distributions in other regions besides Mexico. Of the 116 species we list here as occurring in Mexico (table 13.1), 49 are found in the USA, another 30 are found in the Neotropics south of Mexico, and seven more of the Mexican species occur in all three areas (30 are endemics). Of those species occurring south of Mexico, the Mexican species presumed to be *Leptohyphes nigropunctus* also occurs in Venezuela (McCafferty, 1985) and *Fallceon longifolius* occurs in Cuba (Lugo-Ortiz *et al.*, 1994). All others found south of Mexico are evidently restricted to Central America. We expect the number found in common between the USA and Mexico to increase slightly as our knowledge of mayflies improves; however, we expect the number found in common between Mexico and Central America to increase more dramatically.

We can account for 1 091 total nominal species for the entire Western Hemisphere. The number for North America north of Mexico [based on McCafferty *et al.*, (1990) with modifications of new species and new synonymies since then, esp. McCafferty & Waltz (1990)], is 598. The number occurring in Mexico is 116 (as reported herein). When the 49 species in common between the two areas are discounted, it leaves 665 species total for North America. The current number of species in Central America is 83 (Lugo-Ortiz & McCafferty, unpublished), and the number exclusive of those in the Antilles is 38 (Lugo-Ortiz & McCafferty, unpublished). McCafferty, *et al.*, (1992), indicated approximately 340 species as occurring in South America. Thus in Central America, the Antilles and South America combined we can account for roughly 458 species. When the species number for North America is added to this figure, minus the 32 species held in common between the two areas, we arrive at 1 091 species.

Using the world figure of 2 250 species (McCafferty *et al.*, 1990) we can illustrate the comparative richness of the Mexican Ephemeroptera fauna relative to the other larger areas in which it is nested (figure 13.2). We do expect, however, a substantial number of new species to be discovered throughout Latin America, and thus these proportions are expected to change somewhat.

Table 13.2 shows the hypothesized regional affinities of each of the genera occurring in Mexico. These hypotheses are based primarily on the study of McCafferty *et al.*, (1992) and are based on phylogeny and distributions as well as behavioral and ecological evolutionary data regarding Panamerican genera.

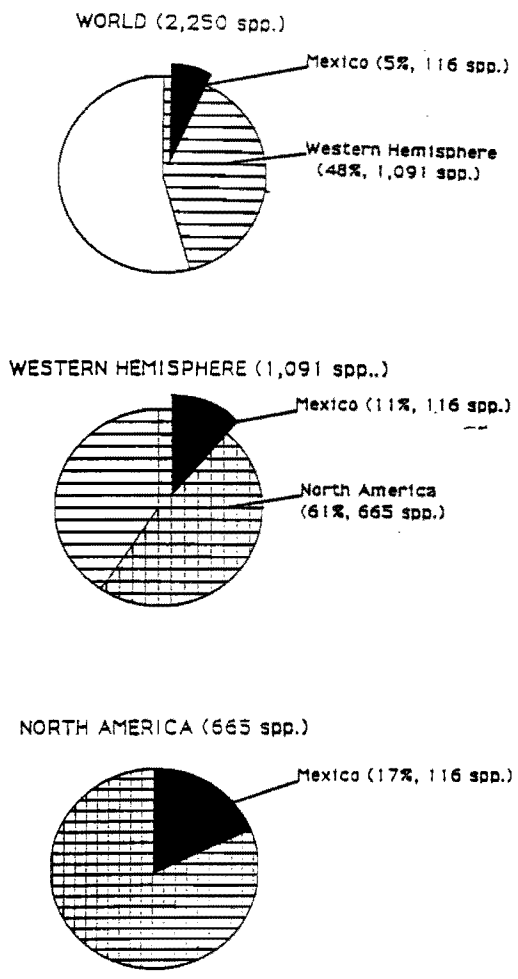

Fig. 13.2. Comparison of mayfly species richness in Mexico with mayfly species richness of larger regions in which Mexico is nested.

Seventeen Mexican genera have evident Neotropical affinities, and another 13 have evident Nearctic affinities. When species demographies within these genera (table 13.2), are considered, certain consistent patterns for the two groups become apparent. At least 84 species in Mexico belong to lineages that we are confident are Neotropical. On the other hand, only 25 species in Mexico belong to lineages that we are confident are Nearctic. These data strongly suggest that the Mexican mayfly fauna is fundamentally a Neotropical one. Most Mexican genera with Neotropical affinities that range into the USA are restricted to the southwestern or western USA, although Texas is well represented by these forms also (Lugo-Ortiz & McCafferty, 1994c). Most Mexican genera with Nearctic affinities are widespread in North America north of Mexico.

The pisciform families Siphlonuridae, Isonychiidae, and Heptageniidae as well as the pannote family Ephemerellidae are represented by very few species in Mexico, and *Siphlonurus occidentalis, Isonychia intermedia, Ironodes nitidus, Nixe salvini,* and all Ephemerellidae (*Drunella flavilinea, Ephemerella altana,* and *Serratella micheneri*) are restricted to northern Mexico. *Iron, Isonychia, Nixe, Rhithrogena,* and *Stenonema* have penetrated southward into Mesoamerica. *Iron, Nixe,* and *Rhithrogena* are primarily found in cool rapid waters at higher altitudes in both the Nearctic and the neotropics. Apparently these taxa have utilized north-south mountain ranges in Mexico as dispersal routes, much as have other insects (cf. *e.g.*, Halffter, 1987). *Isonychia* and *Stenonema,* on the other hand, are primarily eastern North American groups and have evidently penetrated Mesoamerica via lowlands of the eastern coastal region of Mexico.

In the family Baetidae, *Acentrella* and *Baetis* have Nearctic affinities. *Acentrella* has penetrated only northern Mexico, whereas in *Baetis,* it appears that *B. caelestis, B. magnus,* and *B. notos* may have originated in southwestern North America/Mexico (only *B. magnus* has been found south of Mexico), while *B. flavistriga* and *B. tricaudatus* are widespread species in North America and may have originated in more northern latitudes.

Species of *Caenis* in Mexico comprise elements of both Nearctic and Neotropical lineages. *Caenis anceps* and *C. latipennis* clearly represent northern North America lineages, while *C. bajaensis* appears to be related to a Neotropical lineage (Provonsha, 1990) although the species, itself, may have originated in southwestern North America. We expect many more species of *Caenis* eventually to be found in Mexico, and these will probably include new species of Neotropical affinity.

Table 13.2. Hypothesized geographic affinities of Mexican mayfly genera.

NEOTROPICAL		
Acerpenna	Fallceon	*Moribaetis*
Baetodes	*Farrodes*	*Paracloeodes*
Camelobaetidius	*Homoeoneuria*	*Thraulodes*
Campsurus	*Hydrosmilodon*	*Traverella*
Cloedes	*Lachlania*	*Tricorythodes*
Euthyplocia	*Leptohyphes*	
NEARCTIC		
Acentrella	*Ironodes*	*Sarratella*
Baetis	*Isonychia*	*Siphlonurus*
Drunella	*Nixe*	*Stenonema*
Ephemerella	*Paraleptophlebia*	
Iron	*Rhithrogena*	
NEOTROPICAL + NEARCTIC		
Caenis	*Hexagenia*	
INCONCLUSIVE		
Callibaetis	Choroterpes	*Neochoroterpes*

Hexagenia in Mexico is also made up of Nearctic and Neotropical lineages. *Hexagenia bilineata* and *H. limbata* are members of the subgenus *Hexagenia* s.s., which clearly is a northern North America group. *Hexagenia albivitta* and *H. mexicana*, however, are members of the subgenus *Pseudeatonica*, which is clearly a Neotropical group that probably evolved in South America (McCafferty *et al.*, 1992).

Of the Mexican genera that we are confident have Neotropical affinities, *Euthyplocia*, *Hydrosmilodon*, and *Moribaetis* are not found north of Mexico, and *Campsurus*, *Cloeodes*, and *Farrodes* are restricted north of Mexico to nearby adjacent areas. All of these are considered essentially South American genera.

The Mexican genera *Baetodes*, *Camelobaetidius*, *Lachlania*, *Leptohyphes*, *Thraulodes*, *Traverella*, and, to a certain degree, *Tricorythodes* demonstrate the most consistent Nearctic range pattern for Panamerican genera of Neotropical affinity. That is, generic ranges are widespread in Mexico and primarily restricted to the arid southwestern and western regions north of Mexico. *Tricorythodes*, however, has become more widespread north of Mexico, and a species of *Camelobaetidius* has recently been found as far east as Indiana (McCafferty & Klubertanz, 1994).

It appears that the most plesiomorphic species of the baetid genus *Acerpenna* are South American (Lugo-Ortiz *et al.*, 1994) suggesting Neotropical affinities for the genus, although the genus is also found as far north as Canada. *Callibaetis* is found in both North and South America, but we do not have sufficient phylogenetic data at this time to infer which of these regions represents its origin. It may well be that both Nearctic and Neotropical species lineages exist in Mexico, as is the case in *Caenis* and *Hexagenia*.

The Leptophlebiid genera *Choroterpes* and *Neochoroterpes* require species phyletic studies to ascertain their biogeographic affinities. Preliminarily, however, the demographies of the known species of *Neochoroterpes* would

perhaps suggest an origin in Nearctic southwestern North America.

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