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Historical and Life History Factors in the Biogeography of Mayflies[1]

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SYNOPSIS. Cladistic analysis of mayflies suggests that dispersal was very asymmetrical after the new land connection between North and South America. Twenty-one genera apparently moved from South to North and Central America, but there is good evidence for only one North American genus moving into the south. Testable predictions are possible once the boreal (Laurasian) or austral (Gondwanian) designations are made. For example, *Paracloeodes*, a genus of austral origin, was predicted to be found in South America, and in North America in warm rivers north and east of its known distribution. These predictions have been confirmed. Other 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. Merger events and consequent dispersal of organisms have profound influences on distributional patterns, and from such information, biologically useful generalities can be made.

Geographic patterns of living organisms are the result primarily of the processes of diffusional dispersal, dispersal across barriers, vicariant events, merger events and extinctions. This paper concerns itself primarily with the geographic patterns of mayflies resulting from a major merger event, the establishment of a land connection between North and South America via the isthmus of Panama. Some genera dispersed across the former barrier and some apparently did not; some dispersed only a few hundred kilometers and others from South America to northern Canada. A principal purpose of this paper is to show that despite such variation, biologically useful generalities can be made concerning this biogeographic process, and that testable predictions are possible.

Before one can determine which direction groups dispersed, it must be determined whether the genus was originally in North America or in South America. Almost every rule for determining a center of origin has been thrown into doubt except for a substantial fossil record in one area and its absence elsewhere. No significant fossil record is available for mayflies (Ephemeroptera) that bears on this question. For the mayflies my assignment of a genus as being of South American origin or North American origin has been done entirely on the basis of the geography of the group of which the insect is a cladistic member. A simple example is the mayfly genus *Tricorythodes* (Tricorythidae) which ranges from northern Canada to Argentina. The other genera of the subfamily occur in South America (except for one genus in Africa) and the most closely related genus extends north to Utah and Maryland, and a third closely related genus north to Central America. The other subfamilies occur in Africa with one of these extending to Madagascar and the Oriental Realm.

For some genera, no clear decision can be made as to whether the genus is of South American or North American origin, but in most cases even where the cladistics *within* the group are obscure the decision seems reasonably easy. Most New World mayfly genera have clearly had either a Laurasian or Gondwanian evolutionary history.

South American mayflies have a number of interesting vicariant patterns with other Gondwanian land masses. The strongest vicariant patterns are those of southern South American forms with genera, in first, Australia, and, second, New Zealand, and then, New Caledonia. In turn, these

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TABLE 1. *Genera of South American mayflies dispersed to North or Central America.*

Genus	North/east limits	Rank (see text)
Baetidae		
Apobaetis	C., Calif.	11–14
Baetodes	Ariz., Texas	10
Callibaetis	Alaska, N. Canada	20–21
Dactylobaetis	Oregon, Sask., Okla.	16–19
Paracloeodes	Wyo., Minn., Ga.	15
Oligoneuriidae		
Homoeoneuria	Utah, Ind., S.C.	11–14
Lachlania	Utah, Sask.	16–19
Leptophlebiidae		
Farrodes	Texas	8
Hagenulopsis	Honduras	4–6
Hermanella	Honduras	4–6
Hermanellopsis	Panama	1
Thraulodes	Utah, Texas	11–14
Traverella	Wash., Sask., Ohio	16–19
Ulmeritis	Costa Rica	2–3
Euthyplociidae		
Campylocia	Honduras	4–6
Euthyplocia	Vera Cruz, Mex.	7
Polymitaryidae		
Campsurus	Texas	8–9
Tortopus	Man., S.C.	16–19
Tricorythidae		
Haplohyphes	Costa Rica	2–3
Leptohyphes	Utah, Md.	11–14
Tricorythodes	N. Canada	20–21

southern groups have more distant relatives in southern Africa and Madagascar. Many tropical genera have close relatives in Africa. Some lineages are also found in South America and Madagascar but are absent from Africa, paralleling the pattern seen in some lizards, snakes and turtles.

Ephemeroptera are, on the basis of their present distribution pattern, almost exclusively diffusional dispersers. This appears to result primarily from the very short duration and fragility of the winged stages; as will be seen below, tropical forms have an even shorter life as winged stages than do familiar temperate forms.

The dispersal of mayflies between North and South America is overwhelmingly asymmetrical. There is reasonably sound evidence only for a single genus, *Brachycercus* (Caenidae) dispersing from North America to South America. The evidence on *Hexagenia* now strongly favors the belief that the subgenus *Hexagenia* is a North American group and that the subgenus *Pseudeatonica* was in southern Mexico and Central America and spread to South America. It is possible that some South American Baetidae or species referred to *Caenis* (Caenidae) originated in North America but present knowledge of these groups is inadequate to detect any such patterns. No less than 21 genera have moved from South America to North and Central America, with 14 genera extending as far north as the United States and 6 genera in Canada. Table 1 lists these genera, their taxonomic affinity, limits of northward dispersal and rank of dispersal (1, least, to 21, most distance).

Edmunds *et al.* (1976) made a decision for most North and Central American genera whether each genus was boreal (*i.e.*, members of Laurasian lineages) or austral (*i.e.*, members of Gondwanian lineages). Every genus determined as austral is found in South America and extends at least onto the isthmus of Panama and some extend north to Canada. (One genus, *Pentagenia*, is an old North American endemic with its apparent closest relatives in Madagascar and India and it was arbitrarily assigned as austral; we will not discuss it further.) There is considerable advantage to determining the origin of each genus as austral (Gondwanian) or boreal (Laurasian) and then giving the known northern limits for austral genera, and the known southern limits for boreal genera. The general habitats toward the range limits are clearly predicted by such statements. The southerly limits of boreal genera are in the cool streams of highlands and the northern limits of austral genera are in warm, usually silted, lowland streams. My former students and I have used this boreal or austral designation for many years because it is generally predictable of habitat and of heretofore unknown distribution.

For many mayflies there are very incomplete geographic records and hence it is useful to generalize on distribution and predict geographic occurrence. For ex-

ample, Edmunds *et al.* 1976 listed the genus *Paracloeodes* on the basis of cladistic relationships as having an "austral origin," *e.g.*, it originated in South America or from South American ancestors. We noted its "known distribution" is in California, Wyoming, Minnesota, Mississippi, Alabama, Georgia and Puerto Rico. We stated it would not be surprising to find it in "warm rivers north and east" of its known distribution, and it was highly likely to be found in Mexico. Two of these predictions are now confirmed. A larva described by Traver (1944) as "Pseudocloeon??" from Brazil is clearly *Paracloeodes* and the genus occurs in warm silted rivers in Indiana. It almost certainly will be found in Mexico and Central America.

Edmunds *et al.* 1976 noted that in Utah the eggs of species assigned as austral hatch only when the water warms up to about 21°C (70°F), and emerge as adults before the water cools in autumn. The life history patterns of most species belonging to Gondwanian genera in the United States appears to generally follow the pattern of late season hatching (July) and emerging in late August or September. Those mayflies that have been investigated have a critical egg hatching temperature, although tropical genera have not been investigated. It appears that most species of the genera that have dispersed north act as short term summer annuals. It is probable that only those mayflies with relatively short developmental period, *e.g.*, <12 weeks, would have been able to disperse to the United States. I predict that there is a good correlation between the length of time of larval development in the tropics and degree of northward dispersal but at this time there is insufficient data to test this prediction. Certainly, life history length is a much more important factor in the distance each genus has dispersed than the distance an adult can fly during its short life. There has been some adaptive shift. It appears that at least two genera, *Callibaetis* and *Tricorythodes* have a few species that have adapted to cooler climates. Larvae of both genera overwinter in northern Utah.

Tropical lowland mayflies differ from temperate groups in their emergence and mating patterns (Edmunds and Edmunds, 1979). Tropical genera with specialized short lives (*ca.* 2 hr as imago and/or subimago) differ relatively little from temperate forms but there are major differences between tropical and temperate genera whose winged stages last 12 hr to several days. The tropical patterns were primarily established from data from Malaysia but confirmed from published accounts in Africa, and consistent with observations in Madagascar. H. M. Savage (personal communication) has demonstrated that Amazonian mayflies have the same distinctive patterns of emergence and mating times shown by those elsewhere in the tropical lowlands and differing from the pattern in temperate areas.

The emergence and mating pattern of some genera in the United States determined as of South American origin tends to remain as a tropical pattern. The genus *Dactylobaetis* presumably of South American origin was found swarming in Idaho in early evening, a pattern unlike the tropical lowland forms. One of two explanations is possible; the genus may have changed swarming habits or the species may have been derived from tropical highlands forms where some swarming patterns are similar to those in the temperate regions. *Callibaetis,* another genus of presumed South American origin, swarms at midday. This is a common pattern in tropical highlands but midday swarming also is reported for one genus in the Amazon. The emergence and swarming patterns do not unequivocably support South American origin for the genera believed to have originated there, but in genera such as *Tricorythodes* and *Traverella,* emergence and swarming patterns are clearly tropical. Substantially more data are needed on emergence and swarming times to test the generality of the pattern.

In the large silted rivers of North America there is a relatively low diversity of species during the heat of summer, except for the genera of South American origin. In the Green and Colorado Rivers all of the species that emerge in spring and early summer are of Laurasian lineages, and

most of the species emerging in late August and September are of South American origin. The question then arises as to whether tropical mayflies have been successful because they utilized habitats that were poorly exploited or whether the tropical genera displaced warm adapted forms already here. There is only one evidence of the latter possibility. The neoephemerid genus *Potamanthellus* is known from the Miocene of Montana (Lewis, 1977); it is now apparently extinct in North America but it is still extant in Southeast Asia.

One of the prime arguments of the vicariant school of biogeography is that the process of allopatric speciation makes the search for a center of origin a non-question. Nevertheless, we know that groups have long evolutionary histories on one land mass before they enter a second land area by dispersal. The entry into new areas might be dispersal across a barrier or it might be through diffusional dispersal following a merger event. The removal of a barrier by the merger of two land masses is the opposite of a vicariant event. The merger of North and South America had profound influence on the distribution patterns of biota in the New World. It has been treated with considerable generality by a number of biogeographers, of which some notable examples are mammals (see Simpson, 1980) and fishes (Miller, 1966; Myers, 1966).

Most of the organisms analyzed exhibit marked asymmetry of successful dispersal from north to south versus south to north. There is not a consistent directional pattern. It is probable that comparative life history patterns, functional roles in the community and general competitive positions need analysis for each group.

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