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● Biodiversity and Biogeography :
Examples from Global Studies of Ephemeroptera

W.P. McCafferty

(Department of Entomology, Purdue University)

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Examples from Global Studies of Ephemeroptera

W. P. McCafferty

Department of Entomology, Purdue University, West Lafayette, Indiana 47907, U.S.A

ABSTRACT : Biodiversity involves documentation of biota (especially species), of biotic distribution, and of biotic habitats. Pathways for the analysis of such data involve cladistic studies and ecological studies, both of which lead to a necessary understanding of biogeography, or why species or other taxa are where they are today on earth. Biogeography ultimately allows species risk assessment and informed practices of conservation and monitoring of biota and habitats. Examples of biodiversity research and its relationship to biogeography are taken from recent studies of Ephemeroptera, especially in Latin America, Africa, and Madagascar. The power of cladistic analysis for discerning both vicariant and dispersalist biogeography is demonstrated. The origins of exemplary taxa correspond to the breakup of Pangaea, of West Gondwana, of Transantarctica, and of the Afrotropics. Asymmetrical dispersal between regions is apparent among Panamerican and Australasian taxa. Patterns of distribution, phylogenetic relationships, and geotectonic history allow estimates of time and place of origin for many families. North and south temperate restricted families, Laurasian families that are not temperate restricted, Gondwanan families (both Pantropical, and hemisphere restricted), Arctogaeon families, and Pangaeon families are reviewed. Some families appear to be isolated relicts in the wake of the K-T extinctions. Many temperate families are evidently unable to colonize tropical regions. Recent glacial cycles were most decimating

to mayflies in the Palearctic, resulting in a currently greater Nearctic diversity. Data from mayflies suggest that Madagascar has a closer affinity with Africa than it does with India.

As endangerment to species and their habitats increases, both in underdeveloped countries where expanses are often being destroyed at alarming rates, and in industrialized countries where pollution and alterations continue to degrade the environment, the need to discover and describe the earth's still unknown biota is more urgent than ever. Only through such research will our knowledge of biodiversity be sufficient enough for us to determine fully why biota occur where they do. In return, this biogeographic understanding will allow mankind to develop strategies to preserve and monitor earth's biota and habitats. Simply stated, without knowing species makeup and why species are where they are, environmental managers cannot devise sound policies for safeguarding life and the environment, and life forms, including ourselves, will be doomed to suffer the consequences.

The relationships of biodiversity and conservation are shown in the flow chart in Figure 1. Note the critical pathways for developing a knowledge of biogeography from biodiversity by the analysis of biodiversity data both systematically and ecologically. Note also the essential key that biogeography holds for the development of conservation practices.

Biodiversity

Today, knowledge of biodiversity, along with our limited conservation laws and practices, are largely based on terrestrial vertebrates and flowering plants. Even so, it is the insects that constitute more diverse and often more essential roles in terrestrial ecosystems (e.g., Wilson 1992).

Thus, there have been more recent emphases given to the biodiversity of insects, especially the larger orders (e.g., Samways 1994). If we consider that freshwater systems are critical subsets of terrestrial ecosystems, and particularly if we consider our indispensable reliance on freshwater as a fundamental natural resource, then the smaller, aquatic insect orders, such as Ephemeroptera, are obviously of special importance. Although the documentation of aquatic insects has generally lagged behind that of the larger orders (Allan and Flecker 1993), concerted research efforts are now in place to document certain aquatic insect groups as part of understanding and protecting their freshwater habitats.

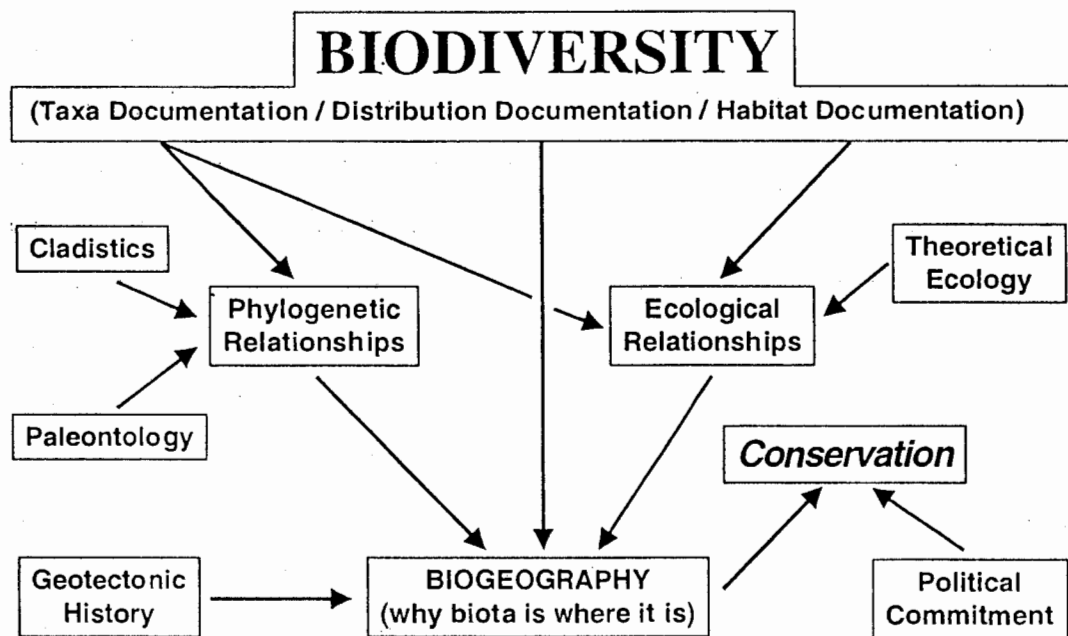


Fig. 1. Relationships of biodiversity, biogeography, and conservation.

Such efforts often falter because of lack of adequate research support or the lack of adequate systematic expertise; however, our research team at Purdue University is giving documentation of the global biodiversity of the Ephemeroptera high priority. Based on our own field work and the acquisition of several important international collections, one of the largest, if not the largest, holding of mayflies now resides at Purdue University. In addition to our discoveries and descriptions of new genera and species in the Southern Hemisphere, we have also received major funding from the National Science Foundation to take biodiversity of Ephemeroptera of North America to an advanced level. This involves the development a computerized database of distributional information associated with the approximately 700 species known from the North American continent. Such data will contribute to risk assessments of species and their habitats.

Other geographic areas we have given considerable attention to have included some of the so-called world hot spots currently undergoing rapid degradation (Myers 1990), in particular, Latin America, Madagascar, and Africa. With respect to Mexico and Central America, for example, the number of mayfly species known from there has more than doubled in the past decade (e.g., McCafferty and Lugo-Ortiz 1996a,b). In the past five years, 17 new genera from South America were described, and several other described genera previously unknown from there were found. In that same time span, another 21 genera from the Afrotropics were described, while several others were reported and revised. These discoveries were reviewed in part by Lugo - Ortiz and McCafferty (1999). The over 200 new species that have been described in the past 15 years are significant because the order had been previously known from only about 2000 species worldwide.

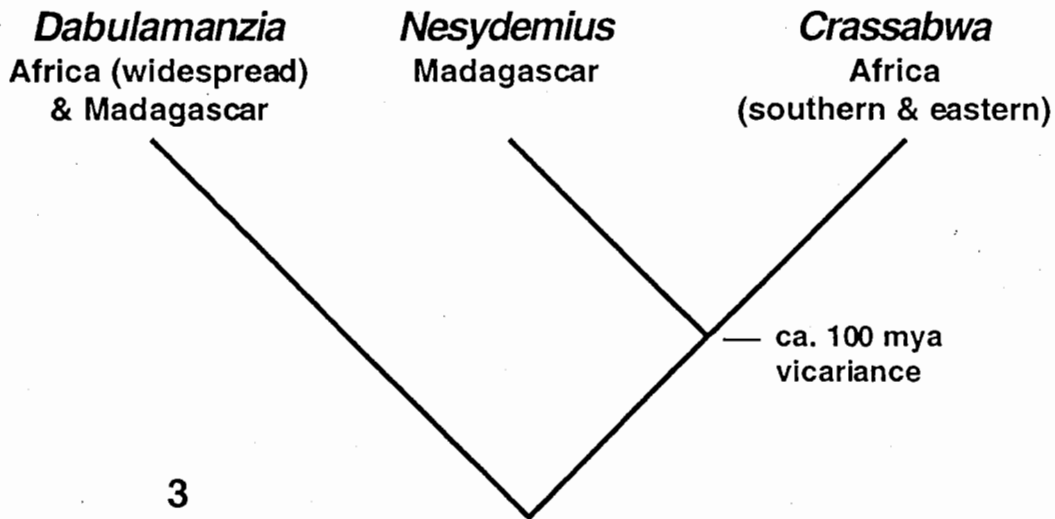
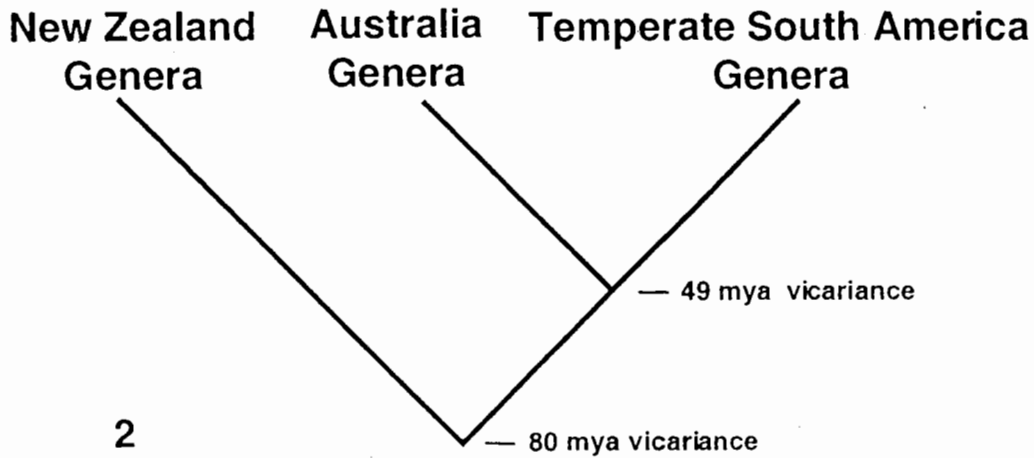
Such discoveries in several instances have allowed elaboration of phylogenetic relationships and biogeography for some taxa that otherwise would have been impossible. For example, the genus *Cloeodes* Traver of the small minnow mayfly family Baetidae had been known from the Neotropics, southwestern North America, and the Oriental region. This enigmatic distribution pattern led to the speculation by our research team that the genus was perhaps Pantropical in distribution. This was subsequently confirmed by more recent discoveries of the genus in Africa, Madagascar, Australia, and throughout Southeast Asia (Waltz and McCafferty 1994, Lugo-Ortiz and McCafferty 1998a, Lugo-Ortiz et al. 1999). We now believe *Cloeodes* perhaps to be the oldest extant small minnow mayfly genus because of what is obviously a Gondwanan pattern at least 135 million years old and possibly as much as 200 million years old. I have recently reported a baetid fossil from Lebanese amber (McCafferty 1997) that dates to the Lower Cretaceous from between 120 and 140 mya (million years ago). The fossil may well be *Cloeodes*, and if so, would add paleontological support for the age hypothesized for this genus.

Historical Biogeography

Biotic lineages become distributed into geographic ranges by dispersal (spreading of ranges) or by a combination of dispersal followed by vicariance (splitting of ranges). Old terrestrial distribution patterns are often related to vicariance, especially continental drift or the splitting of once continuous landmasses, for example, by inundation of seas. Distributional patterns resulting from the connections of landmasses are often due to dispersal.

A classical case of vicariant biogeography in Ephemeroptera involves four strictly Amphinotic families (Edmunds 1975). These families each have one or two genera in temperate South America (southern Chile and Patagonia), one genus in temperate Australia, and one genus in New Zealand. From such a distribution pattern, it may be assumed that each of these families was present in the ancient landmass of Transantarctica, which included Australia, New Zealand, and Antarctica connected to the southern tip of South America. Transantarctica was a distinct landmass about 100 mya (for most dates cited herein, see e.g., Pielou 1979). When the genera of these families undergo cladistic analysis, they each yield the exact same area cladogram (Fig. 2). The first dichotomy among these families involves the New Zealand lineage diverging from that of Australia + temperate South America. The second dichotomy is into an Australian lineage and South American lineage. This sequence matches perfectly the sequence of continental drift affecting these areas, which involved New Zealand splitting off from the rest of Antarctica about 80 mya, then subsequently Australia and South America separating from each other about 50 mya.

Studies of phylogenetic relationships among small minnow mayflies, family Baetidae, in the Afrotropics has revealed evolutionary origins corresponding to the vicariance of Africa and Madagascar. Such historical revelations would not have been possible without concerted biodiversity research on the Afrotropical fauna. One example involves the genera *Dabulamanzia* Lugo-Ortiz and McCafferty, *Crassabwa* Lugo-Ortiz and McCafferty, and *Nesydemius* Lugo-Ortiz and McCafferty. *Dabulamanzia* and *Crassabwa* were first discovered in Africa (Lugo-Ortiz and McCafferty 1996a,b) and later *Dabulamanzia* was discovered in Madagascar (Lugo-Ortiz



Figs. 2 and 3-2. Generic level area-cladogram for each of the Amphinotic families Ameletopsidae, Coloburiscidae, Nesameletidae, and Oniscigastridae. 3. Area-cladogram of the Afrotropical genera *Dabulamanzia*, *Nesydemius*, and *Crassabwa*.

and McCafferty 1997), as was *Nesydemius* (Lugo-Ortiz and McCafferty 1998b). The three genera together constitute a distinct monophyletic clade within a particular complex of related Southern Hemisphere genera. Cladistic analysis (Lugo-Ortiz and McCafferty 1998b) and a resultant area-cladogram shows that the clade was present ancestrally in both Madagascar and Africa (Fig. 3). *Dabulamanzia* is the most ancestral genus in the clade and is present throughout Africa and Madagascar. The dichotomy of the African *Crassabwa* and the Madagascar *Nesydemius* evidently corresponds to the split of Madagascar from east Africa, which may have begun as early as 160 mya, although the two areas may have remained in close proximity until the end of the Cretaceous, about 65 mya.

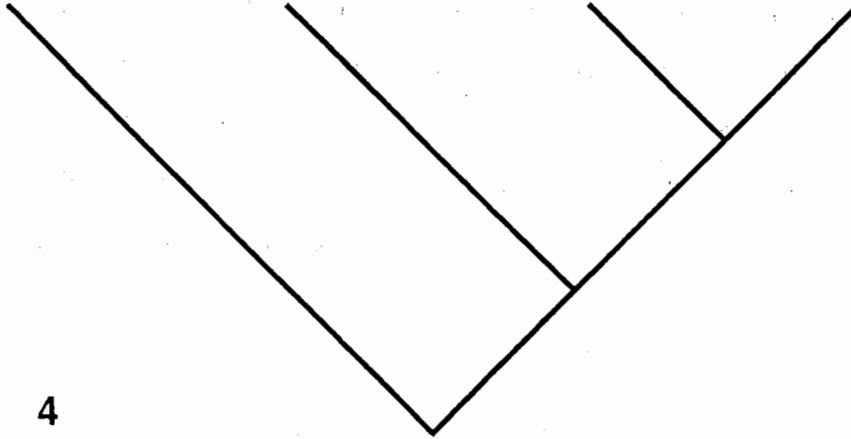
Research in general on the family Baetidae suggests that a much stronger faunal similarity exists between Madagascar and Africa than between Madagascar and India. This may be significant because there is some uncertainty as to the timing of the isolation of India and Madagascar. Some workers maintain that India split from Africa + Madagascar as early as 160 mya (e.g., see Pielou 1979), while others maintain that India and Madagascar remained together for another 100 million years after splitting off from Africa (e.g., see Brown and Lomolino 1998). Our data would favor the theory that India was well separated first and that Africa and Madagascar remained in proximity for some time. Both the relatively low number of shared mayfly genera between India and Madagascar and the relatively high number of shared mayfly genera between Africa and Madagascar support this hypothesis.

Examples of biogeographic patterns in mayflies that involve dispersal at the exclusion of vicariance involve almost all of the genera that are found in both North and South America, and almost all those that are

found in both northern Australia and Southeast Asia. Rather than splitting apart, these landmasses have recently been joined by bridges or archipelagos after having had a long history of separation. In the case of North and South America, significant connection began about six mya, but became very strong in the Pleistocene. In the case of Australia and Southeast Asia, stepping stones archipelagos have been available intermittently for the past 15 million years. Such connections lead to the spread of terrestrial biota.

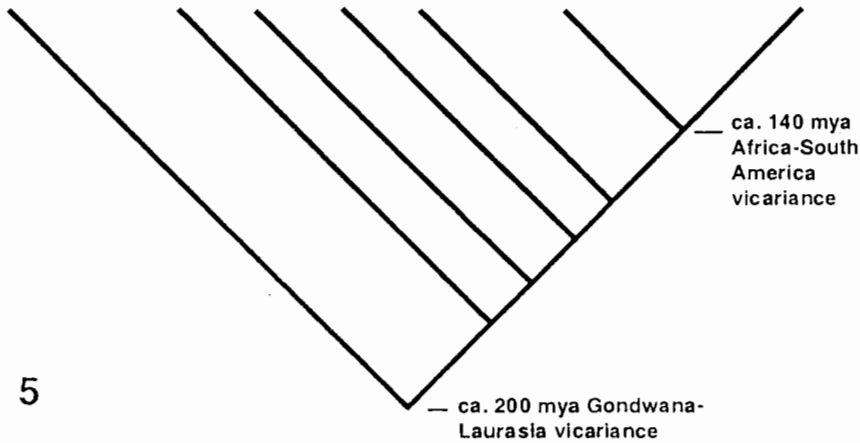
Just as it is with vicariance, cladistics can be a powerful tool in determining historical biogeography involving dispersal, especially for deducing the more subsequent areas of distribution (Ross 1974). For example, the Western Hemisphere small minnow mayfly genus *Baetodes* Needham and Murphy is known from 13 species in South America, nine species in Central America, and 15 species in North America. It can be assumed to have attained this range by recent dispersal because it is found nowhere else in the world. From the distribution pattern alone of this genus, it cannot be determined if it originated in North or South America. Also the genus is so morphologically unique that its relationships within the family Baetidae remained unknown until recent biodiversity research (Lugo-Ortiz and McCafferty 1996c) uncovered a new South American genus that was morphologically intermediate between *Baetodes* and two other Neotropical genera (*Mayobaetis* Waltz and McCafferty and *Moribaetis* Waltz and McCafferty). These four genera form a monophyletic group that can be analyzed using cladistics. Such an analysis (Lugo-Ortiz and McCafferty 1996c) showed that *Baetodes* was the most derived genus and that its ancestral relatives were Neotropical, not Nearctic (Fig. 4). Its origin thus could be deduced to be Neotropical, and that it subsequently dispersed northward and colonized North America.

Moribaetis Neotropical **Mayobaetis** Neotropical **Prebaetodes** Neotropical **Baetodes** Neotropical
Nearctic



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Ephemerellidae Holarctic
Oriental **Other Families** Afrotropical
Australia, Oriental **Tricorythidae** Afrotropical
Oriental **Leptohyphidae** South America
North America



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Figs. 4 and 5-4. Area-cladogram of the *Baetodes* complex genera. 5. Area-cladogram of the major lineages of the superfamily Ephemerelloidea.

This line of deductive reasoning from cladistic relationships and other evidence (McCafferty 1998) has indicated that of some 84 North American genera, 63 originated in the Northern Hemisphere, and of those, 10 have dispersed to Central America, but only four of those 10 have colonized South America. On the other hand, of some 89 genera in South America, 85 originated there or in the Southern Hemisphere. These would include such genera as *Cloeodes* and *Baetodes*, discussed previously. Of these 85 genera, 29 have dispersed into Central America and 21 of those have been able to colonize North America. This northward favored asymmetrical dispersal is similar to the dispersal that has been documented for rainforest birds and plants (see e.g., Stehli and Webb 1985). Most mammals and mountain plants, however, mainly dispersed southward from North America to South America (e.g., Simpson 1940). The theoretical ecological and historical biogeographic explanations that may explain the strong asymmetry of mayfly dispersal between these continents were discussed by McCafferty (1998).

Preliminary data on mayfly genera occurring in both Australia and Southeast Asia indicate that dispersal has been mainly from Southeast Asia south to Australia (e.g., Lugo-Ortiz and McCafferty 1999). It is notable that in North America, South America, and Australasia, temperate mayfly faunas have largely not dispersed into tropical areas, whereas adjacent tropical faunas have been much more prone to invade these temperate areas (see below).

Family Distribution Patterns

Work on mayfly world biodiversity and biogeography suggests a number of broad biogeographic patterns applicable at the family level.

These patterns begin to paint a picture of the history of this primitive order of insects on earth.

There are a number of temperate adapted families that are restricted either to the northern temperate region or the southern temperate region (Table 1). Among the northern families, the Baetiscidae and Pseudironidae are found in the Nearctic, but not in the Palearctic. There are also many more genera and species represented in the Nearctic than there are in the Palearctic in these and other Holarctic families. This appears to be related to differential extinction during the Pleistocene (e.g., Stanley 1989). It has been hypothesized that because mountain ranges tend to run north-south in the Nearctic, but often run east-west in much of the Palearctic, there were more southern migration routes available to biota, including mayflies, in the Nearctic in the face of advancing glaciers from the north. The east-west mountain chains of the Palearctic (see esp. Europe), on the other hand, apparently acted more like barriers for the cyclic migrations associated with the ice ages, and thereby promoted more extinction.

Among the south-temperate families (Table 1), four of them are those Amphinotic families previously discussed that are restricted to Australia, New Zealand, and south-temperate South America. The three other families are endemic to New Zealand. The latter would appear to be either relict groups that have differentially survived only in New Zealand or perhaps evolved in isolation there during the past 80 million years. In the case of Rallidentidae, there are related families in New Zealand, Australia, and temperate South America. In the case of Ichthybotidae, there are no related groups in New Zealand or any other Amphinotic regions, and thus the family is considered an isolated relict. The Siphlaenigmatidae is thought to be the sister group to the family Baetidae (see McCafferty and Edmunds

Table 1. Temperate restricted families of Ephemeroptera.

NORTHERN HEMISPHERE (Laurasian)	SOUTHERN HEMISPHERE (Gondwanan)
Acanthametropodidae	<u>Amphinotic</u>
Ameletidae	Ameletopsidae
Ametropodidae	Coloburiscidae
Baetiscidae	Nesameletidae
Behningiidae	Oniscigastridae
Metretopodidae	
Pseudironidae	<u>New Zealand Only</u>
Siphonuridae	Ichthybotidae
	Rallidentidae
	Siphlaenigmatidae

1979), which is not found in New Zealand (McCafferty 1999) but is otherwise worldwide and at least 135 million years old. These data suggest that Siphlaenigmatidae is also an isolated relict group.

Study of Lower Cretaceous fossils from Brazil (McCafferty 1990) revealed that there was indeed considerable family level extinction in the Southern Hemisphere by the end of the Cretaceous. Clearly, the mayflies were severely affected by the K-T mass extinctions, as were other biota (see, e.g., Raup 1991), and thus the K-T boundary is also the boundary between the ancient Ephemeroptera fauna and the modern Ephemeroptera fauna. Not only did several Mesozoic families and subfamilies disappear, either entirely or from the Southern Hemisphere, but Tertiary mayfly fossils are for the most part made up of extant genera, and Mesozoic fossils are made up of genera that are nearly all extinct.

There are no mayfly families endemic to either Australia or South America, although both regions show a high degree of endemism with respect to genera (e.g., Lugo-Ortiz and McCafferty 1999). The large Western Hemisphere family Leptohephidae, however, appears to have originated in tropical South America and has only recently colonized North America. Cladistic analysis of the pannota mayflies (McCafferty and Wang 1999), to which Leptohephidae belongs, indicates that the origin of Leptohephidae (and its sister group, the Tricorythidae) was associated with the vicariance of South America and Africa, beginning about 140 mya (Fig. 5). The age of the superfamily Ephemerelloidea, to which Leptohephidae belongs, can also be estimated to be perhaps 200 mya or more, based on the Gondwana-Laurasia vicariance corresponding to the first major phyletic dichotomy within the group (Fig. 5).

As shown in Table 2, several other families besides Leptohephidae and Tricorythidae are also Gondwanan and mainly tropical. Also shown in Table 2 are the Laurasian families that are not temperate restricted (i.e., they are also found in the Oriental region).

Finally, the large cosmopolitan families Baetidae, Leptophlebiidae, and Caenidae are apparently of Pangaeian origin (Table 3) and thus originated at least 200 mya. In terms of extant families, this leaves only the Heptageniidae, Oligoneuriidae, Ephemeridae, and Polymitarcyidae (also categorized in Table 3).

Heptageniidae and Ephemeridae show essentially an Arctogaeian distribution pattern (i.e., Holarctic + Oriental + Afrotropical), although the heptageniid genus *Epeorus* Eaton has colonized Colombia from the north, the ephemerid genus *Hexagenia* Walsh is well established in tropical South America, the heptageniid genus *Atopopus* Eaton has possibly colonized northern Australia from Southeast Asia (Wang and McCafferty 1995), and

Table 2. Gondwanan families of Ephemeroptera that are mainly tropical but not Pantropical, and Laurasian families of Ephemeroptera not restricted to temperate regions (Holarctic + Oriental).

GONDWANAN	LAURASIAN
Austremerellidae	Ephemerellidae
Ephemerythidae	Isonychiidae
Leptohyphidae	Neoephemeridae
Machadorythidae	Potamanthidae
Prosopistomatidae	
Teloganellidae	
Teloganodidae	
Tricorythidae	

the ephemerid genus *Plethogenesis* Ulmer is found in Papua New Guinea. Heptageniidae is likely of Laurasian origin, and its two Afrotropical represented genera, *Afronurus* Lestage and *Thalerosphyrus* Eaton, which are also found in the Orient, probably colonized Africa via the Orient. In the case of *Thalerosphyrus* this would have been early enough to have involved Madagascar, where that genus is also known (perhaps as much as 100 mya or more). In the case of *Afronurus*, a more recent tertiary dispersal could have been involved.

As for the family Ephemeridae, which has the two subfamilies Ephemerinae and Palingeniinae represented on Madagascar, it is more probable that its mainly Arctogaeen distribution pattern is the result of an early Pangaeen existence followed by differential extinction. This explanation is more attractive than the Laurasian origin theory because of the existence of Ephemeridae on Papua New Guinea, which appears more biogeographically

Table 3. Pangaeen, Arctogaeen, and Pantropical families of Ephemeroptera.

PANGAEAN	ARCTOGAEAN	PANTROPICAL
Baetidae	<u>Of Pangaeen Origin</u>	Oligoneuriidae
Caenidae	Ephemeridae	Polymitarcyidae
Leptophlebiidae		
	<u>Of Laurasian Origin</u>	
	Heptageniidae	

aligned with Australia than with Southeast Asia, the existence of the closely related family Ichthybotidae in New Zealand, and the prehistoric presence of the related fossil family Australiphemeridae from the Lower Cretaceous of South America.

Oligoneuriidae and Polymitarcyidae are mainly Pantropical groups, of at least Gondwanan origin, that have more recently invaded the Nearctic from the Neotropics, and the Palearctic from the Oriental region. These families are only absent from the south temperate regions, and both have been found in the Lower Cretaceous of South America (McCafferty 1990).

Epilogue

In the above, a philosophy is reviewed regarding biodiversity, the central role of biogeography in understanding biodiversity, and the incorporation of such data and analyses for developing sound conservation practices. The examples of biodiversity studies and biogeographic analyses based on mayflies represent a mere baseline, or starting point, of information, from which a new century of biodiversity research and application will continue and build. Such research will surely lead to a

fuller knowledge of biodiversity and biogeography, and their role in the intelligent use of conservation. We can only hope that this occurs before irreparable damage is done to the environment, and before a wealth of biodiversity on earth is lost.

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“21세기 자연환경 보전과 곤충학”

천안 상록리조트 컨벤션센터

1999年 11月 5日

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1999 한국곤충학회 심포지엄
“21세기 자연환경 보전과 곤충학”

천안 상록리조트 컨벤션센터 1999. 11. 5

일 정

- 12:00 - 1:00 등 록
- 1:00 개 회 (사회: 배연재)
- 1:00 - 1:15 개회사 이병훈 회장
- 1:15 - 1:30 축 사 안영재(환경부 자연보전국장)
- 심포지엄 발표 I (좌장: 윤일병)
- 1:30 - 2:10 Biodiversity and Biogeography: Examples from the Global Studies of Ephemeroptera W.P. McCafferty(Purdue Univ.)
- 2:10 - 2:40 산림생태계 추세과악을 위한 산림곤충의 조사방법론 권태성(임업연구원)
- 2:40 - 3:10 한국산 토양곤충의 현황과 조사방법 김병진(원광대)
- 3:10 - 3:20 보충질의
- 3:20 - 3:40 Break
- 심포지엄 발표 II (좌장: 우건석)
- 3:40 - 4:10 한국산 수서곤충의 연구현황과 조사방법의 표준화 배연재(서울여대)
- 4:10 - 4:40 한국산 육상곤충의 모니터링: 외국의 예를 참고한 방향성 제시 한호연(연세대)
- 4:40 - 5:10 한국산 곤충표본의 보존실태와 효율적인 관리방안 권용정(경북대)
- 5:10 - 5:20 보충질의
- 5:20 - 5:40 종합토의 및 폐회 (좌장: 김진일)

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