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The family Baetidae (Insecta: Ephemeroptera): synthesis and future challenges

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The systematics of the Baetidae has been the subject of much attention during the last three decades, with descriptions of new species and genera as well as several generic revisions. The family now encompasses about 100 genera and 900 species which constitute one-quarter of the world's mayfly diversity. It is thus an opportune time to evaluate the pertinence of these works. The diversity of the Baetidae of the different realms is discussed with emphasis on the rate of endemism and biogeographic affinities. We have also tried to identify the geographical areas where we need more data. The Afrotropics and Neotropics possess the most diversified fauna with the highest degree of endemism. The faunas of the Palaearctic and Nearctic realms are better known but are less diversified especially at a generic level. Oriental and Australasian faunas are still poorly known but are expected to be diversified especially in the tropical regions.

Keywords: Baetidae; biogeographic realms; diversity; systematics

Introduction

In 1815, Leach divided the tribe Ephemerides into two families, depending on the number of caudal filaments in the imaginal stage. He established the family Baetidae for species with two caudal filaments and the Ephemeridae for species with three filaments. In the Baetidae, he established two genera: *Baetis* for species with four wings and *Cloeon* for species with two wings. In the last 200 years, the systematics of the Baetidae has greatly improved, and this family now encompasses about 100 genera and 900 species which constitute one-quarter of the world's mayfly diversity. Except for Antarctica and New Zealand, Baetidae present a cosmopolitan distribution.

Baetidae constitute a relatively homogenous family. They are distinguished in the imaginal stage by the presence of turbinate eyes in the male imago (except in the single Neotropical genus *Aturbina* (Lugo-Ortiz and McCafferty 1996a)), detached IMA and MA_2 forewing veins, the presence of simple or double free intercalary veins in the forewing (partially or completely reduced in a few taxa), hind wing

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reduced or absent, three-segmented mid and hind tarsi and membranous penis (Edmunds et al. 1976). Larvae are also unique among mayflies in having the lateral branches of the epicranial suture anterior to the lateral ocelli and the ventral orientation of the dorsal lobe at the apex of femora (Wang and McCafferty 1996). Larvae are pisciform, they generally possess long antennae and simple or double ovoid gills on segments I–VII or II–VII.

Baetidae are very common in any kind of freshwater; they are mainly diversified in unpolluted running water, especially in the tropics. Although they are less diversified in standing waters, with genera like *Cloeon*, the Baetidae constitute an important part of the insect biomass in ponds. Most species of Baetidae are collector-gatherers, feeding mainly on detritus. Unusual adaptations to peculiar diets occur in a few genera. Twelve species belonging to nine genera are considered to be carnivorous. They feed mainly on larvae of Diptera, but some are specialised in feeding on other mayflies (Gattolliat and Sartori 2001; McCafferty and Sun 2005). Although these carnivorous genera present similar adaptations of the mouthparts, they clearly belong to different lineages (Monaghan et al. 2005). In several lineages, species or genera show adaptations for scrapping algae on the top of stones (Lugo-Ortiz and McCafferty 1997; Gattolliat 2001b). Some genera have an advanced evolution of the mouthparts and/or legs for filtering organic material in water (Elouard et al. 1990; Gillies et al. 1990; Nieto 2003b). A different feeding behaviour like herbivorous feeding on vascular plants rarely occurs (Gattolliat and Sartori 2003).

Convergent evolution can be observed in the different genera living in fast flow. In these genera the median caudal filament is considerably reduced, and there are rows of abundant thin setae on the dorsal margin of legs. In some cases there is a simple or double carena on the abdominal tergites developed (Waltz and McCafferty 1987c, Gillies 1991a, Gattolliat 2001b). On the contrary, other genera like *Pseudocentroptiloides* are considered as psammophilous, showing long and slender legs and tarsal claws (Glazaczow 1997). The genera *Symbiocloeon* and *Mutelocloeon* present a unique adaptation among mayflies as their larvae are obligatory commensals inside mussels (Müller-Liebenau and Heard 1979, Gillies and Elouard 1990).

The systematics of Baetidae has been the subject of a lot of attention over the last three decades. Areas previously poorly known such as Madagascar, West Africa, Taiwan, or Cuba were subject to intensive sampling and systematic research with the discovery of several new species and genera. During his long life devoted to mayflies, G. F. Edmunds collected mayflies from almost all over the world. His huge collection was the source of numerous systematic works led at Purdue University, Indiana, USA. The genus concept has also evolved greatly: firstly by taking into account larval characters rather than only imaginal ones and secondly by the use of phylogenetic methods and the splitting of paraphyletic and polyphyletic genera. The evolution of the global concept of *Baetis* or *Centroptilum* and *Afroptilum* in the Afrotropics perfectly illustrate this new approach (Lugo-Ortiz 1999; Gattolliat et al. 2008). While the systematic generic classification of Baetidae has been greatly improved recently, the suprageneric classification of the Baetidae remains unclear. Historically, two conflicting concepts have been proposed: the division of the Baetidae into different subfamilies (Gillies 1991a) or the gathering of genera in several complexes (Waltz et al. 1994, Lugo-Ortiz and McCafferty 1996b, 1998a, 1998f). However, recent molecular reconstruction showed that the division in

subfamilies is too simplistic and most of the complexes are not monophyletic (Gattolliat et al. 2008).

Recently, under the directory of Freshwater Animal Diversity Assessment Project (FADA), a worldwide global synthesis on Ephemeroptera was published, providing the current numbers of known species and generic diversity globally, identifying the main distribution pattern and biogeographical affinity, and highlighting the main areas of endemicity and possible gaps (Barber-James et al. 2008). Subsequently, FADA has undertaken to create a worldwide electronic database including all freshwaters animals. For this purpose, a database at the specific level of the Ephemeroptera was created, including the Baetidae (Sartori et al. unpublished data). Despite this mayfly database being compiled by largely the same authors, there are some noticeable discrepancies in the number of species per realm, especially in Palearctic and Nearctic realms. While we may expect a few recently described species to be included since publication, the main reason for these differences is the omission of some poorly known species in Barber-James et al. (2008). Cross-checking with the electronic database "Ephemeroptera of the World" of Nikita Kluge (2009) was of great help to fill in this gap, for example for species from the former USSR or China. The results presented in the present study are based on the Sartori et al. database.

In the present study, we discuss the Baetidae diversity of the different biogeographic realms with their rate of endemism and biogeographic affinities. We also try to show the present state of knowledge of the different faunas and to highlight those requiring the most attention.

Palearctic realm

With 212 species, the Palearctic has a high specific diversity (Table 1, Figure 1). This diversity reflects the good knowledge of a great part of the realm rather than a higher diversity than in other parts of the world. The single genus *Baetis* itself represents about half of the species, part of them having a restricted distribution. Most of the 17 genera present a wide distribution including other realms. The carnivorous *Raptobaetopus* and the rheophilous *Acentrella* are the only genera occurring in the Palearctic realm that show important adaptations; all other genera are collector-gathers and have no or few adaptations to environmental factors.

Four of the eight species of mayflies described by Linnaeus were from the Palearctic realm. In the middle of the nineteenth century, a few species were described from Western Europe (Rambur 1842, Pictet 1843–1845). The contribution

Table 1. Generic and specific diversity by realm. Endemicity: % of taxa endemic from the different realm.

	No. genera	Endemicity %	No. species	Endemicity %
Palearctic	17	12	212	98
Afrotropics	40	82	190	100
Oriental	23	38	124	99
Neotropical	27	66	210	92
Neartic	20	25	135	84
Australasian	12	50	40	98

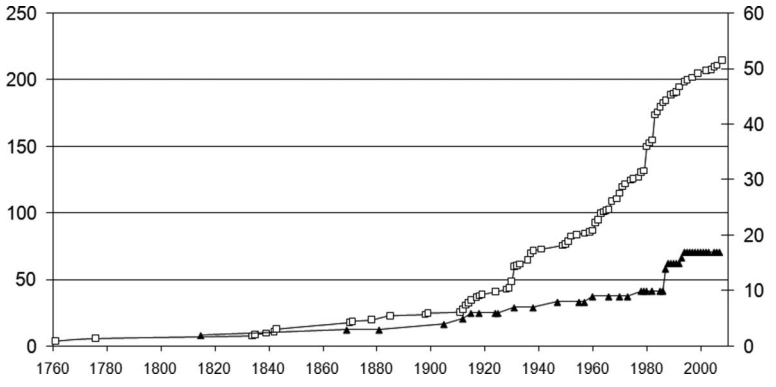

Figure 1. Specific and generic diversity in Palearctic realm: Square: total number of species (left scale). Triangle: total number of genera (right scale).

of Eaton to the knowledge of European Baetidae was essential in the description of new species and a new genus, including the various monographs on mayflies he published and also with his comprehensive study of the mayflies of England (Eaton 1870; Eaton 1871; Eaton 1883–1888). His work was outstanding due to the precision of his drawings and the accuracy of the description. He was also the first to have a concept of the mayfly systematics which is still largely accurate.

At the beginning of the twentieth century, Bengtsson described several taxa based on material from Scandinavia (Bengtsson 1912, 1914, 1917). Some of them were found to have a much broader distribution in the West Palearctic. Mainly based on single specimens pinned in different museums, Navás described dozens of new species from Europe, China and Japan (Navás 1911, 1913, 1917, 1931b). Only a few of them are still considered as valid; most of them have never been mentioned since the original description. Most species described after 1950 from Western Europe represent alpine or insular vicariants (Thomas and Gazagnes 1984; Thomas 1986; Thomas and Soldán 1987; Soldán and Godunko 2006). Several species were described from East Europe (Bogoesco and Tabacaru 1957) and from East Palearctic (Kazlauskas 1963). The fauna of the Himalayas was subject to some attention but more studies are required (Kapur and Kripalani 1963; Dubey 1971). The Japanese fauna encompasses 11 genera and 39 species; most species are endemic to the archipelago (Fujitani 2008). A great part of them were described before 1950, but the main contribution was made by Gose (1980) with the description of 14 species. Fujitani presented revisions of the Japanese Baetidae and described the larval stage for several species (Fujitani et al. 2003a, 2003b). The Baetidae from Korea are also quite well-known, but mainly included species with a wide distribution (Park et al. 1996; Bae 1997; Bae and Park 1998). In China, several taxa in most of the families of Ephemeroptera were recently described or revised (Zhou et al. 2000; Zhou and Zheng 2001; Zhou and Braasch 2003; Zhou and Peters 2003; Zhou and Zheng 2003, 2004), but nothing has been undertaken concerning the Baetidae.

The study of North African fauna is relatively recent. The Moroccan and Algerian faunas possess several endemic species and show close relationships with West Palearctic fauna mainly through the Iberian Peninsula (Soldán and Thomas 1983a, 1983b; Thomas and Gagneur 1994; Thomas 1998). Afrotropical affinities are limited to the single genus *Cheleocloeon* (Soldán and Thomas 1985). Levant and the

Arabian Peninsula have been also subject to attention recently; as for North Africa, this fauna possesses endemic species but a generic composition mainly similar to the European one (Thomas and Dia 1984, 1985; Thomas and Sartori 1989).

Afrotropical realm

The Afrotropical fauna of Baetidae presently encompasses 40 genera and 190 species (Figure 2); they represent about half of the generic and specific diversity of African mayflies. All of the species and 82% of the genera of Baetidae are endemics from this realm; the non-endemic genera possess a wide distribution including at least the Palearctic and Oriental realms (*Baetis, Cloeon* and *Nigrobaetis* for example). The Afrotropics clearly represent an important centre of diversity for the Baetidae.

The distribution of some species covers a great part of the Afrotropics or even in the case of *Cloeon smaeleni* the whole realm (Gattolliat and Rabeantoandro 2002). The specific distribution is sometimes greatly underestimated in part due to the low degree of knowledge of some faunas but also due to the description of the same taxon under various names in different areas (Gattolliat, unpublished data). Due to peculiar ecological conditions or geographic isolation, some taxa have a restricted distribution. Madagascar, the Drakensberg and Cape area in South Africa as well as the volcanic mountain ranges in East and Central Africa are probably the main areas of microendemism.

Ulmer (1909) described the first species of Afrotropical Baetidae from Madagascar and the Comoros. Subsequently a few other European researchers described new taxa based on very restricted samples by generalist collectors, which ended in European museums (Esben-Petersen 1913; Lestage 1918; Navás 1930, 1931a). Barnard was the first true African ephemeropterist; he published the first monograph on South African mayflies mainly from Western Cape (Barnard 1932). He was also one of the first who paid attention to the larval stage by rearing mayflies to obtain larva–adult association. This pioneer study was followed by Crass (1947) and Agnew (1961, 1963), contributing to the knowledge of the South African fauna. After these three studies, this fauna already comprised 26 species of Baetidae (compared to the 34 presently known). Most of them were described on a large series of specimens from different localities usually both at larval and imaginal stages.

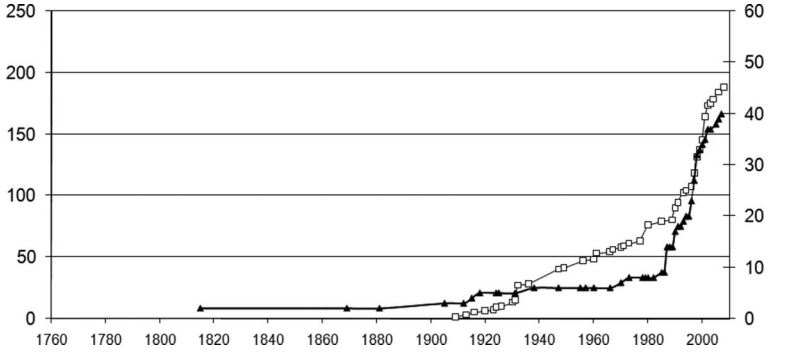

Figure 2. Specific and generic diversity in Afrotropical realm: Square: total number of species (left scale). Triangle: total number of genera (right scale).

Kimmins (1956) described a few species from Uganda. Demoulin (1964a, 1964b, 1965, 1966, 1967, 1968) reported several species of Baetidae collected during various expeditions. In most cases, he described them completely but refrained from naming them. In 1970, he published the first catalogue of the African mayfly fauna, including all the citations from the Afrotropical area (Demoulin 1970). Based on more than 20,000 imagines Kopelke (1980) described 12 new species from the Kalengo mountains near Lake Kivu in Zaire. This study was only based on the imaginal stage and the larva-imago association was subsequently possible only for a few species.

Gillies contributed greatly to the knowledge of African Baetidae. He first worked in East Africa, mainly in Tanzania, describing several species from this area (Gillies 1985, 1988, 1990, 1991a, 1991b, 1994, 1998; Gillies and Wuillot 1997). In the 1970s and 1980s, the French ORSTOM team collected aquatic macroinvertebrates repeatedly in about 100 localities, mainly in Guinea, Ivory Coast, Mali and Sénégal. These collections constituted part of an important onchocerciasis control programme (Lévêque et al. 2003). Elouard and Wuillot, in close collaboration with Gillies, investigated this fauna, and they described seven genera and about 20 species from this area (Gillies 1990; Elouard and Hideux 1991; Wuillot and Gillies 1993, 1994).

The first mention of Baetidae in Madagascar was provided by Ulmer (1909). Until the middle of the 1990s, little work on Malagasy Baetidae had been done: at that time eight species were described but only four of them are now considered as valid (Gattolliat and Sartori 2003). In less than 10 years, 19 genera and 51 species were described or reported from this island, highlighting the great diversity of this fauna; this faunistic and systematic work was largely based on the material collected by J.-M. Elouard and his Malagasy team (Elouard and Gibon 2001). To illustrate the originality and the highly adaptive nature of this fauna, we can mention the three endemic carnivorous genera (Gattolliat and Sartori 2001), the larva of *Edmulmeatus grandis* feeding only on vascular plants (Gattolliat and Sartori 2003), and the adaptation for scraping algae from rocks occurring independently in several genera (Lugo-Ortiz and McCafferty 1997; Gattolliat and Sartori 2000; Gattolliat 2001a, 2001b, 2002a, 2002b, 2004). Compared to other areas of the Afrotropics, the Malagasy fauna can be considered as well known even if some systematics problems need to be solved and a few new species and genera still await description (Gattolliat and Sartori 2003; Gattolliat et al. 2008).

Part of the Arabian Peninsula is also considered as belonging to the Afrotropical realm. Despite a great part of this area being desert, a limited but original fauna occurs there (Gattolliat and Sartori 2008). This fauna shows direct influence from both the Palearctic and Afrotropical realms.

In the 1980s and 1990s, Waltz and McCafferty, then Lugo-Ortiz and McCafferty revised the systematics of the Baetidae at the generic level. They established respectively three and 14 new genera (Lugo-Ortiz and McCafferty 1999b). It clearly represented an important improvement of our knowledge of Afrotropical Baetidae, but still more systematic work is required before having a complete understanding of this fauna. In the series ''Guides to the Freshwater Invertebrates of Southern Africa'', Barber-James and Lugo-Ortiz (2003) offered a key to the generic level for larvae of all the Afrotropical mayflies; distribution, diagnosis and ecology of each genus are discussed and an updated version of the checklist is available online (Barber-James 2007).

We can consider that the faunas of South, West and East Africa as well as of Madagascar are relatively well known. In all of these regions, there are most certainly several species and genera that remain unknown because of restricted distribution or unusual habitat. The fauna of the whole Atlantic side of Africa (from Cameroon to Angola) remains almost completely unknown. This fauna probably encompasses some taxa with a broad distribution like *Centroptiloides bifasciata* or *Ophelmatostoma camerunse;* but it certainly contains several new taxa. The area of the Ruwenzori mountain range is also poorly known and probably possesses a high degree of endemism. Almost no report of Baetidae is available from Northeastern Africa north to Kenya.

Oriental realm

The first species of Baetidae from the Oriental realm were described from Sri Lanka and India (Hagen 1858; Eaton 1883–1888) (Figure 3). In his work on the mayflies of the Sunda Islands, Ulmer (1939) provided the first comprehensive review of an Oriental fauna with complete and accurate descriptions of new species at both larval and imaginal stages. Kimmins (1947) and Gillies (1949) both contributed to the knowledge of the Baetidae from India by respectively describing three and 11 species from the imaginal stage. Apart from these works, the Oriental fauna remained very poorly known until the 1980s. Müller-Liebenau described about 60 new species from the larval stage (about 50% of the species presently known from this area!) and six new genera (Müller-Liebenau 1980a, 1980b, 1981, 1982a, 1982b, 1982c, 1983, 1984a, 1984b, 1985; Müller-Liebenau and Heard 1979; Müller-Liebenau and Morihara 1982; Müller-Liebenau and Hubbard 1985). She mainly described species from Sri Lanka, Malaysia and the Philippines. Her work constituted the major contribution to the knowledge of Oriental fauna. Waltz and McCafferty helped to clarify the supra-specific classification by establishing new genera and complexes of genera (Waltz and McCafferty 1987a, 1987c; Waltz et al. 1994).

The Baetidae from Taiwan were the subject of an extensive study allowing the description of 14 species (Kang et al. 1994, Kang and Yang 1996). The fauna from running waters can be considered as well known, but the fauna from still and

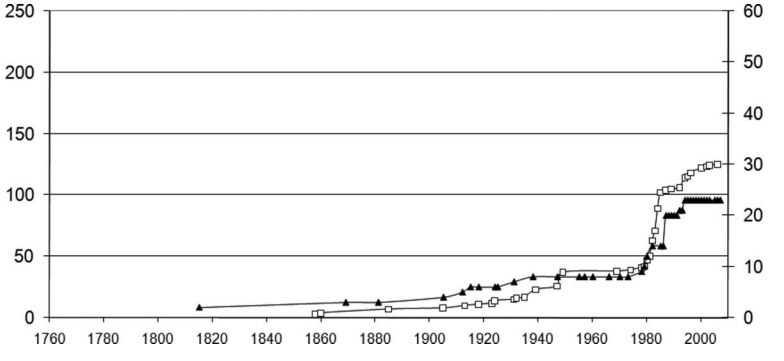

Figure 3. Specific and generic diversity in Oriental realm: Square: total number of species (left scale). Triangle: total number of genera (right scale).

standing water remained unknown. The fauna of Hong Kong has recently been subject to close attention with the description of five new species (Tong and Dudgeon 2000, 2003).

Although some islands like Sri Lanka, Taiwan or Hong Kong were the subject of important studies, the majority of the Oriental realm remains virtually unknown. For example, only provisional checklists of Baetidae at generic level are available for Vietnam and Thailand. India, especially the southern part of this subcontinent, probably possesses a much more diversified fauna than the scattered reports seem to indicate. There are also almost no reports from countries with potentially high diversity such as Cambodia or Myanmar. If we consider that in a 85 km^2 area in Kalimantan (Borneo), intensive sampling allowed the collection of 12 genera of Baetidae, five of them probably being new to science (Sartori et al. 2003), we can easily imagine that only a tiny part of Oriental fauna is presently known. Most faunas are too poorly known to correctly estimate the distribution of the different specimens, but preliminary results based on our own collections seem to indicate that at least some species show a wide distribution including a great part of South East Asia. It is extremely difficult to estimate the specific and generic diversity of the Oriental realm even for restricted regions; it is probably not overstated to consider that the species presently known represent less than a half or even a third of the real diversity.

Neotropical realm

With a total surface of 19 million of km^2 the Neotropical realm is the fourth biogeographical region. The Baetidae there now encompass 210 species and 27 genera (Table 1). The first species of Baetidae from the Neotropics were described by Pictet (1843–1845), Eaton (1871, 1883–1888) and Weyenbergh (1883) (Figure 4). As for the Afrotropics, the descriptions were based on restricted collections of imagines deposited in European museums. Navás was the most prolific author, unfortunately he described the same species several times under different names: he described 26 species of *Callibaetis* but only eight are presently considering as valid (Domínguez et al. 2006). Most of the species described by these first authors have been transferred to new genera or synonymised.

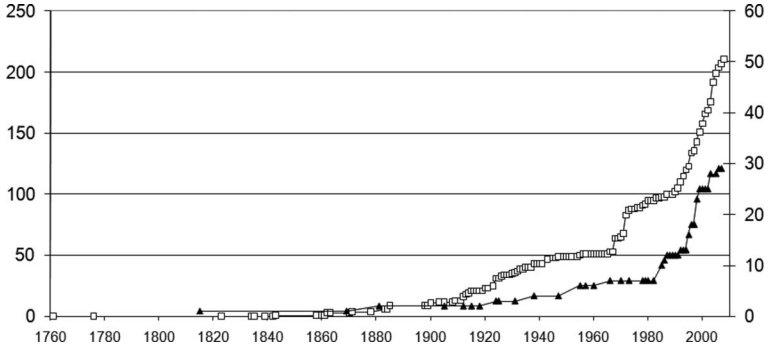

Figure 4. Specific and generic diversity in Neotropical realm: Square: total number of species (left scale). Triangle: total number of genera (right scale).

Traver and Edmunds (1968) greatly improved the knowledge of the highly diversified genus *Camelobaetidius*. Mol (1986) established the only carnivorous genus for this region, *Harpagobaetis*. Lugo-Ortiz and McCafferty (1995, 1996a, 1998c, 1999e), described 12 new genera from the Neotropics; other genera have been recently established by Nieto (2003b) and McCafferty and Baumgardner (2003). Finally, Domínguez et al. (2006) published the first comprehensive review of all South America species of Ephemeroptera with a chapter on the family Baetidae including a key, illustrations, distribution and ecology for each taxon.

The isolation of this continent for millions of years is one of the most important reasons why 2/3 of the Neotropical genera and more than 90% of the species are endemics from this realm. Only seven genera are shared with the Nearctic region, with a generally higher specific richness in the Neotropics (*Apobaetis, Baetodes, Callibaetis, Camelobaetidius* and *Paracloeodes*); only *Americabaetis* and *Baetis* are more diversified in the Nearctic (McCafferty 1998). Several South American species were originally described in the genus *Baetis* and *Pseudocloeon*, but they were all subsequently transferred to other genera such as *Camelobaetidius, Cloeodes, Fallceon* and *Moribaetis* (Lugo-Ortiz and McCafferty 1999d; McCafferty 2000). *Baetis magnus* is the only true *Baetis* which is present in the Neotropical realm; its distribution encompasses a great part of Central America and the South of USA. *Baetis* is present therefore in all the realms. *Fallceon* certainly also has a Panamerican distribution; the generic attribution of *F. candidus* from Taiwan is clearly a mistake and consequently *Fallceon* is not present in the Oriental realm. *Cloeodes* is in fact the only genus present in South America with a wide distribution as species attributed to this genus have been reported from the whole Pantropical area. Most genera possessing an almost worldwide distribution such as *Cloeon* or *Labiobaetis*/*Pseudocloeon* are only missing in the Neotropics; this absence also greatly contributes to the originality of the Neotropical fauna.

Several Neotropical taxa present peculiar adaptations. *Aturbina* is the only genus of the Baetidae without turbinate eyes. *Callibaetis* is one of the few viviparous genera in the Ephemeroptera. *Chane* is a spectacular genus with labium and maxillae extremely well developed for collecting and filtering (Nieto 2003b), presenting similarities with the Afroptropical genus *Ophelmatostoma* (Gillies et al. 1990). Mayo (1973) described the first species collected in a waterfall, *Baetis ellenae*, later transferred to *Mayobaetis* (Waltz and McCafferty 1985). *Cloeodes hydation* is tolerant to short periods of habitat desiccation, this species occurs in small temporary rock pools (Nolte et al. 1996).

Knowledge of the Baetidae from this region has been greatly improved in the last few decades: new species and genera were described (Dominique et al. 2002; Nieto 2003a, 2003b; 2004a, 2004b; Thomas and Peru 2003) and other genera were reviewed (Nieto 2004c; Nieto and Salles 2006; Nieto and Richard 2008). However, there are still regions or even countries with poorly known faunas such as Bolivia, Chile, Peru, Ecuador, Uruguay, and Venezuela; these areas almost certainly possess some endemic taxa which remain to be found. Recent samplings in Brazilian Amazonia allowed the discovery of several new species (Salles and Batista 2004; Salles and Francischetti 2004; Salles et al. 2004, 2005; Salles 2007; Salles and Polegatto 2008), but a great part of this fauna remains unknown (Salles, personal communication).

Nearctic realm

Being the second largest biogeographic region (22.9 million km^2), the Nearctic region encompasses only 20 described genera (Table 1). The rate of endemism is also low. Only five genera have a distribution restricted to this area (25%). Seven genera are shared with the Neotropical region; other genera present a distribution including the Palearctic and/or Oriental areas. Most genera are collector-gatherers or collector-scrapers; no carnivorous Baetidae have been recorded from this region. From the 135 Nearctic species, 114 are endemic (84%), four Holarctic and 17 Panamerican.

The first ephemeropterologists working in this region were Hagen (1861), Walsh (1863a, 1863b) and Eaton (1869, 1870, 1871, 1881, 1883–1888). Banks (1900, 1914, 1918) described eight species of *Callibaetis*, five of which are still valid. With 42 species, McDunnough was the main knowledgeable contributor to Nearctic Baetidae (McDunnough 1922, 1923, 1924, 1925, 1926, 1929, 1931, 1932, 1936, 1939) (Figure 5).

The first accurate revision of all the species from North America was made by Needham et al. (1935). At that time, the concept of Baetidae encompassed several taxonomic groups that are presently considered as separate families. Edmunds' work on mayflies was significant also in this area. He proposed one of the first checklists of mayflies from North America and Mexico (Edmunds and Allen 1957a). His contribution to the biogeography and evolution of Ephemeroptera is still largely accurate (Edmunds 1972, 1975). In 1976, he published, in collaboration with Jensen and Berner, a book with all the species known at that time from North and Central America (Edmunds et al. 1976). In the Baetidae, he described and reassigned several species (Edmunds 1954; Edmunds and Allen 1957b).

In the Nearctic region, contemporary authors such as Jacobus (Jacobus and McCafferty 2005a, 2005b, 2006), Lugo-Ortiz and McCafferty (Lugo-Ortiz and McCafferty 1998d), Waltz (Waltz and McCafferty 1986, 1987b, 1989), and Wiersema (Wiersema, 2000; Wiersema and McCafferty 2004; Wiersema et al. 2004) also contributed to the advanced knowledge of this fauna by the description of genera and species as well as several revisions with generic reassignments. They sustain an actualised web page with a checklist and general information of the mayflies of North and Central America (McCafferty 2009).

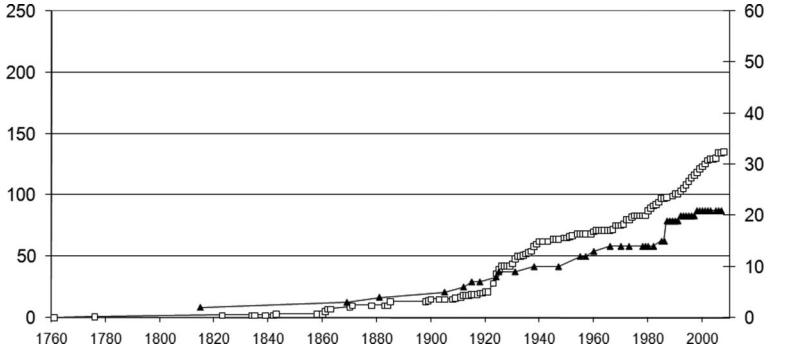

Figure 5. Specific and generic diversity in Nearctic realm: Square: total number of species (left scale). Triangle: total number of genera (right scale).

After 150 years of intensive works, the systematics of Baetidae can be considered as relatively well known, even if some taxomomic problems are still not completely solved. The validity of some species needs to be reviewed: a few of them have never been mentioned since their original description.

Australasian realm

The Australasian realm presently encompasses 40 known species, all of them endemic except for *Cloeon virens*, which is also distributed in the Oriental realm. Twelve genera occur in this area, only six of them being endemic (50%) (Table 1). The non-endemic genera are also distributed in the Oriental region. The presence of some typical Palearctic genera such as *Centroptilum* in Australasia is doubtful and should be clarified in the near future.

Offadens soror was the first species described from this region by Ulmer in 1908. Following Ulmer, Tillyard and Harker provided the only significant works on Australian Baetidae (Tillyard 1936; Harker 1950, 1954, 1957) and until recently (Figure 6). Suter greatly improved the knowledge of the Ephemeroptera fauna in the Australian region, providing the first key for the larval stage of mayflies (Suter 1979). At that time the Baetidae encompassed only 12 species and five genera and interestingly *Bungona* was the only genus which was endemic from this area, all the other Australian species being attributed to Palearctic or Holarctic genera. Later on, Suter described new species and redescribed some genera (Suter 1986, 2000, 2001; Suter and Pearson 2001). He also provided a key specifically for the larvae of Baetidae which included several undescribed species and genera (Suter 1997).

As in other biogeographic regions, Lugo-Ortiz and McCafferty played an important role by describing several species and four endemic genera from this region (Lugo-Ortiz and McCafferty 1998e, 1999a, 1999c) and by reporting genera such as *Cloeodes* or *Labiobaetis*/*Pseudocloeon* (Lugo-Ortiz and McCafferty 1998b; Lugo-Ortiz et al. 1999). They also described several new taxa from New Guinea (Lugo-Ortiz and McCafferty 1999c, Lugo-Ortiz et al. 1999). Baetidae were one of the two families of mayflies reported from the Fiji Islands; although it was only a preliminary study, the diversity was relatively high with 12 species and three genera (Flowers 1990).

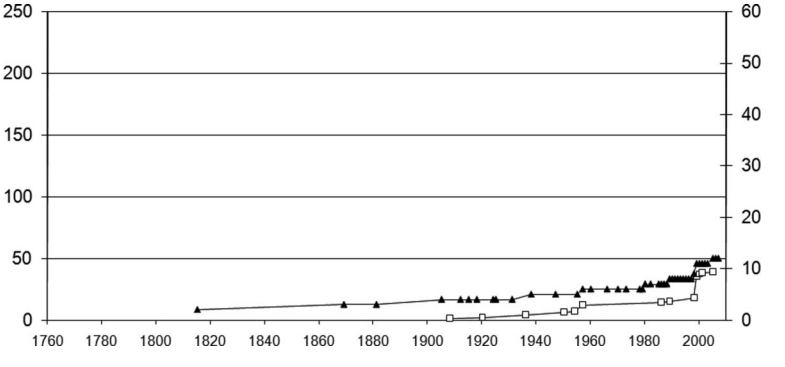

Figure 6. Specific and generic diversity in Australasian realm: Square: total number of species (left scale). Triangle: total number of genera (right scale).

Although the predaceous habit is very unusual in Baetidae, two of the 12 genera of this region are carnivorous: *Echinobaetis* from Sulawesi (Mol, 1989) and *Mystaxyops* from New Guinea (McCafferty and Sun 2005).

New Zealand is the only important landmass where mayflies are present and Baetidae have never been found. This gap remains an enigma. These islands are quite isolated and possess endemic families such as Siphlaenigmatidae and Rallidentidae, but also the widespread family Leptophlebiidae. The Baetidae were also considered to be absent from New Caledonia (Peters 2001). However, in material recently collected in standing waters, half a dozen larvae of *Cloeon* were included (unpublished data). Because of the absence of Baetidae in previous intensive samplings and the high power of dispersion of *Cloeon*, it seems likely that a recent colonisation of the island may be related to human activity. If the Leptophlebiidae were able to remain established on these islands after the break-off of the Gondwana or to colonise the islands afterwards, why were the Baetidae not able to do the same? The question remains open.

Despite recent improvements, the fauna of this region remains insufficiently known in Australia and even more so on other islands and archipelagos. For Australia, a recent estimation established that only about half of the Australian species of Baetidae are described and probably some new genera still need to be established (Jeff Webb, personal communication).

The biogeographic affinities of this region need to be analysed in detail. All the non-endemic genera are also distributed in the Oriental region; they are mainly diversified in the North East of Australasia and had probably dispersed step by step through South East Asia into Australia where their distribution is limited to the North (Lugo-Ortiz and McCafferty 1999b). The genus *Cloeodes* clearly connects this area with the history of Gondwana and the continents placed in the South Hemisphere. Endemic genera such *Edmundsiops*, *Offadens* and *Bungona* may be related to South American taxa (Jeff Webb, personal communication).

Conclusion

Since the establishment of the Baetidae in 1815, their knowledge has been hugely increased due to the efforts of many authors around the world. In 1999, Lugo-Ortiz and McCafferty provided the first worldwide synthesis of this family. They estimated the diversity of this family at 650 species and 87 genera (Lugo-Ortiz and McCafferty 1999b). Ten years later, the number of species has increased by almost one third to reach 894 species. During these 10 years, 142 new species were described, mainly from South America, Madagascar and West Africa. It means that the increase of the total number of species is mainly due to the description of new species, but Lugo-Ortiz and McCafferty had also underestimated the number of species of Baetidae by about 100 species. During these 10 years, 17 genera were described and four were synonymised.

Baetidae are mostly diversified and possess a much higher rate of generic endemism in the Tropics and Southern Hemisphere than in the Northern Hemisphere (Barber-James et al. 2008). The Afrotropics and Neotropics possess by far the most diversified faunas. Despite common Gondwanian origins, these faunas have almost no affinities. The Palearctic fauna shares most genera with the Oriental and/or Afrotropical faunas, as well as the Nearctic fauna. Stepwise colonisation could have occurred through the Palearctic region. Central America

constitutes a bridge between North and South Americas and is under the influence of both areas (McCafferty 1998). The affinities of the Nearctic and Neotropical faunas are mainly due to the presence of North American taxa in Central America. The Oriental fauna is still only partially known: regions of biogeographic importance and with a high potential diversity, such as the Indian subcontinent and South East Asia, remain almost completely unknown. Local studies clearly indicate that the diversity is quite high, but the distribution of the taxa remains unknown. The Oriental realm is therefore probably the most promising and challenging area. Even if the global diversity is probably lower in Australasia, the lack of knowledge of the fauna is obvious, especially in the tropical part of this area such as New Guinea.

The knowledge on systematics and faunistic composition are the first inevitable steps to understand and preserve a natural system. Most of the remaining unknown or poorly known faunas are under a direct human threat. This underlines the urgency of this work before these faunas are definitively lost; this is especially true in most of the tropical rain forest areas where a primordial aquatic fauna is still present. For areas with sufficient knowledge, it is also the duty of the systematists to offer the necessary tools for a correct identification of the taxa. We can only encourage everyone to make our knowledge accessible to others scientists, especially by creating keys and checklists at different systematic levels.

A comprehensive reconstruction of the phylogeny of the Baetidae is also highly necessary. Such a reconstruction should be based on modern tools and include both molecular and morphological characters. It is the only way to solve contradictory suprageneric relationships. Such studies would allow a more accurate understanding of the relationships between the different areas in a global biogeographic approach. They would help to understand the historical influence of Gondwana and Laurasia on the mayfly fauna.

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