

Global diversity of mayflies (Ephemeroptera, Insecta) in freshwater

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Abstract

The extant global Ephemeroptera fauna is represented by over 3000 described species in 42 families and more than 400 genera. The highest generic diversity occurs in the Neotropics, with a correspondingly high species diversity, while the Palaearctic has the lowest generic diversity but a high species diversity. Such distribution patterns may relate to how long evolutionary processes have been carrying on in isolation in a bioregion. Over an extended period, there may be extinction of species but evolution of more genera. Dramatic extinction events such as the K-T mass extinction have affected current mayfly diversity and distribution. Climatic history plays an important role in the rate of speciation in an area, with regions which have been climatically stable over long periods having fewer species per genus when compared to regions subjected to climatic stresses such as glaciation. Thirteen families are endemic to specific bioregions, with eight among them being monospecific. Most of these have restricted distributions which may be the result of them being the relict of a previously more diverse but presently almost completely extinct family, or may be the consequence of vicariance events, resulting from evolution due to long term isolation.

1. Introduction

The Ephemeroptera (mayflies) are an ancient lineage of insects, dating back to the late Carboniferous or early Permian periods, some 290mya. It is thought that they attained their highest diversity during the Mesozoic (Brittain & Sartori, 2003). They are clearly the most primitive and ancient of the extant insect groups (Edmunds & McCafferty, 1988). The relationship of Ephemeroptera with other modern winged insects is still a subject of debate. Together with the Odonata, mayflies were traditionally placed in the Paleoptera, which was considered the sister group of all other extant primarily winged orders (Kukalová-Peck, 1991). More recently, it was suggested that Ephemeroptera *per se* are the sister group of Odonata + Neoptera. This is based on a number of morphological features unique to mayflies as well as on recent DNA-based phylogeny (Ogden & Whiting, 2003; Wheeler et al., 2001).

The nymphal stage of mayflies (Fig. 1) is the dominant life history stage, and is always aquatic. The nymphs undergo a series of moults as they grow, the precise number being variable within a species, depending on external factors such as temperature, food availability and current velocity (Brittain & Sartori, 2003). Ranges from 10 to 50 instars have been reported (Ruffieux et al., 1996). Typically, nymphs have up to seven pairs of

abdominal gills, usually three caudal filaments, and mouthparts generally adapted for collector/gatherer and deposit feeding. A few species are predaceous and some are scrapers. Certain groups are burrowers, and have variously developed mandibular tusks and frontal processes to loosen the substrate, and flattened legs for digging. Burrowers usually have feathery gills which are folded over the abdomen and used to create a current through their burrow. Mayfly nymphs colonize all types of freshwaters but are more diversified in running waters than in lakes or ponds. A couple of species can even be found in brackish waters.

Mayflies undergo hemimetabolous metamorphosis, having a unique maturation stage between the nymph and adult, the subimago. Subimagos appear superficially similar to the adults, but are sexually immature. Their wings and abdomens are covered with small water-resistant microtrichia, which help them to leave the water after moulting from the final instar nymph (Edmunds & McCafferty, 1988). Except for a few exceptions, such as female Polymitarcyidae and Palingeniidae (which are mature as subimagos), most adults have transparent wings and glossy abdomens, having shed the subimaginal cuticle, and males have extended forelegs for grasping the female during mating. Usually, mayfly adults live from a few hours to a few weeks depending on the species. Many species have male mating swarms forming at dawn or dusk. Females have various methods of oviposition and the number of eggs laid varies according to species and size of female and eggs (Sartori & Sartori-Fausel, 1991; Brittain and Sartori, 2003). Length and number of life cycles per year depend largely on geographic locality and size of the species, with large burrowers in temperate climates taking over two years to mature, while tropical species may have several generations in a year.

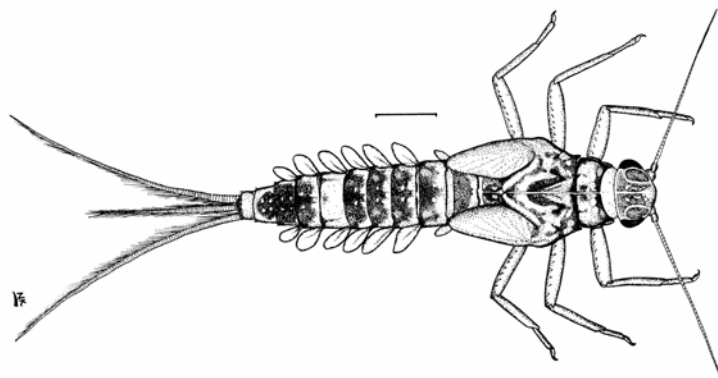


Fig. 1. Typical mayfly nymph (Baetidae)

2. Species and generic diversity

Ephemeroptera are represented by 42 families (Tables 1 and 2), with a little over 3000 described species (Table 1) in ca 400 genera (Table 2). Studies of their taxonomy are still in progress and numerous unknown species and genera await description, mainly in tropical areas. This synthesis includes studies up to October 2005. The supraspecific nomenclature has been the subject of numerous changes over the last few years, with a great increase in the number of recognized genera and families. Some of these changes are due to the fact that more

and more phylogenetic studies are now being undertaken, leading to more monophyletic clades (Brittain & Sartori, 2003).

Species and generic diversity is presented in Fig. 2. Clearly, collecting effort is reflected in the diversity pattern seen. The Holarctic Realm exhibits the highest species diversity and is also where the fauna is the best known. The faunas of the Afrotropical and Oriental Realms are probably underestimated because large areas are still “terrae incognitae” (e.g. Central Africa, parts of South America and Southeast Asia). A recent 80 km² survey of the mayfly fauna of a lowland tropical forest in Borneo led to the discovery of at least ten new genera and tens of new species (Sartori et al., 2003). Mayflies are unknown from Antarctica. The only significant Pacific components are located in New Caledonia, comprising 18 genera and 37 species of Leptophlebiidae, all strictly endemic (Peters et al. 1978; Peters and Peters, 1980, 1981a, 1981b). They have been considered as part of Australasia in the following discussion.

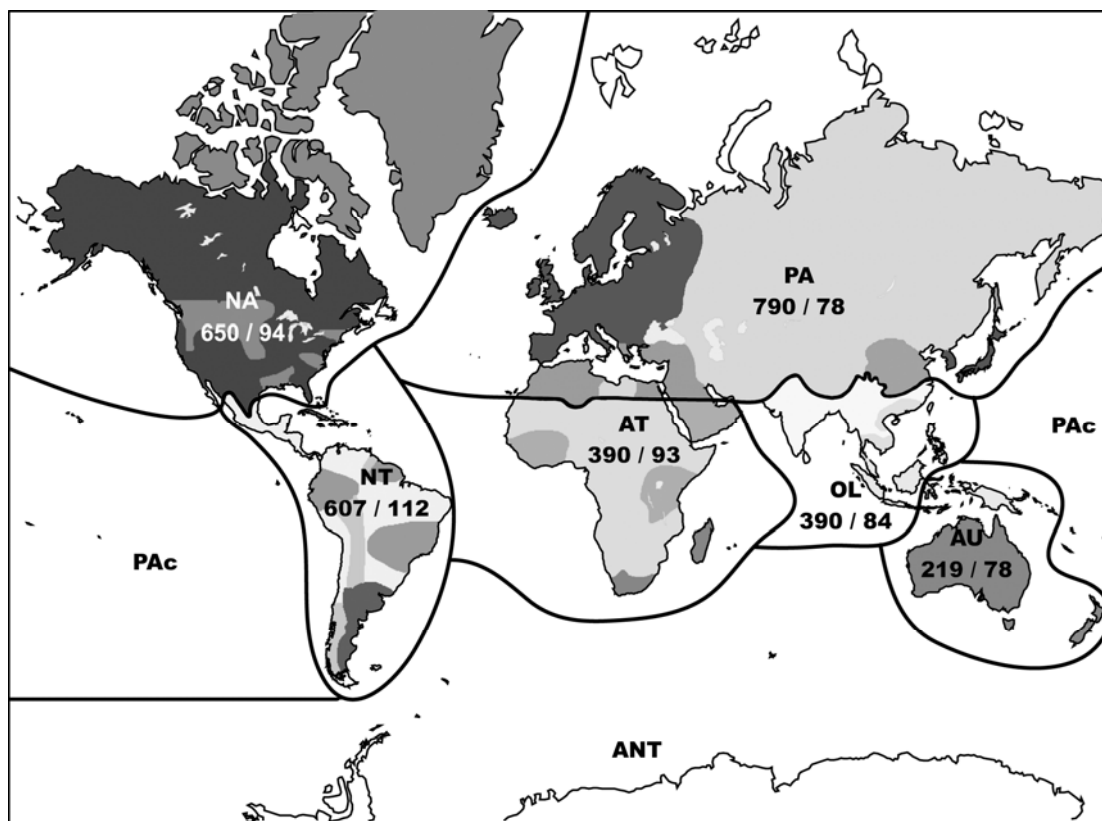


Fig. 2. Ephemeroptera diversity: number of species / number of genera per realm as of October 2005. Dark colour indicates well known fauna, medium colour indicates data available, pale indicates paucity of data. PA: Palearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, Au: Australasian (including the Pacific realm PAC), ANT Antarctic.

The generic diversity (Table 2) reflects a different pattern to species diversity (Table 1) when viewed by bioregion. For example, the Palearctic realm has the highest species diversity but the lowest generic diversity. As a whole, the Northern Hemisphere (Holarctic Realm) possesses fewer genera than the Southern Hemisphere. The diversity among families is very heterogeneous. Within the families, 40% (17 families) are monogeneric, suggesting that they represent isolated and relict branches of formerly more diversified lineages, or relatively young recently evolved groups. They are fairly evenly distributed between the Southern and Northern

Hemispheres. Approximately three quarters of the species (Table 1) and genera (Table 2) belong to only five families. The Leptophlebiidae is the most diverse mayfly family at the generic level, while the Baetidae have more species in fewer genera. In Australasia and the Neotropics, Leptophlebiidae represent 62% and 35% of their mayfly species respectively, while they range from 8% to 15% in other bioregions. In contrast, Baetidae are more evenly distributed among the bioregions, making up 20-25% of the species, with the exception of the Afrotropical and Oriental regions, where they represent 47% and 36% respectively. The Heptageniidae have the third highest diversity. They are notably more diverse in the Northern Hemisphere, and contribute to 41% and 20% of the Palearctic and the Nearctic mayfly species respectively. They constitute a minor group in other bioregions, but are absent from Australia. Although distributed worldwide, the Caenidae play a less important role in mayfly biodiversity (less than 8%) in all regions except in the Afrotropics (11%), although it should be noted that in terms of biomass they may at times exceed any other group. The Ephemerellidae, although absent from several regions, contribute to 11% of the diversity in the Nearctic, 8% in the Palearctic and 5% in the Oriental.

Table1. Number of Ephemeroptera species per realm, as of October 2005.

Family	Palearctic	Nearctic	Neotropical	Afrotropical	Oriental	Australasian	World
Acanthametropodidae	1	2	0	0	0	0	3
Ameletidae	20	34	0	0	2	0	56
Ameletopsidae	0	0	3	0	0	4	7
Ametropodidae	1	2	0	0	0	0	3
Arthropleidae	1	1	0	0	0	0	2
Vietnamellidae	0	0	0	0	6	1	7
Baetidae	156	153	161	185	139	39	833
Baetiscidae	0	12	0	0	0	0	12
Behningiidae	4	1	0	0	1	0	6
Caenidae	54	27	35	44	28	12	200
Chromarcyidae	0	0	0	0	2	0	2
Coloburiscidae	0	0	1	0	0	5	6
Coryphoridae	0	0	1	0	0	0	1
Dipteromimidae	2	0	0	0	0	0	2
Ephemerellidae	63	71	0	0	21	0	155
Ephemeridae	27	14	3	13	31	0	88
Ephemerythidae	0	0	0	5	0	0	5
Euthyplociidae	0	1	7	8	3	0	19
Heptageniidae	322	129	3	20	35	0	509
Ichthybotidae	0	0	0	0	0	2	2
Isonychiidae	6	16	1	0	7	0	30
Leptohyphidae	0	38	100	0	0	0	138
Leptophlebiidae	62	87	212	52	59	136	608
Machadorythidae	0	0	0	1	0	0	1
Melanemerellidae	0	0	1	0	0	0	1
Metretopodidae	4	9	0	0	0	0	13
Neophemeridae	3	4	0	0	4	0	11
Nesameletidae	0	0	1	0	0	6	7
Oligoneuriidae	12	8	20	11	0	0	51
Oniscigastridae	0	0	2	0	0	6	8

Palingeniidae	10	2	0	3	15	4	34
Polymitarciidae	5	7	56	4	12	0	84
Potamanthidae	8	5	0	0	10	0	23
Prosopistomatidae	5	0	0	4	8	2	19
Pseudironidae	0	1	0	0	0	0	1
Rallidentidae	0	0	0	0	0	1	1
Siphlaenigmatidae	0	0	0	0	0	1	1
Siphonuridae	23	26	0	0	0	0	49
Siphuriscidae	1	0	0	0	0	0	1
Teloganellidae	0	0	0	0	1	0	1
Teloganodidae	0	0	0	8	5	0	13
Tricorythidae	0	0	0	32	1	0	33
TOTAL	790	650	607	390	390	219	3046

Table 2. Number of Ephemeroptera genera per realm, as of October 2005; total number mentioned in the last column differs from the total of all realms because some genera may be found in several realms.

Family	Palaearctic	Nearctic	Neotropical	Afrotropical	Oriental	Australasian	World
Acanthametropodidae	1	2	0	0	0	0	2
Ameletidae	2	1	0	0	1	0	2
Ameletopsidae	0	0	2	0	0	2	4
Ametropodidae	1	1	0	0	0	0	1
Arthropleidae	1	1	0	0	0	0	1
Vietnamellidae	0	0	0	0	1	1	2
Baetidae	16	23	29	41	21	11	97
Baetiscidae	0	1	0	0	0	0	1
Behningiidae	2	1	0	0	1	0	3
Caenidae	2	4	5	8	5	3	17
Chromarcyidae	0	0	0	0	1	0	1
Coloburiscidae	0	0	1	0	0	2	3
Coryphoridae	0	0	1	0	0	0	1
Dipteromimidae	1	0	0	0	0	0	1
Ephemerellidae	8	10	0	0	8	0	18
Ephemeridae	1	3	1	3	2	0	6
Ephemerythidae	0	0	0	1	0	0	1
Euthyplociidae	0	1	3	1	1	0	5
Heptageniidae	14	16	3	2	11	0	31
Ichthybotidae	0	0	0	0	0	1	1
Isonychiidae	1	1	1	0	1	0	1
Leptohyphidae	0	4	9	0	0	0	10
Leptophlebiidae	9	10	45	17	19	50	131
Machadorythidae	0	0	0	1	0	0	1
Melanemerellidae	0	0	1	0	0	0	1
Metretopodidae	2	2	0	0	0	0	3
Neophemeridae	3	1	0	0	1	0	3
Nesameletidae	0	0	1	0	0	2	3
Oligoneuriidae	3	2	6	3	0	0	11
Oniscigastridae	0	0	1	0	0	2	3
Palingeniidae	4	1	0	1	2	1	8
Polymitarciidae	1	3	3	4	2	0	7
Potamanthidae	2	1	0	0	2	0	3
Prosopistomatidae	1	0	0	1	1	1	1
Pseudironidae	0	1	0	0	0	0	1
Rallidentidae	0	0	0	0	0	1	1

Siphlaenigmatidae	0	0	0	0	0	1	1
Siphonuridae	2	4	0	0	0	0	4
Siphuriscidae	1	0	0	0	0	0	1
Teloganellidae	0	0	0	0	1	0	1
Teloganodidae	0	0	0	5	2	0	7
Tricorythidae	0	0	0	5	1	0	5
TOTAL	78	94	112	93	84	78	405

Twelve genera encompass one third of the total mayfly species richness worldwide (Table 3). They have a wide range extension, being present in at least three bioregions, with the exception of two genera restricted to the Americas. On the other hand, 37% (149) of the genera are monospecific with a strong proportion biased towards ancient Gondwanan relicts of the South Hemisphere. They contribute 27% and 22% of the generic richness of the Neotropics and Australasia, but only 7% and 11% of the Palearctic and Nearctic, respectively.

Table 3. The twelve most diverse genera among Ephemeroptera, with number of described species and main distribution

Genus	Family	Total spp.	Distribution
<i>Baetis</i> Leach	Baetidae	158	Cosmopolitan except South America
<i>Caenis</i> Stephens	Caenidae	135	Cosmopolitan except Australasia
<i>Rhithrogena</i> Eaton	Heptageniidae	134	Holarctic and Neotropical
<i>Epeorus</i> Eaton	Heptageniidae	71	Holarctic and Oriental
<i>Cloeon</i> Leach	Baetidae	66	Cosmopolitan except Neotropics
<i>Thraulodes</i> Ulmer	Leptophlebiidae	61	Panamerican
<i>Ephemera</i> Linnaeus	Ephemeridae	59	Holarctic, Oriental, Afrotropical
<i>Ecdyonurus</i> Eaton	Heptageniidae	59	Holarctic and Neotropical
<i>Pseudocloeon</i> Klapálek/ <i>Labiobaetis</i> N. & K.	Baetidae	58	Cosmopolitan except Neotropics
<i>Paraleptophlebia</i> Lestage	Leptophlebiidae	56	Holarctic and Oriental
<i>Ameletus</i> Eaton	Ameletidae	55	Holarctic and Oriental
<i>Tricorythodes</i> Ulmer	Leptohephidae	54	Panamerican
TOTAL		966 (32%)	

One may question why one area may be more diverse than another at species level and yet have fewer genera, or the converse. Past changes in the earth's climate and the availability of suitable habitats may have a major role in influencing the patterns seen today. Populations may have been evolving in isolation in some bioregions (such as the Afrotropics) for longer than in others (such as the Oriental Region) resulting in extinction of species but evolution of more genera through time. When comparing the mean number of species between different realms, the effect of different climatic histories in different areas becomes apparent. For example, there is a mean of three species per genus in Australasia, which has been stable over millions of years, compared to ten in the Palearctic, which has been affected by orogenesis and recent glaciation.

A number of authors have recently produced a series of chapters, which make useful supplementary reading, summarizing the history and extent of knowledge of Ephemeroptera biodiversity and systematics (see Alba-

Tercedor (2001) and subsequent authors in the same series). A still growing number of catalogs are available and can be reached through the website “Ephemeroptera Galactica” and subsequent links (Hubbard, 2006).

3. Phylogeny and Historical processes

The Ephemeroptera are the oldest extant order of winged insects, and the taxa present today represent the surviving branches of evolution. It is likely that a large degree of extinction of the phylum has occurred and some basal lineages have disappeared. The first comprehensive work on the systematics of mayflies was that of Eaton (1883 -1888). His division of the mayflies into sections constituted the basis of the modern classification and remained almost unchanged for a century except for the hierarchical ranks of the sections.

Edmunds (1962) made the first attempt to reconstruct the phylogeny of the order, then McCafferty & Edmunds (1979) divided the mayflies in two suborders, Pannota and Schistonota. This reconstruction was widely used and constituted the basis for McCafferty's (1991) higher classification, where the Schistonota concept was considered paraphyletic, and replaced by three new suborders, Retracheata, Setisura and Pisciforma. Recently, Kluge (2004) proposed revisions at different levels of the phylogeny of the mayflies and summarised them in the first comprehensive modern treatment including all mayfly lineages (except Leptophlebiidae and Baetidae). Unfortunately, the approach of Kluge's work remains difficult for most workers because of the use of non-ranking nomenclature (including plesiomorphons). McCafferty's (updated with his subsequent partial reconstructions, quoted below) and Kluge's systems are roughly congruent (Fig. 3). They divide the order into four main lineages: 1) Carapacea (McCafferty) / Posteritorna (Kluge); 2) Furcatergalia; 3) Setisura; 4) Pisciforma (McCafferty) / Tridentisata (Kluge). Although the four main lineages are generally accepted, the relationships between and among them, the placement of some taxa and the rankings remain problematic. The most confusing lineages are the Siphonuroidea, the Ephemerelloidea and the Ephemeroidea. Since the appearance of McCafferty's (1991) system, about ten cladistic studies have been undertaken on family and superfamily relationships helping to better understand aspects of mayfly phylogeny, but none of them have included the entire order (eg. Kluge, 2003; Kluge et al., 1995; McCafferty & Wang, 2000; Molineri & Dominguez, 2003; Wang & McCafferty, 2004; McCafferty, 2004). A phylogeny based on molecular data was proposed and will greatly help to understand the higher relationships within the order (Ogden & Whiting, 2005); note that this was constructed before the publication of McCafferty's (2004) reclassification of the Scaphnodonta, which now includes the family Palingeniidae. It is likely that the details of phylogenies will continue to be debated in the light of further new information in the future.

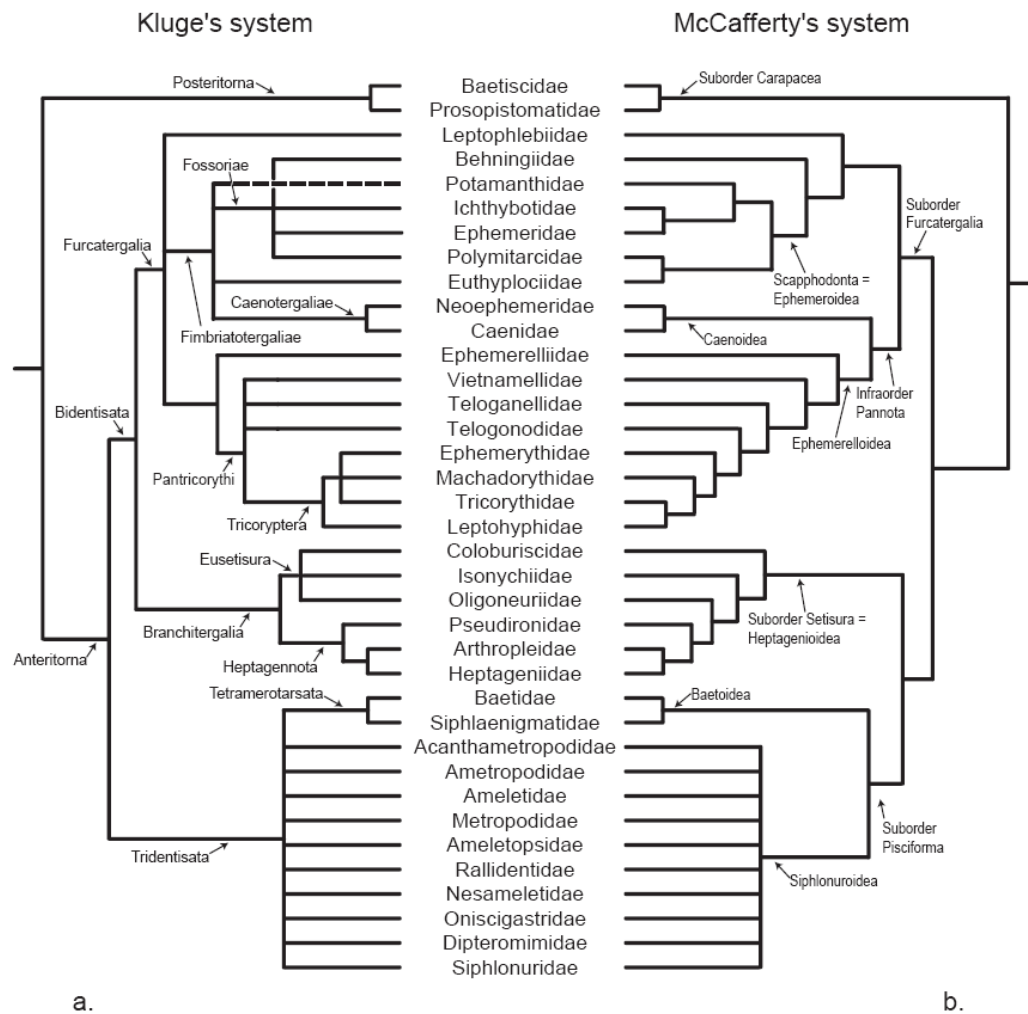


Fig. 3: Comparison of two recent phylogenetic reconstructions for the Ephemeroptera order, a. Kluge, b. McCafferty (from Ogden & Whiting (2005), with permission).

4. Distribution and endemism

Historically, mayflies were considered as having very low dispersal ability with oceans or mountain ranges constituting barriers to dispersal. Therefore, the present distribution was believed to be explained only by vicariance, radiation and extinction events and was a reflection of geological events, especially the break-off and drifting of the continents (Edmunds, 1972; Edmunds, 1975). Interchanges were considered to be restricted to regions directly in touch (McCafferty, 1998). Recent evidence has shown that the power of dispersal of mayflies had been greatly underestimated. The Baetidae in the South East Indian Ocean illustrate this case: the molecular reconstructions of the Afrotropical Baetidae phylogeny shows that there are strong affinities between Madagascar and continental Africa and very low affinities with other realms (opposing reliance upon the tectonic plate theory alone) and that transoceanic dispersal had occurred between Madagascar and continental Africa in both directions until recently (Monaghan et al., 2005). Simultaneously, the discovery of two species on the recent volcanic island of la Réunion indicates unambiguously that mayflies can disperse over more than 700 km (Gattolliat, 2004). Consequently, vicariance, radiation and dispersal must be taken into account to explain present faunal composition and distribution.

Ephemeroptera have a worldwide distribution, being absent only from Antarctica and some remote oceanic islands (Hubbard, unpubl. results). Only three of the 42 families possess such a distribution (Baetidae, Caenidae, and Leptophlebiidae, Tables 1 and 2). The origin of the Leptophlebiidae and Baetidae is probably Pangean, but the former has greater diversity and presents the highest degree of endemism in the Neotropics and Australasia, and the latter in the Neotropical and Afrotropical regions. Caenidae are mainly diversified at the specific level in the Palearctic realm and at the generic in the Australasian, Afrotropical and Neotropical realms. It seems evident in regard to the almost cosmopolitan distribution of some genera included in these families (*Baetis* and *Cloeon* for the Baetidae, *Choroterpes* for the Leptophlebiidae and *Caenis* for the Caenidae) that dispersal events between regions must have taken place after the initial splitting of the Gondwanan plates. Heptageniidae, Ephemeridae and Polymitarcyidae have a similar distribution except that they do not enter the Australasian realm, suggesting they have a Laurasian origin and reached the Southern Hemisphere well after the Gondwanan separation. This is emphasized by the fact that Heptageniidae only enter the Neotropics in Central America and are absent from South America. The monogeneric family Prosopistomatidae is present in all regions except the Americas, where it is replaced in the Nearctic by its sister family Baetiscidae. This distribution can be hypothetically explained by a relatively recent origin of the family (possibly Afrotropical or Oriental) and a secondary colonization of the other regions. Although this chapter has not discussed fossil mayflies, these do shed an interesting light on some of the distributions. For example, a fossil prosopistomatid has been described from Burmese amber (Sinitshenkova, 2000), dating at about 100 million years (Cruikshank & Ko, 2003), indicating the long-term presence of the family in the Oriental region. Staniczek et al. (2002) report a fossil Baetiscidae from Baltic amber, indicating a once more widespread Laurasian distribution of this family. Both discoveries indicate a relatively recent origin of the Carapacea.

Another important aspect to consider at this point is the effect of extinction on the mayfly fauna. Although background extinction takes place more or less constantly (eg. Raup, 1994), mass extinction has had a notable effect on the composition of the mayfly families and genera. McCafferty (1990, 1991) points out that the Mesozoic mayfly fauna was considerably different compared to the Cenozoic fauna, following the mass Cretaceous-Tertiary (K-T) extinctions.

Looking at extant distributions, five families have a strict Holarctic distribution (Acanthametropodidae, Ametropodidae, Arthropleidae, Metretropodidae, Siphonuridae) and five others (Ameletidae, Behningiidae, Ephemerellidae, Neoephemeridae, Potamanthidae) extend their Holarctic range (through the Palearctic) to the Oriental realm (Tables 1 and 2). It seems reasonable to conclude that these all have a Laurasian origin. Four families are amphitropic (Ameletopsidae, Coloburiscidae, Nesameletidae, Oniscigastridae) which confirm that South America, Australia and New Zealand share the same Gondwanan origin. Two families, Teloganodidae and Tricorythidae are spread through the Oriental and Afrotropical bioregions, including Madagascar, possibly indicating a more tropical Gondwanan origin.

The distribution of the Palingeniidae is puzzling as they are absent from the Neotropics and Continental Africa, but present in Madagascar. A once worldwide distribution with a complete extinction in South America and

continental Africa seems quite unlikely. A Lemurian (Madagascar and Deccan plate) origin with subsequent colonization of the Palearctic and introgression to Papua New Guinea could be more appropriate but does not explain adequately the presence of *Pentagenia* in the Nearctic. However, as Edmunds (1972) stated, with the immensity of time, improbable dispersals can become probable.

Considering endemism, thirteen families are endemic to specific bioregions, with eight among them being monospecific. Most of these have restricted distributions and greatly contribute to the distinctness of the fauna in that region (e.g. the monospecific Rallidentidae and Siphlaenigmatidae for New Zealand; Dipteromimidae for Japan; Coryphoridae in the Amazonian basin). The restricted size of these families can be explained by two possible processes; they can be the relict of a previously more diversified but presently almost completely extinct family, in other words, refugial (e.g. Siphuriscidae in China), while other families, especially those endemic to islands, may be the consequence of vicariance events, resulting from evolution due to long term isolation.

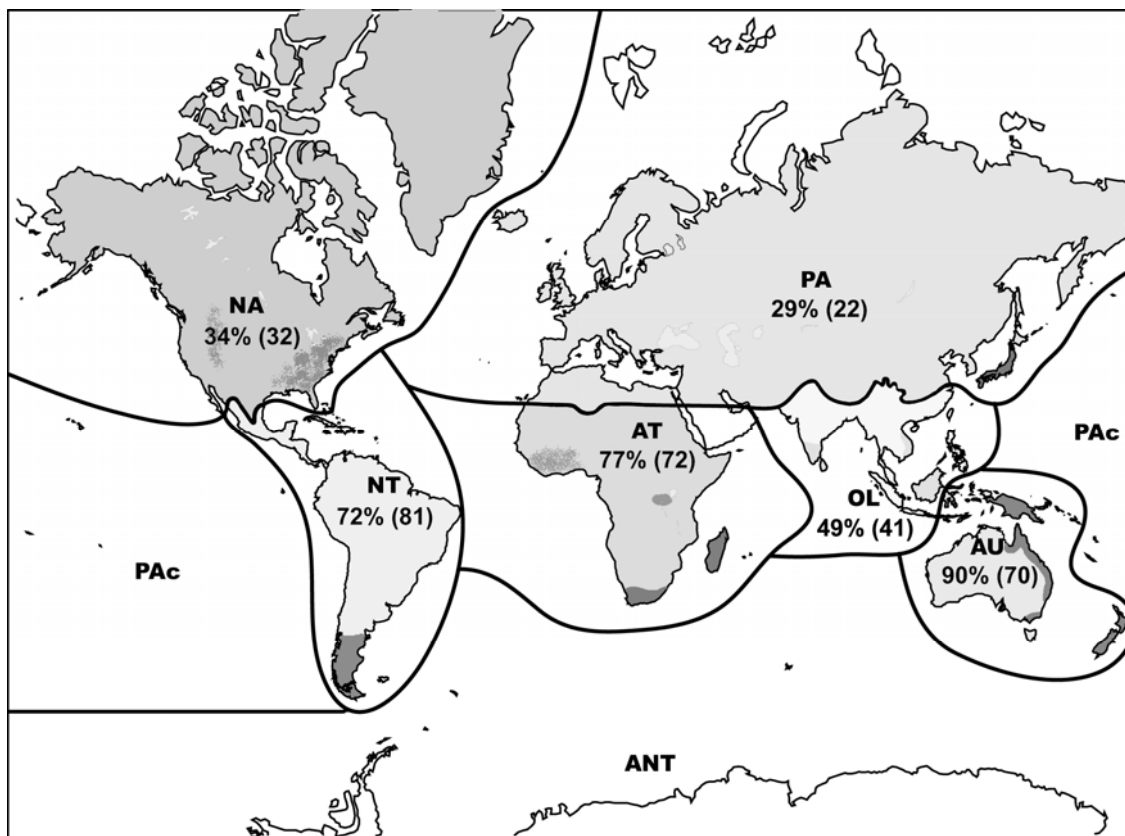


Fig. 4. Ephemeroptera endemism: percentage of endemic genera, number of endemic genera in brackets. Dark colour indicates high level of endemism.

In contrast to the widely distributed genera (Table 3), it is worth noting that 79% of the 405 known genera are endemic to a single realm. No genera exhibit an amphinotic distribution, attesting to the ancient splitting of Gondwanaland. For others, it has to be mentioned that 21 (5%) are Panamerican, whereas 13 (3%) are Holarctic. The extant distribution of some genera can be explained, as for the families, by introgression into an adjacent bioregion: from Palearctic to Oriental (e.g. *Torleya*) or from Oriental to Palearctic (e.g. *Baetiella*). A

single genus may present a disjunctive distribution, eg. *Habrophlebiodes* (Leptophlebiidae) being represented in the eastern Nearctic and Oriental by four species in each realm. It has been suggested that this vicariant distribution could be associated with the Arcto-Tertiary forest that covered most of the Northern Hemisphere during the Early Tertiary into the Pleistocene (Peters, 1988).

Of the 3046 species reported here, just over 60 (2%) are distributed among two bioregions. The main patterns are:

- Circumpolar (Arctic) species, (10 species, such as some Baetidae, Ephemerellidae and Siphonuridae);
- Panamerican species with a Neotropical origin, with introgression into the Nearctic (32 species, mainly Baetidae, Leptophlebiidae and Tricorythidae);
- Panamerican species with a Nearctic origin, with introgression into the Neotropics (8 species, mainly Heptageniidae);
- Palearctic species with introgression into the Oriental realm (6 species, mainly Baetidae and Heptageniidae)
- Oriental species with introgression into the Palearctic (4 species, mainly Ephemerellidae);
- Transpacific distribution (2 species within Baetidae and Heptageniidae seem to have a transpacific distribution, being present in the Eastern Palearctic and Western Nearctic).

Southern and Northern Hemisphere regions not only differ in the generic richness but also notably in the degree of endemism (Fig. 4). The different faunas from the Southern Hemisphere possess a high degree of generic endemism (comprising between 72 and 90%). Moreover, most of the centers of endemism are in the Southern Hemisphere (Southern South America, Southeastern South Africa, Madagascar, Eastern coast of Australia, New Zealand, New Caledonia). Affinities between Southern Hemisphere regions are low. The Australasian fauna is the most distinctive. With a generic degree of endemism of 90%, it shares only a few cosmopolitan genera with other regions, although intermittent stepping-stone archipelagos have been available intermittently for dispersal between the Oriental and Australasian realm (McCafferty, 1999). This can explain the presence of the Prosopistomatidae in northern Australia, and on several of the islands between Australia and Asia, these having migrated southwards during times of lower sea level.

The Neotropical fauna also has low affinities with other Southern hemisphere regions. It seems much closer to the Nearctic fauna. This is mainly due to the formation of the Central American landbridge during the Pliocene allowing introgression (or Great American Interchange) from both sides during the Pleistocene and Holocene (McCafferty, 1998; but see Savage et al., 2005 for an alternate view). Africa has been separated for so long that it has little in common with South America or Australasia, except for some of the globally dispersed families such as Baetidae and Leptophlebiidae. The only remnants of cold adapted taxa in this area may be some of the endemic genera of the Leptophlebiidae (eg. *Aprionyx*, and *Castanophlebia*), in the southern and south-western tip of Africa. Amphinotic families, such as Nesameletidae, encompass vicariant genera restricted to Southern South America (*Metamonius*), New Zealand (*Nesameletus*) and Australia (*Ameletoides*). The sharing of fauna

between these two regions is well documented (eg. Alexander, 1929; Edmunds, 1972; Edmunds, 1975; Brundin 1966), and indicates that there was once an important centre of evolution in the south, with Antarctica being a part of that centre.

Contrary to the Southern Hemisphere, Northern Hemisphere bioregions possess a low level of endemism, both at family and generic levels. Only Japan (with the endemic family Dipteromimidae), and China (with the monotypic family Siphuriscidae) as well as some parts of North America (with Baetiscidae (once more widespread, discussed above) and Pseudironidae) can be considered as important centers of endemism. Most of the taxa present a wide distribution at the same latitude.

The Oriental realm presents an intermediate situation between the Northern and Southern Hemispheres. About half of the genera are endemic to this region. This is clearly more than the Holarctic fauna but it is still lower than regions in the Southern Hemisphere, even if some new endemic genera are still undescribed (mainly from Malaysia and Indonesia). The Oriental region shows important affinities with both the Holarctic and Afrotropical realms; this is probably partially due to the dual origin of the region, with India belonging to Gondwana and the remaining part of Laurasian origin.

Table 4 summarises affinities of the mayfly fauna between realms both at the family and the generic levels.

Table 4. Sørensen's index of similarities between the different realms at the family level (above) and generic level (below). The higher the value, the more similar are the faunas.

	Neotropical	Nearctic	Palaearctic	Oriental	Australasian	Afrotropical
Neotropical		0.51	0.42	0.44	0.48	0.53
Nearctic	0.30		0.84	0.65	0.22	0.49
Palaearctic	0.06	0.42		0.67	0.29	0.50
Oriental	0.06	0.24	0.43		0.36	0.65
Australasian	0.01	0.06	0.06	0.09		0.37
Afrotropical	0.03	0.10	0.18	0.20	0.07	

Important differences in the diversity and endemism between Northern and Southern Hemispheres have been elucidated. These can be explained by several different hypotheses:

- The Gondwanan fauna was originally much more diverse than the Laurasian fauna;
- A higher level of extinction occurred in the Northern Hemisphere (due for instance to the climate changes in the Pleistocene);
- In the Northern Hemisphere, bioregions are oriented East-West where similar latitudes (especially in the Palaearctic) imply much more homogenous environments. In the Southern Hemisphere, bioregions are oriented North-South meaning they are much more subject to climatic changes;
- The main islands suitable for vicariance and radiation events of the mayflies are present in the Southern Hemisphere (Madagascar, New Zealand, Australia, New Guinea, Borneo).

5. Human impacts

Deforestation is one of the primary threats to mayfly biodiversity and conservation in the tropics (eg. Madagascar, Borneo) (Benstead et al., 2003; Benstead & Pringle, 2004; Dudgeon, 2000a, 2000b) whereas pollution (Rosenberg & Resh, 1993) and/or building and reshaping of the banks leading to a lack of connectivity with the floodplain (Buijse et al., 2002) or habitat fragmentation (Zwick, 1992) are the main causes in temperate areas.

Many studies have been carried out in recent year on the effects of climate changes on mayflies. Clearly, climate changes are affecting the behaviour and ultimately the ecology of some mayflies: for example, small increases in temperature (3°C) over the short term cause early emergence (McKee and Atkinson, 2000), possibly when the flow regime is not right for successful egg laying (Harper and Peckarsky, 2005). Climate changes alter precipitation pattern, leading to greater flood magnitude and frequency in certain rivers. This results in changes in ecological structure and function, and loss of diversity through too frequent scouring (Poff, 2002). Beniston (2006) reviews climatic changes in the Alps, and notes that with the warming trend observed, glaciers have considerably reduced in volume and area over the last 150 years. With the continuing trend of temperature increase, the proportion of glacial melt and snow melt waters will change and lead to drastic changes in macroinvertebrate communities, including mayflies (Brown et al., 2003; Brown et al., 2006).

Stream acidification is another negative human effect. In Europe acidification is still having a negative impact on invertebrate communities: in the Vosges mountains (France), Guerold et al. (2000) found a high reduction in diversity for many aquatic species and that Ephemeroptera totally disappeared from some streams.

Very few mayflies have been listed under the IUCN red listing criteria, although this is probably because of a lack of knowledge of specific ecologies, rather than an indication of the state of the fauna. The 1998 Red List of the German fauna (Malzacher et al., 1998) lists a much larger number of mayflies, probably because the environmental requirements are better known there than most places.

Some species are thought to have undergone recent extinction, *Palingenia robusta* (USA) (Palingeniidae), *Isonychia diversa* (USA) (Isonychiidae), *Siphonurus luridipennis* (USA) (Siphonuridae), *Ephemera compar* (USA) and *Ephemera mooiana* (South Africa) (Ephemeridae), all inhabitants of large rivers, though it is possible some may yet be rediscovered. The largest and one of the most vulnerable European mayfly, *Palingenia longicauda* (Palingeniidae) has been recently added to the Bern Convention of the Council of Europe (Sartori & Landolt, 1998); formerly distributed in large rivers throughout Europe, it is now restricted to the Tisza watershed in Hungary. Many more species need to be added to this list, as more and more habitat destruction takes place.

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7. References

- Alba-Tercedor, J., 2001. Introduction to the panel discussion "The status and knowledge of Ephemeroptera". In Dominguez, E. (ed), Trends in Research in Ephemeroptera and Plecoptera. Kluwer Academic/ Plenum Publishers, New York, 1-2.
- Alexander, C.P., 1929. Diptera of Patagonia and South Chile. Part 1. Crane flies. British Museum of Natural History, London. 240pp.
- Benstead, J. P., P. H. de Rham, J-L. Gattolliat, F. M. Gibon, P. V. Loisel, M. Sartori & J. S. Sparks, 2003. Conserving Madagascar's freshwater biodiversity. *Bioscience* 53:1101-1111.
- Benstead, J. P. & C. M. Pringle, 2004. Deforestation alters the resource base and biomass of endemic stream insects in eastern Madagascar. *Freshwater Biology* 49: 490-501.
- Beniston, M., 2006. Mountain weather and climate: A general overview and a focus on climatic change in the Alps. *Hydrobiologia* 562: 3-16.
- Brittain, J. E. & M. Sartori, 2003. Ephemeroptera. In Resh V. H. & R. T. Cardé (eds), Encyclopedia of insects. Academic Press, Amsterdam, 373-380.
- Brown, L. E., D. M. Hannah & A. M. Milner, 2003. Alpine stream habitat classification: An alternative approach incorporating the role of dynamic water source contributions. *Arctic Antarctic and Alpine Research* 35: 313-322.
- Brown, L. E., A. M. Milner & D. M. Hannah, 2006. Stability and persistence of alpine stream macroinvertebrate communities and the role of physicochemical habitat variables. *Hydrobiologia* 560:159-173.
- Brundin, L., 1966. Transantarctic relationships and their significance as evidenced by chironomid midges. Almqvist & Wiksell, Stockholm, 1- 472.
- Buijse, A. D., H. Coops, M. Staras, L. H. Jans, G. J. Van Geest, R. E. Grift & B. W. Ibelings, 2002. Restoration strategies for river floodplains along large lowland rivers in Europe. *Freshwater Biology* 47: 889-907.
- Cruickshank R.D. & K. Ko, 2003. Geology of an amber locality in Hukawng Valley, Northern Myanmar. *Journal of Asian Earth Sciences* 21: 441-455.
- Dudgeon, D., 2000a. The ecology of tropical Asian rivers and streams in relation to biodiversity conservation. *Annual Review of Ecology and Systematics* 31:239-263.
- Dudgeon, D., 2000b. Riverine biodiversity in Asia: a challenge for conservation biology. *Hydrobiologia* 418:1-13.
- Eaton, A. E., 1883 -1888. A revisional monograph of recent Ephemeridae or mayflies. Transactions of the Linnean Society of London, 2nd Series. *Zoology* 3: 1-352.
- Edmunds, G. F., 1962. The principles applied in determining the hierarchic level of the higher categories of Ephemeroptera. *Systematic Zoology* 11: 22-31.
- Edmunds, G. F., 1972. Biogeography and evolution of Ephemeroptera. *Annual Review of Entomology* 17: 21-42.
- Edmunds, G. F., 1975. Phylogenetic biogeography of mayflies. *Annals of the Missouri Botanical Garden* 62: 251-263.
- Edmunds, G. F. & W. P. McCafferty, 1988. The mayfly subimago. *Annual Review of Entomology* 33: 509-529.
- Gattolliat, J-L., 2004. First reports of the genus *Nigrobaetis* Novikova & Kluge (Ephemeroptera: Baetidae) from Madagascar and La Réunion with observations on Afrotropical biogeography. *Revue Suisse de Zoologie* 111:657-669.

- Guerold, F., J-P. Boudot, G. Jacquemin, D. Vein, D. Merlet & J. Rouiller, 2000. Macroinvertebrate community loss as a result of headwater stream acidification in the Vosges Mountains (N-E France). *Biodiversity and Conservation* 9: 767–783,
- Harper, M.P & B. L. Peckarsky, 2005. Emergence Cues of a Mayfly in a High-Altitude Stream Ecosystem: Potential Response to Climate Change. *Ecological Applications* 16: 612–621.
- Hubbard, M. D., 2006. <http://www.famu.org/mayfly/>
- Kluge, N. J., 2003. System and phylogeny of Pinnatitergaliae (Ephemeroptera). In Gaino, E. ed. *Research Update on Ephemeroptera and Plecoptera*. University of Perugia, Italy, 145-152.
- Kluge, N.J., 2004. *The phylogenetic system of Ephemeroptera.*, Kluwer Academic Publishers, Dordrecht 1-442.
- Kluge, N. J., D. Studemann, P. Landolt & T. Gonser, 1995. A reclassification of Siphonuroidea (Ephemeroptera). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 68: 103-132.
- Kukalová-Peck, J., 1991. Fossil history and the evolution of hexapod structures. In Naumann, I.D. (ed), *The Insects of Australia*. Second Edition vol 1. CSIRO. Melbourne University Press, Australia, 141-179.
- Malzacher, P., U. Jacob, A. Haybach & H. Reusch, 1998. Rote Liste der Eintagsfliegen (Ephemeroptera). In Naturschutz B. F., (ed), *Rote Liste gefährdeter Tiere in Deutschland*, Bonn, 264-267.
- McCafferty, W. P., 1990. Chapter 2. Ephemeroptera. In Grimaldi D. A., (ed), *Insects from the Santana Formation, Lower Cretaceous, of Brazil*. *Bulletin America Museum of Natural History*, 20-25.
- McCafferty, W. P., 1991. Toward a phylogenetic classification of the Ephemeroptera (Insecta): a commentary on systematics. *Annals of the Entomological Society of America* 84: 343-360.
- McCafferty, W.P., 1998. Ephemeroptera and the great American interchange. *Journal of the North American Benthological Society* 17: 1-20.
- McCafferty, W.P., 1999. Biodiversity and Biogeography: Examples from Global Studies of Ephemeroptera. *Proceedings of the Symposium on Nature Conservation and Entomology in the 21st Century*. The Entomological Society of Korea. 3-22.
- McCafferty, W.P., 2004. Higher classification of the burrowing mayflies (Ephemeroptera: Scappodonta). *Entomological News* 115: 84-92.
- McCafferty, W. P. & G. F. Edmunds, 1979. The higher classification of the Ephemeroptera and its evolutionary basis. *Annals of the Entomological Society of America* 72: 5-12.
- McCafferty, W. P. & T.-Q. Wang, 2000. Phylogenetic systematics of the major lineages of Pannote mayflies (Ephemeroptera, Pannota). *Transactions of the American Entomological Society* 126: 9-101.
- McKee, D. & D. Atkinson, 2000. The influence of climate change scenarios on populations of the mayfly *Cloeon dipterum*. *Hydrobiologia* 441: 55–62.
- Molineri, C. & E. Dominguez, 2003. Nymph and egg of *Melanemerella brasiliiana* (Ephemeroptera: Ephemeroidea: Melanemerellidae), with comments on its systematic position and the higher classification of Ephemeroidea. *Journal of the North American Benthological Society* 22: 263-275.
- Monaghan, M. T., J-L Gattolliat, M. Sartori, J-M. Elouard, H. M. James, P. Derleth, O. Glazot, F. de Moor & A. P. Vogler, 2005. Trans-oceanic and endemic origins of the small minnow mayflies (Ephemeroptera, Baetidae) of Madagascar. *Proceedings of the Royal Society. B.* 272: 1829–1836.

- Ogden, T. H. & M. F. Whiting, 2003. The problem with "the Paleoptera Problem:" sense and sensitivity. *Cladistics - the International Journal of the Willi Hennig Society* 19: 432-442.
- Ogden, T. H., & M. F. Whiting, 2005. Phylogeny of Ephemeroptera (mayflies) based on molecular evidence. *Molecular Phylogenetics and Evolution*. 37: 625-643.
- Peters, W. L., J. G. Peters & G. F. Edmunds, 1978, The Leptophlebiidae of New Caledonia (Ephemeroptera). Part I. Introduction and systematics. *Cahiers de l'ORSTOM, série Hydrobiologie* 12: 97-117.
- Peters, W. L. & J. G. Peters, 1980. The Leptophlebiidae of New Caledonia (Ephemeroptera). Part II. Systematics. *Cahiers O.R.S.T.O.M., Series Hydrobiologie* 13: 61-82.
- Peters, W. L. & J. G. Peters, 1981a. The Leptophlebiidae: Atalophlebiinae of New Caledonia (Ephemeroptera). Part III - Systematics. *Revue d'Hydrobiologie Tropical* 14: 233-243
- Peters, W. L. & J. G. Peters, 1981b. The Leptophlebiidae: Atalophlebiinae of New Caledonia (Ephemeroptera). Part IV. - Systematics. *Revue d'Hydrobiologie Tropical* 14: 245-252.
- Peters, W. L., 1988. Origins of the North American Ephemeroptera fauna, especially the Leptophlebiidae. *Memoirs of the Entomological Society of Canada* 144: 13-24.
- Poff, N. R., 2002. Ecological response to and management of increased flooding caused by climate change. *Philosophical Transactions of the Royal Society of London A* 360: 1497-1510.
- Raup, D. M. 1994. The role of extinction in evolution. *Proceedings of the National Academy of Sciences of the United States of America* 91: 6758-6763.
- Rosenberg, D. M., & V. Resh, 1993. *Freshwater biomonitoring and benthic macroinvertebrates*. Chapman & Hall, New York, 1-488.
- Ruffieux, L., M. Sartori & G. L'Eplattenier, 1996. Palmen body: a reliable structure to estimate the number of instars in *Siphonurus aestivalis* (Eaton) (Ephemeroptera: Siphonuridae). *International Journal of Insect Morphology and Embryology* 25: 341-344.
- Sartori, M. & A. Sartori-Fausel, 1991. Variabilité de la durée du stade subimaginal et de la fécondité chez *Siphonurus aestivalis* (Eaton) (Ephemeroptera; Siphonuridae). *Revue Suisse de Zoologie* 98: 717-723.
- Sartori, M. & P. Landolt, 1998. Memorandum concernant la candidature de *Palingenia longicauda* (Olivier, 1791) (Insecta Ephemeroptera) à son inscription en annexe de la Convention de Berne. Strasbourg, Document T-PVS (98) 15, Council of Europe, 1-9.
- Sartori, M., P. Derleth & J. L. Gattolliat, 2003. New data about the mayflies (Ephemeroptera) from Borneo. In Gaino, E., (ed), *Research Update on Ephemeroptera and Plecoptera*. Perugia, University of Perugia, Italy, 403-406.
- Savage, H.M., R.W. Flowers & V.W. Porras, 2005. Rediscovery of *Choroterpes atramentum* in Costa Rica, type species of *Tikuna* new genus (Ephemeroptera: Leptophlebiidae: Atalophlebiinae), and its role in the "Great American Interchange". *Zootaxa* 932:1-14.
- Sinitshenkova, N. D., 2000. The first fossil prosopistomatid mayfly from Burmese amber (Ephemeroptera: Prosopistomatidae). *Bulletin of the Natural History Museum, London (Geology)* 56: 25-28.
- Staniczek, A. H., T. Bechly & G. Bechly, 2002. First fossil record of the mayfly family Baetiscidae from Baltic amber (Insecta: Ephemeroptera). *Stuttgarter Beiträge zur Naturkunde B (Geologie und Paläontologie)* 322: 1-11.
- Wang, T. Q. & W. P. McCafferty, 2004. Heptageniidae (Ephemeroptera) of the world. Part I: Phylogenetic higher classification. *Transactions of the American Entomological Society* 130: 11-45.

Wheeler, W. C., M. Whiting, Q. D. Wheeler & J. M. Carpenter, 2001. The phylogeny of the extant hexapod orders. *Cladistics - the International Journal of the Willi Hennig Society* 17: 113-169.

Zwick, P., 1992. Stream habitat fragmentation - a threat to biodiversity. *Biodiversity and Conservation* 1: 80-97.