ORIGINS OF THE NORTH AMERICAN EPHEMEROPTERA FAUNA, ESPECIALLY THE LEPTOPHLEBIIDAE

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Abstract

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The complex origins of the North American Ephemeroptera fauna extended from the Lower Permian to the Recent. This paper discusses origins of North American genera of the cosmopolitan family Leptophlebiidae with a few examples from other mayfly families. The two extant subfamilies, Leptophlebiinae and Atalophlebiinae, probably evolved at least by the mid-Cretaceous, or about 100 million years before present. The primitive Leptophlebiinae are distributed throughout most of the Northern Hemisphere and the ancestors of the *Leptophlebia–Paraleptophlebia* complex within this subfamily dispersed widely by the North Atlantic route as early as the mid-Cretaceous and later probably by northern trans-Pacific dispersals through Beringia. The ancestors of *Habrophlebia* dispersed through the North Atlantic route at an early time, but the vicariant distribution of *Habrophlebiodes* in several areas of the Oriental Region and eastern North America correlates with the Arcto-Tertiary forest that covered most of the Northern Hemisphere including Beringia from the Early Tertiary into the Pleistocene. Within the nearly cosmopolitan Atalophlebiinae, *Traverella* is austral in origin and probably dispersed north through the Mexican Transition Zone during the mid-Tertiary as an ancient dispersal and then dispersed to its northern and eastern limits following the last Pleistocene deglaciation by way of the Missouri River tributaries. *Thraulodes* and *Farrodes* are both austral in origin and probably dispersed north through the Mexican Transition Zone during the Early Pleistocene as a relatively recent dispersal. The origins of *Choroterpes sensu stricto* and *Neochoroterpes* in North America are unknown. The mayfly fauna of the West Indies is Neotropical in origins, and no affinities between the West Indies and North America through Florida have ever been confirmed.

Résumé

Les origines complexes des Ephemeroptera d'Amérique du Nord s'étendent du Permien inférieur jusqu'au Récent. Cet article discute des origines des genres nord américains de la famille cosmopolite des Leptophlebiidae et de quelques membres d'autres familles. Les deux sous-familles contemporaines Leptophlebiinae et Atalophlebiinae sont apparues au moins depuis la mi-Crétacé, il y a environ 100 millions d'années. Les Leptophlebiinae sont répartis sur la majeure partie de l'Hémisphère Nord et les ancêtres du complexe *Leptophlebia–Paraleptophlebia* de cette sous-famille se sont dispersés largement, d'abord par la route de l'Atlantique Nord depuis le milieu du Crétacé, et plus tard par des dispersions trans-pacifiques via la route du Beringia. Les ancêtres d'*Habrophlebia* se sont dispersés par la route de l'Atlantique Nord à une époque ancienne, mais la répartition d'*Habrophlebiodes* dans plusieurs parties de la Région Orientale et l'est de l'Amérique du Nord est corrélée avec la forêt arcto-Tertiaire qui recouvrait la majeure partie de l'Hémisphère Nord du début du Tertiaire jusqu'au Pléistocène. Parmi les Atalophlebiinae cosmopolites, *Traverella* est d'origine australe et s'est probablement dispersé au nord par la Zone de Transition Mexicaine au milieu du Tertiaire dans un premier temps, et a ensuite atteint ses limites nordique et orientale après la dernière déglaciation du Pléistocène, via les tributaires du Missouri. *Thraulodes* et *Farrodes* sont tous deux d'origine australe et se sont probablement dispersés au nord par la Zone de Transition Mexicaine tôt au cours du Pléistocène, lors d'une dispersion relativement récente. Les origines de *Choroterpes sensu stricto* et de *Neochoroterpes* en Amérique du Nord sont inconnues. La faune éphéméroptérienne des Caraïbes est d'origine neotropicale, aucune affinité n'ayant été confirmée entre les Caraïbes et l'Amérique du Nord via la Floride.

Introduction

The origins of the North American Ephemeroptera fauna are rather complex and extend over a vast period of geologic time to the Recent. The Ephemeroptera are the most ancient living order of winged insects, and the oldest known fossil mayflies in North America are those from the Lower Permian from Kansas and Oklahoma. All of these are representatives of extinct families (Kukalová 1968; Hubbard and Kukalová-Peck 1980). The Jurassic has yielded mayflies in the Northern Hemisphere clearly assignable to modern families of Ephemeroptera as pointed out by Tshernova (1970), Riek (1973), Demoulin (1970*b*) and Sinitchenkova (1984). Tshernova (1980) listed approximately 20 genera of mayflies known from the Palaeocene, 10 of which also occur in the Recent fauna. Therefore, recognizable mayflies have occurred in the Northern Hemisphere at least since 250 million years before present (m.y.B.P.) and the origins of the present North American Ephemeroptera date from the Lower Permian to the Recent.

Edmunds (1972) indicated that dispersal of mayflies is sharply limited as the nymphs are restricted to aquatic habitats and the adults are short-lived with limited flight capabilities. Among examples given by Edmunds (1972), some boreal genera and numerous species of mayflies have failed to cross the plains of the Snake River and southern Wyoming to reach suitable habitat in the southern Rocky Mountains. Mackerras (1970) suggested that mayflies have a history of conservative dispersal and should be ideal subjects for biogeographic analysis. Research in the past 25 years on the phylogeny and zoogeography of various groups of mayflies supports Mackerras' view (see Edmunds 1975, for Siphlonuridae; Peters 1980, Pescador and Peters 1980, Towns and Peters 1980, Landa, Soldán and Peters 1980, for Leptophlebiidae; Allen 1980, for Ephemerellidae; McCafferty 1973, McCafferty and Gillies 1979, McCafferty and Sinitshenkova 1983, for Ephemeridae).

Leptophlebiidae

It would be impossible to discuss here the complex origins of all the diverse mayfly groups in North America. Not only do the groups cover a varying period of geologic time, but the systematics and complete geographical ranges of many North American groups are incompletely known. Therefore, this paper will concern primarily the family Leptophlebiidae with a few examples from other mayfly families.

Several of my students, faculty and associates have worked on the taxonomy, phylogeny, and zoogeography of the cosmopolitan family Leptophlebiidae over a number of years. Results from our work have shown that the Leptophlebiidae is one of the most diversified, oldest and largest families in number of species and genera within the Ephemeroptera. Although most of our research has concerned the Southern Hemisphere representatives, sufficient work has been completed in the Northern Hemisphere to review the origins of the North American Leptophlebiidae.

McCafferty and Edmunds (1979), in their phylogenetic model of the extant superfamilies of the Ephemeroptera, noted the ancient nature of the leptophlebiid-like nymph. An ancestor, which was most likely leptophlebiid-like, gave rise on the one hand to the suborder Pannota and on the other hand to the common ancestor of the Leptophlebioidea and Ephemeroidea. The common ancestor of the Leptophlebioidea and Ephemeroidea was most likely a leptophlebioid. McCafferty and Edmunds (1979) suggested that the highly derived Ephemeroidea has its origin within the Leptophlebiidae; however, confirmation of this paraphyly could take years, as it is extremely difficult to find shared derived character states for such ancient furcations.

The Leptophlebiidae comprise two extant subfamilies, Leptophlebiinae and Atalophlebiinae as defined by Peters (1980), and the fossil subfamily Mesonetinae currently assigned to the Leptophlebiidae based on the genus *Cretoneta* (Tshernova 1971). Generic and subgeneric limits for the Leptophlebiidae are defined by criteria given in Peters and

Edmunds (1970). These criteria use the degree of morphological differences in both nymphs and adults to differentiate genera and subgenera.

Hubbard and Savage (1981) discussed the fossil Leptophlebiidae. As both extant subfamilies occur in Baltic amber, they concluded that the separation of the two subfamilies had definitely occurred more that 50 m.y.B.P. Mesonetinae have been found in the Upper Cretaceous of Siberia and thus existed at least 85 m.y.B.P.

Modern representatives of the subfamily Leptophlebiinae are distributed throughout most of the Northern Hemisphere with only eight named genera (Peters and Edmunds 1970). The genera of the subfamily are more primitive than the representatives of the subfamily Atalophlebiinae. Demoulin (1970*a*) placed four fossil species from Baltic amber in the extant *Paraleptophlebia* which I consider to be one of the most primitive genera in the Leptophlebiinae. Based on what is known about the phylogeny and zoogeography of the entire family, I consider the two extant subfamilies to have evolved at least by the mid-Cretaceous, or about 100 m.y.B.P.

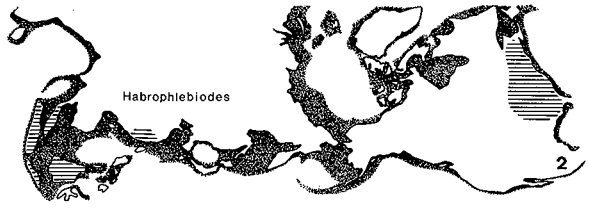
Modern representatives of the subfamily Atalophlebiinae are distributed worldwide and represent about 90% of the total diversity within the Leptophlebiidae. The subfamily is especially diverse in genera in the Southern Hemisphere with many specialized nymphal and adult adaptations. Some recent systematic revisions and discussions on the phylogeny and zoogeography of various genera in the subfamily have included Peters *et al.* (1978); Towns and Peters (1979); Landa *et al.* (1980); Pescador and Peters (1982); Savage and Peters (1983); Peters and Edmunds (1984); and Sivaramakrishnan and Peters (1984). Within the Atalophlebiinae there are several major phyletic lineages which may eventually be recognized as tribes (Peters 1980) and in many cases these lineages have interesting vicariant Gondwanian patterns. In most cases, these patterns include New Caledonia, New Zealand, Australia, southern South America, rarely southern Africa (probably because of a high extinction rate), Madagascar, and sometimes southern India and Sri Lanka (Pescador and Peters 1980; Towns and Peters 1980; Hubbard and Peters 1984).

Leptophlebiinae

Presently four genera of the Leptophlebiinae occur in North America (Peters and Edmunds 1970). As currently defined, these are *Leptophlebia, Paraleptophlebia, Habrophlebiodes*, and *Habrophlebia (Hesperaphlebia)*.

The *Leptophlebia–Paraleptophlebia* complex occurs throughout most of the Holarctic Region and is the most primitive extant complex within the Leptophlebiidae. This complex of two genera has several ancient phyletic groupings and these groupings occur widely in both the Nearctic and Palaearctic Regions. As systematic studies are completed, these lineages may well be defined as genera or subgenera.

Based on Laurasian events as summarized by McKenna (1973), Smith *et al.* (1973), Herron *et al.* (1974), and Raven and Axelrod (1974), the most plausible dispersal route for the ancestors of these ancient lineages was the North Atlantic as the Bering area was at a higher latitude. Commencement of these ancient dispersals could have occurred as early as the mid-Cretaceous (about 100 m.y.B.P.) (Schwarzbach and Pflug 1957). The exact origin of the *Leptophlebia–Paraleptophlebia* complex within Laurasia will probably never be known, as almost every rule for determining centres of origins has been thrown into doubt (Edmunds 1981; Croizat 1958). Without additional systematic studies, it is not known if northern trans-Pacific dispersals through Beringia occurred within the *Leptophlebia–Paraleptophlebia* complex. Levanidova (1982), in her study of the zoogeography of Ephemeroptera, Plecoptera, and Trichoptera of the mountainous regions of the Far Eastern USSR, noted records of only three extant species of *Paraleptophlebia* and none for *Leptophlebia*. In North America, *Paraleptophlebia* is known from Alaska and western Canada, and *Leptophlebia* is known from the Yukon Territory and Northwest Territories (Edmunds *et al.* 1976; Harper and Harper 1981; McCafferty 1985). However, all the



FIGS. 1, 2. 1, Distribution of genus *Habrophlebia*. 2, Distribution of genus *Habroplebiodes*. Stippled area shows approximate margins of continental shelf.

eastern Palaearctic species should be compared with all the North American representatives before any conclusions can be reached.

Habrophlebia occurs throughout Europe and in eastern North America from the mountain streams in eastern Canada to the lowland streams of north Florida (Fig. 1). Peters (1979) recognized the single North American species as a separate subgenus *Hesperaphlebia*. *Habrophlebia* is one of the most primitive genera within the subfamily and a common ancestor probably dispersed through the North Atlantic at an early time.

The last North American genus of the Leptophlebiinae, *Habrophlebiodes*, occurs in several areas of the Oriental Region and in eastern North America from the mountain streams in eastern Canada to the lowland streams of northern Florida and west to the Ozark Mountains (Fig. 2). Adults of this genus are highly specialized although the nymphs retain the primitive characters of *Paraleptophlebia*-type nymphs (Peters and Edmunds 1970). A similar distribution is known for many other insects such as the *Wormaldia kisoensis* (Tsuda) complex of caddisflies (Ross 1956) and the longhorn beetle genus *Calloides* (Linsley 1963). These vicariant distributions are associated with the Arcto-Tertiary forest that covered most of the Northern Hemisphere, including Beringia, during the Early Tertiary into the Pleistocene (Pielou 1979; Li 1952).

Other boreal mayfly dispersals

Many genera or species groups in other mayfly families are boreal with widespread ancestral dispersals through the North Atlantic and the Bering Straits. Evidence indicates

mayflies dispersed widely through both the North Atlantic and Beringia from the Late Cretaceous. Unfortunately the cladistics and distributional patterns of most of these boreal groups have not been studied in any detail.

In his review of northern trans-Pacific dispersal patterns of mayflies, Edmunds (1981) pointed out that more than half of the genera and subgenera of mayflies in North America north of Mexico are found also in Eurasia. He further noted vicariant species pairs of mayflies in Asia and western North America in genera such as *Rhithrogena* and *Heptagenia*. Other groupings within the heptageniids, such as *Cinygmula* and the subgenera *Iron* and *Ironopsis* of the genus *Epeorus*, show strong northern trans-Pacific patterns. Among the ephemerellids, *Ephemerella, Drunella, Serratella*, and *Attenella* occur in both eastern and western North America and Asia. Cobb and Flannagan (1980) and Harper and Harper (1981) discussed additional northern trans-Pacific dispersals based on new species records from Alaska and northern Canada. Recently, McCafferty and Sinitshenkova (1983) described a fossil species of *Litobrancha* collected in Oligocene deposits from Sikhote Alin, USSR. The Recent distribution of this genus only includes eastern North America (McCafferty 1975).

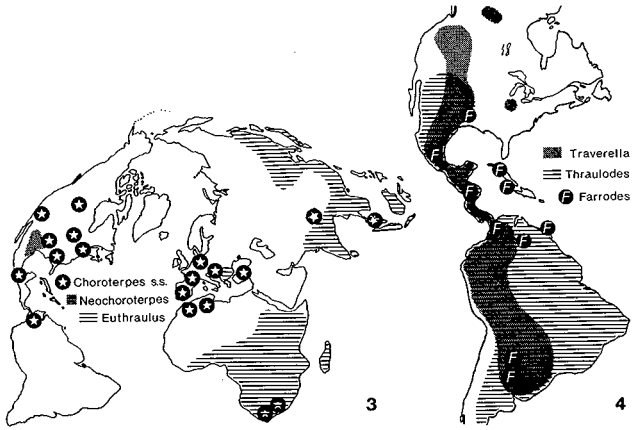
Levanidova (1982) reviewed the mayfly fauna of the Far Eastern USSR and its relationships to North America. Although this book gives us much new information on the mayfly fauna of the region, it is surprising how little is known concerning the relationships of that mayfly fauna to North America. The book does discuss in detail the relationships of the stonefly and caddisfly fauna in Far Eastern USSR with those of North America.

Even less is known concerning the North Atlantic dispersals of other mayfly groups. Present distributions of several genera and species groups of mayflies include only Europe and North America and these distributions may well be explained by North Atlantic dispersals. For example, one species of *Arthroplea* is known from central and northern Europe and a second species occurs in eastern North America south and west to Massachusetts, Ohio, and Wisconsin (Edmunds *et al.* 1976). Müller–Liebenau (1970) noted that several European species groups of *Baetis* are widespread throughout North America.

Trans-Atlantic species are known in several families of mayflies. Morihara and McCafferty (1979) discussed the trans-Atlantic pond species *Baetis macani* Kimmins. In their paper, they recognized two subspecies: *B. macani macani* known from northern Europe south to approximately 60°N (Müller–Liebenau 1970), and *B. macani bundyae* Lehmkuhl known from the tundra of central Canada (Lehmkuhl 1973). Traver (1962) and Flowers (1978) noted that *Cloeon cognatum* Stephens is a common species in continental Europe, the British Isles, Pennsylvania, Ohio, and Illinois. *Cloeon cognatum* is a pond species and quite likely was transported to North America by man (Burks 1953).

Several mayfly species are apparently circumpolar in the Northern Hemisphere. For example, *Ephemerella aurivillii* (Bengtsson) is known from northwestern Europe, central and northeastern Asia, and disjunct populations in eastern and northwestern North America (Allen and Edmunds 1965). Although *E. aurivillii* may be polytypic, the group could well have dispersed through both the Bering Straits and the North Atlantic to obtain its present distribution. The nymphal populations from eastern North America are morphologically distinct from the western North America populations, and nymphal populations from northeastern Asia are similar to those in western North America. The nymphs from northern Europe have never been compared with those in eastern North America. It is interesting that western populations of the species occur in the Pribilof Islands in the Bering Sea.

Metretopus borealis (Eaton) is known in Eurasia from Scandinavia to the Kamchatka Peninsula and in North America completely across Canada and south into Michigan and Maine. Both Edmunds (1957) and Berner (1978) pointed out that the European and Canadian populations are conspecific and apparently indistinguishable, but Berner (1978) noted the specimens from Alaska differ slightly. The Asian populations have not been compared



FIGS. 3, 4. 3, Distribution of subgenera of genus *Choroterpes*. 4, Distribution of the genera *Traverella, Thraulodes* and *Farrodes*.

with those in North America. Lestage (1938), Leonard and Leonard (1962), and Levanidova (1976) all believed the present distribution of the species is the result of post-glacial invasion.

Flannagan and Flannagan (1982, 1984) discussed the present distribution and post-glacial origins of mayflies, stoneflies, and caddisflies in Manitoba. In their studies of 258 species, they delineated six basic post-glacial distributional patterns in North America. Although a number of mayfly faunal studies have been completed in North America, additional studies on distributional patterns must be made to understand better the origins of their present ranges within the continent.

Atalophlebiinae

Presently, the subfamily Atalophlebiinae includes over 100 genera, four of which occur in North America north of Mexico (Peters 1980). As I will discuss, three genera (*Traverella, Thraulodes,* and *Farrodes*) are austral in origin, but the origins of *Choroterpes sensu stricto* and *Neochoroterpes* are unknown.

Dispersal of Choroterpes

Choroterpes currently is divided into three subgenera — *Choroterpes s.s., Euthraulus,* and *Neochoroterpes*. Although neither the biosystematics nor zoogeography of this nearly worldwide genus are understood, a discussion of the distributional patterns and probable relationships of the subgenera is realistic.

Choroterpes s.s., which may itself represent more than one genus or subgenus, occurs throughout Europe, northern India and Nepal, Sumatra, the more temperate areas of northern and southern Africa, and scattered localities throughout North America south to Mexico and Columbia (Fig. 3) (Peters and Edmunds 1970; Allen 1974; unpublished data). The subgenus has not been reported from Far Eastern USSR (Levanidova 1982) or continental southeastern Asia.

Traver (1947) described two species of *Choroterpes s.s.* from Costa Rica and Needham and Murphy (1924) described two additional species from Peru and Guyana. For many years *Choroterpes s.s.* has been listed as a genus of the Neotropical fauna with representatives in continental South America (Allen and Brusca 1973). However, Savage and Peters (1983) transferred *Choroterpes emersoni* Needham and Murphy to *Miroculitus* and Savage (pers. comm.) will transfer the remaining three species to genera in the *Terpides* lineage. Hence, *Choroterpes s.s.* will no longer be recorded in the literature from continental South America. Recently, however, I studied nymphs from Colombia that definitely belong to *Choroterpes s.s.*, but the adults of this species are unknown. These montane Colombian nymphs are the first authenticated record of *Choroterpes s.s.* in continental South America.

The subgenus *Euthraulus* is widespread throughout the Ethiopian and Oriental Regions, southern Europe, and in the eastern Palaearctic. I know of no records of the subgenus from the Western Hemisphere.

The subgenus *Neochoroterpes* is restricted to Texas, Arizona, New Mexico and Mexico (Fig. 3) (Allen 1974). Nymphs of *Euthraulus* resemble nymphs of *Neochoroterpes*. The abdominal gill shape is strikingly similar; however, this similarity is probably due to adaptation to warmer environments (see Peters and Tsui [1972] for a similar discussion on the abdominal gills of *Thraulus*) and is not indicative of sister-group relations.

The origin and dispersal of the Western Hemisphere representatives of *Choroterpes* are unknown. I believe the ancestors of *Choroterpes* arose from the Gondwanian mayfly fauna and dispersed northward through Africa giving rise to *Choroterpes s.s.* and the derived *Euthraulus*. However, I cannot find any relationships between the Eastern and Western Hemisphere members of the genus. The origins of the North American *Choroterpes s.s.* could be either boreal or austral, or both, and until detailed studies of the genus are completed origins of the genus in North America are problematic.

Dispersal of other Atalophlebiinae

Three North American genera of the Atalophlebiinae are entirely austral in origin. Edmunds (1982) reviewed the dispersal of mayflies between North and South America. He concluded that no fewer than 21 genera of mayflies have moved from South to North and Central America, with 14 genera extending as far north as the United States and six genera into Canada. He stated further that there is good evidence for only two North American genera, *Brachycercus* and *Hexagenia*, moving into South America. Halffter (1974) offered similar conclusions based on his worldwide studies of the Scarabaeinae, and outlined the dispersal patterns responsible for the present composition of the entomofauna of the Nearctic and Neotropical Regions. Based on Edmunds' (1982) work on origins and Halffter's (1974) model of dispersal patterns, it is now possible to discuss the biogeography of many North American mayflies with austral distributions. Allen and Allen have made such studies (1989). As a published example, McCafferty (1984) noted that *Stenonema mexicanum* (Ulmer) occurs from the Great Lakes in the United States to Panama with two distinct subspecies *S.m. mexicanum* and *S.m. integrum* (McDunnough). He indicated the disjunct distributional pattern of the northern and southern subspecies is explicable in terms of Pleistocene climatic events which led to the dispersal of the species from the north into middle America. For lack of space, I will confine my comments on austral origins to the Atalophlebiinae.

Traverella occurs throughout the tropical areas of the Neotropical Region and extends up warm rivers north to Washington, Alberta, Saskatchewan, and Ohio (Fig. 4) (Allen 1973). The nymphal mouthparts are highly specialized for filtering algae and detritus from the water. Phylogenetic studies support Edmunds' (1982) conclusion that *Traverella* evolved in continental South America and my studies suggest the genus is a derivative of an ancient Gondwanian lineage. Based on Halffter's (1974) model of dispersal, it can be

Table 1. Endemic genera of Ephemeroptera of the West Indies

Family	Genus	Distribution
Leptophlebiidae	*Neohagenulus*	Puerto Rico
	Traverina	Cuba
	Careospina	Cuba, Haiti
	Borinquena	Puerto Rico, Haiti
	Hagenulus	Puerto Rico, Haiti, Jamaica, Cuba, Trinidad

concluded that *Traverella* probably dispersed north through the Mexican Transition Zone during the mid-Tertiary and, as discussed by Lehmkuhl (1976) for *Baetisca, Analetris* and *Lachlania*, dispersed to its northern and eastern limits following the last Pleistocene deglaciation by way of the Missouri River tributaries.

Thraulodes is widespread throughout the Neotropical Region and extends north to Arizona, New Mexico, Utah, and central Texas (Fig. 4) (Allen and Brusca 1978). Phylogenetic studies support Edmunds' (1982) conclusion that *Thraulodes* evolved in continental South America and my studies suggest the genus is a derivative of an ancient Gondwanian lineage. Based on Halffter's (1974) model of dispersal, *Thraulodes* probably dispersed north through the Mexican Transition Zone during the early Pleistocene. *Thraulodes* did not disperse northward as the deserts of western North America began to develop in the mid-Tertiary (Raven and Axelrod 1974; Whyte 1976) and xeric habitats began to spread in the Pliocene (Solbrig 1976).

Farrodes is widespread throughout the tropical areas of continental South America to as far south as Sante Fe, Argentina, and extends north to the West Indies (Grenada, Cuba, and Jamaica) and through Mexico to Texas (Fig. 4) (Dominguez and Savage 1987; Edmunds 1984). Recent phylogenetic studies indicate that *Farrodes* evolved in continental South America. Based on Halffter's (1974) model of dispersal, it can be concluded that *Farrodes* probably dispersed through the Mexican Transition Zone during the early Pleistocene.

Other austral mayfly dispersals

Although vicariance and merger events can help explain the present distribution of mayflies in North America, the biology and ecology of ancestral mayflies are also important in understanding present distributions. Edmunds and Edmunds (1980) noted there is some evidence that ancestral emergence and swarming habits may persist when mayflies disperse to new areas, and Edmunds (1982) suggested that some characteristics of tropical mayflies, such as length of larval period and emergence and mating patterns, may be used to predict habitats and characteristics of present North American genera. Unfortunately, the biology and ecology of most boreal mayflies have not been studied in any great detail, although some work is in progress, and even less is known about austral mayflies.

West Indian mayfly fauna

The relationships of the West Indian mayflies to continental North and South America and to Central America are interesting. Peters (1971) studied the West Indian Leptophlebiidae and listed other mayflies occurring in these islands. At present, there are 16 genera of mayflies known from the West Indies. Five of these genera, all belonging to the Leptophlebiidae (Table 1), are endemic to the West Indies with sister-group relations in the Neotropics (Edmunds, Jensen and Berner 1976; unpubl. data). Eight of these genera (Table 2) occur in the West Indies and are widely spread in the Neotropics (Edmunds 1982; Flowers, pers. comm.; unpubl. data). All genera of Table 2, except *Terpides* and *Euthyplocia*, also occur in North America north of Mexico. Edmunds (1982) noted that these genera were austral in origin. Species of *Farrodes* and *Terpides* in the West Indies

Table 2. Genera of the Ephemeroptera of the East Indies with austral affinities

Family	Genus	Distribution
Baetidae	*Paracloeodes*	Brazil to Minnesota, California, Georgia
	Cloeodes	Argentina to Mexico
Leptophlebiidae	*Farrodes*	Argentina to Texas
	Terpides	Brazil to Costa Rica
Euthyplociidae	*Euthyplocia*	Brazil, Peru to Mexico
Tricorythidae	*Leptohyphes*	Argentina to Maryland
	Tricorythodes	Uruguay, Peru to British Columbia, Saskatchewan, Quebec
Oligoneuriidae	*Lachlania*	Argentina to Saskatchewan

Table 3. Genera of the Ephemeroptera of the West Indies with broad distributions

Family	Genus	Distribution
Baetidae	*Callibaetis*	Western Hemisphere (Chile to Alaska)
	Baetis	Cosmopolitan
Caenidae	*Caenis*	Cosmopolitan

appear to be related to those on continental South America (Dominguez and Savage 1987; Savage 1986). Three genera (Table 3) are widespread throughout the Western Hemisphere (Edmunds *et al.* 1976). Species of these genera in the West Indies may be more closely related to those in the Neotropics than to species occurring in Florida (Berner 1950; unpubl. data).

Although the mayfly fauna of the West Indies is Neotropical in origin, the affinities of the fauna to either continental South America or Central America have not been determined. Within the Leptophlebiidae, four genera (*Farrodes, Hagenulus, Borinquena,* and *Terpides*) are distributed in the Antilles; and in the case of *Farrodes* and *Terpides*, both genera occur along the northern coast of South America. The present distribution of *Farrodes* and *Terpides* could easily be explained by wind currents from the northern coast of South America. A similar explanation could be given for the ancestors of *Hagenulus* and *Borinquena*. The remaining three genera (*Neohagenulus, Traverina,* and *Careospina*) are all endemic to the Greater Antilles, and may be phylogenetically related to *Hagenulus* and *Borinquena*. Although the present distribution of the three genera might be explained by northern dispersal of ancestors by wind currents, we cannot discount affinities with Central America until its leptophlebiid fauna has been studied in more detail.

Although many groups of insects indicate a faunal connection between Florida and the West Indies, I have never confirmed a single record for the mayflies. Leech (1972) found the same results for Amaurobiid spiders. Berner (1950) stated that such a faunal connection probably has never been established for mayflies because of ecological conditions in southern Florida. The great majority of mayflies occurring in the West Indies are inhabitants of mountain streams, and even if these mayflies were accidentally introduced into Florida, establishment would be impossible in the lowland sand-bottomed streams.

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