Ephemeroptera and the great American interchange

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Abstract. The Panamerican Ephemeroptera fauna is evaluated with respect to the interchange of generic lineages and species between the Americas, and comparisons are drawn with classical studies of the American interchange based on other biota. Cladistic, distributional, and behavioral data are presented or reviewed that support the following hypotheses and conclusions: The Central American corridor has strongly favored northward dispersal, with 29 of 85 potential South American donor genera having infiltrated Central America, and 21 of those having further penetrated Nearctic North America. Only 10 of 63 potential North American donor genera have dispersed into Central America, and of those only *Cercobrachys, Choroterpes, Epeorus,* and *Hexagenia* have broached the Central American corridor. Only 8 species among the genera *Campylocia, Cloeodes, Euthyplocia, Guajirolus, Hexagenia, Mayobaetis,* and *Tortopus* co-occur in South and Central America. All belong to South American lineages, and 5 are large, relatively strong flying ephemeroid mayflies—the 3 belonging to *Euthyplocia* and *Hexagenia* having further penetrated North America. Species range extensions between North and Central American are less restricted, with 34 species of genera of South American origin and 9 species of genera of North American origin co-occurring in the continental Neotropics ("Central America") and Nearctic region ("North America") of the Northern Hemisphere. Late Neogene and Holocene dispersal can account for most infiltration of Central America as well as interchanges across the corridor. Bi-directional dispersal is evident in *Caenis* and *Hexagenia.* Vicariance has evidently affected the Panamerican distribution of *Hexagenia* and *Homoeoneuria.* Mid-Tertiary or earlier southward and more recent northward dispersal of *Hexagenia* is consistent with the distribution and phylogeny of the genus. A relatively early northward dispersal of *Homoeoneuria* is suggested by the presence of a distinct lineage in South America and the Holarctic sister relationship of *Homoeoneuria* and *Oligoneurisca.* Distributional pattern analysis predicts that the widespread Panamerican genus *Callibaetis* is of South American origin.

Key words: American interchange, Ephemeroptera, biogeography, dispersal, Central American corridor, Panamerican faunistics.

The Central American land bridge and its function as a historical dispersal route for terrestrial and freshwater biota between South America and Central-North America (as elucidated foremost by the paleontological mammal studies of Simpson [e.g., 1940, 1965]) have become standard textbook examples illustrating biotic interchange between major land masses and biogeographic phenomena such as corridors and filters (see also McKenna 1973). The interchange of biota via this corridor is often referred to as the "great American interchange". The present Isthmus of Panama land bridge was evidently formed during the Pliocene, 5.7 million years ago (mya) (e.g., Raven and Axelrod 1974), although some geologists give a date closer to 3.5 mya (e.g., Stanley 1989). Earlier linkages, probably incomplete, between the southern and northern American land masses, however, were apparently also present in the Mid Tertiary and Early Cretaceous (e.g., Rosen 1975, Stehli and Webb 1985). Studies of this dynamic corridor have been centered mainly on vertebrates and flowering plants, with studies of freshwater benthos in this respect being very limited. Among pertinent insects studies, that of scarabaeine beetle biogeography by Halffter (1974) is 1 of the most notable.

Fauna and flora that have undergone detailed study with respect to the American interchange show asymmetry in that the predominant movement has been either southward or northward between the continents (e.g., see Stehli and Webb 1985, Vermeij 1991). The movements of some groups, such as mammal genera were mainly southward, whereas that of rainforest plants and birds has been mainly northward. The main purpose of this work is to address the great American interchange in terms of how a major group of freshwater benthic organisms—the Ephemeroptera, or mayflies—participated in this phenomenon. Moreover, present biogeographic data and conclusions are presented in such a way as to be informative to general bi-

ologists and benthologists who may be interest-
ed in comparing the historical spatial movement
of an important group of benthic organisms in
the Western Hemisphere with those of more
well-known groups of organisms that are com-
monly used to exemplify such dynamic biolog-
ical events.

The studies of Edmunds (1982) and Mc-
Cafferty et al. (1992), although far from treating
the entire fauna shared by the Nearctic and
Neotropical biogeographic regions, suggested
that the American interchange of Ephemerop-
tera lineages has had a northward bias, both in
terms of the number of lineages involved and
degree of penetration. The early hypotheses of
this asymmetry can only now be elaborated
with confidence because of the much more com-
plete data on Western Hemisphere Ephemerop-
tera that have recently become available (e.g.,
the documented mayfly fauna of Central Amer-
ica and Mexico has essentially doubled since
1992 to close to 200 species).

Published information on the Latin American
mayfly fauna has increased with the availability
of new collections, emphasis on biodiversity and
its description, and data from revisionary sys-
tematics of certain genera occurring in this area
(especially within the diverse families Baetidae
and Leptophlebiidae). These factors have al-
lowed the 1st comprehensive inventory of the
mayflies of Central America (McCafferty and
Lugo-Ortiz 1996a) and Mexico (McCafferty and
Lugo-Ortiz 1996b), and substantial modifica-
tions to Hubbard's (1982) list of South American
species. Furthermore, recent systematic studies
of several baetid lineages (e.g., Lugo-Ortiz and
McCafferty 1995, 1996a, 1996d) and leptophle-
biid lineages (e.g., Pescador and Peters 1987,
Flowers and Domínguez 1991, Wang and
McCafferty 1996) in the tropical and subtropical
Neotropics suggest that the fauna is, to a large
degree, insular, having evolved in South Amer-
ica since that continent's geographic isolation
from other Gondwanan land masses, especially
Africa. Demonstration of significant extinction
of Ephemeroptera, including entire families and
subfamilies, in South America by the end of the
Cretaceous, as shown by the fossil studies of
McCafferty (1990), lends additional credence to
this generality.

Previous analyses of Nearctic-Neotropical
mayfly distributions treated at least in part by
Allen and Brusca (1973), Edmunds et al. (1976),

Edmunds (1982), Peters (1988), and Allen (1990)
were, to various degrees, anecdotal. The histor-
ical biogeography of the Mesoamerican Ephem-
eroptera fauna was analyzed by McCafferty et
al. (1992) based on available data, including cla-
distic data associated with distribution, and in
lieu of compelling data of that type, secondary
lines of evidence were used as will be explained
below. Data were prioritized for drawing bio-
geographic inferences and thus followed a hi-
erarchical methodological approach (Myers and
Giller 1988).

Methods

Various methods and philosophies have been
used for inferring historical biogeography that
has resulted in the present distributions of ex-
tant biota, and thus the methods alluded to
above and incorporated in the study of Pan-
american mayflies must be explained. Mc-
Cafferty et al. (1992) indicated that the major
biogeographic question about Panamerican
mayflies was whether a genus was of recent Ne-
arctic or Neotropical affinity. That question,
which certainly addresses the American inter-
change and the subject of this study, itself in-
vokes assumptions of dispersal (spread) rather
than vicariance (splitting of former widespread
distributions). I maintain that explanatory bio-
geography (see Patterson 1983) that assumes
dispersal-driven processes to explain Panamer-
ican pattern is appropriate given the over-
whelming data showing the Central American
corridor/Mexican transition zone as a repetitive
north–south dispersal corridor for general Ne-
arctic and Neotropical biota (Stehli and Webb
1985). The classical examples of the great Amer-
ican interchange mentioned above as well as in-
sects (e.g., Halffter 1976) support this conclu-
sion. In fact, Noonan (1988) went so far as to
state that methods of vicariance-oriented ex-
planatory biogeography were inadequate with
respect to historical biogeography of insects (in-
cluding stoneflies) in the area of interchange.
Because North and South America are connect-
ed and have been for some appreciable geolog-
ical time, vicariance is not an a priori assump-
tion in the analysis of interchange of Panamer-
ican mayfly genera. This study therefore does
not rely on vicariance methods, as have been
promoted by Rosen (1975, 1978) and many oth-
ers. Although vicariance methods have been ap-

plied in studies of mayfly groups found in both Western and Eastern Hemispheres and affected by continental drift (whether primarily Southern Hemisphere [e.g., Edmunds 1975] or Northern Hemisphere [e.g., Bae and McCafferty 1991]), dispersal has been shown to be the primary mechanism for recent Transamerican interchange in Western Hemisphere biota and the mechanism is not expected to differ in Ephemeroptera.

Vicariance methods are generally used in most current studies where, for example, biota are found on continents separated as a result of continental drift. As such, area-cladograms (essentially phylogenetic trees overlaid with distributions of all the lineages, or taxa, being compared) are an essential tool for inferring vicariant historical biogeography. This is because branching of lineages can often be expected to parallel the splitting of distributional ranges, such as the break up of major land masses in the case of terrestrial biota (e.g., see Nelson and Platnick 1981). The exact same kind of data, however, can also be a powerful deductive tool in the analysis of historical biogeography when dispersal is the primary causative factor of present distributions, as explained by Ross (1974). Thus, the 1st line of evidence in McCafferty et al. (1992) and herein for hypothesizing whether the recent center of origin of a Panamerican mayfly genus was in North or South America involves area-cladograms of mayfly taxa as can be produced from published hypothesized cladistic studies and reported distributions. As Ross (1974) showed, by tracing the ancestry of lineages in a family tree back to more removed divergences (more ancestral branchings), a reasonable distributional ancestry may be hypothesized. A simplistic example of how this works can be seen in 3 closely related genera A, B, and C, where A and B represent the most recently derived pair and whose common stem diverged earlier from the line leading to C. If A is distributed in both North and South America and we wish to ascertain whether it was originally in North or South America, we can examine the distribution of its relatives. If its sister genus B is found only in South America, there is some probability that the common ancestor to both genera originated in South America. If genus C is also found in South America the probability becomes even stronger for the South America origin of A, and if the ancestry can be further

traced to South America or the general Southern Hemisphere (Gondwanaland), the hypothesis grows even stronger.

To a certain degree, a component of so-called Hennigian biogeography is inherent in the tracing of geographic ancestry as reasoned above. That component is the assumption that more primitive species will generally be found nearer the recent center of origin of the genus and the more derived species will be found more peripherally, as advocated, for example, by Brundin (1966). McAllister et al. (1986) tested this Hennigian assumption with 173 species and 34 genera of the fish family Cyprinidae in North America and found that on a continental-wide basis the Hennigian hypothesis generally held up. It does not hold up, however, on a more regional basis. It would appear to be of value when generic inter-relations of a Panamerican genus are inclonclusive but when species of that genus are demonstrably more ancestral or derived in either North or South America.

Despite the general assumption of dispersal to explain present distributions of Panamerican biota, including mayfly genera, large-scale vicariance cannot be disregarded as a possibly viable component of North and South American relationships when it is suggested from available cladistic data. Again, an illustration of this can be given by using a simplistic model of area-cladogram data, where genera A, B, and C are related as given above, but A is found in North and South America, B is North American and C is Holarctic (general Northern Hemisphere). This arrangement strongly suggests a North American origin of the Panamerican genus A. In this case, however, further examination of cladistic data indicates that genus A consists of 2 cladistic subgroups of species, 1 of which is Nearctic and 1 of which is Neotropical. The subgroup distribution suggests that these 2 subgroups possibly evolved as a result of a geographic vicariant event such as the separation of North and South America. Such would be possible if the original migration to South America of genus A had occurred at a time previous to 1 of the paleogeographically demonstrable breaks between North and South America. Such data also allow additional hypotheses regarding the relative age of such groups, since the separation and joining times are generally known.

There remain cases in certain families of mayflies where cladistic relationships have not been

resolved or even hypothesized. In these cases, secondary lines of evidence must be used to infer whether a Panamerican genus has a recent North or South American center of dispersal. Details of such cases can be found in McCafferty et al. (1992); they consist of several lines of reasoning that can be briefly reviewed here. Edmunds and Edmunds (1980) and Edmunds (1982) indicated that certain behavioral traits were generally associated with tropical mayflies. For example, late-night emergence and swarming is most common in the tropics. This type of behavior, when found in north-temperate regions, may indicate the retention of a trait in a genus evolved in the tropics. One adaptation of tropical groups to cold winters associated with severe seasonality of north-temperate regions is to shorten the entire postembryonic life (length of time spent in the larval and alate stages) for the relatively short, warm growing season and to prolong the overwintering period in the egg stage. McCafferty et al. (1992) found that most Panamerican genera that could be hypothesized from cladistic data to be South American in origin were primarily or exclusively found in the lowlands of North America (arid northern Mexico and the southwestern USA). Thus, this pattern can suggest a South American center of dispersal for certain Panamerican genera when other data for them are not available. On the other hand, cladistic analysis has indicated that Panamerican genera that are distributed in mountain ranges of western North America include lineages that have infiltrated the Neotropics via highland and cooler water habitats (McCafferty et al. 1992). Finally, numbers of species of Panamerican genera in Neotropical vs. Nearctic areas may be suggestive. The assumption is that, if the dispersal has been recent, more species will be found in the continent of origin. I refer to this assumption simply as distributional data, but without accompanying cladistic data, it certainly is not foolproof. In most cases when cladistic data are also known the assumption is validated, but there are considerable exceptions. In addition, distribution data alone can be limited by the fact that our knowledge of the species-level fauna in South America is still fragmentary.

Because dispersal mechanisms are fundamental to this study, what exactly are the mechanisms? Relative vagility (ability to disperse) of mayflies was discussed in detail by McCafferty

et al. (1992; see also Ross et al. 1967, Scudder 1979, Flannagan and Flannagan 1982). Briefly, the rate of mayfly dispersal is limited in the aquatic larval stage by drainage systems, and in the alate stages by generally short lives and relatively weak flying ability of gravid females. A range of vagility is apparent and is a function of both power of flight and fitness for colonizing new or unstable habitats, for example, either as a function of dispersal vs maintenance phenotypes (see e.g., Bush 1975, Bruton 1989) or alternative reproductive or life-history strategies (see e.g., Edmunds et al. 1976, McCafferty and Morihara 1979, Gray 1981, Edmunds 1982, McCafferty et al. 1992, Nolte et al. 1996). Past dispersal of mayflies at the species level is reflected by both wide-ranging species resulting from diffusion dispersal (range expansions of individual species; Edmunds 1982, McCafferty 1985) and geographically radiating species diversity resulting from secular migration (dispersal of a lineage via expansion and the division of ranges of species leading to the process of geographic speciation; Mason 1954). The latter type of dispersal or spread over time thus results from series of vicariant events on a small scale. Secular migration as such clouds some of the traditional arguments between dispersal and vicariance biogeography, particularly if the argument assumes they are mutually exclusive. Obviously, diffusion dispersal at some point always precedes vicariance, and small vicariance (geographic speciation) contributes to dispersal via secular migration.

Below, data for each mayfly genus are reviewed alphabetically under **Panamerican mayfly fauna**. Phylogenetic trees or cladograms of taxa, which are prima-facie evidence for conclusions concerning historical biogeography, whether involving dispersal or vicariance, are reviewed briefly, and although not pictorially duplicated, appropriate references are given to those papers in which they have appeared. Species accounting for North America is based in part on McCafferty (1996). Mexico east of the Isthmus of Tehuantepec is considered Neotropical, and therefore the mayfly fauna known from the far southern Mexican states of Campeche, Chiapas, and Tabasco are included with the Central American fauna. The functional demarcation of "Central America" from the northern Isthmus of Tehuantepec to the eastern border of the southern Isthmus of Panama is used in this

study, and "North America" does not include the southern Mexican states mentioned above. Concluding generalizations regarding faunal interchange via the Central American land bridge and broad relationships of the Americas that may now be induced from the entire data set are discussed under the section **Patterns and interchange of the American fauna**.

Panamerican mayfly fauna

Baetidae

Americabaetis Kluge.—This genus (=*Acerpenna* Waltz and McCafferty in part, see Lugo-Ortiz and McCafferty [1997a]) is Neotropical, except that the species *A. pleturus* (Lugo-Ortiz and McCafferty) is known from both Central America and Northern Mexico. Besides 2 species known from Central America (Lugo-Ortiz and McCafferty 1994), 4 species are now known from South America (Lugo-Ortiz and McCafferty 1997a). No species are known to co-occur in both Central and South America. The plesiotypic nature of South American species suggests a South American origin of this genus (Lugo-Ortiz and McCafferty 1997a).

Apobaetis Day.—Historically this genus has been known only from 2 species in North America. It is now known to be a Panamerican genus based on the recent discovery of a species in South America by Lugo-Ortiz and McCafferty (1997b). Those authors hypothesized a South American origin for *Apobaetis* based on cladistic evidence. Although there are no species presently known from Central America, it is highly likely that the genus eventually will be confirmed from there.

Baetis Leach.—Although 14 nominal South American species are currently classified in the genus *Baetis* , exhaustive examination of materials from South America by C. R. Lugo-Ortiz (Purdue University, personal communication) has revealed that true *Baetis* is not represented in South America and that those species have been incorrectly assigned. Two species of *Baetis* are known from Central America, and 36 species are known from Nearctic North America. *Baetis flavistriga* McDunnough and *B. magnus* McCafferty and Waltz co-occur in Central America and North America. *Baetis* essentially is Arctogaean (world continent = Holarctic + Oriental + Afrotropical), and the Central Amer-

ican representatives of this genus clearly appear to be of North American origin. *Baetis notos* Allen and Murvosh and *B. tricaudatus* Dodds have reached southern Mexico but have not yet broached the Isthmus of Tehuantepec.

Baetodes Needham and Murphy.—Thirteen species of this strictly Panamerican genus are known from South America, 9 species are known from Central America, and 15 species are known from North America. No species are known to co-occur in Central and South America. Although I collected numerous *Baetodes* from Colombia, and Rojas de Hernández et al. (1995) reported unnamed species from there, these species are yet to be identified and described, and no reports of nominal species from Colombia exist. Three species co-occur in Central and North America (Table 1). The North American fauna ranges through Mexico and southwestern USA, and the genus is hypothesized to be of South American origin based on both distributional data (McCafferty et al. 1992) and cladistic relationships of the genus (Lugo-Ortiz and McCafferty 1996a).

Callibaetis Eaton.—Fifteen species of this strictly Panamerican genus are known from South America, 4 species are known from Central America, and 11 species occur in North America. No species are known to co-occur in Central and South America. No nominal species have as yet been reported for either Panama or Colombia. Three species co-occur in Central America and North America (Table 1). No hypothesis as to the origin of *Callibaetis* was given by McCafferty et al. (1992) because species cladistics are unknown and the genus is diverse in both South and North America. However, if one now considers that no Panamerican genera of Neotropical origin are Palearctic in distribution, and nearly all Panamerican genera of recent Nearctic origin are more widespread (i.e., Holarctic and often Arctogaean), then *Callibaetis* would certainly fit the predominant pattern of the Panamerican genera of Neotropical origin. Thus, I deduce a Neotropical origin for *Callibaetis*.

Camelobaetidius Demoulin.—Seven species are known from South America, 3 species are known from Central America, and 7 species occur in North America. No species are known to co-occur in Central and South America. Although no nominal species are known from Colombia, Rojas de Hernández et al. (1995) have reported unnamed species. Three species co-oc-

TABLE 1. Mayfly species co-occurring in the Americas. Records from Chiapas and Tabasco states, Mexico, are assigned to Central America.

Central and South America		
Campylocia anceps	*Mayobaetis ellenae*	*Hexagenia mexicana*
Cloeodes redactus	*Guajirolus ektrapeloglossa*	*Tortopus unguiculatus*
Euthyplocia hecuba	*Hexagenia albivitta*	

Central and North America		
Americabaetis pleturus	*Cloeodes excogitatus*	*Leptohyphes lestes*
Baetis flavistriga	*Epeorus metlacensis*	*Leptohyphes lumas*
Baetis magnus	*Euthyplocia hecuba*	*Leptohyphes packeri*
Baetodes deficiens	*Fallceon quilleri*	*Moribaetis macaferti*
Baetodes fuscipes	*Farrodes texanus*	*Neochoroterpes oklahoma*
Baetodes tritus	*Hexagenia albivitta*	*Paracloeodes minutus*
Caenis bajaensis	*Hexagenia mexicana*	*Rhithrogena notialis*
Caenis diminuta	*Hydrosmilodon primanus*	*Stenonema mexicanum*
Caenis latipennis	*Isonychia sicca*	*Thraulodes brunneus*
Callibaetis floridanus	*Lachlania iops*	*Thraulodes speciosus*
Callibaetis montanus	*Leptohyphes brunneus*	*Thraulodes zonalis*
Callibaetis pictus	*Leptohyphes castaneus*	*Traverella albertana*
Camelobaetidius mexicanus	*Leptohyphes ferruginus*	*Traverella longifrons*
Camelobaetidius musseri	*Leptohyphes hispidus*	*Traverella promifrons*
Camelobaetidius warreni		

cur in Central America and Nearctic North America (Table 1). All except 1 North American species are western and arid-favored and therefore the genus is most probably of Neotropical origin (McCafferty et al. 1992).

Cloeodes Traver.—Seven species are known from South America, 2 species are known from Central America, and 3 species are known from southwestern North America. One species, *C. redactus* Waltz and McCafferty is common to South America (Peru [Waltz and McCafferty 1987]) and Central America (Honduras [McCafferty and Lugo-Ortiz 1996a]), and *C. excogitatus* Waltz and McCafferty co-occurs in Central America and Nearctic North America. *Cloeodes* is now known to be Pantropical (Waltz and McCafferty 1994). As pointed out by McCafferty et al. (1992), South America evidently represents the recent center of dispersal in the Western Hemisphere.

Fallceon Waltz and McCafferty.—This genus is known only from North America and Mesoamerica (both Central America and the Antilles). Two species are known from Central America, and 3 species are known from North America. *Fallceon quilleri* (Dodds) co-occurs in Central America and North America. The distribution of this genus, as it is currently defined (Lugo-Ortiz et al. 1994), is unique. All other Panamerican genera under consideration reflect 1 of the 2 general distributional patterns mentioned under *Callibaetis*, above. The anomalous distribution of *Fallceon* and lack of any definitive phyletic data make any hypothesis of the geographic origin of the genus somewhat speculative. Although it is restricted in its Northern Hemisphere distribution, which otherwise is consistent with a South American origin, it is not known from South America. This apparent absence, however, may be an artifact of collecting because much of tropical South America remains to be sampled for Ephemeroptera. There is also the possibility that it originated in Central America or the Greater Antilles (Lugo-Ortiz et al. 1994). Because of the uncertainties remaining about this genus, a hypothesis of a South American origin at this time is based on suggestive distributional data along with the assumption that the genus will be found in South America.

Guajirolus Flowers.—This genus is entirely Neotropical. Two species are known from Central America, 1 of which (*G. ektrapeloglossa* Flowers) is also known from South America (Panama and Colombia, respectively [Flowers 1985]). The possibility of a relationship with the Afrotropical genus *Pseudopannota* Waltz and McCafferty (Lugo-Ortiz and McCafferty, unpublished data)

would suggest a Gondwanan origin, and therefore a northern dispersal into Central America.

Mayobaetis Waltz and McCafferty.—Cladistic data of Lugo-Ortiz and McCafferty (1996a) showed *Mayobaetis* to be a genus distinct from *Moribaetis* Waltz and McCafferty, under which it was originally classified as a subgenus (Waltz and McCafferty 1985). The only described species of this Neotropical genus, *M. ellenae* (Mayo), is known from both Central and South America (Costa Rica, Ecuador, and Peru [Waltz and McCafferty 1985]). The basal cladistic position of this genus relative to *Baetodes* and *Prebaetodes* Lugo-Ortiz and McCafferty, both of which originated in South America, clearly suggests a South American origin.

Moribaetis Waltz and McCafferty.—As now delimited (Lugo-Ortiz and McCafferty 1996a), this genus is essentially Central American with 1 of its 3 species, *M. macaferti* Waltz, extending into extreme southern Mexico as far as Veracruz and Puebla (technically North America) (Lugo-Ortiz and McCafferty 1996e), and thus it should be listed with other Panamerican genera. Although the genus eventually may be found in South America, the false report of its presence there by Lugo-Ortiz and McCafferty (1996a) was inadvertent. It is not known whether the *Moribaetis* from Colombia cited by Rojas de Hernández et al. (1995) applies to *Mayobaetis* or *Moribaetis*. From the plesiotypic position of this genus relative to *Baetodes* complex lineages of South American origin (Lugo- Ortiz and McCafferty 1996a), the genus would also have originated in South America.

Paracloeodes Day.—Four species were recently described from South America by Lugo-Ortiz and McCafferty (1996c), and 1 species, *P. minutus* (Daggy), is known from both Central America and North America. No species co-occur in Central and South America. Cladistic data suggest a South American origin (Lugo-Ortiz and McCafferty 1996c).

Additional considerations.—Nine South American species are currently listed in the genus *Pseudocloeon* Klapálek, and many North American species were originally classified in *Pseudocloeon* but have since been recombined (see McCafferty and Waltz 1990). True *Pseudocloeon* apparently is restricted to the Orient. The correct recombinations for the South American species still assigned to *Pseudocloeon* and *Baetis* are currently being researched.

Caenidae

Caenis Stephens.—Fifteen species are known from South America, 3 species are known from Central America (McCafferty and Lugo-Ortiz 1992, 1996a, Lugo-Ortiz and McCafferty 1996e), and 8 species are known from North America. No species are known to be common to Central and South America, but 3 species co-occur in Central America and North America (Table 1). *Caenis* is a cosmopolitan genus of considerable antiquity, possibly of Pangaean origin. All of the North American *Caenis*, except *C. bajaensis*, represent Holarctic lineages (Provonsha 1990). The aforementioned species, however, apparently belongs to a South American lineage (P. Malzacher, Ludwigsburg, Germany and A. V. Provonsha, Purdue University, personal communication). The Central American fauna, therefore, is represented by elements (*C. diminuta* Walker and *C. latipennis* Banks) of 1 of the North American lineages and, concurrently, *C. bajaensis*, which is representative of a South American lineage. Only the South American lineage has thus far broached the Central-South American boundary. Such bi-directional dispersal involving northern and southern lineages suggests that *Caenis* was well established in both North and South America prior to the Tertiary, which in turn lends additional support to the assumed antiquity of the genus.

Cercobrachys Soldán.—Two nominal species are known from South America, and 2 are known from North America. An unnamed species of this genus has been seen in Panama by R. W. Flowers (Florida A & M University, personal communication). No species are known to co-occur in any of the Americas. Soldán (1986) reported this genus from the Holarctic, Oriental, and Neotropical regions. This distribution pattern, and the boreal Holarctic distribution of the closely related genus *Brachycercus* Curtis, led McCafferty et al. (1992) to hypothesize a Nearctic center of dispersal for the Western Hemisphere component of *Cercobrachys*. The known penetration of South America is somewhat shallow, including only Colombia and Peru.

Additional considerations.—The species *Brachycercus tenella* (Navás) is known from adults only from Argentina. Otherwise, *Brachycercus* is a Northern Hemisphere genus. The genus is evidently not Panamerican as once thought, and I agree with the suggestion of Thew (1960) that

the generic assignment of *B. tenella* is incorrect and remains to be resolved.

Ephemeridae

Hexagenia Walsh.—Three species are known from South America, 2 species are known from Central America, and 7 species are known from North America. *Hexagenia albivitta* (Walker) and *H. mexicana* Eaton co-occur in Central America and South America. The former is widespread in tropical and subtropical South America, and the latter is known from Colombia, Ecuador, and Peru. Both of these species are also known from Nearctic regions of southern Mexico, and they therefore represent 2 of the 3 mayfly species known from both North and South America. Based on phyletic data presented by McCafferty (1979), *Hexagenia* is hypothesized to have a Nearctic or Holarctic center of origin. If this is the case, then it is an exceptional example of deep penetration into the Neotropics from the north. The South-Central American lineage constitutes the subgenus *Pseudeatonica* Spieth, which evidently evolved from colonizing *Hexagenia* that became isolated in South America (McCafferty et al. 1992). A hypothesized relatively early penetration of South America could have taken place via a possible Mid-Tertiary archipelago or land bridge (Stehli and Webb 1985) or even earlier via a Proto-Antilles archipelago during the Early Cretaceous (Malfait and Dinkleman 1972). Such an initial penetration and subsequent vicariance may be explained by 1) the relatively high vagility demonstrated by these large and strong-flying mayflies, and 2) the substantial period of isolation of the 2 continental land masses from the time of disruption of the initially used land bridge and establishment of subsequent land bridges, the most recent formed in the Pliocene. This explanation also presumes a recent invasion of Central America and Nearctic southern Mexico by the subgenus *Pseudeatonica* from a South American center of dispersal. The Nearctic species *H. bilineata* (Say) and *H. limbata* (Serville) of the subgenus *Hexagenia* s.s. have also recently dispersed southward into southern Mexico, but have not yet broached the Isthmus of Tehuantepec.

Heptageniidae

Epeorus Eaton.—One unnamed species of *Epeorus* has recently been found in Colombia by M. Zuñiga del Cardoso and her colleagues (C. R. Lugo-Ortiz, Purdue University, J. Alba-Tercedor, University of Granada, Spain, personal communication), 2 species are known from Central America, and 20 species occur in North America. No species are known to co-occur in Central and South America; however, the Colombian species may eventually prove to be *E. packeri* Allen and Cohen, which is known as far south as Panama in Central America (Allen and Cohen 1977). One species co-occurs in Central and North America (Table 1). Although there is minor representation in Central and South America, *Epeorus* is essentially a Holarctic and Oriental genus. Dispersal from the Nearctic along mountain corridors clearly appears to be the explanation for its presence in Central and South America.

Rhithrogena Eaton.—No species are known from South America, 1 species is known from Central America, and 23 species occur in North America. *Rhithrogena notialis* Allen and Cohen is known only from tropical southern Mexico and Central America, and thus technically co-occurs in Central and North America although it does not cross biogeographic regions. This genus is clearly of Holarctic origin, and McCafferty et al. (1992) hypothesized that it dispersed southward via mountain corridors in western North America.

Stenonema Traver.—No species are known from South America, 1 species is known from Central America, and 18 species are known from North America. *Stenonema mexicanum* (Ulmer) co-occurs in Central and North America. Bednarik and McCafferty (1979) showed *Stenonema* to be of North American origin, and McCafferty et al. (1992) postulated that *S. mexicanum* dispersed southward from east-central North America via the Gulf of Mexico maritime corridor lowlands.

Additional considerations.—All assignments of mayflies to the family Heptageniidae in South America, other than to *Epeorus* in Colombia, are insupportable at this time. The family, therefore, should continue to be considered essentially Arctogaean, despite the fact that there has been a minor recent invasion of the Neotropics by the *Epeorus, Rhithrogena,* and *Stenonema* lineages, and a further shallow invasion of South America by *Epeorus.* The North American genera *Leucrocuta* Flowers and *Nixe* Flowers were considered by McCafferty et al. (1992) to be recent invaders

of the Neotropics from the north. The extensive work of Lugo-Ortiz and McCafferty on the Mesoamerican fauna, however, has not confirmed their presence in the Neotropics. *Nixe* is represented in southern Mexico by *N. bella* (Allen and Cohen), but the genus has not broached the Isthmus of Tehuantepec.

Isonychiidae

Isonychia Eaton.—No species are known from South America, 1 species is known from Central America, and 17 species are known from North America. *Isonychia sicca* (Walsh) co-occurs in Central and North America (see recent species synonymies by McCafferty 1996). Based on its Holarctic-Oriental distribution and basal phyletic position relative to Oligoneuriidae (McCafferty (1991a), *Isonychia* appears to be a Laurasian remnant of an old lineage with a recent North American center of dispersal in the Western Hemisphere.

Leptohyphidae

Haplohyphes Allen.—Three species are known from South America (Argentina and Peru), 2 species are known from Central America (Costa Rica), and no species are known from North America. No species are known to co-occur in Central and South America, although I collected *Haplohyphes* larvae from central Colombia that may prove to be the larvae of *H. mithras* (Traver), which is presently known only from adults from Costa Rica (Traver 1958). Distributional pattern alone suggests that this genus has recently spread northward into Central America from South America, and I expect that future cladistic studies will show that the Central American species are relatively derived within this Neotropical lineage.

Leptohyphes Eaton.—Thirty-four species are known from South America, 18 species are known from Central America, and 25 species are known from North America. No species are known to co-occur in Central and South America, but 7 species co-occur in Central and North America (Table 1). The fauna of this species-rich genus is arid-favored in north-temperate regions and the genus clearly appears to be Neotropical in origin, most likely South American (McCafferty et al. 1992).

Tricorythodes Ulmer.—Nine species are known

from South America, 2 species are known from Central America, and 19 species are known from North America. No species are known to co-occur in any of these areas. This strictly Panamerican genus was inferred by Edmunds (1982) to have a Neotropical, probably South American, origin. Although the genus is generally distributed and most radiated in the Nearctic, species there demonstrate a presumably plesiotypic nocturnal flight periodicity typical of lowland tropical mayflies (Edmunds and Edmunds 1980). Furthermore, recent phyletic studies by T. -Q. Wang (University of Missouri) and McCafferty (unpublished data) clearly show Leptohyphidae and closely related families to be of Gondwanan origin.

Leptophlebiidae

Atopophlebia Flowers.—Three species are known from South America, 1 species is known from Central America, and no species are known from North America. No species co-occur in Central and South America. This strictly Neotropical genus is a sister group to the *Thraulodes* complex, according to Flowers (1987), and it most probably is of South American origin.

Choroterpes Eaton.—One unnamed species is known from South America (Colombia [Peters 1988]), 1 species is currently authenticated from Central America (Chiapas, Mexico), and 5 species are known from North America. Three nominal species of this problematic genus that have been recorded for Central America proper and 1 nominal species recorded for South America are, according to Peters (1988), not assigned correctly and are all to be recombined with other leptophlebiid genera. Lugo-Ortiz and McCafferty (1996b), however, recently described *C. ungulus*, as cited above for Central America. The species appears related to Nearctic *Choroterpes*. The systematics of *Choroterpes* remains dubious. Except for the remote possibility that the North and South American elements of *Choroterpes* represent ancient and separate lineages within the genus, as is the case for *Caenis*, it seems reasonable to hypothesize that a single Panamerican *Choroterpes* lineage has a most recent center of dispersal in North America. This hypothesis is based on distributional data alone, particularly the number and distribution of species in North America and a shallow South American representation apparently limited to Colombia, which

is a pattern similar to other Panamerican genera of recent northern origin.

Farrodes Peters.—Presently 7 species are known from South America, 4 species are known from Central America, and 1 species is known from North America. No species are known to co-occur in Central and South America, but *F. texanus* Davis ranges from Guatemala (McCafferty and Lugo-Ortiz 1996a) through Mexico (Lugo-Ortiz and McCafferty 1996e) to southern Texas. The origin of the genus is apparently South American (Domínguez and Savage 1987), and the genus is currently undergoing a considerable revision (Domínguez et al. 1996), with additional species shortly to be described from Mexico, and Central and South America by Domínguez.

Hagenulopsis Ulmer.—Two species are known from South America, 2 species have recently been described from Central America (Lugo-Ortiz and McCafferty 1996b), and no species are known from North America. No species are known to co-occur in Central and South America. Although it may be assumed that the origin of this strictly Neotropical genus is South American, confirmation by cladistic data is needed.

Hydrosmilodon Flowers and Domínguez.— Flowers and Domínguez (1992) described *H. saltensis* from Argentina but also noted that there may be additional species from Peru and Brazil. *Hydrosmilodon primanus* (Eaton) occurs in North America (southern Nearctic Mexico) as well as Central America. No species are known to co-occur in Central and South America. The close relationship of this genus with the South American *Needhamella* Domínguez and Flowers (Flowers and Domínguez 1992) suggests a South American origin.

Neochoroterpes Allen.—No species are known from South America, 1 species is known from Central America (Chiapas, Mexico), and 3 species are known from North America. *Neochoroterpes oklahoma* (Traver) was recently discovered in Neotropical far-southern Mexico by Lugo-Ortiz and McCafferty (1996e) and thus represents the single co-occurrence of a species of this group in Central and North America. Based on the distribution of this genus and phylogeny of its respective species (Henry 1993, 1995), it appears to have originated recently in southwestern North America. *Neochoroterpes* apparently represents an apotypic branch of a few species derived from within *Choroterpes* (not at the base

of *Choroterpes*). Therefore, *Neochoroterpes*, even as a subgenus as originally conceived by Allen (1974), makes *Choroterpes* s.s., by definition, a paraphyletic grouping.

Terpides Demoulin.—Two species are known from South America, 2 species are known from Central America, and no species are known from North America. No species are known to co-occur in Central and South America. The known South American fauna consists of *T. guyanensis* Demoulin from Surinam and an unnamed species found in Ecuador by C. R. Lugo-Ortiz (Purdue University, personal communication). The basal position of the lineage in the cladogram of related genera given by Flowers and Domínguez (1991) suggests a relatively old South American origin.

Thraulodes Ulmer.—Twenty-three species are known from South America, 16 species are known from Central America (including Chiapas, Mexico), and 7 species are known from Nearctic North America. No species are known to co-occur in Central and South America; however, Traver and Edmunds (1967) suggested that *T. ephippiatus* Traver and Edmunds, from Chiapas, may be the same as *T. colombiae* (Walker), from Colombia. Three species co-occur in Central and North America (Table 1). Peters (1988) stated that he had unpublished phylogenetic data indicating a South American origin for the genus, and McCafferty et al. (1992) hypothesized a Neotropical recent center of dispersal for this Panamerican genus based on distribution patterns.

Traverella Edmunds.—Four species are known from South America, 5 species are known from Central America, and 5 species are known from Nearctic North America. No species co-occur in Central and South America, but 3 species co-occur in Central and North America (Table 1). There can be little doubt that this group's primary affinities are Neotropical. Peters (1988) stated that the genus arose in South America, and McCafferty et al. (1992) reviewed both distributional and behavioral data that support such a hypothesis.

Ulmeritoides Traver.—Two species of this strictly Neotropical genus are known from Central America, and 7 species are known from South America. No species are known to be common to both areas. The phylogeny of *Ulmeritoides* and its cognates, as hypothesized by

Domínguez (1995), suggests a South American origin of the genus.

Additional considerations.—A reference to *Ulmeritus* in Panama by Flowers (1991) is evidently referable to *Ulmeritoides*. Treatments of certain Central American mayflies by Edmunds et al. (1976), under the generic names *Hermanella* Needham and Murphy, *Hermanellopsis* Demoulin, and *Homothraulus* Demoulin, were based on preliminary information and are now recognized to be incorrect.

Oligoneuriidae

Homoeoneuria Eaton.—One species is known from South America, 1 other species is known from Central America, and 5 species are known from North America. No species are known to co-occur in any of the Americas. Although this Panamerican lineage is apparently most diverse in North America (possibly only because adequate collections have not been made from sandy bottomed rivers in South America), the phylogenetic data presented by Pescador and Peters (1980) indicate a South American origin. Different lines of evidence indicate that the northern dispersal of *Homoeoneuria* may have been relatively early, compared with most such dispersals considered here: Pescador and Peters (1980) placed South American *Homoeoneuria* in a separate subgenus *Notochora* Pescador and Peters. Those 2 daughter lineages, therefore, may have evolved as a consequence of vicariance of the 2 major land masses after Mid-Tertiary dispersal or possibly Early Cretaceous dispersal because the family was already established throughout Gondwana (based on the known Pantropical distribution of the family, South American fossil data from the Early Cretaceous, and phyletic relationships of the subfamilies [McCafferty 1990]). Also, Edmunds (1979) indicated that *Homoeoneuria* was a sister lineage of the Palearctic genus *Oligoneurisca* Lestage. This relationship suggests that northward dispersal was early enough to have allowed additional spread in the Holarctic prior to the evolution of Nearctic and Palearctic sister genera via continental vicariance. If this indeed is the correct sequence of phyletic and biogeographic events, then the current classification of *Homoeoneuria* into South and North-Central American subgenera is paraphyletic, and, as McCafferty et al. (1992) suggested, full generic status of the South

American subgenus *Notochora* is warranted. There is no current evidence that either the *Homoeoneuria* s.s. or *Notochora* lineages have crossed the Central American-South American boundary in recent times. The relatively plesiotypic phyletic position hypothesized for the Central American species *H. salviniae* Eaton by Pescador and Peters (1980) suggests that it is representative of the early northward dispersal, rather than representing a more recent subsequent dispersal from the north.

Lachlania Hagen.—Five species are known from South America, 4 species are known from Central America, and 3 species are known from North America. No species co-occur in Central and South America, but 1 species co-occurs in Central and North America (Table 1). Edmunds et al. (1976) indicated that *Lachlania* develops as a short summer annual in north-temperate areas of North America, spending most of the year in the egg stage. Because this life-history feature is believed to be a phenological adaptation of a tropical lineage to a temperate regime (Edmunds 1982), McCafferty et al. (1992) hypothesized a South American center of dispersal for the genus. The fact that the family Oligoneuriidae is mainly Pantropical supports a South American origin.

Polymitarcyidae

Campsurus Eaton.—Forty-three species are known from South America, 2 species are known from Central America, and 2 species are known from North America. No species co-occur in Central and South America, and 1 species co-occurs in Central and North America (Table 1). Although species cladistics are unknown for the group, distributional data alone allowed McCafferty et al. (1992) to infer a South American origin for the genus. The species taxonomy of *Campsurus* in the Neotropics is poorly known and may preclude the accurate recognition of many species. If these mayflies follow the trend exhibited by other large burrowing mayflies, I would expect 1 or more species eventually to be found to co-occur in Central and South America.

Campylocia Needham and Murphy.—Three species are known from South America, 1 species is known from Central America, and no species are known from North America. One widespread South American species, *C. anceps*

(Eaton), is common to Central and South America. Cladistic relationships of the subfamily Euthyplociinae (to which *Campylocia* belongs), as indicated in both the interpretation of McCafferty (1991b) and Bae and McCafferty (1995), suggest a Gondwanan origin. It follows, therefore, that Panamerican dispersal of *Campylocia* was from South America to Central America.

Euthyplocia Eaton.—Two species are known from South America, 1 species is known from Central America, and 1 species occurs in North America. *Euthyplocia hecuba* (Hagen) co-occurs in Central and South America. For the same reasons as stated above for *Campylocia*, a dispersal of *Euthyplocia* from South America to Central America is hypothesized. *Euthyplocia hecuba* has penetrated as far north as Veracruz, and therefore is 1 of 3 mayfly species that occur in both South and North America.

Tortopus Needham and Murphy.—Eight species are known from South America, 2 species are known from Central America, and 3 species are known from North America. One species, *T. unguiculatus* (Ulmer), is widespread in Central America and is also known from Colombia, but no species co-occur in Central and North America. McCafferty et al. (1992) hypothesized a South American origin of *Tortopus* based on its sister relationship with *Campsurus*. The eastern North American distribution of *Tortopus* (excluding eastern mountain regions), which is somewhat atypical of North American genera of Neotropical origin (McCafferty et al. 1992), may be a function of relatively early lowland dispersal via the Gulf of Mexico maritime corridor. If *Tortopus* mayflies are relatively good dispersers, however, dispersal from the Neotropics could have been relatively recent.

Patterns and interchange of the American fauna

Overall mayfly faunal similarity between the Americas can be visualized from Venn diagrams of family and generic distribution as shown in Fig. 1, where the exclusive distributions of the 25 families and 148 genera that are known from the study area are indicated . (Genera that have been reported from South America in older literature but that cannot be confirmed are not included in the South American count [Fig. 1B].) No families are known exclusively from Central America, but the 8 families occur-
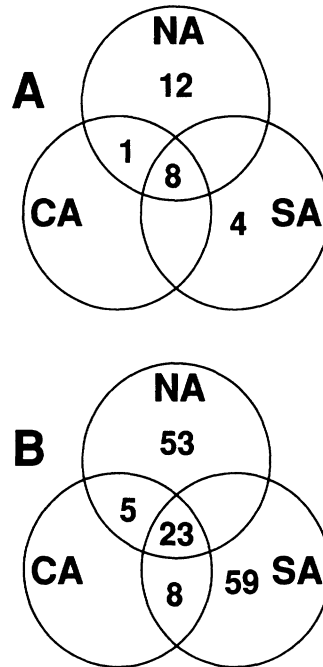

FIG. 1. Venn diagrams of distribution of Ephemeroptera taxa in North America (NA), Central America (CA), and South America (SA) and any combinations of the Americas. A.—Distribution of 25 families. B.—Distribution of 148 genera.

ring in all 3 areas and the 1 found in North and Central America (Fig. 1A) are those that were treated in detail above. Those families known only from either North or South America are temperate-adapted groups. In South America, they include the Amphinotic families Ameletopsidae, Coloburiscidae, Nesameletidae, and Oniscigastridae. These families are found in south-temperate Chile and Argentina and have Transantarctic affinities (i. e., they are also found in Australia and New Zealand). Families found in North America but nowhere else in the Western Hemisphere include Acanthametropodidae, Ameletidae, Ametropodidae, Arthropleidae, Baetiscidae, Behningiidae, Ephemerellidae, Metretopodidae, Neoephemeridae, Potamanthidae, Pseudironidae, and Siphlonuridae. Note that those families that are confined either to North or South America in the Western Hemisphere, with the exception of Ephemerellidae and Siphlonuridae, consist of only 1 or 2 genera in those areas. The considerably greater diversity of non-Panamerican families in North America vs non-Panamerican families in South American may

reflect 1) the long period available for faunal interchange among the Arctogaean land masses since the Cretaceous while South America was isolated, 2) possibly less catastrophic extinction events in Laurasia having occurred by the end of the Cretaceous than were experienced in Gondwana (McCafferty 1991b), and 3) little success of mayflies in southward dispersal (because of limited opportunity or difficulty adapting to tropical environs, as discussed below).

Figure 1B illustrates the distribution of the 148 Panamerican genera in the Americas; however, genera exclusive to the Antilles are not represented. The diversity of genera in South America largely reflects the considerable insular evolution that has occurred on that continent over a prolonged period of isolation, and the resulting generally large degree of endemicity (58 known endemic mayfly genera) associated with the biota of South America. South America is 2nd only to Australia in degree of endemicity of vertebrate groups (e.g., Cox and Moore 1973). The diversity of North American mayfly genera is not greatly influenced by endemicity (only 28 endemic genera), but rather reflects the considerable number of Holarctic and Arctogaean genera present in North America.

Species of Ephemeroptera that are shared by the Americas are itemized in Table 1, where it can be seen that 8 species co-occur in Central and South America, 43 species co-occur in Central and North America, and only 3 species are known from all 3 areas. The species similarity data, alone, suggest a much stronger local interrelationship between Central and North America than Central and South America. Apparently, dispersal across the Isthmus of Tehuantepec has been more amenable to diffusion dispersal (spread via species range extension not accompanied by speciation), while the Isthmus of Panama has acted more as an intermittent barrier, with dispersals across it often accompanied by more geographic speciation. Thus, secular migration has been a common mode of crossing the South and Central American boundary, as reflected by the low relative number of species overlapping in Central and South America.

Numbers of taxa shown in Fig. 1 can also be used to generate coefficients of similarity between the Americas. By using Sorensen's coefficient of similarity (= $2a/[2a + b + c]$, where a = taxa in common between 2 areas, b = taxa exclusive to 1 area, and c = taxa exclusive to the other area), the similarity of South and Central America based on family taxa occurrences is 0.76 (1.00 = the maximum similarity possible), the similarity between North and Central America is 0.60, and the similarity between South and North America is 0.48. Based on genus occurrences, the similarity both between South and Central America and between North and Central America is 0.51, and that between South and North America is 0.29. The numbers suggest that Central America is truly a bridge between the 2 main continental areas, being about equally influenced at the generic level by North and South America. Species are not compared by coefficients because the Latin American species fauna remains so poorly described.

Historical dispersal can be taken as the general basis of the similarities shown above and in Fig. 1; however, I reiterate that historical dispersal does not preclude consideration of the interplay of broad-scale vicariance where appropriate. Table 2 itemizes all of the data and hypotheses reviewed or presented herein with respect to dispersal directionality and lineage origin of the Panamerican Ephemeroptera genera. Twenty-nine genera are hypothesized to have dispersed from South America to Central America, and 21 of those are shown to have penetrated even deeper into Nearctic North America. Only 10 genera are hypothesized to have dispersed from North America to Central America, and only 4 of those have broached the Central American corridor and entered South America. The difference between the northward and southward dispersals is considerable and demonstrates a strong bias to northward dispersal. This dramatic asymmetry is depicted in Fig. 2. Potential donor genera in South America include the hypothetically occurring genera *Fallceon* and *Moribaetis* (see discussions of those genera, above).

All species common to both Central and South America (Table 1) belong to lineages hypothesized to be of South American origin (Table 2). The presence of the same species in both areas suggests very recent dispersal. *Guajirolus* and *Mayobaetis* are genera that may be limited in distribution to the approximate adjoining areas of Central and South America. *Campylocia, Euthyplocia, Hexagenia,* and *Tortopus* are genera of burrowing mayflies that are all relatively large-bodied, strong-flying forms with comparatively widespread species. Relatively high vagility in

TABLE 2. Mayfly lineage interchange between South America, Central America (including Chiapas and Tabasco, Mexico), and North America. [ ] = nominal species not yet confirmed in Central America. *Caenis* and *Hexagenia* show bi-directional movement by different lineages within them.

South America to Central America	South America to North America
Americabaetis	Americabaetis
[Apobaetis]	Apobaetis
Baetodes	Baetodes
Caenis	Caenis
Callibaetis	Callibaetis
Camelobaetidius	Camelobaetidius
Campsurus	Campsurus
Campylocia	
Cloeodes	Cloeodes
Euthyplocia	Euthyplocia
Fallceon	Fallceon
Farrodes	Farrodes
Guajirolus	
Hagenulopsis	
Haplohyphes	
Hexagenia (Pseudeatonica)	Hexagenia (Pseudeatonica)
Homoeoneuria	Homoeoneuria
Hydrosmilodon	
Lachlania	Lachlania
Leptohyphes	Leptohyphes
Mayobaetis	
Moribaetis	Moribaetis
Paracloeodes	Paracloeodes
Terpides	
Thraulodes	Thraulodes
Tortopus	Tortopus
Traverella	Traverella
Tricorythodes	Tricorythodes
Ulmeritoides	

North America to Central America	North America to South America
Baetis	
Caenis	
[Cercobrachys]	Cercobrachys
Choroterpes	Choroterpes
Epeorus	Epeorus
Hexagenia (ancestral)	Hexagenia (ancestral)
Isonychia	
Neochoroterpes	
Rhithrogena	
Stenonema	

terms of range expansion is most evident in the species *E. hecuba, H. albivitta,* and *H. mexicana,* and these are the species that co-occur in South and North America. Of the species that co-occur in Central and North America, 34 belong to genera of hypothesized South American origin, and only 9 belong to genera of hypothesized North American origin. Among those Nearctic lineages that have penetrated into Central America (Table 2), it is almost always the same species that represents the occurrence in both areas: *Baetis flavistriga, B. magnus, Caenis diminuta, C. latipennis, Isonychia sicca, Epeorus metlacensis, Rhithrogena notialis,* and *Stenonema mexicanum.* These species ranges are thought to be the result of relatively recent diffusion dispersal via the Mexican transition zone (e.g., Noonan 1988).

The pattern of biotic interchange through a corridor, once a former barrier has been removed, is often highly asymmetrical (Vermeij 1991). Recent Panamerican interchange of savannah-adapted mammals and mountain plants was mainly southward; however, dispersal of rainforest mammals, birds, and plants was mainly northward (e.g., Simpson 1940, Gentry 1982, Marshall et al. 1982, Stehli and Webb 1985). Overall, during the Pleistocene, 11% of the North American mammal genera invaded South America, but only 2% of the South American genera invaded North America. Although the Panamerican interchange of Ephemeroptera genera may not have been exclusively Pleistocene, a comparison of percentages is instructive. In contrast to mammals, 25% of the potential donor genera of South America mayflies dispersed to North America, and only 6% of the potential donor genera of North America dispersed to South America. Halffter (1974) found a similar northward bias for the scarab beetles.

Causal biogeography of Panamerican mayflies should include an attempt to explain the observed interchange asymmetry. I doubt there is a simple explanation for this asymmetry because so many paleogeographic, paleoecological, and biotic factors could have contributed to the observed pattern. Pattern analysis of mayflies compared with that of some other biota, however, may offer pertinent clues. Mayfly lineages that have moved south from the Nearctic (see above) are mainly highland, or mountain adapted, with *Stenonema mexicanum* being an example of the few obvious exceptions (McCafferty et al. 1992). This mainly southward
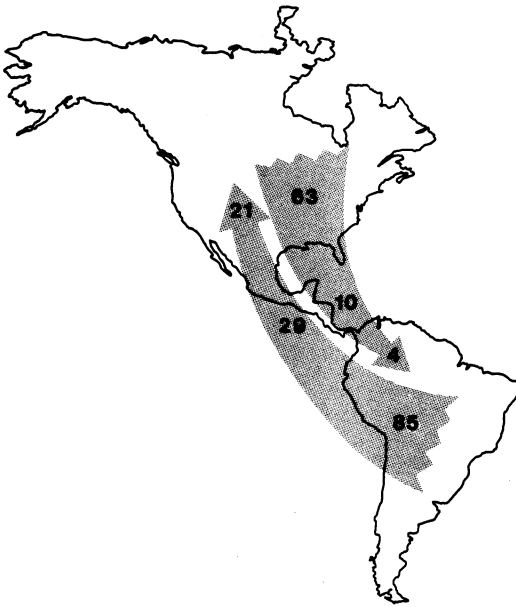
FIG. 2. North, Central, and South America showing the directions and relative degree of dispersal of Ephemeroptera genera between regions. The number of potential donor genera is indicated at the base of arrows in North and South America; numbers within the arrows adjacent to Central America are the number of the respective donor genera that have reached Central America; and numbers in the tip of the arrows are the number of the respective donor genera that have reached South or North America.

movement via highlands may suggest some general (but not universal) inherent difficulty in the adaptation of temperate biota to tropical environs. This difficulty can also be seen in the southward dispersal of entomofauna in general (Halffter 1987), and in plants that are largely limited to mountain corridors, as cited above. Nonetheless, historical circumstances may have played another primary role in the asymmetry. Given Neogene orogenesis (mountain building) and the cyclic disturbances of pluvial and xeric periods in western and southwestern North America during the Pleistocene (e.g., Stanley 1989), the number of mayflies actually available, or poised, for possible dispersal southward when there was a land bridge present in Central America may have been severely limited. Smith (1981) postulated a high probability of extinction of fishes and other aquatic biota and depressed rates of dispersal because of barriers and long-term instability of aquatic habitats in western North America during the Pleistocene. With respect to stoneflies, only a relatively small number are thought to have dispersed southward in the past 1,800,000 y (Sargent et al. 1991, Baumann and Kondratieff 1996).

Circumstances for austral donor lineages would have been considerably different from that hypothesized for Nearctic donor lineages. Mayfly lineages dispersing northward are of tropical or subtropical origin and evidently have largely dispersed along lowland routes into North America. There are exceptions such as *Baetodes*, which may have evolved in the Andes and is often associated with moderate- to high-gradient streams (Lugo-Ortiz and McCafferty 1996a). A considerable period of time since the formation of the Isthmus of Panama land bridge has been available for dispersal into Central America by South American mayfly lineages, as is demonstrated by the predominant northward directionality observed for rainforest biota cited above. During the Pleistocene cycles of disturbance, many South American lineages may already have been poised in Central America for further dispersal into North America. In the wake of retreating ice in the east and the end of cyclic pluvial and xeric periods and associated dispersal barriers in the west, a stabilizing North America may have been especially amenable to colonization from invading austral mayfly lineages that have been variously able to adapt to temperate seasonality. Vermeij (1991), for example, has argued that disturbance or local extinctions cause areas to be highly suceptible to invasion immediately thereafter, whereas the presence of a well-established community of incumbent species in the recipient area has an inhibitory effect on potential invasion.

Most of the Panamerican interchanges that are apparent from known extant taxa of mayflies probably occurred relatively recently, since the Pliocene formation of the Isthmus of Panama land bridge. Significant evidence for this conclusion involves: 1) the overlap of species in different regions of the Americas, 2) shallow penetrations of genera invading South America from the north, and 3) the fact that none of the Neotropical derived lineages in North America are found in regions outside of North America in the Northern Hemisphere. Furthermore, generally, Panamerican generic lineages do not require earlier scenarios to explain their intraspecific relationships or present distributional pat-

terns. There are, however, apparent notable exceptions to this generality. Some dispersal of *Hexagenia* and *Homoeoneuria* may have occurred via the Mid-Tertiary Central American land bridge or archipelago, or even less possibly via the Early Cretaceous Proto-Antilles archipelago. These genera, unlike any of the other genera involved in the interchange, appear to have evolved into major daughter lineages possibly coinciding with vicariance between the 2 major land masses. In the case of *Hexagenia*, this evolution most likely followed an initial dispersal to South America from the north—possibly Mid Tertiary—then isolation of the land masses and faunas, and vicariant evolution of lineages now recognized as separate subgenera. When the land masses were once again united in the Pliocene, a northward dispersal of what had evolved into the subgenus *Pseudeatonica* would account for its presence today in Central America. In the case of *Homoeoneuria*, a northern dispersal would have been followed by a vicariant event between North and South America early enough to have allowed additional spread of the northern lineage and subsequent evolution of it into the sister genera *Homoeoneuria* and *Oligoneurisca* in the Nearctic and Palearctic, respectively. *Cloeodes* is a Pantropical genus that evidently was present generally in Gondwana. The age of this genus alone and the fact that it survived the theorized mass extinction by the end of the Cretaceous would make it a candidate for possible early dispersal, but such early dispersal to Central and North America is not apparent from present data.

One possible measure of the relative success at dispersal among the several North American generic lineages of South American origin can be gleaned from the data summarized in Table 3. Ten of these 21 austral lineages have not dispersed beyond southwestern North America (= beyond the Middle America + Southwest areas of McCafferty and Waltz [1990]; regional distributions of each North American species are given by McCafferty [http://www.entm.purdue.edu/entomology/mayfly/contents.html]). This pattern perhaps indicates a very recent invasion or poor ability to adapt to north-temperate conditions. As also can be seen from Table 3, those genera that have more than ½ their North American species distributed beyond southwestern North America may represent relatively old invasions; however, only in the case of *Homoeoneu-*

TABLE 3. The relative northern dispersal of Nearctic North American (NA) genera of South American origin. Only sublineages of South American origin are represented for *Caenis* and *Hexagenia*.

Genus	No. of NA spp	No. of NA spp beyond south-western NA	% NA spp beyond south-western NA
Americabaetis	1	0	0
Apobaetis	2	2	100
Baetodes	15	0	0
Caenis	1	0	0
Callibaetis	11	9	81
Camelobaetidius	7	2	29
Campsurus	1	0	0
Cloeodes	3	0	0
Euthyplocia	1	0	0
Fallceon	3	1	33
Farrodes	1	0	0
Hexagenia	2	0	0
Homoeoneuria	5	4	80
Lachlania	3	1	33
Leptohyphes	25	2	8
Moribaetis	1	0	0
Paracloeodes	1	1	100
Thraulodes	7	0	0
Tortopus	3	2	67
Traverella	5	2	40
Tricorythodes	19	10	53

ria, as discussed above, is there strong evidence from phyletic information of an older invasion. Still, the other austral lineages could be relative early invaders within the time frame of the recent 6,000,000-y land bridge. The fact that *Tricorythodes* is both widespread and species rich in North America suggests a relatively high rate of vagility that is associated with a relatively high rate of speciation. Relatively high vagility in *Callibaetis* may also be partly related to rate of speciation; however, the vagility of *Callibaetis* is also related to its propensity to colonize unstable habitats, as discussed by McCafferty et al. (1992). *Tortopus* mayflies, found throughout much of lowland eastern North America, are evidently good dispersers, as mentioned previously, but are limited in the larval stage to submergent clay banks of warm-water streams and rivers.

Transamerican dispersal of Panamerican mayfly genera has apparently been unidirec-

tional, except with respect to 2 genera. The present distribution and phyletic relationships of *Hexagenia,* explained above, are consistent with bi-directional dispersal at different times. The phyletic relationships and distributions within the Western Hemisphere components of the cosmopolitan genus *Caenis* may also be explained by bi-directional dispersal in the Americas. *Caenis* apparently is old enough to have participated in both southward and northward dispersal concurrently. Recent dispersals in the genus are seen by the southern lineage represented by 1 species in the Nearctic, and by 1 of the 2 Holarctic lineages in North America represented by 2 species in the Neotropics. The theorized antiquity of *Caenis* (possibly of Pangaean origin) is suggested by its phyletic position (Wang and McCafferty, unpublished data) and its widespread world distribution, in light of an indication from the Panamerican data that *Caenis* mayflies are not especially good dispersers.

One final notable and useful generality that has resulted from this study is that Panamerican lineages of Ephemeroptera originating in South America have world distributions limited to North America in the Northern Hemisphere, i.e., they are not Palearctic (e.g., *Tortopus, Tricorythodes*), and besides being Neotropical, a few also are Gondwanan or Pantropical (e.g., *Cloeodes*). Those Panamerican lineages that colonized the Neotropics from North America show a variety of distribution patterns, such as Nearctic (e.g., *Stenonema*), Holarctic + Oriental (e.g., *Cercobrachys, Epeorus*), and Arctogaean (e.g., *Baetis*); and with the possible exception of *Hexagenia,* all those that have penetrated South America (Table 2) are distributed beyond the Western Hemisphere. These general world patterns of Panamerican genera served as a predictor for the hypothesis that the species-rich and widespread Panamerican genus *Callibaetis* has a South American, rather than North American, origin.

Acknowledgements

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