THE GENTLE QUEST: 200 YEARS IN SEARCH OF NORTH AMERICAN MAYFLIES

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ABSTRACT

The first 200 years of mayfly faunistics in North America are reviewed. After meager beginnings for most of the Nineteenth Century, a burst of descriptive activity occurred in the 1920's and 1930's, the Golden Age of ephemeropterology, when over half of the currently known valid species were described, mainly by John McDunnough and Jay Traver. Thirteen of the 77 authors of North American mayflies species in the past 200 years have contributed over 80% of the known fauna, and represent all time periods and regions. The North American fauna currently consists of close to 700 species, with only moderate increases expected in the next century. Growth of the known fauna over time, contributions by decade, changes in family and generic classification, regional inventories, pertinent revisions, and major researchers are reviewed. Current status and recommendations for future research are also outlined.

OVERVIEW

As the Twentieth Century comes to a close, it is most befitting to review the historical development of our knowledge of the Ephemeroptera fauna of North America. I refer to the activity of discovering and describing mayflies, and refining our knowledge of them, as the "gentle quest" because of the dedication and labor of love that workers have long demonstrated in their searches for these delicate, exquisite, and challenging aquatic insects.

Because of the relative recent colonization of North America (N. A. hereafter) by Europeans and the subsequent scientific explorations of its vast territories and environments, it was not until the Nineteenth Century (and by far the latter half) that naturalists began to make significant inroads in describing mayflies from the "New World." Initially, small collections from various expeditions in N. A. were being sent to European museums and specialists, with only a few early pioneering American and Canadian naturalists able to study and describe mayflies. It was in the Twentieth Century that home-grown workers took over the task of describing the fauna and that a comprehensive knowledge of its diversity and distribution

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was acquired. In fact, by the end of the Twentieth Century, the major vast diversity of N. A. mayflies will have been discovered.

In the future, remaining voids in N. A. faunistics (especially species ranges) will be filled at an accelerated rate and necessary systematic revisions will continue to be performed. The following historical review of ephemeropterology in N. A. will hopefully provide both perspective and direction for the Ephemeroptera workers of the Twenty-First Century. Clearly, in the Twenty-First Century the outstanding priority of mayfly faunistics and biodiversity will be its dynamic synthesis, including the electronic management and dissemination of data for not only the purposes of deducing the evolutionary history of the fauna and its many ramifications, but predicting the future of the fauna in the face of its special ecological requirements and any impending or potential natural or unnatural alterations to the environment. The rudiments of such efforts are already present in these waning years of the Twentieth Century.

Considerable data are referenced in this historical review, but the numerous particulars concerning the nomenclature of the Mayflies of N. A. that cannot be given in the short space allotted here may be found at *Mayfly Central* at <http://www.entm.purdue.edu/entomology/research/mayfly/mayfly.html>. Descriptive Ephemeroptera literature not cited herein may be found in Needham et al. (1935), McCafferty and Randolph (1998), and revisionary and faunistic works that are referenced herein. Species counts are given principally for their comparative value, considering that exact counts of valid species are subject to revision and thus transitory. Unpublished reports or theses are not referenced or accounted for in the data sets.

The Nineteenth Century

No N. A. mayflies were to be found in the 1758 edition of Linnaeus' «Systema Naturae.» The first recognizable mayfly species known in N. A. was *Ephoron leukon* Williamson, described from New Jersey in 1802. *Siphlonurus noveboracana* (Lichtenstein), which was described from New York in 1796, represents the only description of a mayfly originally taken in N. A. previous to the Nineteenth Century; however, it remains an unresolved nomen dubium. In all, 96 valid species were described from N. A. in the Nineteenth Century.

European specialists who described species in the Nineteenth Century from N. A. included foremost the Reverend Alfred E. Eaton. He authored 42 valid N. A. species from 1871 to 1892, including the renaming of six species. Two of the 42 Eaton species were originally described from elsewhere and only subsequently discovered in N. A. by other workers. Eaton's (1883-88) world monograph was seminal to much of the N. A. research well into the Twentieth Century.

Early Nineteenth Century N. A. descriptions by Europeans included an obscure species described in H. C. C. Burmeister's 1832 "Handbuch der Entomologie." Also, however, Jean Serville, in Guérin-Méneville's 1829 "Iconographie du Règne Animal de C. Cuvier . . ." described what today is arguably the best known species in N. A., the common burrower *Hexagenia limbata* (Serville), often called the Giant Michigan Mayfly. François Pictet had access to certain N. A. materials, and three of his 1843 N. A. species remain valid, although *Stenonema flaveolum* (Pictet) must be regarded as a nomen dubium (McCafferty and Bae, 1992). In 1853, Francis Walker (who in his lifetime proposed a record ca. 20,000 insect names) described 17 Canadian mayflies housed in the British Museum (only seven remain valid). While still in Prussia, Herman Hagen described seven valid new species from N. A. Four homonymic Hagen species were later renamed by Eaton. *Ephemera compar* Hagen, described in 1875 from the Colorado Territory (see Edmunds and McCafferty, 1984) after Hagen moved to America, is now considered extinct (McCafferty, 1996a).

Of the N. A. naturalists who contributed to the faunistics of mayflies in the Nineteenth Century, Williamson's single pioneering contribution has already been mentioned. The famous American naturalist Thomas Say made significant early contributions in the 1820's and 30's with 10 valid species. The less famous, but important Benjamin Walsh described 15 currently valid species from Illinois and added significantly to generic classification. The

Table 1. Notable reviews and revisions since Edmunds et al. (1976). See References for complete citations of works. Numbers of new species, new synonyms, and new combinations are applicable to North American species only. Some earlier reviews are cited in the narrative.

Taxon	Reference	n. sp. / n. syn. / n. comb.		
Ameletus	Zloty (1996)	7	9	0
Acerpenna s.l.	Lugo-Ortiz & McCafferty (1994)	2	0	0
Americabaetis	Lugo-Ortiz & McCafferty (1996a)	0	0	2
Ametropus	Allen & Edmunds (1976)	1	0	0
Anthopotamus	Bae & McCafferty (1991)	0	4	0
Baetis s.l.	Morihara & McCafferty (1979a)	0	13	0
	Waltz & McCafferty (1987a)	0	0	9
	McCafferty & Waltz (1990)	2	3	8
	Lugo-Ortiz & McCafferty (1998)	0	0	10
Baetisca	Pescador & Berner (1981)	0	2	0
Barbaetis s.l.	Lugo-Ortiz & McCafferty (1998)	0	0	1
Brachycercus	Soldán (1986)	5	0	0
Caenis	Provonsha (1990)	1	5	0
Callibaetis	McCafferty & Waltz (1990)	0	10	0
	Lugo-Ortiz & McCafferty (1996b)	1	1	0
Camelobaetidius	Lugo-Ortiz & McCafferty (1995c)	1	5	0
Centroptilum s.l.	McCafferty & Waltz (1990)	0	0	19
Choroterpes	Burian (1995)	0	3	0
Cloeodes	Waltz & McCafferty (1987b)	3	0	0
Cloeon s.l.	McCafferty & Waltz (1990)	0	0	11
Ephemerella s.l.	McCafferty (1977)	0	0	1
	Allen (1980)	0	0	55
Eurylophella	Funk & Sweeney (1994)	3	0	0
	McCafferty & Wang (1994)	0	0	1
Fallceon	Lugo-Ortiz, McCafferty & Waltz (1994)	0	0	1
Farrodes	Domínguez, Molineri & Peters (1996)	1	0	0
Heptagenia s.l.	Flowers (1980)	0	0	20
Heterocloeon	Morihara & McCafferty (1979b)	0	0	1
Homoeoneuria	Pescador & Peters (1980)	2	0	0
Labiobaetis	Morihara & McCafferty (1979c)	1	3	0
Isonychia	Kondratieff & Voshell (1984)	2	11	0
Macdunnoa	Flowers (1982)	1	0	2
Metretopus	Berner (1978)	0	0	0
Moribaetis	Waltz & McCafferty (1985)	1	0	1
Neoephemera	Bae & McCafferty (1998)	0	0	0
Neochoroterpes	Henry (1993)	1	2	3
Pseudiron	Pescador (1985)	0	1	0
Pseudocloeon s.l.	McCafferty & Waltz (1990)	0	3	17
Siphloplecton	Berner (1978)	3	1	0
Stenonema	Bednarik & McCafferty (1979)	0	9	0
Timpanoga	McCafferty & Wang (1994)	0	1	3

demise of Walsh's types in the great Chicago fire of 1871 and subsequent actions to validate the species were discussed by Burks (1953). The considerable descriptive work in the 1860's depicted in Fig. 1 is attributable to Walsh along with Hagen. The French Canadian Léon Provancher studied mayflies from Quebec, which he referred to as the "Petit Faune." The three species he described in 1876 and 1878 are still recognized, although one is dubious. In the final year of the Nineteenth Century, the American Nathan Banks (1900) added four species in the first of his several works that would include mayflies.

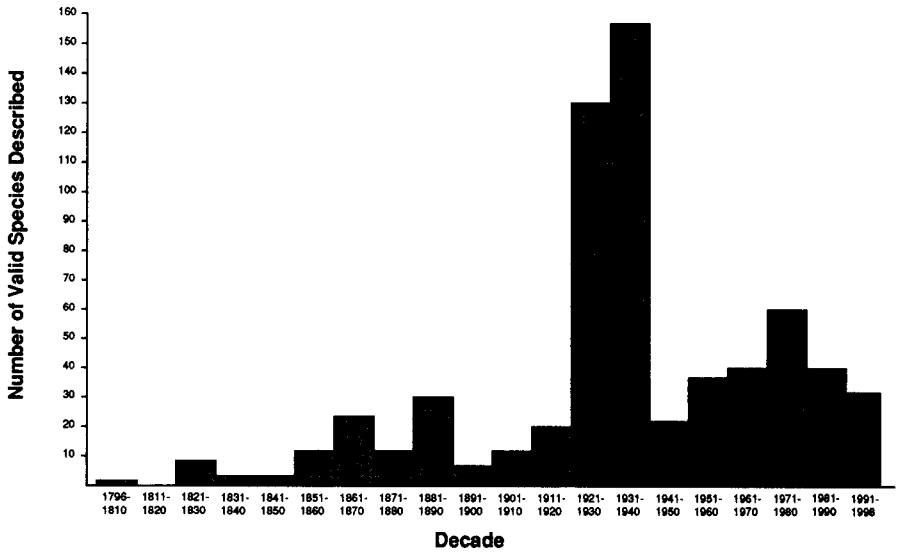

Fig. 1. Relative numbers of mayfly species described from N. A. by decade from 1796 to 1998. Only junior synonyms not counted (homonyms are counted in the decade of original description). The 1990 decade is modified for an additional five new species known to be in preparation.

The Twentieth Century

In the first two decades of the Twentieth Century, 33 valid species were added to the N. A. mayfly fauna. This was a somewhat inauspicious beginning to the century, given the past activity in the late Nineteenth Century and that which was to follow in the 1920's and 30's (Figs. 1 and 2). Contributions to the known fauna were by Banks; by W. A. Clemens; by one of the forefathers of aquatic entomology, James Needham and one of his protégés, Anna Haven Morgan; and by Georg Ulmer. In one sense, N. A. entomology was truly coming of age in this period, because only one species was described by a European (Ulmer).

What surely must be considered the *Golden Age* of N. A. ephemeropterology in terms of discovery and description of new species occurred in the third and fourth decades of the Twentieth Century. This Golden Age is due primarily to the outstanding descriptive works of two of the most prolific mayfly taxonomists the world has ever known: the Canadian John McDunnough and the American Jay Traver. McDunnough proposed 208 species names from 1921 to 1943, and of those, 161 remain valid at the species level; three are now recognized as subspecies only, two are homonymic and have been renamed, and 42 have proven to be junior synonyms. Nearly all of McDunnough's species were described from Canada, and all but one valid species was described in the 1920's and 30's. A complete review of McDunnough's descriptive literature can be found in McCafferty and Randolph (1998). Traver proposed 124 species names in the 1930's. Of those, 84 remain valid and 40 have fallen as synonyms. Although McDunnough essentially finished his Ephemeroptera work by the early 1940's, Traver continued to describe N. A. mayflies through 1968, resulting in 106 valid N. A. species authored by her.

Besides the contribution of over 240 descriptions of valid N. A. species during the 1920's and 30's by McDunnough and Traver, these workers also provided important faunal accounts for N. A. McDunnough (1925) gave a first substantial list for Canada and its provinces, and Traver (1935) reviewed 517 species recognized in N. A. north of Mexico at that

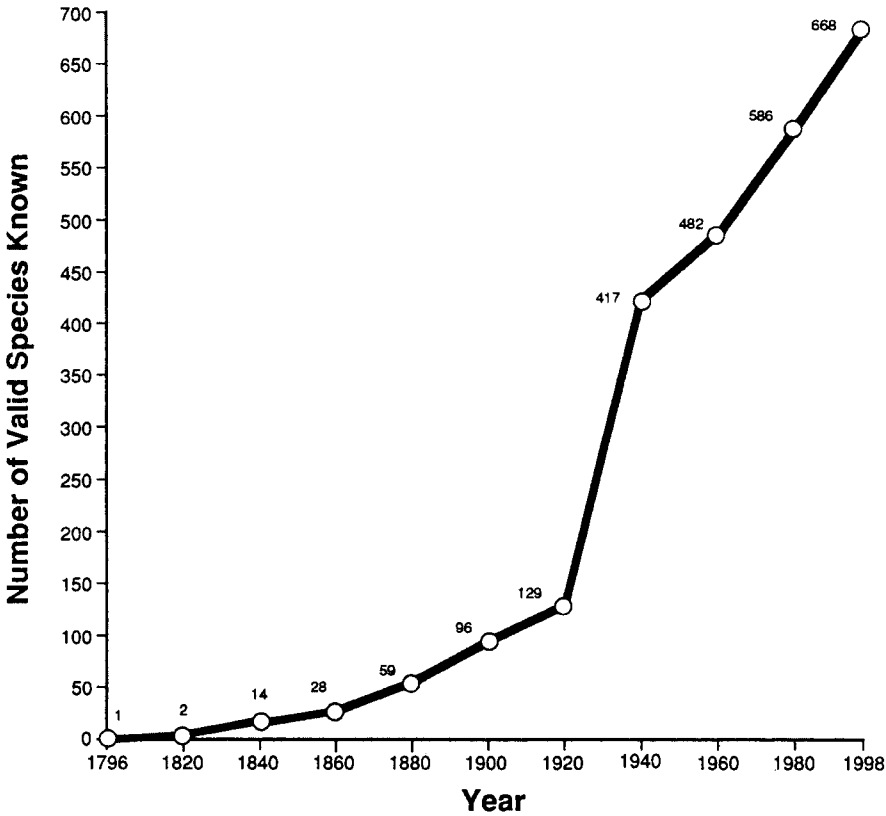

Fig. 2. Growth of the known valid mayfly fauna of N. A., accounting for species originally described from N. A. and subsequently discovered species originally described elsewhere.

time. Traver's synopsis was a remarkable achievement and continued to be of value for the remainder of the Twentieth Century. It should be noted, however, especially for the purposes of tracking faunistic developments, that based on subsequent research, there were actually 137 junior synonyms, two homonyms, and at least one misidentification treated as species, making in actuality a currently valid 370 species treated by Traver (1935). Still, this number represented about a ten-fold increase of N. A. species known since Eaton's monograph. In addition, by 1935 there were an additional 10 N. A. species known that were restricted to Mexico.

Besides the valid McDunnough and Traver species described during the Golden Age, another 31 valid N. A. species were described by the Americans Banks, Lewis Berner, G. S. Dodds, Justin Leonard, Velma Knox Mayo, Needham, Theresa Seemann, and Herman Spieth, and the Canadians Clemens and Fred Ide. These workers tended to be more regional in their scope; for example, Berner worked in Florida, Dodds in Colorado, Ide in Ontario, and Seemann in California. The Englishman D. E. Kimmins described another two species from Mexico, and the Spanish Jesuit P. Longinos Navás described one species from Mexico during this period. New descriptions along with discoveries of European species in N. A during the period resulted in a total of 417 valid species known from N. A. by the end of 1940. The steep growth curve for N. A. known species during the Golden Age is most evident from the graph shown in Fig. 2.

Table 2. Notable North American regional faunistic reports published since Edmunds *et al.* (1976). See References for complete citations of works. Earlier faunistics works are cited in the narrative.

Region	Author	Year
Alabama	Kondratieff & Harris	1986
Alaska	McCafferty	1985
Alberta	McCafferty & Randolph	1998
Arizona	Lugo-Ortiz & McCafferty	1995a
Arkansas	McCafferty & Provonsha	1978
British Columbia	McCafferty & Randolph	1998
Colorado	McCafferty, Durfee & Kondratieff	1993
Connecticut	Burian & Bednarik	1994
Florida	Berner & Pescador	1988
Illinois	Randolph & McCafferty	1998
Indiana	Randolph & McCafferty	1998
Iowa	Klubertanz	1995
Kentucky	Randolph & McCafferty	1998
Maine	Burian & Gibbs	1991
Manitoba	Flannagan & Flannagan	1982
	McCafferty & Randolph	1998
Mexico	McCafferty & Lugo-Ortiz	1996
Michigan	Randolph & McCafferty	1998
Missouri	Sarver & Kondratieff	1997
New Brunswick	Petersen	1989
	McCafferty & Randolph	1998
Newfoundland	Larson & Colbo	1983
	McCafferty & Randolph	1998
New Mexico	McCafferty, Lugo-Ortiz & Jacobi	1997
North Carolina	Unzicker & Carlson	1982
Northern Canada	Harper & Harper	1981
	Cobb & Flannagan	1980
	McCafferty & Randolph	1998
Nova Scotia	Petersen	1989
	McCafferty & Randolph	1998
Ohio	Randolph & McCafferty	1998
Oklahoma	McCafferty, Heth & Waltz	1997
Ontario	McCafferty & Randolph	1998
Saskatchewan	Lehmkuhl	1976
	McCafferty & Randolph	1998
South Carolina	Unzicker & Carlson	1982
South Dakota	McCafferty	1990
Quebec	Dulude	1992
	McCafferty & Randolph	1998
Tennessee	Long & Kondratieff	1997
Texas	Lugo-Ortiz & McCafferty	1995b
Virginia	Kondratieff & Voshell	1983
Wisconsin	Hilsenhoff	1995
	Randolph & McCafferty	1998
West Virginia	Faulkner & Tarter	1977
Yukon	Harper & Harper	1997
	McCafferty & Randolph	1998

Far fewer valid N. A. species were described in the 1940's and 50's (Fig. 1), perhaps because many of the common species had already been described, but also because of the precedence of World War II in the 1940's and its aftermath. The major contributors from the

Table 3. Major historical authors of the North American mayfly fauna (with 10 or more currently valid species). Periods are those in which species counted were named. Species counts are of currently valid North American species.

Worker	Period	Species
Say, T.	1823 - 1839	10
Walsh, B. D.	1862 - 1863	15
Eaton, A. E.	1871 - 1892	42
Banks, N.	1900 - 1924	13
Needham, J. G.	1903 - 1932	13
McDunnough, J.	1921 - 1943	161
Traver, J. R.	1931 - 1968	106
Mayo, V. K.	1939 - 1973	11
Berner, L.	1940 - 1978	22
Day, W. C.	1952 - 1954	12
Edmunds, G. F.	1957 - 1976	23
Allen, R. K.	1957 - 1988	72
McCafferty, W. P.	1977 - 1998	33

period tended to be regional in their scope and included Berner (Southeast), B. D. Burks (Illinois), Richard Daggy (Minnesota), Bill Day (California), and Mayo (West and Southwest). Traver also described eight valid species during this period. Minor descriptive contributions were made by Dick Allen, George Edmunds, Ide, McDunnough, Bill Peters, and Ulmer (the latter being the only non-N. A. species author in the period).

The 1950's did, however, witness the first of regional checklists or more comprehensive regional faunal accounts of mayflies in N. A. Two of the works, in particular, were noteworthy because of the wealth of specific information they contained: the Florida fauna was treated extensively by Berner (1950) and the Illinois fauna extensively by Burks (1953). A work on California by Day (1956) contained keys but was quite preliminary, and checklists were given for Utah by Edmunds (1954) and Oregon by Allen and Edmunds (1956).

Dick Allen led the way in descriptive taxonomy in the next two decades in authoring or co-authoring 58 of the 99 valid N. A. species described between 1961 and 1980. A good deal of the species discoveries were from the relatively poorly known southwestern and Mexican regions. In particular, this involved major contributions to the knowledge of the austral genera *Baetodes* by Cohen and Allen (1972), *Thraulodes* by Traver and Edmunds (1967), *Camelobaetidius* by Traver and Edmunds (1968), and *Leptohyphes* by Allen and Brusca (1973). Many of Allen's singular descriptions were also from this area, for example, from his work on *Tricorythodes* (Allen, 1967). In addition to the authors mentioned above, minor descriptive contributions were made by Berner, F. L. Carle, E. S. M. Chao, D. L. Collins, Françoise Harper, Steve Jensen, J. I. Kilgore, Ralph Kirchner, Dick Koss, Dennis Lehmkuhl, Phil Lewis, Mayo, Pat McCafferty, Dennis Morihara, Chad Murvosh, Ingrid Müller-Liebenau (the only non-N. A. species author in this period), Manny Pescador, Peters, R. F. Schneider, and Donald Tarter. The few contributions to regional faunas published during this period involved Michigan (Leonard and Leonard, 1962), British Columbia (Scudder, 1975), and Arkansas (McCafferty and Provonsha, 1978).

The advent of co-authorship of taxonomic descriptions also became apparent in this time period, although one species had already been co-authored by Clemens and Leonard earlier. The renowned American ephemeropterist George Edmunds can be credited as much as anyone with this new trend. In the 1960's he co-authored descriptions by Edmunds and Allen; Edmunds and Traver; Edmunds, Berner and Traver; and Allen and Edmunds (see McCafferty, 1995). Such co-authorship marked the beginning of a new era of team work and schools among mayfly taxonomists. Beginning in the 1970's, Allen co-authored species with

Table 4. Evolution of family classification of the North American mayfly fauna in the Twentieth Century. Listing order of modern families does not necessarily indicate relationships.

Needham *et al.* (1935)	Burks (1953)	Edmunds *et al.* (1976)	McCafferty (1997)
Baetidae	=Baetidae	=Baetidae	=Baetidae
		+Siphlonuridae	=Siphlonuridae
			+Acanthametropodidae[1]
			+Ameletidae
			+Isonychiidae
	+Ametropodidae	=Ametropodidae	=Ametropodidae
		+Metretopodidae	=Metretopodidae
		+Heptageniidae partim	=Pseudironidae
	+Baetiscidae	=Baetiscidae	=Baetiscidae
	+Caenidae	=Caenidae	=Caenidae
		+Tricorythidae	=Leptohyphidae
	+Ephemerellidae	=Ephemerellidae	=Ephemerellidae
	+Leptophlebiidae	=Leptophlebiidae	=Leptophlebiidae
	+Oligoneuriidae[2]	=Oligoneuriidae	=Oligoneuriidae
Heptageniidae	=Heptageniidae	=Heptageniidae partim	=Heptageniidae
			+Arthropleidae
Ephemeridae	=Ephemeridae	=Ephemeridae	=Ephemeridae
		+Behningiidae[1]	=Behningiidae
		+Polymitarcyidae	=Polymitarcyidae
		+Potamanthidae	=Potamanthidae
	+Neoephemeridae	=Neoephemeridae	=Neoephemeridae

[1] Taxa not known in North America in 1935 or 1953.
[2] Taxa not known in North America in 1935.

seven different workers. Such collaborative efforts were commonplace for the remainder of the Twentieth Century.

Edmunds (1962) provided a useful account of the type localities of all of the N. A. species recognized at that time. The pivotal "The Mayflies of North and Central America," by Edmunds, Jensen, and Berner, appeared in 1976. This work concentrated on generic treatments, but also listed a total of 657 N. A. species. Also, of considerable significance in the 1960's was the first comprehensive restudy and review of an entire large group of N. A. mayflies: the outstanding series dealing with the family Ephemerellidae by Allen and Edmunds (1959, 1961ab, 1962ab, 1963ab, 1965). Both new species and new synonymies were included in the latter, but perhaps their most useful aspects were extensive species keys for what are now considered seven genera.

Near the end of the period, major revisionary works were published for the large and problematic genera *Baetis* by Morihara and McCafferty (1979a) and *Stenonema* by Bednarik and McCafferty (1979). These revisions were the first to demonstrate that there were a large number of synonyms amongst the N. A. species names, thus indicating that a tendency toward typology had been common among many early workers. For example, of those 657 N. A. species listed by Edmunds et al. (1976), actually only 535 are currently considered valid. Other revisionary works in the final two decades of the Twentieth Century (see Table 1), such as that of Kondratieff and Voshell (1984) on *Isonychia* and McCafferty and Waltz (1990) on Baetidae in general would continue to demonstrate that the fauna had been over-described. Table 1 indicates that among combined revisionary works, synonyms have largely outnumbered new species in the last quarter of the century. Additions subsequent to the publication of Edmunds et al. (1976) with respect to new descriptions and to discoveries of species originally described from the Palearctic or Neotropics are greater than might be suggested in Fig. 2. This is because considerable synonymyzing of previously proposed species names also took place after 1976.

Table 5. Growth of genera as recognized in North America, based on current, valid genera discovered or described from North America, raised to rank or changed in name by the interval dates indicated. For authors of genera, see *Mayfly Central.*

Known by 1900	Added 1901-1935	Added 1936-1976	Added 1977-1997
Ameletus	*Ametropus*	*Acanthametropus*	*Acanthomola*
Baetis	*Anepeorus*	*Analetris*	*Acentrella*
Baetisca	*Arthroplea*	*Apobaetis*	*Acerpenna*
Brachycercus	*Centroptilum*	*Baetodes*	*Amercaenis*
Caenis	*Cinygmula*	*Cloeon*	*Americabaetis*
Callibaetis	*Habrophlebia*	*Dolania*	*Anthopotamus*
Campsurus	*Habrophlebiodes*	*Edmundsius*	*Attenella*
Choroterpes	*Heterocloeon*	*Epeorus*	*Barbaetis*
Cinygma	*Ironodes*	*Homoeoneuria*	*Camelobaetidius*
Ephemera	*Metretopus*	*Lachlania*	*Caudatella*
Ephemerella	*Neoephemera*	*Leptohyphes*	*Caurinella*
Ephoron	*Paraleptophlebia*	*Litobrancha*	*Cercobrachys*
Euthyplocia	*Parameletus*	*Paracloeodes*	*Cloeodes*
Heptagenia	*Pseudiron*	*Stenacron*	*Diphetor*
Hexagenia	*Siphlonisca*	*Tortopus*	*Drunella*
Isonychia	*Siphloplecton*	*Traverella*	*Eurylophella*
Leptophlebia	*Stenonema*		*Fallceon*
Pentagenia	*Thraulodes*		*Farrodes*
Rhithrogena	*Tricorythodes*		*Hydrosmilodon*
Siphlonurus			*Labiobaetis*
			Leucrocuta
			Macdunnoa
			Moribaetis
			Neochoroterpes
			Nixe
			Procloeon
			Pseudocentroptiloides
			Raptoheptagenia
			Serratella
			Timpanoga

Some 69 valid N. A. species were described between 1981 and the time of this writing (1998). I know of at least five more that will be published by the end of the century. McCafferty authored or co-authored 29 species in this period. His co-authors included Carlos Lugo-Ortiz, Arwin Provonsha, Bob Waltz, and Nick Wiersema, all of whom were major contributors in their own right (see e.g., Tables 1 and 2). The other 40 species were authored by an array of workers, with Thomas Soldán from the Czech Republic and Jack Zloty from Alberta each contributing seven species. More minor contributions were made by Javier Alba-Tercedor (the only non-N. A. species author besides Soldán in the period), R. K. (Dick, above) Allen, R. T. Allen, W. F. Botts, W. L. Burrows, J. R. Davis, Richard Durfee, J. L. Evans, John Flannagan, Wills Flowers, D. H. Funk, F. Harper, P. Harper, Brad Henry, Boris Kondratieff, J. H. Kennedy, Lehmkuhl, R. G. Lowen, Murvosh, G. Roemhild, J. R. Voshell, and Eric Whiting.

There have been major advances in our knowledge of distributional ranges of N. A. species in the last two decades of the Twentieth Century. These data have been contributed via numerous small published reports of individual species records as well as from a variety of faunistic studies and inventories (Table 2), ranging from basic checklists to extensive faunal analyses (some partial state inventories are not shown). The most extensive study is that of Randolph and McCafferty (1998) for the U. S. states of Kentucky, Illinois, Indiana, Michigan, Ohio, and Wisconsin, where not only were extensive habitat, drainage system,

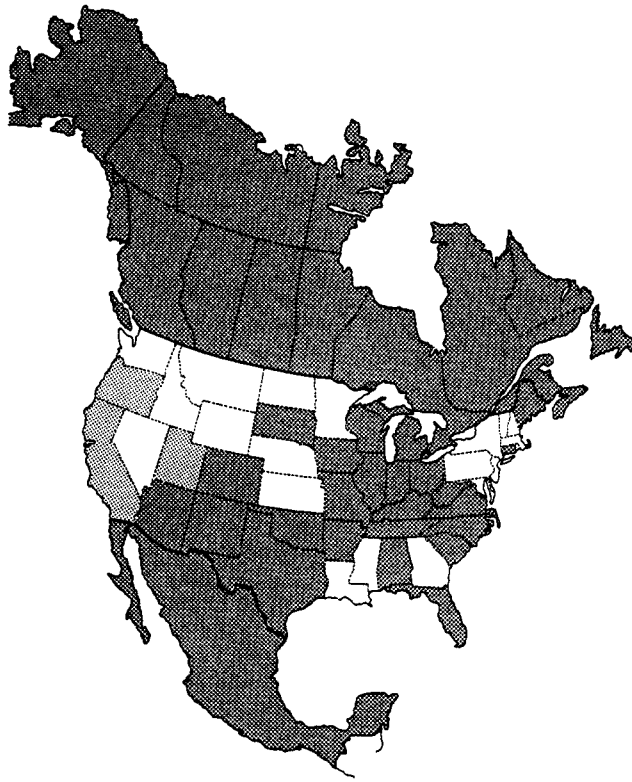

Fig. 3. North American subregions with significant inventories (those inventoried only previous to 1976 shown by slight shading; those since 1976 are darkly shaded; unpublished surveys and some partial inventories not shown).

historical geology, and fine geography detailed, but also risk analyses of species included. Studies of the Maine and New Mexico faunas are also especially notable (see Table 2). During the 1990's, comprehensive documentation of the entire faunas of Canada (McCafferty and Randolph, 1998), including provincial and territorial distributions, and Mexico (McCafferty and Lugo-Ortiz, 1996) were provided for the first time. Regions that have been surveyed are highlighted in Fig. 3. Those studied only prior to 1976 undoubtedly require considerable updating as do some others.

As of this writing, there are close to 700 valid species of mayflies in N. A. The net growth of the known fauna over time can be visualized from Fig. 2. The growth has been relatively steady since the Golden Age in the 1920's and 30's (see also Fig. 1). Eventually when lesser known subregions such as Alaska and Mexico are more fully documented, I expect the growth curve (Fig. 2) to flatten out, with species discoveries more or less balanced by new synonyms. Also as of this writing, some 321 species are currently known from Canada (McCafferty and Randolph, 1998), 124 species from Mexico (McCafferty and Lugo-Ortiz, 1996; McCafferty et al., 1997; McCafferty, unpublished), 564 species from the conterminous United States (McCafferty, unpublished), and only 19 species from Alaska (McCafferty, 1985, 1994). Updates of these numbers may be found on the WWW at *Mayfly Central*. The 13 primary authors of N. A. mayflies and their contributions of 543 valid species, or over 80% of the known fauna mentioned above, are summarized in Table 3.

Nine N. A. species were originally described from Europe and later discovered in N. A. (similarly, five species originally described from N. A. were later discovered to occur in the Palearctic) (Flowers, 1989; McCafferty, 1985, 1994; McCafferty and Randolph, 1998). Also several species were originally described from Central America, South America, or the Antilles and only subsequently discovered in Mexico. The dynamic biogeographic interchange of lineages between North and South America was detailed by McCafferty (1998). *Euthyplocia hecuba* (Hagen), *Hexagenia albivitta* (Walker), and *H. mexicana* Eaton are the only species known to co-occur in North and South America. The only mayfly known from every subregion of N. A. (including Alaska and the Yukon) is *Baetis tricaudatus* Dodds; interestingly, however, it is not known beyond N. A.

This review has dealt essentially with species discoveries; however, higher classification has also developed immensely during the Twentieth Century. Transitions reflect not only a change from a phenetic to an evolutionary to a phylogenetic basis (see Edmunds and Traver, 1954; McCafferty and Edmunds, 1979; McCafferty, 1991), but also reflect the intent to impart substantial information content with more finite taxa, such as genera. Tables 4 and 5 illustrate the major transitions and advancements in familial and generic classification, respectively, as they have pertained to the N. A. fauna.

The last published checklist for the entire N. A. continent was given by McCafferty (1996a). However, the rate of change in nomenclature instigated by on going revisionary work can and often does necessitate modifications to such lists before they appear in print. To alleviate this problem and to provide immediately available, up to date tracking of the fauna and its nomenclature, "The Mayflies of North America" has existed on the WWW as part of *Mayfly Central* since 1995 (McCafferty 1996b). It provides a full listing of species and facilitates searching any name (synonym, homonym, misspelling, generic combination, etc.) applicable to any species. It also provides regional distribution data for each species. Such data management and presentation are previews of the kind of utilitarian information that is in store for the Twenty-First Century as the gentle quest continues.

The Future

A status report for the systematics of N. A. Ephemeroptera was given by McCafferty et al. (1990), and many recommendations for future priorities of research indicated at that time still hold. The fauna of special habitats of large rivers continue to require study, as does the general fauna of several geographical regions that were indicated. Regional priorities are best judged from Table 2 and Fig. 3. Certainly, there remain genera that require revision. This is particularly true for many of the heptageniid genera. The most needed revisionary work in the Baetidae involves the genera *Centroptilum* and *Procloeon*, and they are now being comprehensively studied. The leptohyphid genera *Leptohyphes* and *Tricorythodes* require revision because they were probably largely over-described as species and surely involve several additional genera. The caenid genus *Brachycercus* also remains problematic. The large leptophlebiid genus *Paraleptophlebia* and siphlonurid genus *Siphlonurus* may appear to require revision; however, that remains to be seen because I have found that most current species have morphological integrity as adults. The challenge will be to delineate the species of these genera in the larval stage.

As our knowledge of species improves appreciably, species keys, now unavailable for many genera, must be provided. Larval and adult stages need to be associated for the many species known only as one or the other. Distributional work needs to be taken to the next level by plotting species against numerous parameters at a finer level, and incorporating modern GIS (geographic information systems) analysis to help explain past and present distributions. Perhaps most importantly, data should be used to determine species at risk from present, impending, or potential environmental degradation.

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