

Biogeographic Classification of the Neotropical Leptophlebiidae (Ephemeroptera) based upon Geological Centers of Ancestral Origin and Ecology

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Thirty-four genera belonging to the Gondwanian subfamily Atalophlebiinae are known from the Neotropics. Development of the lower Central American isthmus was marked only by dispersal of Gondwanian Atalophlebiinae from South America into Central America. No member of the Laurasian subfamily, the Leptophlebiinae, has dispersed from North America into Central or South America. The Antilles were colonized entirely by Atalophlebiinae from South and Central America. Genera of Neotropical Atalophlebiinae are placed into one of two faunal components: either the Patagonian Shield, South Andean, Cold-Adapted Genera; or the Guiana & Brazilian Shields, Warm-Adapted Genera. The 10 Patagonian Shield Genera are primarily associated with cold-water streams of southern South America. Secondary diversification has occurred in the southern coastal mountains of Brazil, and at high elevations in the central and northern Andes. Phylogenetically, Patagonian Shield Genera are related to diverse genera on several Gondwanian continents. The 24 Warm-Adapted Genera share a common heritage stemming from isolation on the Guiana and Brazilian Shields and independent evolution of the Warm-Adapted attribute. The Warm-Adapted Genera are composed of endemic monophyletic lineages of 2-4 genera. Presence of endemic lineages with distant relationships to other Atalophlebiinae reflects the isolation experienced by the Guiana and Brazilian Shields between formation of the northern South Atlantic Ocean 80 mya and the lower Central American isthmus about 5 mya. Warm-Adapted Genera are widely distributed in warm to cool streams of the northern Neotropics at elevations below 2000 m. The Warm-Adapted Genera are further subdivided based primarily upon the area of maximum species diversification into three faunal elements: the Guiana & Brazilian Shields Associated Genera; the North Andean, Central American Genera, and the Antillean Genera. The 12 Guiana & Brazilian Shields Associated Genera are principally associated with the Guiana and Brazilian Shields and surrounding lowlands such as the Amazon, São Francisco and Paraná Basins. This faunal element is restricted to elevations of less than 700 m along the eastern slopes of the Andes and does not occur in the Antilles. Maximum species diversification in the 8 North Andean, Central American Genera occurs in the northern Andes and Central America with occasional invasions by isolated species-groups into the Antilles and/or North America. The 4 Antillean Genera are endemic to the Antilles, and are both geographically and phylogenetically most closely related to taxa of the North Andean, Central American Genera.

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Introduction

The Leptophlebiidae are a dominant element of the ephemeropteran fauna in streams and small to moderate-sized rivers in the Neotropics. Currently 34 genera of Leptophlebiidae, all of which belong to the subfamily Atalophlebiinae Peters, are known to occur in the Neotropics. The Atalophlebiinae are Gondwanian in origin and this subfamily displays its maximum diversity and abundance in streams of the Southern Hemisphere. The other extant subfamily of Leptophlebiidae, the Leptophlebiinae Banks, is of Laurasian origin and forms an important, but less dominate element of the stream fauna in the Northern Hemisphere and Asia.

In the New World the Leptophlebiinae are common in streams of Canada, northern and central portions of the western United States, and throughout the U.S.A. east of the Mississippi River. The Leptophlebiinae are presently not known to occur south of the U.S.A.-Mexican border (Edmunds et al. 1976).

The development of the Central American Land Bridge in late Miocene to Pleistocene Times was marked only by northward dispersal of Gondwanian Atalophlebiinae from South America into Central America. In sharp contrast to dispersal patterns in other groups of organisms (Simpson 1969, Raven & Axelrod 1974) no member of the Laurasian subfamily, the Leptophlebiinae, has dispersed from North America into Central or South America. The Antilles were colonized entirely from South and Central America by members of the Gondwanian Atalophlebiinae, and no Leptophlebiidae of North American origin are present on the islands. Therefore, the Neotropical leptophlebiid fauna is composed entirely of the subfamily Atalophlebiinae.

The 34 genera of Neotropical Atalophlebiinae are generally restricted to the Neotropics as classically defined by biologists. However, two genera, *Farrodes* and *Thraulodes*, are known to extend north into the southwestern U.S.A.; while *Traverella*, the most northerly distributed Neotropical genus, has been recorded as far north as Saskatchewan, Canada, and east to Ohio in North America (Edmunds et al. 1976).

This initial biogeographic classification of genera is made possible by the considerable progress that has been made on the taxonomy and phylogeny of the Neotropical Atalophlebiinae during the last 16 years. Certainly, a comprehensive understanding of the biogeography and evolution of the Neotropical Atalophlebiinae awaits future revisionary work and much additional collecting and rearing in the Neotropics. However, the distributions of most genera can be realistically estimated from recent revisions (e.g., Peters 1971, Peters & Edmunds 1972, Pescador & Peters 1980b, 1982, Savage 1983a, 1986, Savage & Peters 1982), and examination of undescribed species is available in the Ephemeroptera Collections at Florida A & M University, Tallahassee, and at the University of Utah, Salt Lake City. The generic concept employed in the Ephemeroptera (Edmunds 1962, Peters & Edmunds 1970) results in genera that are eco-morphological units of monophyletic origin. Due to this generic concept, an initial understanding of Neotropical biogeography must first focus at this level of organization.

Geographic terminology

The definition of geographic areas employed herein (Table 1) largely follows standard definitions except for a few modifications discussed below.

The Neotropics as classically defined by biologists includes South America, the Antilles, and Central America south of the Mexican Plateau in a narrow region between the Bay of Campeche and the Gulf of Tehuantepec at approximately 95°W longitude. Frequently, Neotropical taxa extend north of this imaginary line in low coastal areas. I define Neotropical Leptophlebiidae as genera of Leptophlebiidae that evolved in the Neotropics despite their current distributions.

South America includes continental South America south of the Venezuelan-Panamanian border plus the island of Trinidad. I have modified the traditional definition of South America to include Trinidad as a recent collection forwarded to me by Dr. W.L. Peters, Tallahassee, indicates that the leptophlebiid fauna of this island corresponds to that of the nearby mainland. Trinidad appears to have been readily accessible to mainland Leptophlebiidae either by direct land connections with the Peninsula de Paria during Pleistocene sea-level reductions or by overwater dispersal aided by air currents and/or the flow of the Orinoco River.

Central America refers to Latin America between the Panamanian-Venezuelan border and the southern limit of the Mexican Plateau.

North America includes Canada, the U.S.A. and Mexico north of the southern limit of the Mexican Plateau.

The Antilles include the islands of the West Indies except the Bahamas. The Antilles are further divided into the Greater Antilles, including the large islands of Cuba, Hispaniola, Jamaica and Puerto Rico, and the Lesser Antilles, including the Leeward and Windward Islands, and Barbados.

Geologic terminology and development of the Neotropics

Continental South America is composed of three extensive, ancient, structural units or shields (Harrington 1962): the Guiana Shield, the Brazilian Shield, and the Patagonian Island Shields. These shields are early Precambrian-early Cambrian structural units of crystalline rock that have experienced long terrestrial histories (Harrington 1962, Beurlen 1983). In Fig. 1, the Guiana Shield is the structural unit located north of the present-day Amazon River, while the Brazilian Shield is the massive, irregular, structural unit lying south of the Amazon River. The Patagonian Island Shields, herein collectively referred to as the Patagonian Shield, consist of three smaller shields. These three island shields from north to south are (Harrington 1962): the Pampean Ranges Shield; the Patagonian Island Shield; and the Deseado Shield. The Brazilian and Guiana Shields have retained a terrestrial nature throughout geological time (Harrington 1962). Only occasionally, during the Triassic over part of the Guiana Shield, and during the Cretaceous over parts of the Brazilian Shield, have continental

sedimentary deposits accumulated on these shields (Harrington 1962, Putzer 1969). The Patagonian Island Shields have displayed a more variable history. The most northern island shield, the Pampean Ranges Shield, has always retained a terrestrial nature. The two southern island shields, while generally terrestrial, have experienced periods of marine introgression (Harrington 1962, Putzer 1969). Generally, terrestrial tendencies among the three Patagonian Islands Shields decrease from north to south. The representation of shield areas in continental South America (Fig. 1) closely follows geological interpretations (Harrington 1962, Putzer 1969, Fittkau 1974, Beurlen 1983), and emphasizes the representation of areas consistently or nearly consistently suitable for terrestrial and freshwater faunas.

The common practice of representing South America by its current configuration in Mesozoic plate reconstructions is misleading. Future investigations on the breakup of Gondwanaland should focus on the locations and movements of the Patagonian, Brazilian and Guiana Shields. Southern South America, represented by the Patagonian Shield and a low-elevation pre-Andean Cordillera, began to drift away from Southern Africa as the South Atlantic developed by seafloor spreading about 130 mya in the Cretaceous (Tarling 1981). During the early Cretaceous, the Brazilian Shield and Africa remained in close association (Beurlen 1983). The widening of the South Atlantic during the lower Cretaceous was associated with continued uplifting of the southern pre-Andean Cordillera. The northward developing South Atlantic Ocean reached the Belém, Brazil area about 100 mya. Approximately 110 mya, the northern and southern portions of the South Atlantic began to open at equal rates due to a shift in the relative direction of plate motions associated with linkage of the South and Central American spreading systems (Tarling 1981, Duncan & Hargraves 1984). The linkage of these spreading systems had profound effects resulting in the early orogenesis of the northern Andes, and the initial development of the Greater Antilles. Following the separation of the Patagonian Shield region from southern Africa, and the Guiana and Brazilian Shields from north-central Africa, the intervening and marginal areas of continental South America began to acquire an increasingly terrestrial nature, a process that would continue into the late Pliocene.

Although, the separation of South America from Africa is geologically well documented (Tarling 1981, Beurlen 1983), geological data on the separation of the southern Patagonian Shield region and Antarctica remain limited (Tarling 1981). The marginal basin between southern South America and Antarctica appears to have closed in the late Cretaceous about 74 mya (Tarling 1981). Destruction of this southern South America-Antarctica connection by seafloor spreading occurred in the Oligocene, with development of the cool circum-Antarctic Current at the Oligocene-Miocene boundary (Barker & Burrell 1977, Tarling 1981). Therefore, a terrestrial connection between the southern Patagonian Shield region and Antarctica appears probable during the interval 74-27 mya. During this interval Australia and Antarctica parted. Separation of the continental margins of Australia and Antarctica occurred about 49 mya, but some migration between Antarctica and Australia via the South Tasman Rise may have been possible until 39 mya (Raven & Axelrod 1974, Tarling 1981). The southward movement of Antarctica during the last 55 my into polar regions, and

the extensive glaciation that developed in the Miocene have resulted in the near extermination of Antarctica's plant and animal fauna (Raven & Axelrod 1974).

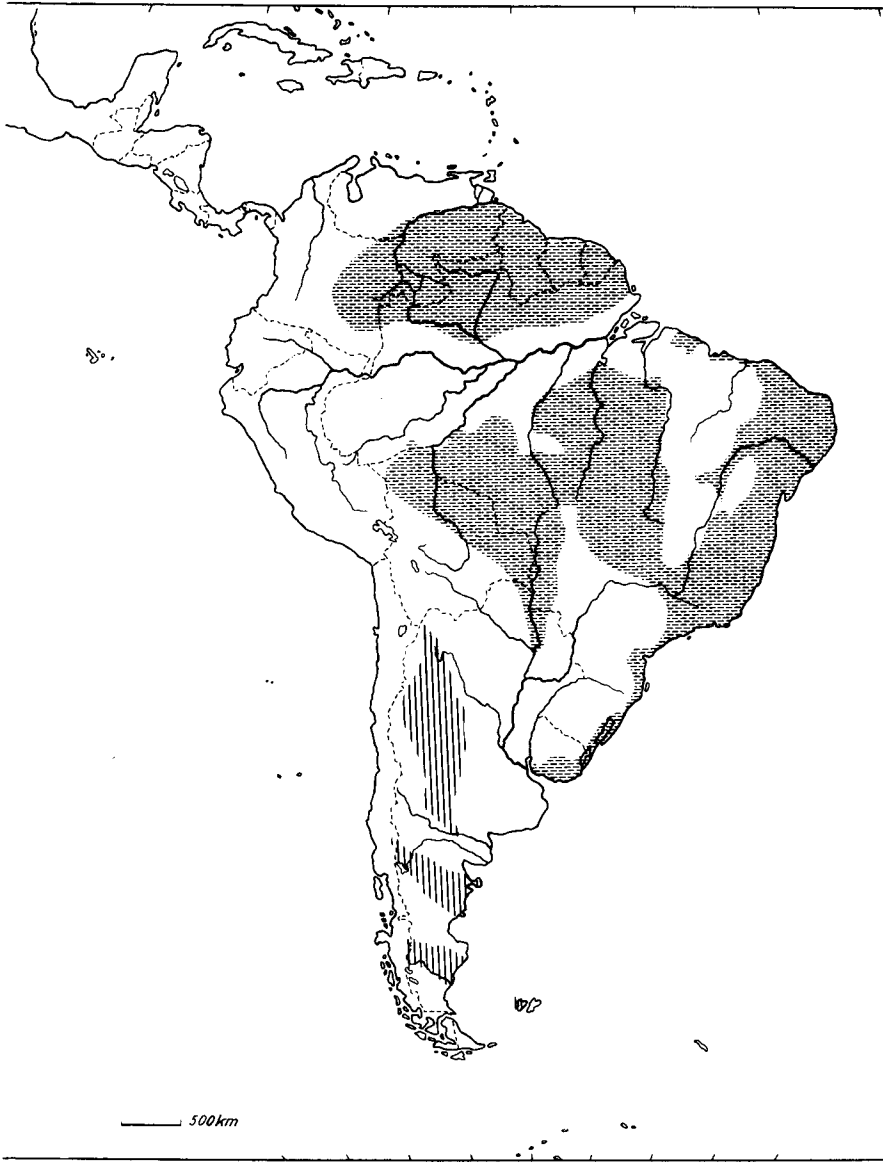


Fig. 1. Location of ancient, geological shields in the Neotropics (after Harrington 1962 and others).

Vertical lines — Patagonian Island Shields. Horizontal dashes — Guiana & Brazilian Shields; Guiana Shield is located north of the Amazon River, Brazilian Shield is located south of the Amazon River.

The history of Central America and the Antilles is particularly uncertain, and has been subject to much recent debate among biologists (Rosen 1975, Pregill 1981, Briggs 1984) and geologists (Sykes et al. 1982, Donnelly 1985, Smith 1985). The origin and development of the Caribbean region vary greatly among authors. However, nearly all models incorporate three broad phases (Burke et al. 1984). The initial phase corresponds to Jurassic-Lower Cretaceous Caribbean basin development by extension between South America and North America and an associated Chortis block representing nuclear northern Central America (Anderson & Schmidt 1983). The extension phase was followed by Cretaceous-Paleogene convergence (Burke et al. 1984) between North and South America beginning about 85 mya (Donnelly 1985). This convergence resulted in the formation of several island arcs including the incipient Greater Antilles. The third phase corresponds to post-Eocene eastward motion of the Caribbean plate relative to both South and North America. This eastward motion produced the Lesser Antilles by subduction of Atlantic crust, and the recent unification of North and South America by impact of a Costa Rica-Panamanian arc with northwestern South America. Even though the above three phases are represented in most models, the origin, direction and extent of motion of various entities (arcs, plates, etc.) differ greatly among models (Smith 1985). The following summary includes the principal features found in most models.

North America began to separate from northern South America-Africa forming the Caribbean about 170 mya in the Jurassic. During the Cretaceous, the Caribbean reached its maximum development and began to slowly close. At this time, the southern limit of the North American plate including the Mexican Plateau, and the Chortis block representing nuclear northern Central America lie roughly 3000 km to the north of northern South America, represented by the Guiana Shield (Raven & Axelrod 1974). Most models envision the Caribbean plate as an oceanic plateau formed in the Pacific west of its present location, and incorporate considerable, subsequent eastward motion (Sykes et al. 1982, Duce & Hargraves 1984, Mattson 1984, Burke et al. 1984). However, Donnelly (1985) believes that extension between South and North America created a huge zone of dispersed igneous centers surrounded by a peripheral margin of island arcs. These dispersed igneous centers in a prolonged extensional environment resulted in immense basaltic volcanism producing the Caribbean plate largely in place. Generally, mobilist models place the incipient Greater Antilles south of the Chortis block along a plate boundary in the Pacific 110-100 mya in the Cretaceous. In contrast, Donnelly (1985) places the incipient Greater Antilles only slightly west of their present location just east of Yucatán.

At 85 mya, most models show radical changes in the Caribbean area (Ladd 1976, Burke et al. 1984, Donnelly 1985). Mobilist models show an oceanic plateau moving between Mexico and South America in a northeasterly direction. This motion forces the Greater Antilles past Yucatán with Jamaica and the Nicaraguan Rise sliding past or colliding with southern Yucatán along an extended Montagua fault-Cayman trough system (Burke et al. 1984). Tectonic activity along the extended Montagua fault-Cayman trough system led to uplift of the Nicaraguan Rise, and the development of Jamaica, eastern Cuba, Hispaniola and Puerto Rico (Perfit & Heezen 1978). During the late Cretaceous, the Greater Antilles and Nicaraguan Rise were apparently sites of numerous

small terrestrial volcanic islands stretching to nuclear Central America (Perfit & Heezen 1978, Mattson 1984). Contemporaneously, northern Central America was represented by numerous terrestrial islands including the Maya Mountains of Belize, and parts of Chiapas, Honduras, Nicaragua and Guatemala (Raven & Axelrod 1974). By late Cretaceous, convergence along the southwest edge of the Caribbean plate resulted in the initial development of a submarine Costa Rica-Panamanian arc with formation of the Nicoya Complex in Costa Rica (Donnelly 1985).

In the Eocene, approximately 53 mya, the Greater Antilles collided with the Bahamian Platform with eastern and central Cuba becoming firmly welded onto the North American plate. The submarine Costa Rica-Panamanian arc joined the Chortis block along the Caribbean plate's western margin forming an unified, incipient Central America (Burke et al. 1984, Donnelly 1985).

In the late Eocene, the northeastern motion of the Caribbean plate was blocked by the Bahamian Platform (Duncan & Hargraves 1984). The Caribbean plate then began to move eastward with respect to both North and South America about 38 mya. Simultaneously, volcanic activity decreased along the extended Montagua fault-Cayman trough system and the Greater Antilles, except for Hispaniola (Bracey & Vogt 1970), are characterized by a lack of post-Eocene andesitic volcanism (Malfait & Dinkelman 1972). Post-Eocene movements in the Greater Antilles have been largely vertical, and Malfait & Dinkelman (1972) suggest that the end of underthrusting in the north Caribbean led to the post-Eocene uplift of the Greater Antilles.

In response to the new eastward motion, both the eastern and western sides of the Caribbean became active with Atlantic plate subduction to the east and Pacific-Farallon plate subduction to the west. The eastern subduction added significantly to the development of the Lesser Antilles, while subduction of the Pacific-Farallon plate along an extended Middle America Trench resulted in volcanism in western Central America (Malfait & Dinkelman 1972). Jamaica and Hispaniola moved slightly eastward with respect to Cuba, which remained firmly sutured to the North American plate, and experienced shearing along strike-slip faults, particularly in Hispaniola. The eastward motion of Central America including a submarine Costa Rica-Panamanian arc terminated deep ocean circulation between the Pacific and Atlantic Oceans at the end of the Eocene (Donnelly 1985). The Chortis block of northern Central America continued eastward motion along the Montagua fault reaching its present location approximately 21 mya (Burke et al. 1984).

Volcanism and the development of Lower Central America appear to have slowed from the middle Oligocene to the early Miocene. However, this quiescent period came to an abrupt end during the middle and late Miocene with uplift, deformation and volcanism in Costa Rica and western Panama (Malfait & Dinkelman 1972). The most intensive uplift period in northwest South America was associated with widespread tectonic activity in the Western Cordillera of Colombia during the early Miocene (Jacobs et al. 1963). Uplift in northwestern South America continued during the late Miocene and into the Pleistocene producing the present North Andean relief (Malfait & Dinkelman 1972, Giegengack 1984). Collision of the Costa Rica-Panamanian arc with northwestern South America resulted in coalescence of a permanent Central-South

American land bridge about 5 mya (Smith 1985). During the Quaternary, substantial uplifting centered on the Windward Passage resulted in 165-600 m of uplift in Cuba and Hispaniola (Horsfield 1975, Mattson 1984).

The Neotropical Atalophlebiinae

Genera of Neotropical Atalophlebiinae may be placed into one of two major faunal components (Table 1): either as a member of the Patagonian Shield, South Andean, Cold-Adapted Genera; or the Guiana & Brazilian Shields, Warm-Adapted Genera. The common distribution patterns displayed by members of these two faunal components (Figs. 2-3) stem from the geological history of the Neotropics and the ecological tolerances of these taxa, particularly to stream-water temperature. Each faunal component (Table 1) is associated with a geological area of ancestral origin (Fig. 1), and the two major distribution patterns are a result of isolation and diversification within these geological areas and subsequent dispersal.

The Guiana & Brazilian Shields, Warm-Adapted Genera are further subdivided based primarily upon the area of maximum species diversification into one of three faunal elements: the Guiana & Brazilian Shields Associated Genera; the North Andean, Central American Genera; or the Antillean Genera.

Patagonian Shield, South Andean, Cold-Adapted Genera

The evolution of the 10 genera composing the Patagonian Shield, South Andean Cold-Adapted Genera (Table 1) is closely associated with the Patagonian Shield region of southern South America. I have included South Andean in the formal title to emphasize the role of the southern Andes on the biogeographic relationships of these genera, and because of the different geological histories of the southern and northern Andes. The ancestors of the Patagonian Shield Genera colonized the southern Andes from the Patagonian Shield as uplift progressed, and currently these genera are primarily associated with cold-water streams in Chile and Argentina.

Patagonian Shield Genera, based on the significant contributions of Pescador and Peters (Peters & Edmunds 1972, Pescador & Peters 1980a, b, 1982, Towns & Peters 1980), may be placed into one of five monophyletic lineages. Only one of these lineages, the *Penaphlebia* lineage, represented by *Penaphlebia* and *Massartella* is restricted to South America. The remaining 4 lineages are large assemblages of genera with representatives on other Gondwanian continents. The *Hapsiphlebia* lineage presently includes *Hapsiphlebia*, 4 Australian genera, and one genus each in New Zealand, New Caledonia and Africa. The *Atalonella* lineage includes *Nousia*, *Archethraulodes*, *Rhigotopus*, several new genera in New Caledonia, and one genus each in New Zealand and Australia. The *Meridialaris* lineage includes *Meridialaris*, *Massartellopsis*, *Secochela*, two genera in New Zealand, and one genus each in Australia and Madagascar. The *Zephlebia* lineage, includes *Demoulinellus*, the New Zealand genus *Zephlebia*, and several new genera from New Caledonia. Although, a more detailed analysis awaits

phylogenetic analysis of the New Caledonian Leptophlebiidae (Peters, in prep.), it is presently obvious that the Patagonian Shield Genera have their primary relationships with diverse genera on several Gondwanian continents. Generally, relationships within a lineage indicate a most recent connection between the Patagonian Shield Region and Australia, secondarily with New Zealand and New Caledonia, and more distantly with Africa and Madagascar.

Table 1. Biogeographic classification of the Neotropical Leptophlebiidae. Known distributions for genera are indicated as follows: SA - South America; CA - Central America; NA - North America; GA - Greater Antilles; and LA - Lesser Antilles. See terminology sections for definition of geographic regions and shields.

I. PATAGONIAN SHIELD, SOUTH ANDEAN, COLD-ADAPTED GENERA

<i>Archethraulodes</i> Pescador & Peters - SA	<i>Demoulinellus</i> Pescador & Peters - SA
<i>Hapsiphlebia</i> Peters & Edmunds - SA	<i>Massartella</i> Lestage - SA
<i>Massartellopsis</i> Demoulin - SA	<i>Meridialaris</i> Peters & Edmunds - SA
<i>Nousia</i> Navás - SA	<i>Penaphlebia</i> Peters & Edmunds - SA
<i>Rhigotopus</i> Pescador & Peters - SA	<i>Secochela</i> Pescador & Peters - SA

II. GUIANA & BRAZILIAN SHIELDS, WARM-ADAPTED GENERA

II.a. GUIANA & BRAZILIAN SHIELDS ASSOCIATED GENERA

<i>Askola</i> Peters - SA	<i>Fittkaulus</i> Savage & Peters - SA
<i>Hermanella</i> Needham & Murphy - SA, CA	<i>Hermanellopsis</i> Demoulin - SA
<i>Homothraulius</i> Demoulin - SA	<i>Leentvaaria</i> Demoulin - SA
<i>Microphlebia</i> Savage & Peters - SA	<i>Miroculis</i> Edmunds - SA
<i>Miroculitus</i> Savage & Peters - SA	<i>Perissophlebiodes</i> Savage - SA
<i>Simothraulopsis</i> Demoulin - SA	<i>Ulmeritus</i> - SA, CA

II.b. NORTH ANDEAN, CENTRAL AMERICAN GENERA

<i>Atopophlebia</i> Flowers - SA, CA	<i>Farrodes</i> Peters - SA, CA, NA, GA, LA
<i>Hagenulopsis</i> Ulmer - SA, CA	<i>Hagenulus</i> Eaton - SA, GA
<i>Terpides</i> Demoulin - SA, CA, LA	<i>Thraulodes</i> Ulmer - SA, CA, NA
gen. n. of <i>Terpides</i> lineage - SA, CA	<i>Traverella</i> Edmunds - SA, CA, NA

II.c. ANTILLEAN GENERA

<i>Borinquena</i> Traver - GA, LA	<i>Careospina</i> Peters - GA
<i>Neohagenulus</i> Traver - GA	<i>Traverina</i> Peters - GA

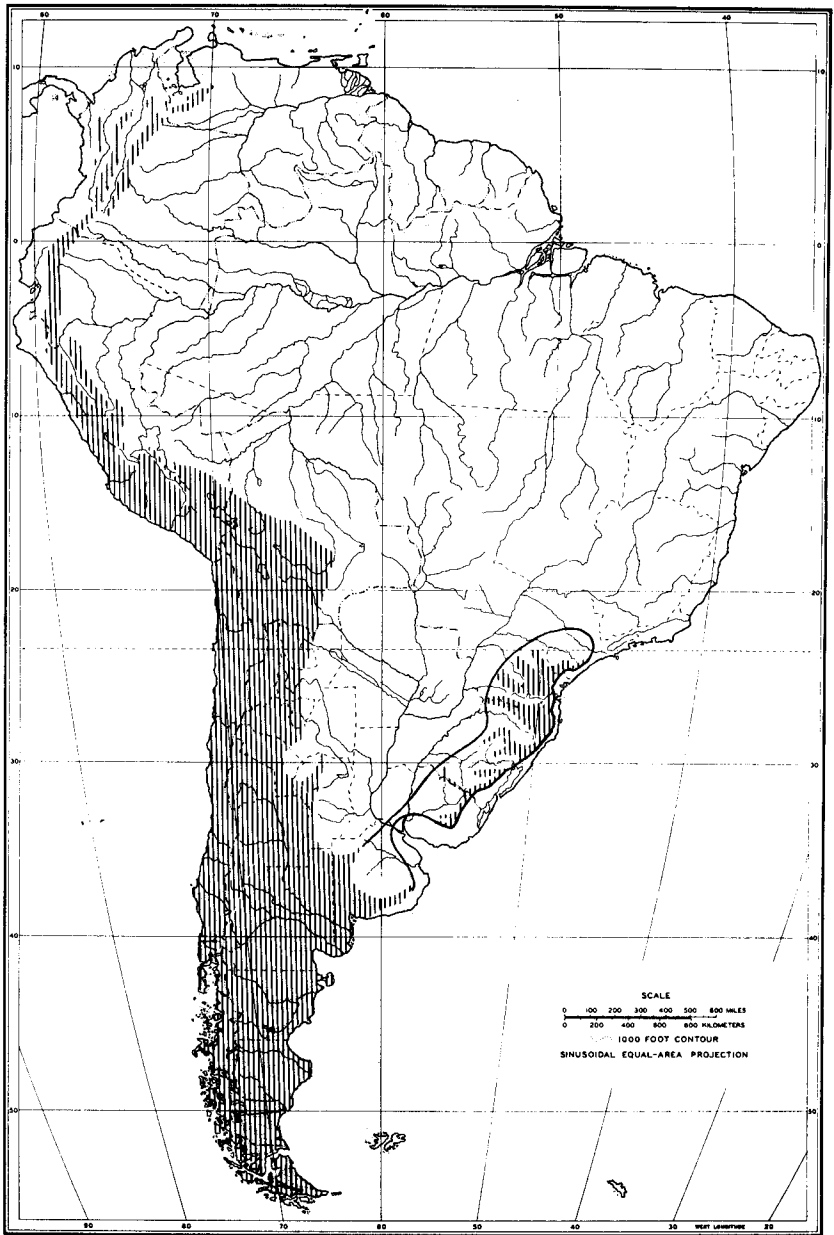


Fig. 2. Distribution of Patagonian Shield, South Andean, Cold-Adapted Genera of Atalophlebiinae (Table 1).



Fig. 3. Distribution of Guiana & Brazilian Shields, Warm-Adapted Genera of Atalophlebiinae (Table 1).

Based on the above summaries of the geological history of the Neotropics and the phylogenetic relationships of the Patagonian Shield Genera, ancestors of the Patagonian Shield Genera became isolated initially from Africa and Madagascar as the South Atlantic began to form about 130 mya. The development of the southern Andes allowed interchange via Antarctica to Australia, New Zealand and New Caledonia until a later date, perhaps 80 mya (Raven & Axelrod 1974). After the rifting of New Zealand and New Caledonia, a Patagonian Shield Region-Australian connection via Antarctica appears probable during the interval 74-39 mya. The late rifting of Australia and Antarctica, and the southern movement of Antarctica into polar regions result in the present close faunal relationships between the Patagonian Shield Genera and the Australian Leptophlebiidae.

Maximal generic and species diversification within the Patagonian Shield Genera occurs in the cold mountain streams of the southern Andes and southernmost South America. Secondary diversification occurs in portions of the southern coastal mountains of Brazil, and at high elevations in the central and northern Andes (Fig. 2). Generally, the present distribution of this group is limited by an ecological restriction to cold stream-water temperatures. The evolution of the cold-adapted attribute appears ancient and resulted from the cool climates present over much of the southern Gondwanian landmasses during the Mesozoic. This general cold-adaptiveness appears to be a general phenomenon among southern Gondwanian lineages and is obvious in such unrelated groups as Plecoptera (Illies 1969), Chironomidae (Brundin 1966), and Scarabaeidae (Halffter 1974). Due largely to the cold-adapted attribute, members of this faunal component become increasingly restricted to higher elevations in the warmer, northern portions of South America.

In the Aconquija Mountains near Tucumán, Argentina, at 27° S latitude, the leptophlebiid fauna between 2,000-4,300 m is composed entirely of Patagonian Shield Genera with *Meridialaris* and *Massartellopsis* being particularly abundant (Dominguez & Savage 1987). In contrast, the leptophlebiid fauna below 1,000 m is composed entirely of the Guiana & Brazilian Shields, Warm-Adapted Genera *Thraulodes* and *Farrodes* (Dominguez & Savage 1987). Streams between 1,000-2,000 m in the Aconquija Mountains remain uncollected. However, collections made by Dominguez in the neighboring hills of Medina and Burruyacú demonstrate that *Farrodes* and *Thraulodes* are abundant at 1,550 m in the absence of Patagonian Shield Genera. Unfortunately, streams between 1,550-2,000 m at this latitude remain uncollected, and the elevation and conditions at which faunal mixing or replacement occurs remain unknown.

Patagonian Shield Genera appear to be restricted to even higher elevations at warmer northern localities due primarily to the cold-adapted attribute. Presently, little is known concerning the distribution of Patagonian Shield Genera in northern areas because collections from above 2,500 m in the central and northern Andes are extremely rare. Study of numerous collections from elevations of 2,500 m or less between 17° S and 10°30' N latitude reveals only members of the Guiana & Brazilian Shields, Warm-Adapted Genera (Table 1). Current distribution records for Patagonian Shield Genera north of 17° S latitude are limited to three collections that have been made at elevations above 3,000 m. A collection made at 3,750 m in the mountains of Ecuador (Ecuador:

Imbaburu Prov., 0° 37' N) is composed entirely of a new taxon of the *Atalonella* lineage related to *Nousia* of the Patagonian Shield Genera (Table 1). A series of collections from the Rio Huallaga of Peru indicates that members of the Patagonian Shield Genera are present at elevations above 3,600 m between 10° 43' -9° 08' S (Illies 1964). Although the present location of the specimens collected by Illies is unknown (Zwick, pers. comm.), the fact that Illies recognized an *Atalophlebia* dominated fauna at sites between 3,600-4,100 m (*Atalophlebia* is currently recognized as a member of the *Hapsiphlebia* lineage and restricted to Australia), and a *Thraulodes* dominated fauna at lower elevations supports the contention that Patagonian Shield Genera are restricted to elevations above 3000 m in the central and northern Andes. The occurrence of Patagonian Shield Genera throughout the high Andes is documented by the presence of a new species of *Massartella* collected in the Cordillera de Merida, Venezuela, at 8° 24' N latitude (Pescador, pers. comm.).

Members of the Patagonian Shield Genera present in the central Andes likely colonized high North Andean mountain habitats as they were formed in Pliocene-Pleistocene times (Hammen 1974). Northward migration would have been facilitated during Pleistocene glacial periods because cooler temperatures would have decreased the elevation and increased the area of cold stream, high mountain habitats. The occurrence of Patagonian Shield Genera outside continental South America appears extremely unlikely, due to their recent arrival in the northern Andes, and the lack of an appropriate continuous or semi-continuous habitat in Panama.

It has been suggested that the stream fauna of the high North and Central Andes is low in species-richness (Illies 1964, Fittkau, pers. comm.). Although, the mayfly data is too scarce to evaluate, a low species-richness associated with the high northern Andes may result from: the recent origin of the high North Andean habitat (Hammen 1974, Giegengack 1984); the island and peninsular nature of areas of elevation over 3,000 m; and the limited area of the high North Andean habitat and area associated effects.

Even though the distribution of the Patagonian Shield Genera is strongly associated with cold stream-water temperatures, secondary adaptation at the species-level to cool and warm water streams may occur. The recent description of an unusually small species of *Penaphlebia* (Dominguez & Pescador 1983) from Rio Negro Prov., Argentina, suggests recent adaptation within a primary cold-adapted genus to cool and warm, summer, stream-water temperatures in southern areas at low elevations. Noting the possibility of recent secondary adaptation to warmer stream-water temperatures, I have emphasized the geological origin of these taxa by commonly employing the name Patagonian Shield Genera.

Guiana & Brazilian Shields, Warm-Adapted Genera

The remaining 24 known genera of Neotropical Atalophlebiinae represent a number of separate phyletic lineages that share a common ancient heritage stemming from isolation on the Guiana & Brazilian Shields (Fig. 1), and independent evolution of the warm-adapted attribute. The Guiana & Brazilian Shields, Warm-Adapted Genera (II, Table 1) presently include a diverse assemblage of genera. Taxonomically, most genera are represented by only a few described species, and most species of this fauna remain undescribed. To prepare this manuscript, I have of necessity based generic distributions largely on undescribed species. Therefore, future revisionary and phylogenetic studies will likely result in an improved understanding of relationships within the Guiana & Brazilian Shields, Warm-Adapted Genera.

In sharp contrast to the Patagonian Shield Genera, the Guiana & Brazilian Shields, Warm-Adapted Genera appear to be not only composed of endemic genera, but of endemic monophyletic lineages that are each composed of 2-4 endemic genera. Two lineages, the *Terpides* lineage (Savage 1983a, 1986) including *Terpides*, *Fittkaulus* and a new genus, and the *Hermanella* lineage (Flowers & Peters, pers. comm.), including *Hermanella*, *Leentvaaria* and *Traverella*, are defined by a number of distinct apomorphic characters associated with exploitation of atypical niches. Members of the *Hermanella* lineage have evolved a filter feeding habit, while members of the *Terpides* lineage have caudal filaments with long, dense setae and employ swimming movements typical of the family Baetidae (Savage 1986). The *Miroculis* lineage (Savage & Peters 1982, Savage 1983b) includes the 4 subgenera of *Miroculis* and the genera *Miroculitus*, *Microphlebia* and *Hermanellopsis*. Although the 4 subgenera of *Miroculis* and *Miroculitus* are obviously very closely related, their association with *Microphlebia* is more distant, and the phylogenetic placement of *Hermanellopsis* remains preliminary because the nymphal stage of this unusual genus remains unknown. Based on initial studies without documented phylogenetic analyses the following additional lineages seem apparent: the *Farrodes* lineage including *Farrodes*, *Simothraulopsis* and *Homothraululus*; the *Hagenulopsis* lineage including *Hagenulopsis*, *Borinquena* and *Askola*; the *Hagenulus* lineage including *Hagenulus* and *Neohagenulus*; and the *Careospina* lineage including *Careospina* and *Traverina*. In addition, the *Hagenulopsis*, *Hagenulus* and *Careospina* lineages may constitute a larger super-*Hagenulopsis* lineage. The remaining 4 genera, *Atopophlebia*, *Perissophlebiodes*, *Thraulodes* and *Ulmeritus* remain phylogenetically enigmatic, although *Ulmeritus* appears to be related to members of the *Hermanella* lineage, and *Thraulodes* appears to share a common ancestor with members of the *Meridialaris* lineage of the Patagonian Shield Genera.

The phylogenetic relationships among the above warm-adapted lineages and other lineages of Atalophlebiinae remain obscure, and sister-group relationships with lineages on other continents are not readily apparent. The presence of endemic monophyletic lineages with distant relationships to other Atalophlebiinae reflects the isolation experienced by the Guiana & Brazilian Shields between the formation of the northern South Atlantic Ocean about 80 mya and the formation of the lower Central American isthmus approximately 5 mya. Although distant, phylogenetic relationships of the warm-adapted lineages appear to be of two types: those related to African taxa, and those related to

lineages of the Patagonian Shield Genera. For example, the *Miroculis* lineage may be related to *Adenophlebiodes* Ulmer of Africa, while *Thraulodes* as mentioned previously appears to share a common ancestor with members of the *Meridialis* lineage of the Patagonian Shield Genera.

Members of the Guiana & Brazilian Shields, Warm-Adapted Genera are widely distributed in warm to cool streams of the northern Neotropics (Fig. 2). Although most Warm-Adapted Genera are restricted to the Neotropics as indicated in Fig. 2, three genera, *Farrodes*, *Thraulodes* and *Traverella* have dispersed into North America (Table 1). In the northern Andes, Warm-Adapted Genera have been recorded up to elevations of 2,500 m. Although, presently available collections at this elevation include only members of the genus *Thraulodes*, and most Warm-Adapted Genera appear to be common only at elevations of less than 2,000 m. In Fig. 2, the distribution of Warm-Adapted Genera is portrayed as being continuous to the west of the northern Andes in the following areas: along the coastal areas of Venezuela and Colombia; through an area of lower elevation near San Cristóbal, Venezuela, which separates the Cordillera de Merida in Venezuela from the eastern Cordillera of Colombia; in the headwater regions of the north flowing Rio Magdalena and the east flowing Rio Caqueta near Garzón, Colombia; and through tributaries of the Rio Huancabamba, a northern tributary of the Rio Marañón, and tributaries of the west flowing Rio Cascajal and Rio Piura near Huarmaca, Peru. However, there are a number of additional areas north of the Rio Marañón that could act as channels for the Guiana & Brazilian Shields, Warm-Adapted Genera. In fact, narrow areas of moderate elevation between east and west draining streams north of the Rio Marañón may be so numerous that this area acts more like a sieve than a barrier. In contrast, to the south of the Rio Huancabamba-Rio Chamaya area of Peru, E-W connections via valleys and headwater areas of low and moderate elevations become increasingly rare due to development of the high Peruvian Andes and the Altiplano.

I have subdivided the Guiana & Brazilian Shields, Warm-Adapted Genera into three faunal elements (Table 1) based upon the available distributional data and my field experiences in South America. The categorization of genera into the first two faunal elements, the Guiana & Brazilian Shields Associated Genera, and the North Andean, Central American Genera is based upon the geographic distribution of the genus, the area of maximum species diversification, and habitat preference. In contrast, group IIc, the Antillean Genera, is defined to include only genera that are endemic to the Antilles (Table 1). Therefore, the geographic distributions of the Antillean Genera are strictly defined, while the distributions of genera in the first two faunal elements commonly overlap. In addition, isolated species-groups of some genera of the North Andean, Central American Genera have recently, since the Miocene, invaded the Antilles.

The 12 Guiana & Brazilian Shields Associated Genera (IIa, Table 1) are principally associated with the Guiana and Brazilian Shields and surrounding lowlands such as the Amazon, São Francisco and Paraná Basins. Based on available collections, genera of this faunal element are restricted to elevations of less than 700 m along the eastern slopes of the Andes, do not occur in the Antilles, and with the exceptions of *Hermanella* and *Ulmeritus* do not occur in Central America. *Hermanella* is classified as a member of the Guiana & Brazilian

Shields Associated Genera despite its presence in Central America, because maximum species diversification within this genus occurs in stony streams of the Guiana and Brazilian Shields, and associated lowland areas such as the Paraná and Amazon Basins. In Central Amazonia where sandy or sandy-clay bottomed streams dominate, *Hermanella* occurs on hard wood substrates in areas of fast to moderate current.

Miroculis is taxonomically and geographically the best understood genus within the Guiana & Brazilian Shields Associated Genera and provides a distribution typical of this faunal element (Fig. 4). The distribution of *Miroculis* is strongly associated with the Guiana & Brazilian Shields and the intervening Amazonian lowlands (Savage & Peters 1982, Savage - submitted manuscript). *Miroculis* is a major component of the stream fauna in the indicated area (Fig. 4). However, 6 weeks of collecting in the Andes and coastal mountains of Venezuela by the author, and extensive field work by Flowers in Panamá (Flowers, pers. comm.) indicate that *Miroculis* has failed to cross the Andes. *Miroculis* is known from the island of Trinidad, which is biogeographically a part of continental South America, but is unknown from the Antilles.

The second faunal element within the Warm-Adapted Genera, the North Andean, Central American Genera (IIB, Table 1), includes 8 genera whose maximum species diversification occurs in the northern Andes and Central America with occasional invasions by isolated species-groups into the islands of the Antilles and/or North America. These taxa, except for gen.n. of the *Terpides* lineage, and some species-groups of *Terpides*, display ecological preferences for stony substrates and moderate to swift currents. *Terpides* (Fig. 5) displays a distribution pattern representative of the North Andean, Central American Genera, which includes the eastern slopes of the central and northern Andes, the coastal ranges of Venezuela and Colombia, Central America, one or more of the Antillean islands (St. Vincent), and streams draining the Guiana Shield (Savage 1983a). Three of the 8 North Andean, Central American Genera, *Atopophlebia*, *Hagenulopsis* and gen.n. of the *Terpides* lineage, are presently known only from northern South America and Central America. *Hagenulus* is known from Ecuador, Trinidad, and all four islands of the Greater Antilles (Peters, pers. comm.). Two genera, *Farrodes* and *Thraulodes*, are widely distributed throughout northern South America including the island of Trinidad, occur in Central America and northward into the southwestern U.S. In addition, *Farrodes* is known from both the Lesser and Greater Antilles (Peters 1971). In North America, *Thraulodes* is common in Mexico and is known from Utah, Arizona, New Mexico and Texas (Traver & Edmunds 1967, Edmunds 1982, Peters - submitted manuscript), while *Farrodes* is known from southern Mexico and Texas. The third genus to successfully colonize North America, *Traverella*, is widely distributed in both South and Central America. *Traverella* is unusual in that it has successfully invaded the Mississippi drainage basin and occurs north to Saskatchewan and Alberta, and east to Ohio.

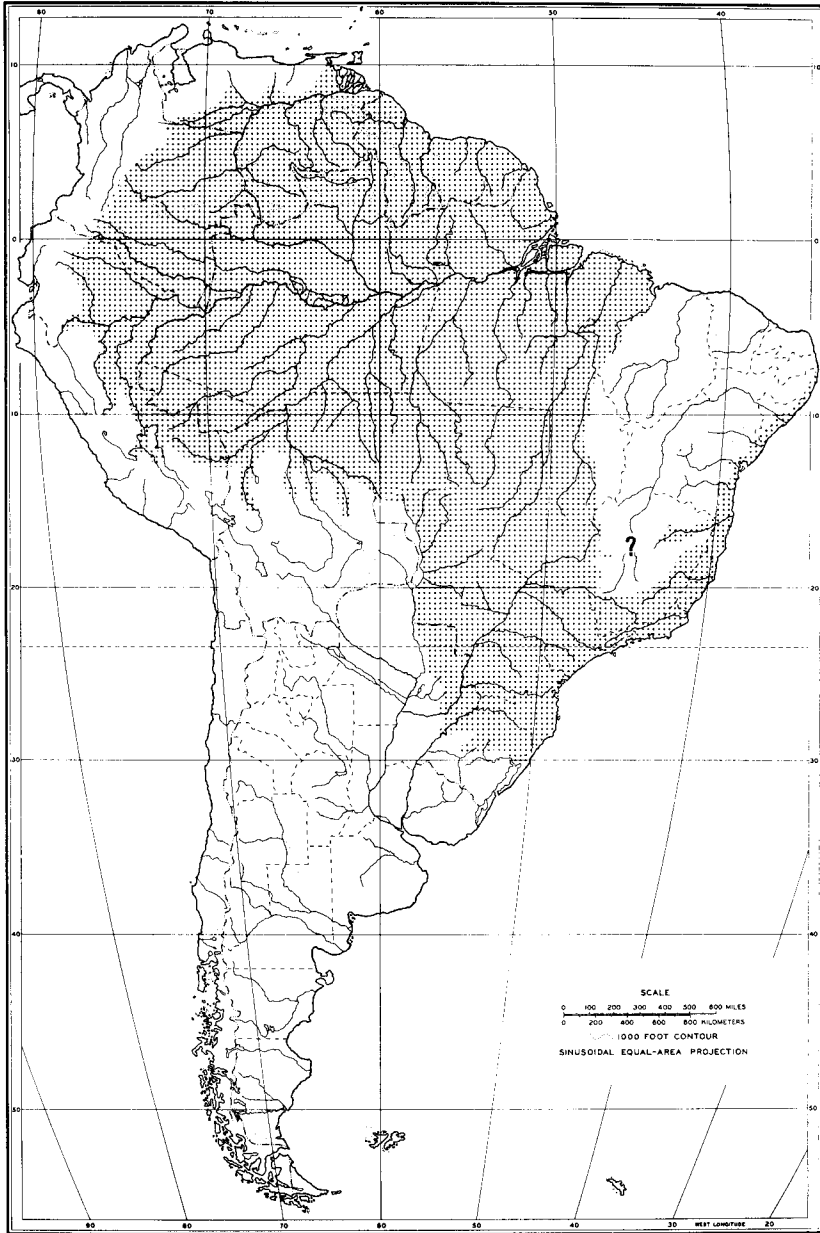


Fig. 4. Distribution of *Miroculis*, a genus of the Guiana & Brazilian Shields Associated Genera (Table 1).



Fig. 5. Distribution of *Terpides*, a genus of the North Andean, Central American Genera (Table 1).

The colonization of Central America by most genera of the North Andean, Central American Genera (Table 1), and subsequent dispersal by three genera into North America appears to be a function of their historical association with North Andean streams, their ecological preferences for stony substrates and warm stream-water temperatures, and development of the Lower Central American isthmus. Possession of particular life history characteristics, such as a relatively short developmental period (Edmunds 1982), likely played an important role in the successful colonization of North America. Unfortunately, life history data on Neotropical Ephemeroptera remain too limited to properly evaluate the role of these factors.

The distinction between Guiana & Brazilian Shields Associated Genera and North Andean, Central American Genera is based upon differences in generic distributions and species-richness patterns. These differences stem from both ecological and historical factors, and the relative role of these two variables may vary among genera. Members of the North Andean, Central American Genera, except for gen.n. of the *Terpides* lineage, typically display stronger preferences for stony substrates and swifter currents. In contrast, genera of the Guiana & Brazilian Shields Associated Genera appear better adapted to hard wood substrates, leaf packs, and moderate currents. However, the strengths of these preferences are sufficiently variable to allow considerable habitat overlap, and these preferences should be viewed as general trends rather than hard and fast rules.

Members of these two faunal elements may exhibit strong habitat segregation at one location; yet, occur in the same microhabitat at another location. At Mission Cutivireni, on the eastern slopes of the Peruvian Andes at an elevation of 435 m, distinct habitat segregation occurs between *Thraulodes* and *Farrodes* of the North Andean, Central American Genera, and *Miroculis* of the Guiana & Brazilian Shields Associated Genera. The dominant mayflies in the Rio Mamiri, a medium-sized, shallow, rocky river with moderate to swift currents, are *Thraulodes* and *Farrodes*. *Thraulodes* completely dominates the mayfly fauna of the Rio Mamiri in terms of both numbers and biomass, and is a principal component of the aquatic insect fauna. *Miroculis* (Fig. 4), a member of the Guiana & Brazilian Shields Associated Genera, is also present in the Mission Cutivireni area, but occurs on wood detritus in sandy-bottomed, oxbow-like streams that drain isolated swampy areas. These streams have sandy-clay bottoms, little to moderate current, much wood and leaf detritus, and resemble streams of Central Amazonia. The dichotomy at Mission Cutivireni was distinct, with *Thraulodes* dominating rocky streams, and *Miroculis* dominating sandy streams within 10 m of each other. However, this ecological separation blurs in Central Amazonia where stony substrates are rare. In Central Amazonia, *Thraulodes* occurs on solid wood substrates in areas of moderate to fast current, and *Thraulodes* and *Miroculis*, particularly members of the subgenus *M.* (*Miroculis*), may occur in the same microhabitat, e.g., on sticks below the waterfall on Igarape Acará at Reserva Ducke near Manaus.

The distribution maps (Figs. 4-5) representative of these two faunal elements also suggest differences in food items associated with hydrogeochemical features of the northern Neotropics. The distribution of North Andean, Central American Genera (Fig. 5) frequently overlaps the distribution of recently

uplifted, rapidly eroding rocks. The presence of recently exposed rocks in the northern and central Andes has been correlated with higher stream-nutrient levels, higher primary productivity and correspondingly higher diatom biomass (Fittkau 1964, Fittkau et al. 1975). In contrast, the distributions of *Miroculis* (Fig. 4) and other Guiana & Brazilian Shields Associated Genera typically include electrolyte-poor streams draining heavily weathered geological formations of Central Amazonia and shield areas. Genera that are particularly well adapted to nutrient-poor Amazonian streams such as *Miroculis* apparently have adapted to detritus, fungi and bacteria based diets. Dietary data for Neotropical Atalophlebiinae to test this hypothesis remain lacking. However, the inference is supported by a similar pattern in the Chironomidae, where typical diatom-feeding taxa are absent or rare in nutrient-poor Amazonian streams (Fittkau, pers. comm.).

While the distinction between Guiana & Brazilian Shields Associated Genera and North Andean, Central American Genera typically contains an ecological component, distinctly different distributional and species-richness patterns between closely related sister-genera may occur in the absence of ecological differentiation. This biogeographic differentiation between ecologically similar sister-genera documents the role of historical vicariance events in the generation of distribution patterns displayed by these two faunal elements. A well-documented example of divergence in the absence of ecological differentiation is provided by the sister-genera *Fittkaulus* and gen.n. of the *Terpides* lineage (Savage 1983a, 1986). *Fittkaulus* is a common genus known from the eastern Guiana Shield and surrounding lowland areas, the eastern Amazon Basin, and southward across the Brazilian Shield to the northern Rio Paraguay Basin in Mato Grosso. Gen.n. of the *Terpides* lineage in contrast displays a distribution typical of the north Andean, Central American Genera. This genus occurs from northern Argentina north along the eastern slopes of the Andes to Colombia and Venezuela, and in Central America north to Costa Rica with a single wide ranging species occurring east to central Amazonia and Surinam. Ecologically nymphs of both genera occupy a Baetidae-like habitat. Nymphs cling to solid substrates especially trailing tree roots and vegetation in areas of slow to moderate currents, and employ the slightly flattened abdomen and setal rows on the caudal filaments for swimming in the fashion typical of Baetidae (Savage 1986). Thus, ecological preferences definitely can not be invoked to explain differences in species-richness and distribution patterns in these two genera. The evolutionary divergence of these two sister-genera likely stems from isolation of the northern Andes from the Guiana and Brazilian Shields by large freshwater and brackish water lagoons during the mid-Tertiary (Fittkau 1974). This vicariance event apparently at least in these two genera leads to divergence without ecological differentiation.

The third faunal element of the Warm-Adapted Genera, the Antillean Genera (IIc, Table 1), is a smaller and more homogeneous assemblage because membership is restricted to endemic genera. Currently, four genera of Atalophlebiinae are believed to be endemic to the Antilles, with three of these four genera being endemic to the Greater Antilles (Table 1). *Traverina* and *Careospina* are known from Cuba, while *Neohagenulus* is known from Puerto Rico (Peters 1971). *Borinquena* is composed of two subgenera: *B. (Borinquena)* known from

Puerto Rico; and *B. (Australophlebia)* known from the Lesser Antillean islands of St. Lucia and Dominica (Peters 1971).

The four Antillean Genera are both geographically and phylogenetically most closely related to taxa of the North Andean, Central American Genera (Table 1), particularly to *Hagenulus* and *Hagenulopsis*. Unfortunately, detailed studies on the phylogenetic relationships of the Antillean Genera are lacking, and the islands of the Antilles remain largely uncollected. Presently, *Traverina* and *Careospina* appear to constitute a lineage endemic to the Greater Antilles. *Neohagenulus*, which is endemic to the Greater Antilles, appears most closely related to *Hagenulus*, which is a member of the North Andean, Central American Genera and is known to occur in Ecuador, Trinidad, and all four of the Greater Antillean Islands. *Borinquena* is very closely related to *Hagenulopsis* of the North Andean, Central American Genera. *Hagenulopsis* is not known to occur in the Antilles, but it is a common and widespread continental genus occurring from southern Brazil to Honduras. Whether *Borinquena* evolved from a common ancestor shared by all continental species of *Hagenulopsis*, or from a common ancestor of an isolated species-group of *Hagenulopsis* awaits revision and phylogenetic analysis of *Hagenulopsis* and the description of numerous undescribed continental species.

The islands of the Antilles, particularly the islands of the Lesser Antilles, remain largely uncollected and new distribution records and descriptions of new taxa will undoubtedly change our interpretation of the historical biogeography of this region. For example, 16 years ago, six genera of Atalophlebiinae were known from the Antilles and all were believed to be closely related and endemic (Peters 1971). This implied that the evolution of the Antillean fauna could be explained by a single vicariance or dispersal event. Currently, seven genera are known from the Antilles (Table 2), and of these seven only four are believed to be endemic to the Antilles. Preliminary phylogenetic analysis suggests that a minimum of 5 biogeographic events, dispersal or vicariance, are required to explain the evolution of the Antillean Atalophlebiinae at the generic level (Table 2). Although some of these events could have been synchronous, it is apparent that with increasing distributional data the historical biogeography of the Antillean Atalophlebiinae will become increasingly complex.

Table 2. Minimum number of biogeographic events required to explain the evolution of the Antillean Atalophlebiinae at the generic level.

<i>Taxa</i>	<i>Events</i>
species-groups of <i>Terpides</i>	1
species-group(s) of <i>Farrodes</i>	1 - 2
species-group of <i>Hagenulus</i>	1
<i>Neohagenulus</i>	0 - 1
<i>Borinquena</i>	1
<i>Careospina</i> - <i>Traverina</i>	1 - 2
	5 - 10

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The printer mailed the page proofs for this manuscript to me by surface mail. Consequently, I received my copy of the page proofs about 2 months after the deadline to return them to the editor. The editor, not wanting to delay the issue or to drop my article decided to proof read my article himself. As a result a number of errors went undetected and a few new errors were added by the editor. They are as follows:

<u>page #</u>	<u>location</u>	<u>error</u>	<u>correction</u>
199	1st line	Neotropica	Neotropical
199	last line	43543	43542
200	3 para	Pleistocene Times	Pleistocene times
200	3 para	the islands	these islands
200	5 para	species is available	species available
202	top para	Islands Shields	Island Shields
204	2 para	Ducan	Duncan
204	3 para	Cayman through	Cayman trough
211	top para	43'	43'
211	top para	08'	08'
211	top para	Cordillera de Merida	Cordillera do Merida
213	2 para	Cordillera de Merida	Cordillera do Merida
213	2 para	Rio Mananon	Rio Maranon
218	2 para	leads	lead
219	1st line	<i>Australophlebia</i>	<i>Australphlebia</i>
219	2 lines above Table	data the	data that the
219	Table	species-groups of <i>Terpides</i>	species-group of <i>Terpides</i>
219	Table	5-10	5-8

The interpretation of the geographic history of *Hagenulus*, the classification of *Hagenulus* in Table 1, and the biogeographic events in Table 2 considered information on an unpublished record of *Hagenulus* from Ecuador conveyed to me by letter in 1986 and cited as Peters (pers. comm.). Recent studies by J.G. and W.L. Peters, reveal that the original interpretation was in error and that the specimens from Ecuador are not *Hagenulus* but an allied new genus (J.G. and W.L. Peters, in letter, 1988). Therefore, *Hagenulus* is known only from the Greater Antilles and should have been placed as a member of the Antillean Genera (II.c.) in Table 1. I have also redone Table 2 (see below) to include only taxa published before January 21, 1989 because the exact phylogenetic position of the unpublished taxon from Ecuador is unclear.

TABLE 2. Minimum number of biogeographic events required to explain the evolution of the Antillean Atalophlebiinae at the generic level. (Only taxa published before January 21, 1989 are considered.)

<u>Taxa</u>	<u>Events</u>
species-group of <i>Terpides</i>	1
species-group(s) of <i>Farrodes</i>	1 - 2
<i>Borinquena</i>	1
<i>Hagenulus-Neohagenulus</i>	1 - 2
<i>Careospina-Traverina</i>	<u>1 - 2</u> 5 - 8