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THE BIOGEOGRAPHY OF MESOAMERICAN MAYFLIES

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ABSTRACT

Mayflies (Insecta: Ephemeroptera) of Mesoamerica are known from 135 species in 39 or more genera; five ^{genera} are endemic, 15 are strictly Neotropical, and others are Pan-American (Nearctic + Neotropical). When mayfly genera are considered, Mesoamerica shows a stronger affinity with South America than North America, more so if amphinotic genera are excluded from comparisons. Dispersal is initially assumed to explain most Pan-American patterns; the cyclic nature of the American interchange and the presence of only temporary or weak historical barriers in the Mexican transition zone indicate that vicariant methodology may not be applicable. Several genera previously reported from Mesoamerica are based on erroneous or doubtful placement of species. Recent centers of dispersal for Pan-American genera are distinguished from centers of origin, and hypotheses of recent biogeographic history are based on cladistics, demographics, adaptive behavior, and ecological limitations. Among Pan-American genera, hypotheses are offered that *Baetodes*, *Camelobaetidius*, *Campsurus*, *Cloeodes*, *Farrodes*, *Homoeoneuria*, *Lachlania*, *Leptohyphes*, *Thraulodes*, *Tortopus*, *Traverella*, and *Tricorythodes* have recent Neotropical centers of dispersal, and that *Cercobrachys*, *Iron*, *Isonychia*, *Leucrocota*, *Nixe*, *Rhithrogena*, and *Stenonema* have recent Nearctic centers of dispersal. An initial spread of *Hexagenia* into South America was possibly followed by continental vicariance resulting in subgenera, and then more recent dispersals both north and south into Mesoamerica. Mesoamerican *Caenis* is shown to consist of both an old South American lineage and a more recent Holarctic lineage. Records of *Fallceon* and *Paracloeodes* in the West Indies and North America only, make hypotheses difficult, but their eventual confirmation in Central America would suggest a Neotropical affinity. Lack of substantial data does not allow a hypothesis about the history of *Callibaetis*. Distributional patterns and ecological factors indicate that nearly all genera

Tulane Studies in Zoology and Botany, Supplementary Publication number 1, 1992. Purdue University Experiment Station Journal number 10215. Manuscript revised September, 1991.

hypothesized to have recent Neotropical centers of dispersal are arid restricted or favored in the Nearctic, and several are warm-water sublimited; the few with broader or more eastern Nearctic patterns may reflect a longer history in North America. Most genera hypothesized to have a recent Nearctic center of dispersal are broadly distributed there; those that are highland sublimited in the Neotropics, some of which are rapid-water sublimited, probably dispersed along mountainous corridors; those found in tropical lowlands probably dispersed via the eastern maritime corridor. Mesoamerican interchanges^{and} speciation involving Pan-American genera can be explained primarily within the context of complex cyclic geological and climatological events beginning in the Miocene.

INTRODUCTION

The mayfly fauna of Central America, the West Indies, and tropical southern Mexico (together constituting the region we refer to as Mesoamerica) is typical of many freshwater insect faunas of the region in that it remains relatively poorly known but has received considerable recent attention. This is demonstrated by the fact that well over half of the presently known mayfly species of Mesoamerica have been described since 1967. Research on the mayfly fauna has dealt primarily with alpha taxonomy. Although some 20 ephemeropterists have described Mesoamerican species, the most significant historical taxonomic contributions are the late Nineteenth Century work of the Rev. A. E. Eaton (e.g., Eaton, 1871, 1883-88), the mid Twentieth Century work, especially of Jay R. Traver and her co-workers (e.g., Traver, 1938, 1946, 1947a, 1947b, 1950, 1958, 1960; Traver & Edmunds, 1967, 1968) and the more recent work by Richard K. Allen and his co-workers (Allen, 1973a, 1973b, 1974, 1977, 1978, 1985, 1990a, 1990b; Allen & Brusca, 1973a, 1973b, 1978; Allen & Cohen, 1977; Cohen & Allen, 1978).

We have engaged in research in Mesoamerican Ephemeroptera (McCafferty 1968, 1970, 1984, 1985a; Flowers 1979, 1980, 1985, 1987; Flowers & Peters, 1981; Waltz & McCafferty, 1985, 1987a, 1987b; Dominguez & Flowers, 1989; McCafferty & Waltz, 1990) in order to elucidate the fauna, its historical biogeography, and its revisionary impact on the systematics of widespread taxa, especially the families Baetidae and Leptophlebiidae. In this paper, we update and analyze the descriptive faunistics of Mesoamerican mayflies and apply analytical methodology for examining elements of the fauna in terms of their casual biogeography. Emphasis is placed on genera mainly because most Mesoamerican mayfly species (approximately 86%) are endemic.

Reported occurrences of *Apobaetis*, *Baetis*, and *Hermanella* in Mesoamerica have recently been shown to be incorrect (Dominguez & Flowers, 1989; McCafferty & Waltz, 1990). In addition, other reported occurrences of *Baetis*, *Choroterpes*, *Hermanellopsis*, *Homothraulius*, *Thraulius*, and *Ulmeritus* cannot be validated because the assignments of respective Mesoamerican species to these genera remain problematic and in all likelihood are incorrect (see, e.g., Peters, 1988; McCafferty & Waltz, 1990). Therefore, these genera, although reported from Mesoamerican, are not included in the tables or analysis herein.

FAUNISTICS

Our northern demarcation for a biogeographic construct of Mesoamerica corresponds to the northern limit most consistently found for the southern vicariads of genera having a major north-south disjunction between Central America/southern Mexico and northern Mexico/United States. It is a line roughly bordering the northern and western limits of the Isthmus of Tehuantepec, but with northern fingers encompassing tropical forest areas to about Poza Rica, Mexico. This conceptual line, besides demarcating North America from Mesoamerica, also divides the Nearctic and Neotropical realms for the purposes of our discussion. This construct of Mesoamerica does not agree with that of Allen (1990a) because we include the West Indies and describe a slightly different northern demarcation. The "Middle America" of McCafferty and Waltz (1990) agrees with our concept of Mesoamerica except only the Greater Antilles were included in their Middle America and all of Mexico south of the Tropic of Cancer was somewhat arbitrarily included.

Presently described and authenticated extant Mesoamerican genera are presented by family in Table 1. Familial classification is after McCafferty (1991a).

TABLE 1. Systematic list of extant Mesoamerican mayfly genera, indicating familial classification and (in parentheses) the number of presently valid nominal Mesoamerican species. No number denotes the record is based on undescribed species. *Apobaetis*, *Baetis*, *Choroterpes*, *Hermanella*, *Hermanellopsis*, *Homothraulius*, and *Ulmeritus* are unlisted because they have been erroneously reported or are of highly dubious taxonomic status in the region.

Baetidae	Leptophlebiidae
<i>Baetodes</i> (13)	<i>Atopophlebia</i> (1)
<i>Callibaetis</i> (5)	<i>Borinquena</i> (3)
<i>Camelobaetidius</i> (5)	<i>Careospina</i> (3)
<i>Cloeodes</i> (2)	<i>Farrodes</i> (3)
<i>Fallceon</i> (2)	<i>Hagenulopsis</i>
<i>Guajirolus</i> (1)	<i>Hagenulus</i> (5)
<i>Moribaetis</i> (3)	<i>Neohagenulus</i> (3)
<i>Paracloeodes</i> (1)	<i>Terpides</i> (1)
	<i>Thraulodes</i> (13)
Caenidae	<i>Traverella</i> (2)
<i>Caenis</i> (2)	<i>Traverina</i> (1)
<i>Cercobrachys</i>	<i>Ulmeritoides</i>
<i>Isulibrachys</i> (1)	
	Oligoneuriidae
Ephemeridae	<i>Homoeneuria</i> (1)
<i>Hexagenia</i> (2)	<i>Lachlania</i> (5)
Heptageniidae	Polymitarcyidae
<i>Iron</i> (2)	<i>Campsurus</i> (2)
<i>Leucrocota</i>	<i>Campylocia</i> (1)
<i>Nixe</i> (1)	<i>Euthyplocia</i> (1)
<i>Rhithrogena</i> (1)	<i>Tortopus</i> (1)
<i>Stenonema</i> (1)	
Isonychiidae	Tricorythidae
<i>Isonychia</i> (1)	<i>Haplohyphes</i> (1)
	<i>Leptohyphes</i> (25)
	<i>Tricorythodes</i> (6)

Atopophlebia, *Borinquena*, *Campylocia*, *Careospina*, *Euthyplocia*, *Guajirolus*, *Hagenulopsis*, *Hagenulus*, *Haplohyphes*, *Insulibrachys*, *Moribaetis*, *Neohagenulus*, *Terpides*, *Traverina*, and *Ulmeritoides* are known only as Neotropical genera. Of these, the West Indian genera *Careospina*, *Hagenulus*, *Insulibrachys*, *Neohagenulus*, and *Traverina* are presently thought to be endemic to Mesoamerica (Peters, 1971; Soldán, 1986), and all but the caenid *Insulibrachys* are members of the Leptophlebiidae, a family known for its propensity for insular evolution. The remaining 24 extant genera are both Nearctic and Neotropical and thus are here referred to as Pan-American. Many Pan-American genera demonstrate broadly disjunct distributions between North America and Mesoamerica; however, *Baetodes*, *Callibaetis*, *Isonychia*, *Leptohyphes*, *Thraulodes*, and *Traverella* range relatively continuously through Mexico either along mountainous corridors or the Gulf of Mexico maritime corridor. *Hexagenia* and *Lachlania* are narrowly disjunct.

Only the genera *Cercobrachys*, *Cloeon*, and *Pseudocloeon* have previously been reported from North and South America but not Mesoamerica. However, Flowers (unpublished) has recently collected *Cercobrachys* in Panama, and the *Cloeon* and *Pseudocloeon* records are inconsequential because any applicable identifications of such would have been based on no longer acceptable taxonomic concepts (Waltz & McCafferty, 1987c; McCafferty & Waltz, 1990).

As of 1991, we can account for approximately 650 described extant mayfly species in North America (see esp., McCafferty et al., 1990; McCafferty & Waltz, 1990), 135 for Mesoamerica, and approximately 340 for South America. In calculating the number of Mesoamerican species we included nominal species that are dubiously assigned to genera not included in this study, and therefore the total cited is greater than the sum from Table 1. Mesoamerica appears relatively rich in mayfly species given its available land mass, but even when all presently known Neotropical species are taken together they do not approach the Nearctic number. Although the expected greater proportion of undiscovered species in the Neotropics undoubtedly explains part of this discrepancy, it may well be that the temperate mayfly fauna is inherently as rich or richer in species numbers than the tropical fauna. McCafferty (unpublished) has generally found this to be the case when comparing Costa Rican streams with a variety of North American streams (e.g., in the Ouachita Mountains of Arkansas) (McCafferty & Provonsha, 1978), and some other workers (e.g., Patrick et al., 1966; Illies, 1969; McElvay et al., 1981; Wolda & Flowers, 1985) showed similar latitudinal relations for certain stream-dwelling insects. The fact that thermal niches and life history strategies are more diverse in temperate regions may be a major factor contributing to this phenomenon.

We account for 39 genera in Mesoamerica, 77 in the Nearctic, and 79 in South America; 25 are in common between Mesoamerica and the Nearctic, 28 between Mesoamerica and South America, and 15 between the Nearctic and South America. Mesoamerica shows less affinity with the Nearctic than with South America. When the cool-adapted Amphitotic genera (16 Chilean–Patagonian genera with exclusively transantarctic affinities) are excluded from the comparison, the Mesoamerican–South American affinity appears even stronger. If species rather than genera are compared, the same relationships are indi-

cated. No species are known to be common to both the Nearctic and South America.

One measure of relative affinity of regions in the Western Hemisphere based on the distribution of mayfly genera can be generated by using Sorensen's coefficient [$= 2a/(2a + b + c)$, where a = genera in common between two regions, b = genera exclusive to one region, and c = genera exclusive to the other region]. If calculated, results show the relationships generally stated above. Another measure of area affinity would be to formulate reduced area cladograms (Rosen, 1978). Preliminarily, it appears as if those would suggest similar overall affinity; however, precise species level cladistics are severely lacking for nearly all genera, and any such cladograms at this point would be generated by incomplete and thus questionable data.

With respect to mayfly distribution patterns, degrees of uniqueness to areas, and shared lineages between areas, four biogeographic regions in the Western Hemisphere could be recognized. These would include 1) the Nearctic region (as we have defined it above), 2) the Mesotropical region (Mesoamerica as we have defined it), 3) the Neotropical region (restricted to tropical and subtropical South America), excluding 4) the Amphitropic region (the temperate Chile-Patagonia area mentioned above). For the purposes of discussion herein, however, we will use more traditional concepts of the Nearctic and Neotropical realms.

Distributions of Pan-American genera are a function of historical biotic events such as dispersal and historical earth events such as vicariance, and at different levels, the interaction between organisms and their physical and biotic environments now and in the past (Myers & Giller, 1988). The first step in examining these functions is faunistics pattern analysis. Therefore, we have faunistically characterized these genera by their more definable geographic and broad ecological patterns. These data, as they may be applied preliminarily at the genus level, are summarized in Table 2.

Nearctic distributions of Pan-American genera are expressed by three patterns: some genera are restricted to western desert and coniferous forest drainages (referred to as Nearctic arid-restricted distributions); at least one Pan-American genus is restricted to eastern prairie and deciduous/mixed forest drainages (Nearctic humid-restricted) (actually several Holarctic genera are restricted to this area); and some genera are found in both eastern and western North America (Nearctic general), although many of these general distributions are predominantly either Nearctic arid or Nearctic humid (additionally referred to as arid-favored or humid-favored distributions).

Although sublimiting factors for some restricted and some favored distributions of mayflies are apparently correlated with atmospheric moisture regimes (in which case the terms arid and humid are more than convenient descriptors), there are many possible sublimiting factors. General distributions, although geographically broad, are in some cases patchy or favored because they are sublimated by certain other ecological factors. Additional factors we selectively present in Table 2 are briefly describable as 1) "cool water" (generally, water that will support trout reproduction and does not increase much in summer temperature), 2) "warm water" (although minimum annual temperatures may

TABLE 2. Nearctic geographic pattern and known ecological factors possibly sublimiting ranges of Pan-American mayfly genera. Sublimiting factors: **W** = Nearctic warm water, **C** = Nearctic cool water, **R** = generally rapid water, **S** = generally still water, **F** = generally fine substrate, **P** = generally plant substrate, **L** = Neotropical lowland, **V** = Neotropical altitude variable, **H** = Neotropical highland. See text for fuller descriptions of ecological categories.

Nearctic General Distribution		
Arid-Favored	Not Favored	Humid-Favored
<i>Camelobaetidius</i> W,V <i>Fallceon</i> <i>Leptohyphes</i> V <i>Traverella</i> W,R	<i>Caenis</i> V <i>Callibaetis</i> S,V <i>Cercobrachys</i> F <i>Iron</i> C/R,H <i>Nixe</i> H <i>Rhithrogena</i> C/R,H <i>Tricorythodes</i>	<i>Hexagenia</i> F,V <i>Homoeoneuria</i> W,F , <i>Isonychia</i> R,V <i>Leucrocuta</i> H <i>Paracloedes</i> W <i>Stenonema</i> L
Nearctic Arid-Restricted		
<i>Baetodes</i> P,V <i>Campsurus</i> W,F,L	<i>Cloeodes</i> V <i>Farodes</i> W	<i>Lachlania</i> W,F <i>Thraulodes</i> V
Nearctic Humid-Restricted		
<i>Tortopus</i> W,F,L		

be comparable with cool water environments, summer maximums are greater), 3) "plant substrate" (plant material is required as a larval foothold), 4) "fine substrate" (larvae are restricted to sand, silt, mud, or clay substrates), 5) "rapid water" (generally over 100 cm/sec), and 6) "still water" (ponds, lakes or quiet pools of streams).

Substrate and current may also be sublimiting within Neotropical ranges of Pan-American genera. There is not a true parallel in the tropics to cool- and warm-water sublimiting factors of the Nearctic; however, an altitudinal distribution may be reasonably comparable in some cases. For example, a genus that is cool-water sublimited in temperate areas may be found only in tropical highlands, and a genus found in tropical lowlands may be sublimited by warmer water temperatures in temperate areas. These data, although incomplete, are included in Table 2; more field research in Mesoamerica is required before these kinds of data will be entirely reliable.

CAUSAL BIOGEOGRAPHY

Mesoamerican mayfly genera that are restricted to the Neotropics include those of presumed South American origin that have spread into Mesoamerica following land merger events, and those, such as West Indian endemics, that have evolved in Mesoamerica but are presumably derived from South American lineages. There is, of course, the possibility that Mesoamerican genera may be discovered that represent sister lineages to Nearctic genera, although this has yet to be demonstrated in mayfly groups for which there is relatively good phylogenetic data (e.g., McCafferty, 1987; Savage, 1987).

Perhaps the most intriguing biogeographic question about genera restricted to the Neotropics concerns their far reaching geographic and evolutionary history. What broad scale continental areas were occupied by them or their immediate ancestors in view of the vicariant paradigm? Answers require cladistic based studies of genera. Familial relationships of these genera are Gondwanan (McCafferty & Edmunds, 1979; Peters, 1988). Southern drift-related vicariance may be suggested by this and in fact has been recently demonstrated for Oligoneuriidae and Polymitarciidae (sens. auctt.) by Brazilian fossils from the Lower Cretaceous (McCafferty, 1990a). However, former Northern Hemispheric distributions followed by extinctions (especially involving Tertiary spread during northern warm pulses) cannot be ruled out. For example, with the discovery of fossil *Litobrancha* from northern Asia and the fossil genus *Denina* from the Palearctic, McCafferty and Sinitshenkova (1983) and McCafferty (1987) demonstrated an extinct Laurasian ancestry for the Hexageniinae particularly in reference to the extant tropical lineages (Oriental *Eatonigenia*, Afrotropical *Eatonica*, and Neotropical *Pseudeatonica*). Furthermore, known Mesoamerican genera do not have close relationships with Amphinotic groups, and it is only the Amphinotic South American genera that show a history of western Transantarctic drift involving Australia, New Zealand, and South America (see e.g., Edmunds, 1975).

Philosophy and Methodology

We are primarily concerned herein with the biogeography of Mesoamerican genera that are Pan-American. Since significant fossil data are limited, inferential data and reliance on hypothetico-deductive reasoning and congruence are necessary (see Rosen, 1988). A major question about Pan-American mayflies is whether a genus is of recent Neotropical or Nearctic affinity; in other words, does it have a most recent southern tropical center of dispersal or a northern temperate one? Such a question invokes assumptions of dispersal rather than vicariance, and this more-or-less has been the premise in other analyses of Pan-American mayflies (Allen & Brusca, 1973a; Edmunds et al., 1976; Edmunds, 1982; Peters, 1988; Allen, 1990b). Such "explanatory" biogeography (see Patterson, 1983), which assumes a dispersal-driven process to explain pattern, appears appropriate in light of overwhelming data showing the Mexican transition zone as a repetitive north-south dispersal corridor for general Nearctic and Neotropical biota (Stehli & Webb, 1985) and insects in particular (e.g., Halffter, 1976, 1987). In this respect, Noonan (1988), in a comprehensive analysis of Mexican and North American insects including the aquatic order Plecoptera, concluded that methods of vicariance-oriented explanatory biogeography were inadequate for explaining the biogeographic history of these insects. He specifically attributed this difficulty to common dispersals across barriers, barriers in the area being recently highly cyclic, extensive range changes in the past, and considerable extinctions. Kohlmann and Halffter (1990) have recently reiterated that Holarctic, Nearctic, and Neotropical lineages of insects appear to have invaded and speciated in parts of Mesoamerica repeatedly.

In light of the above, we have not applied such strict methods of vicariance analysis, such as suggested by Rosen (1975, 1978) and rigorously done in the

analysis of Potamanthidae biogeography by Bae and McCafferty (1991) but with a less rigorous technique in the analysis of Transantarctic Ephemeroptera by Edmunds (1975). Nevertheless, we do regard vicariance as a viable alternative explanation when such is suggested from the lines of evidence we employ (particularly in light of the presumed low vagility of certain mayflies). Thus, while our approach is basically an explanatory one with a prioritized assumption of dispersal, we do not feel bound to adhere to only one process for our explanations.

Any discussion of dispersal must consider the inherent vagility of mayflies. We agree with Edmunds (1982) that mayflies are diffusion dispersers. Rates of diffusion over time, however, vary considerably among species as is evidenced by the fact that some North American species remain essentially restricted to disjunct glacial refugia, whereas others have become continentally widespread within the past 10,000 years (McCafferty, 1985b, 1990b). Secular migration (Mason, 1954) and vicariant events on small scale are evidently important factors for any of the slow-diffusion lineages.

Aquatic insects have been categorized as those that colonize aerially and are most apt to disperse between watersheds, and those that are primarily aquatic dispersers and thus are more limited by drainage systems (Ross et al., 1967; Scudder, 1979; Flannagan & Flannagan, 1982). Such a dichotomy may express only the ends of a continuum of vagilities found among mayflies, but we suspect that ranges primarily change as drainage systems expand, retreat, or become disrupted.

There may be some relationship between the vagility of mayflies and their relative fitness for temporary or unstable versus permanent or stable habitats. In this respect, vagility has been suggested as a function of r- and K-selection, or maintenance and dispersal phenotypes (see e.g., Bush, 1975; Bruton, 1989). Although it is still difficult to neatly categorize all mayflies in this manner, there is growing evidence that mayfly species demonstrating various adaptations to rigorous and unstable habitats (particularly with regard to alternative life history strategies, such as egg dormancy, ovoviviparity, parthenogenesis, and short growing seasons) have exceptional abilities for colonization (see e.g., Edmunds et al., 1976; McCafferty & Morihara, 1979; Gray, 1981; Edmunds, 1982; Sweeney & Vannote, 1987). We will show below that ecologically tolerant species or groups may be among the most vagile of mayflies. Other factors, such as length of adult life, population size, and propensity for flight relate to vagility, but correlated data are currently unavailable in this respect.

Little evidence of jump dispersal in Ephemeroptera exists. In theory, mayflies, which have relatively weak-flying and short-lived gravid females whose eggs generally require an immediate aqueous medium, are poor candidates for jump dispersal. Thus, expanses of saltwater and desert presumably would pose formidable physical barriers to mayflies. Nonetheless, mayflies are known from aeroplankton, and jump dispersal cannot be entirely ruled out.

As suggested above, certain adaptive shifts or predispositions are required by mayflies in order to successfully colonize new ecological and climatological environments. Two such factors appear to be especially pertinent for understanding Pan-American affinities of mayflies. Edmunds et al. (1976) observed

that in some temperate species for which a tropical ancestry can be clearly substantiated, postembryonic life occurs very quickly in summer, taking advantage of seasonal warm temperatures, and eggs remain dormant most of the year (functional diapause, although suggested, has yet to be experimentally demonstrated). Temperate-based seasonality, therefore, may be a barrier that is overcome by a phenological shift from more continuous cyclic development to an annual cycle with a highly prolonged dormancy. Otherwise, a lower larval growth temperature threshold, common among most temperate species, is necessary. This is not to say that we subscribe to the idea that diapause evolved as an adaptation subserving range extension from tropical regions. Instead, it appears that diapause originated in the tropics, where it served more subtle adaptive functions (Tauber & Tauber, 1981) but predisposed insects for dramatic life history adjustments required elsewhere. This generality requires testing in Ephemeroptera but appears credible in light of Wolda's (1978) conclusions that tropical habitats are seasonal and that tropical insect populations are not significantly more stable than temperate populations.

The second possibly pertinent factor is suggested by the study of Edmunds and Edmunds (1980), who indicated, by citing primarily Bishop (1973) and their own work in Malaysia, that emergence in tropical lowland mayflies occurs nocturnally and swarming takes place from before dawn through morning hours. Actually, mayfly swarming can take place during any part of the night in the tropics, depending on the species (McCafferty, unpublished). Regardless, such diel periodicity is allegedly an adaptation to extreme daytime predatory pressure that may be experienced in lowland tropical environments. McCafferty (unpublished) has noted a similar relationship in going from temperate regions to subtropical lowlands in southern Africa; however, the differences are also associated with proportional changes in family-level taxa. For example, caenids and tricorythids are prone to pre-dawn swarming no matter where they occur, but those families may become more prevalent relative to other mayflies in tropical and subtropical areas of Africa. In addition, crepuscular emergence and swarming are also well developed in Afrotropical lowland species.

According to Edmunds and Edmunds (1980), would-be temperate colonizers of tropical lowlands may be limited by their ability to adapt their diel flying periodicity. We will show below that recent invasions of the Neotropics from the North have predominately involved colonization of tropical highlands, not lowlands. With respect to the two lineages for which we are able to hypothesize an invasion of lowland tropics from the north-temperate region, there are no data regarding their swarming habits in the tropics, although they are known to be crepuscular swarmers in North America. Therefore, whereas tropical-derived lineages may retain ancestral swarming modes after invading temperate areas, it is not known if temperate-derived lineages also retain ancestral swarming modes, or if swarming modes may, indeed, preclude colonization of tropical lowlands.

Before reviewing our methods of inference, it should be emphasized that we distinguish concepts of the latest centers of dispersal (*sensu* Udvardy, 1969; Müller, 1972) from centers of origin, although the two could obviously be the same in some cases. Our study addresses only hypotheses as to whether the most

recent center for dispersal was encompassed by the Nearctic, the Neotropics, or both, and thus emphasizes directionality in the recent biogeographic history of the genus. This is a particularly important point when dealing with the North American mayfly fauna because of the cyclic phenomena of widespread extinction, isolation, spread, and speciation mediated, for example, by dramatic Tertiary orogenies and frequent Quaternary climatic shifts. Although we will show that many Pan-American generic distributions are probably the result of Pleistocene and post-Pleistocene events, it is also probable that certain present Pan-American mayfly geographic patterns are attributable to events dating from somewhat earlier to as many as 60 million years ago, as, for example, has been shown from some other kinds of biota (Axelrod, 1975).

We agree with Ross (1967, 1974) and with Nelson and Platnick (1981) that phylogenetic information (cladistics) is crucial to reconstructing historical biogeography, even though the former authors emphasized dispersal, and the latter emphasized vicariance as the predominant mechanism producing pattern. We regard species-level cladistics as our first line of evidence for deciphering recent biogeographic history of genera and as a primary means of testing biogeographic hypotheses based on other observations. In first assuming dispersal as the most likely underlying process for the patterns we observe in Mesoamerica, we generally apply the concept that, in the case of mayflies at least, plesiotypic species tend to remain in original geographic ranges and apotypic species tend to be represented in more recent extensions (see Brundin, 1972).

Generic cladistics, although valuable for inferring a Laurasian versus Gondwanan evolutionary origin, are not necessarily valid for hypothesizing latest centers of dispersal because logically they may differ from centers of origin, given the strong possibility of extinction and expansion having taken place in the meantime. Generic relationships are valuable, however, in supplementing other data used to formulate our hypotheses.

Allen and Brusca (1973a), Edmunds et al. (1976), Edmunds (1982), Peters (1988), and Allen (1990b) have previously discussed geographic spread of genera between Nearctic and Neotropical regions. The criterion of Allen and Brusca (1973a) for indicating direction of movement was the presumed origin of each genus, but the basis or source of these presumptions was never given. Allen (1990b) attempted to test Halffter's (1976) pattern analysis data with mayfly distributions, but his mayfly origins again were evidently assumed without the benefit of any phylogenetic studies or reference to such.

Edmunds et al. (1976) and Edmunds (1982) employed generic phylogeny to offer theories of origins as did Peters (1988); however, it is difficult to always ascertain what phylogenetic methodology was used, and explicit phylogenetic data or reference to such were often lacking. It is also difficult to interpret their conclusions since the emphasis on ascribing either an "austral" or "boreal" designation to each genus suggests that in actuality recent centers of dispersal are sometimes being theorized. Rosen (1978) has emphatically shown the importance of biogeographers making a clear distinction between original biogeographic patterns and subsequent alterations.

When species-level cladistics are incomplete, we maintain that other lines of inference can be used for hypothesis formation with lesser degrees of confidence. Cartographic pattern analysis is useful for hypothesizing a latest center of dispersal (not necessarily a center of origin) when clearly asymmetrical demographics of a genus are indicated. As an example, if a genus is composed of 20 Neotropical species and one Nearctic species, then a most recent Neotropical center of dispersal might be hypothesized. Ross (1974) referred to this as the numerical method (with respect to origin determination) and pointed out that it can be faulty because organisms are not always the most diverse in the older region (Cain, 1944; Ross, 1962). However, this does not prevent such demographic data from being used to formulate a hypothesis to be tested with other data. Any such hypothesis is obviously stronger if species in the minority region are relatively apomorphic (even when complete phylogenies have not been determined). Our demographic data below are based only on nominal species.

A third line of evidence for recent biogeographic history is based on adaptational shifts related to regional colonization or the possible retention of a behavioral mode consistent for the fauna of the region. When north-temperate species demonstrate the phenological shift to short once-a-year postembryonic development (as discussed above) and/or retain flight behavior typical of lowland tropical species (as discussed above), then a dispersal from the tropics may be hypothesized. At this time we know of no comparable kinds of indirect behavioral evidence available for hypothesizing a recent Nearctic center of dispersal.

Hypotheses

A summary of our hypotheses concerning recent biogeographic history of Pan-American mayfly genera is presented in Table 3. The degree of confidence for each of the hypotheses varies considerably from genus to genus, as will be shown below.

Phylogenetic relationships are particularly useful in hypothesizing the recent biogeographic history of three genera (*Cloeodes*, *Homoeoneuria*, and *Hexagenia*). Plesiomorphic species of *Cloeodes* (Waltz & McCafferty, 1978b) and *Homoeoneuria* (Pescador & Peters, 1980) are found in South America, and relatively apomorphic species of these genera occur in Mesoamerica and North America. The most apomorphic species of *Cloeodes* actually occur in eastern Asia (Waltz & McCafferty, unpublished). Generic relations of *Cloeodes* (Waltz & McCafferty, 1987a) indicate a South American and Gondwanan ancestry. Its sister genus, *Bernerius*, is South American.

If cladistics presented by Pescador and Peters (1980) are correct, then *Homoeoneuria* offers a caveat that geographic pattern analysis alone, vis-à-vis the numerical method, does not unequivocally suggest directionality of dispersal, particularly when not strongly skewed. This is because two of the species of the genus are Neotropical (one South American and one Mesoamerican) and five are Nearctic. The South American species, *H. fitzkau*, was placed in the separate subgenus *Notochara* by Pescador and Peters (1980), and very likely will prove to

TABLE 3. Summary of hypotheses of the recent biogeographic history of certain Mesoamerican-Pan-American mayfly genera regarding the Nearctic and Neotropical regions. Arrows indicate hypothesized direction of most recent dispersal of lineages. See text for explanations.

Neotropics → Nearctic	
<i>Baetodes</i>	<i>Lachlania</i>
<i>Camelobaetidius</i>	<i>Leptohyphes</i>
<i>Campsurus</i>	<i>Paracloeodes</i>
<i>Cloeodes</i>	<i>Thraulodes</i>
<i>Fallceon</i>	<i>Tortopus</i>
<i>Farrodes</i>	<i>Traverella</i>
<i>Homoeoneuria</i>	<i>Tricorythodes</i>
Nearctic → Neotropics	
<i>Cercobrachys</i>	<i>Leucrocuta</i>
<i>Hexagenia</i> s.s.	<i>Nixe</i>
<i>Iron</i>	<i>Rhithrogena</i>
<i>Isonychia</i>	<i>Stenonema</i>
Neotropics → ← Nearctic	
<i>Caenis</i>	

be a separate genus once its larval stage is known (McCafferty, unpublished). In this regard, our hypothesis for *Homoeoneuria* (sensu stricto) is that it has a most recent Neotropical center of dispersal in Mesoamerica. Furthermore, recent continental vicariance may have been involved in the evolution (cladogenesis) leading to *Notochara* and *Homoeoneuria*.

Species of the subgenus *Pseudeatonica* (genus *Hexagenia*) are clearly apomorphic and are restricted to the Neotropics (McCafferty, 1979, 1987). Generic phylogeny indicates that *Hexagenia* originated in the Northern Hemisphere (McCafferty, 1987); it spread into the Neotropics, and *Pseudeatonica* evolved as an isolated South American vicariad. The recent center of dispersal for the subgenus is hypothesized to be South America, with spread northward into Mesoamerica following a continental merger via the Isthmus of Panama.

Five Pan-American genera (*Baetodes*, *Campsurus*, *Farrodes*, *Thraulodes*, and *Leptohyphes*) are hypothesized as having recent Neotropical centers of dispersal on the basis of cartographic pattern analysis in the absence of complete species-level cladistics and significant biological data [numerical and phenological data are derived primarily from Edmunds et al. (1976), Allen (1978), Allen and Cohen (1978), Cohen and Allen (1978), and Hubbard (1982)]. There is, however, available genus-level cladistic data that appear to support these hypotheses.

Baetodes is currently reported to contain 12 species in South America, 13 in Mesoamerica, and three in North America. Therefore, *Baetodes* is one mayfly genus for which a Mesoamerican center of origin might be hypothesized. However, Waltz & McCafferty (unpublished) believe that several Mesoamerican species of *Baetodes* will eventually fall to synonymy, thus modifying these species demographics. Furthermore, and more importantly, the most plesiomorphic species of *Baetodes* are South American, and the genus is closely related to the

subgenus *Mayobaetis* of the genus *Moribaetis* (Waltz & McCafferty, unpublished). This subgenus is currently known from Ecuador and Costa Rica (Waltz & McCafferty, 1985). The relationship of *Baetodes* and *Mayobaetis* also suggests that *Mayobaetis* might eventually require full generic status, if a strict phylogenetic classificatory system is imposed.

Campsurus contains 44 species in South America, three in Mesoamerica, and one in North America. The disjunct northern species is restricted to southern Texas. A similar northern disjunction of a single species in Texas is found in the genus *Farrodes*. Three additional species of *Farrodes* occur in the West Indies, but the genus apparently also contains several undescribed or previously misidentified species from southern Mexico through tropical South America (McCafferty, 1985a; Peters, 1988). *Thraulodes* contains 19 species in South America, 13 in Mesoamerica, and six in North America. Peters (1988) indicated that recent (but evidently unpublished) phylogenetic studies showed that *Thraulodes* and *Farrodes* evolved in continental South America (see also Davis, 1987). *Leptohyphes* contains 34 species in South America, 25 in Mesoamerica, and nine in North America.

Three genera (*Lachlania*, *Traverella*, and *Tricorythodes*) are inferred to have recent Neotropical centers of dispersal on the basis of behavioral data, but other indirect evidence also supports the inferences regarding two of the three. The three genera have relatively symmetrical demographics for North and South America, and very little species-level phylogeny has been worked out for them. *Lachlania* develops (from egg eclosion to adult emergence) as a short summer annual in the Nearctic (Edmunds et al., 1976), and both *Traverella* (Edmunds, 1948) and *Tricorythodes* (Hall et al., 1975) demonstrate a lowland tropical diel periodicity in flying, typical of lowlands tropical mayflies. As discussed above, the former behavior suggests an adaptation accompanying a temperate invasion, and the latter behavior may suggest a remnant of a tropical mode of swarming.

The fact that the family Oligoneuriidae, to which *Lachlania* belongs, is essentially a pantropical group (see e.g., McCafferty, 1990a, 1991b) lends support to our hypothesis. Perhaps also lending credence, but without presenting data, Peters (1988) showed that *Traverella* evolved in continental South America. The hypothesis for *Tricorythodes* is relatively weak and certainly open to question since it is based solely on the supposed retention of an early morning swarming behavioral trait that may have originated as an adaptation to the tropics (see further discussion of this genus below).

Phylogenetic data for hypothesizing recent Nearctic centers of dispersal are limited. The subgenus *Hexagenia* (sensu stricto) is restricted to the Nearctic, but apomorphic species extend into Mexico from the northeast as far south as Lake Chapala (McCafferty, unpublished). Recent southward spreading *Hexagenia* have evidently not yet overlapped with the recent northward spreading subgenus *Pseudeatonica* (McCafferty, 1968). As stated previously, a Holarctic center of origin is indicated for the genus. Its widespread distribution in the Western Hemisphere, along with its northern origin, would suggest that its initial spread into South America was much earlier. Late Miocene is one period of evident faunal interchange via the Central American land bridge (Stehli & Webb, 1985) that may correspond to this inferred initial spread. A more recent southward

spread of *Hexagenia* into the Mexican transition zone (Halffter, 1976) may have been as recent as the Pliocene or Quaternary.

Of the 17 Nearctic species comprising *Stenonema*, only one extends disjunctly to Mesoamerica (McCafferty, 1984). Since this species is also relatively apomorphic (Bednarik & McCafferty, 1979), both phylogenetic and demographic evidence suggest a recent Nearctic center of dispersal. The center of origin is also evidently Nearctic (Bednarik & McCafferty, 1979).

Species now placed in the genus *Choroterpes* (the genus does not appear in the Tables) are probably polyphyletic (Peters, 1988); however, there is evidence (Peters, personal communication) that at least one natural subgroup of these species assignable to *Choroterpes* or some other genus, appears to have a recent Nearctic center of dispersal.

Species-level cladistics data are entirely lacking for *Cercobrachys* at the present. Nevertheless, a proposed sister relationship with the Holarctic *Brachycercus* lineage (Soldán, 1986) would suggest at least a Northern Hemisphere center of origin. Demographics of Pan-American species are uninformative and biological data for *Cercobrachys* species are relatively unknown.

Another five genera (*Iron*, *Isonychia*, *Leucrocuta*, *Nixe*, and *Rhithrogena*) are hypothesized to have recent Nearctic centers of dispersal on the basis of highly asymmetrical demographics, with no species known from South America and only one or two in Mesoamerica. These hypotheses are further suggested by familial relations indicating that they all have Laurasian centers of origin (McCafferty & Edmunds, 1979; McCafferty, 1991b). *Iron* contains 19 species in North America and two in Mesoamerica. *Isonychia* contains 17 species in North America and one in Mesoamerica. *Leucrocuta* contains nine species in North America and one in Mesoamerica. *Nixe* contains 13 species in North America and one in Mesoamerica. *Rhithrogena* contains 21 species in North America and one in Mesoamerica. [See Edmunds et al. (1976) and McCafferty et al. (1990) for specific numerical data; the *Leucrocuta* species from Mesoamerica has not been described].

When genera thought to have recent centers of dispersal are examined in light of the distributional and ecological data shown for them in Table 2, certain consistencies among ecological biogeographic patterns allow further deductions about genera for which recent biogeographic history cannot be hypothesized on the basis of primary lines of evidence. Predominantly, genera thus far proposed to have Neotropical centers of dispersal have arid-restricted or arid-favored distributions in the Nearctic. In addition, at least four of those genera are apparently warm-water sublimited (Table 2). This relationship may suggest a significant influence of the arid Mexican transition zone on the evolution of these lineages if, indeed, they had a tropical origin. On the other hand, it may simply be that they invaded primarily by mountainous corridors and there has not been sufficient time for further spread in North America. All groups hypothesized to have recent Nearctic centers of dispersal have general distributions in the Nearctic, some of them humid-favored, but none are arid-favored. Three of these are apparently rapid-water sublimited (Table 2).

From the above we deduce that *Camelobaetidius* may also have had a recent Neotropical center of dispersal because it follows the pattern of having an arid-

avored distribution in the Nearctic and being warm-water sublimited. Because species numbers of *Camelobaetidius* are evenly distributed between North America, Mesoamerica, and South America (Traver & Edmunds, 1968; McCafferty & Waltz, 1990), eventual species-level cladistics will be most enlightening with regard to whether the genus originated in Mesoamerica or South America. Based on preliminary data, Waltz (unpublished) believes that the South American species are the most highly evolved.

It might be deduced that *Caenis* and *Callibaetis* have Nearctic centers of dispersal because they demonstrate a generalized Nearctic distribution pattern common to other genera thus far hypothesized to have Nearctic centers of dispersal. They differ from those genera, however, in being well represented in South America. *Tricorythodes*, hypothesized to be of Neotropical affinity on rather slim inferential data, similarly is distributed in the Nearctic, is not arid-favored, and occurs in South America. Therefore, if *Tricorythodes* does have a recent Neotropical center of dispersal, the trend of Nearctic distributions shown by other Neotropical derived genera is not a universal one. The more general Nearctic pattern of *Tricorythodes* is perhaps correlated with a relatively longer period of infiltration and presence in North America.

Callibaetis appears well adapted for inhabiting temporary and otherwise unstable environments, having been found from road puddles to tide pools and cattle troughs to mangrove swamps (see e.g., Berner & Pescador, 1988). These mayflies are ovoviviparous as well as being relatively ecologically tolerant. We take it then, that among mayflies in general, *Callibaetis* probably has an atypically high potential for dispersal. This could explain its widespread distribution throughout the Americas and further confounds any attempt to deduce its recent history. In fact, we would not be surprised to eventually find the ranges of one or more *Callibaetis* species to extend from North America to South America. Only species-level cladistics will allow meaningful hypotheses concerning recent biogeographic history, since the group's ubiquitous nature has masked all other lines of inference.

If the two *Callibaetis* species known to occur in Mesoamerica and North America, *C. montanus* and *C. pictus*, are examined, we find that they demonstrate western/arid Nearctic patterns. This, in itself, is of no help in deciphering the more ancestral range of these species, and since their phylogenetic relationships are unknown, it does not aid in the analysis of the genus. However, McCafferty (unpublished) has examined *C. montanus* from highland and lowland tropics in Central America, a distribution that suggests an origin in the Neotropical part of its range.

Whereas *Callibaetis* is restricted to the Western Hemisphere, *Caenis* is a truly cosmopolitan genus. All but one of the *Caenis* species found north of Mexico are members of Northern Hemisphere lineages, and the *Caenis* spp. from South America are Gondwanan. Therefore, *Caenis* may represent an unusual situation in which all species of a Pan-American genus do not have a related recent biogeographic history. *Caenis bajaensis*, known from Arizona, California, Colorado, Nebraska, New Mexico, and Mexico (see Provonsha, 1990), is the only species belonging to a Southern Hemisphere lineage (P. Malzacher, personal communication) presently known to have infiltrated northward into the Nearc-

tic. Its distribution is typical of such species as discussed above. On the other hand, McCafferty (unpublished) has studied *Caenis* specimens from Nicaragua that are probably *C. diminuta* and definitely belong to the *diminuta* group, a Northern Hemisphere lineage described by Provonsha (1990). As far as *Caenis* is concerned then, Mesoamerica is apparently a mixing ground consisting of both Nearctic and old South American lineages. It is highly possible that a similar kind of history will be discovered for *Callibaetis*.

Tortopus appears to be warm-water sublimited in the Nearctic just as certain of the genera proposed to have recent Neotropical centers of dispersal are, but it also has a humid-restricted distribution in the Nearctic (McCafferty, 1975). Nevertheless, it likely has a Neotropical center of origin, given its sister relationship with *Campsurus*. Possibly the center of origin of *Tortopus* is also its latest center of dispersal, and this particular geographic disjunction is related to Tertiary events and not the more recent events we suggest as underlying most Pan-American patterns. The presence of *Tortopus* in eastern North America may also reflect a relatively old invasion.

Paracloeodes and *Fallceon* are the only mayfly genera that presently demonstrate a geographic pattern involving only North America and the West Indies, where they occur in the Greater Antilles (McCafferty & Waltz, 1990). *Paracloeodes* appears to be warm-water sublimited and is humid-favored in the Nearctic. *Fallceon* is arid-favored in the Nearctic, which may suggest a recent Neotropical center of dispersal, but other ecological data concerning it are lacking and make any deductive assessment of its biogeography difficult. We suspect, however, that *Paracloeodes* and *Fallceon* will eventually be confirmed as occurring in mainland Mesoamerica; McCafferty & Morihara (1979) previously predicted this for *Fallceon quilleri*. Such a discovery would strongly suggest a Neotropical affinity for these genera.

The latter prediction is based on the fact that the mayfly fauna of the Greater Antilles has a strong affinity with mainland Mesoamerica (e.g., McCafferty, 1985a; Peters, 1988) as do other aquatic insects such as caddisflies and dragonflies (Flint, 1977). With regard to the Lesser Antilles, however, more species-level studies are required to ascertain the degree of presumed relationship between the Lesser Antilles and South America that would be predicted by Rosen's (1975) model of Caribbean biogeography.

Iron, *Isonychia*, *Leucrocuta*, *Nixe*, *Rhithrogena*, *Stenonema*, and a Northern Hemisphere *Caenis* lineage are each represented in the Neotropics by one or two species that are apparently either conspecific with, or closely related to, a Nearctic species. This leads us to further hypothesize that their southward dispersal took place relatively recently, quite possibly during glaciopluvial periods 8,000 years ago. From these genera it is easy to visualize the process of range extension, isolation, and speciation in its early phase and gain insight into how the Mesoamerican interchange has functioned.

It appears that *Iron*, *Isonychia*, *Leucrocuta*, *Nixe*, and *Rhithrogena* dispersed from western North America via mountainous corridors because their Neotropical species are restricted to tropical highlands and apparently have closest affinities with western North American congeners (since we cannot yet place Neotropical *Nixe* to subgenus we are not totally sure that its affinities are with the

western subgenus *Akkarion*). This general Pleistocene, southward, mountainous dispersal pattern is shown by several other taxa (Raven & Axelrod, 1975). Although many Nearctic biotic elements are known to have moved southward along the mountainous corridors in Mexico, the fact that only a few species of mayflies with Nearctic affinities have penetrated south of the Isthmus of Tehuantepec is consistent with data from other insects (Halfpter, 1987). The most recent dearth of aquatic habitats in the Mexican ranges is possibly a factor that has prevented certain mayfly lineages from exploiting these corridors more extensively.

Stenonema is clearly of Nearctic origin, but one species, *S. mexicanum*, is atypically found from throughout eastern North America to tropical Central American lowlands (McCafferty, 1984); it most likely dispersed southward from east-central North America via the Gulf of Mexico maritime corridor lowlands. The only other species of mayflies that fits this particular Nearctic-derived pattern is *Caenis diminuta*, which also represents a Northern Hemisphere lineage, as discussed above. These species are not yet known from the broad Texas-Tamaulipas desert area north of Tampico, Mexico (McCafferty, 1984). The occurrence of *Stenonema* and a northern *Caenis* lineage in tropical lowlands could be considered an anomaly since most lowland tropical species are derived from somewhat older South American lineages.

Although not known, perhaps these species' diel flying periodicity in Mesoamerica is typical of lowland species. In Florida, Berner and Pescador (1988) reported late afternoon and evening emergences for the short-lived *Caenis diminuta*. Interestingly, Berner (1950) considered *C. diminuta* the most tolerant mayfly species he knew, even more so than any *Callibaetis*; and Lewis (1974) considered *Stenonema mexicanum* (as *S. integrum*) to be relatively pollution tolerant. The fact that both of these species can live in a variety of habitats that most mayflies cannot tolerate perhaps is related to their ability to have dispersed southward in the manner we suggest.

The dispersal of Neotropical groups into the Nearctic has apparently involved more secular migration and completed speciation events, perhaps facilitated by isolated pockets of appropriate aquatic habitat in xeric northern Mexico and the arid United States, where those genera with hypothesized recent Neotropical centers of dispersal are primarily found. It is more difficult to propose the age of the mostly older northward dispersals of this group. Quaternary, Tertiary, or older events may have variously been involved, although late Miocene and Pliocene are commonly cited as principal occasions for invasions from South America into the Mexican transition zone (e.g., Kohlmann & Halfpter, 1990). Those genera that demonstrate rather continuous ranges through Mexico (e.g., *Lachlania*, *Leptohyphes*, *Thraulodes*, and *Traverella*) have perhaps not been as dependent on pluvial periods in northern Mexico for trans-Mexican dispersal as have been those that appear to be clearly disjunct. These genera apparently follow the tendency for biota of the Mexican Plateau to be of earlier southern origin than recent biota derived from the north-temperate areas.

Baetodes, *Cloeodes*, and *Leptohyphes*, which are known both from lowland and highland tropical habitats, may have dispersed into the Nearctic via mountainous areas because they can be found (not exclusively) in cool mountain streams

of the southwestern United States. *Camelobaetidius*, *Campsurus*, and *Farrodes* appear to be warm-water sublimated and variously related to fine substrate habitats. *Campsurus* and *Farrodes* may have colonized northern regions relatively recently. The presence of *Camelobaetidius* north into Saskatchewan and the eastern Nearctic distributions of *Tortopus* and *Tricorythodes* suggest a longer period of northern movement for these particular genera.

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