
1 **George Edmunds, ephemeropterist par excellence**

W.P. McCafferty

*Department of Entomology, Purdue University, West Lafayette, IN
47907 USA*

This Seventh International Conference on Ephemeroptera is dedicated to our esteemed colleague Professor George F. Edmunds, Jr. (1920-) in recognition of his life-long contributions to our knowledge of Ephemeroptera and in recognition of his role as perhaps the foremost 20th-century facilitator of such studies. Those who have dealt with mayflies in one way or another and have been advised and encouraged by George Edmunds over the years can attest to his enormous influence on this entire field of study.

On the subject of Ephemeroptera, George has, to date, authored or co-authored one book; 95 monographs, journal articles or scientific notes; two major review articles; eight Ephemeroptera chapters or sections in various texts, encyclopedias and collections; and seven book reviews or discussions. These works are listed in a chronological and numbered Edmunds Ephemeroptera bibliography that is appended below and referenced herein.

George's publications have dealt principally with the elucidation of the taxonomy of mayflies, especially of western North America, and with revising the concepts and taxonomy of numerous genera, for which he importantly incorporated an evolutionary basis and world perspective. Table 1 is an alphabetical checklist of the 35 genera and 79 species of mayflies attributed to George Edmunds either wholly or in part. Actually, there are few genera he has not touched on in one way or another. His systematics works have a strong theoretical framework, and a recurrent theme includes his search for evolutionary relationships and history (e.g., 30, 73, 75), and consistency and practicality in his classifications (e.g., 48, 61). It is also apparent from his systematics that George always regarded larvae and adults equally as character sources. He found that because these different stages often evolved at different rates as a response to their different environmental pressures, they not only made the study of Ephemeroptera phylogeny fascinating but often at the same time made higher classification of the Ephemeroptera a particularly challenging task.

During my doctoral studies with the renown evolutionist Herbert H. Ross, I once asked Herb which of his contemporaries he most admired. While I expected someone such as a Mayr, Huxley, Michener, Simpson, Stebbins, Dobzhansky or Hennig to come to mind, Herb unhesitatingly responded with the name George Edmunds. I am not sure George ever realized this, but I am sure he will regard it as a great tribute from a highly respected colleague.

George's Ephemeroptera contributions have by no means been limited to systematics. His work on the evolution of wings in insects (16) provided a functional morphology of mayfly wing veins and clearly established the primary homologies of Ephemeroptera wing venation. Today, this work is still cited as a major contribution in the study of insect and wing evolution. Field observations of mayfly ecology and behaviour made by George are many and important, and hopefully will not be overlooked even though they are often found couched among discussions in his systematics works. In certain cases, however, i.e., ovoviviparity (1), flight exuviation (18), predatory habits (23, 37) and emergence and mating behaviour (97), he did devote entire papers to the subjects. His works on the life histories of *Ephoron album* (19) and *Parameletus columbiae* (24) are classical studies. His work on the mayfly subimago (110) is monumental, demonstrating his acute ability to synthesize his observations and knowledge of systematics, phylogeny, morphology, paleontology, developmental biology, behaviour and ecology into unified explanatory theories, in this case involving the origin and function of the unique subimago life stage, which is so emblematic of the Ephemeroptera.

George's book on the mayflies of North and Central America (82), written with Steve Jensen and Lewis Berner and published in 1976 after many years of work, brought together all information on the subject and was the first major compilation in the Western Hemisphere since *The Biology of Mayflies* by Needham, Traver and Hsu written in 1935. Although out of print for some years, it remains one of the major sources of utilitarian information on mayflies required by biologists in North America, and serves as the benchmark upon which all subsequent taxonomic research in the area is measured.

More than anything else, George deservedly should be considered the first biogeographer of Ephemeroptera and is unquestionably one of the foremost biogeographers in general of the modern era. While cosmopolitan ephemeropterists that preceded him, such as A. E. Eaton, G. Ulmer and J.-A. Lestage, sought to classify and catalogue mayflies from the far corners of the globe, George, from the very outset of his investigations, sought to discover the dynamic relationships of all biogeographic regions and mayfly faunas of the world, and above all to develop a distributional history of Ephemeroptera (22, 73, 81, 93, 99, 101, 113). Before it was a common practice and before biogeographic applications of cladistics, or cladistics itself for that matter, had been generally accepted, George realized that historical biogeography had to be grounded in solid phylogenetic data.

From 1956 to 1980, George received ten grants from the National Science Foundation in support of his research on Ephemeroptera. These allowed him and his students to collect mayflies from critical biogeographic areas. His around-the-world expeditions not only allowed him to study most world genera first hand and rear innumerable species to obtain necessary larval-adult associations, but also to accumulate the world's premier international collection of mayflies. This collection has served as the basis of much of his research as well as that of many others with whom he has generously shared this valuable resource. Vladimir Landa, Thomas Soldán, Ingrid Müller-Liebenau and Patrick McCafferty conducted extensive research at George's laboratory, and visitors have included such international notables as Joachim Illies, Edjar Riek and Herbert Ross.

Perhaps the most important biogeographic research contribution made by George was his demonstration of the relationships of mayflies from Australia, New Zealand and Chile. Prior to the general confirmation of continental drift via the elaboration of plate tectonics, it was researchers such as Lars Brundin and George Edmunds who discovered clear and precise evidence from the study of insects that these Southern Hemisphere regions must have been connected by a Transantarctica. Not only did George uncover entomological proofs of continental drift, but he was also able to show the sequence of continental breakup of Gondwana from his template of mayfly phylogeny (e.g., 81). In this respect George was an early pioneer of what would come to be known as vicariance biogeography.

Anyone who has engaged George in conversations about mayflies quickly becomes aware of his vast knowledge of the group, and one gets the impression that he must possess more unwritten information about mayflies than he has written, even given his lengthy bibliography. This, I believe, is a fair assessment, and it is why I once, only somewhat facetiously, wrote that a great deal of unpublished information had been stored away in his cerebral database.

George's entire professional career was spent at the University of Utah in Salt Lake City, where he received the Distinguished Research Award in 1974, and in 1989 he received the Distinguished University Service Award from the Utah Academy of Sciences. Although he had lucrative offers for administration or staff positions at larger or more prestigious universities in the midwest and eastern United States, George chose to remain in the city of his birth and to devote his time primarily to Ephemeroptera and other endeavours, among which happened to be hunting and fishing. Administrative duties would have hardly left time for his prolific studies of Ephemeroptera, and no other place of residence could quite match the lure of trout, mule deer and ring neck pheasants he had culled from the countryside over the years, or his favourite of all, the diverse migratory populations of ducks found along the marshes of the Great Salt Lake.

As a teacher at the University of Utah, George incorporated his general and special knowledge into his courses and presentations. My first encounter with George was as a student in an undergraduate course he offered in evolution. I remember being amazed by two things in particular. First, unlike most professors I'd experienced, he would regularly lecture without using notes. Second, he demonstrated an incredible breadth of knowledge of natural history and was able to give examples of phenomena based on his own personal experiences as a biologist. I was getting evolution straight from the horse's mouth. It was in another course from him on principles of systematics that I first learned of the many rules and nuances of zoological nomenclature. These he colourfully accented with examples from mayfly taxonomy, the good, the bad and the ugly.

As a graduate student of Ephemeroptera, George had studied with Jay Traver at the University of Massachusetts. Jay Traver had been James Needham's student at Cornell University, and James Needham had been John Comstock's student at Cornell. John Comstock, of course, is the acknowledged father of entomological education in America, James Needham is regarded by most entomologists to be the father of aquatic entomology, and Jay Traver was one of the primary early contributors of Ephemeroptera research in North America. As a major professor and mentor, George continued this rich entomological heritage, spawning a continuing legacy of Ephemeroptera research for now and in the future. Of his 19 graduate students, eight (Table 2) conducted research on Ephemeroptera topics. Of those eight, three (Allen, Peters and McCafferty) continued their work on Ephemeroptera over the years and have in turn produced another larger generation of ephemeropterists through students of their own. In addition, three postdoctoral fellows have studied mayflies with George (Table 2).

Among George's many accolades and professional memorabilia are two mayfly genera and ten mayfly species (Table 3), not to mention a stonefly, beetle and crane fly, that have thus far been named after him by colleagues.

It is befitting that this dedication of an international conference on Ephemeroptera recognizes George Edmunds, ephemeropterist par excellence, and expresses the continued respect and admiration of everyone who has, like him, marvelled at the extraordinary group of animals known as mayflies.

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Appendix

The George Edmunds Bibliography of Ephemeroptera

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Table 1. Genera and species of Ephemeroptera described by George Edmunds.

Generic Group Names

Aethephemera McCafferty and Edmunds, 1973
Analetris Edmunds, 1972
Attenella Edmunds, 1959
Caudatella Edmunds, 1959
Crinitella Allen and Edmunds, 1963
Dactylobaetis Traver and Edmunds, 1968
Dannella Edmunds, 1959
Dicrephemera McCafferty and Edmunds, 1973
Dolania Edmunds and Traver, 1959
Fasciamirus Peters, Peters and Edmunds, 1990
Gilliesia Peters and Edmunds, 1970
Hapsiphlebia Peters and Edmunds, 1972
Hyrtanella Allen and Edmunds, 1976
Indialis Peters and Edmunds, 1970
Kimminsula Peters and Edmunds, 1970
Kouma Peters, Peters and Edmunds, 1990
Lepegenia Peters, Peters and Edmunds, 1978
Lepeorus Peters, Peters and Edmunds, 1978
Maheathraulius Peters, Gillies and Edmunds, 1964
Masharikella Peters, Gillies and Edmunds, 1964
Megaglena Peters and Edmunds, 1970
Meridialaris Peters and Edmunds, 1972
Minyphlebia Peters and Edmunds, 1970
Miroculus Edmunds, 1963
Nesophlebia Peters and Edmunds, 1964
Notobaetis Morihara and Edmunds, 1980

Table 1. (continued)

Notophlebia Peters and Edmunds, 1970
Penaphlebia Peters and Edmunds, 1972
Serratella Edmunds, 1959
Simulacala Peters, Peters and Edmunds, 1990
Spinadis Edmunds and Jensen, 1974
Stygifloris Bae, McCafferty and Edmunds, 1990
Sulawesi Peters and Edmunds, 1990
Tanycola Peters and Edmunds, 1970
Traverella Edmunds, 1948

Species Group Names

Ametropus ammophilus Allen and Edmunds, 1976
Analetris eximia Edmunds, 1972
Baetis caurinus Edmunds and Allen, 1957
Baetisca columbiana Edmunds, 1960
Camelobaetidius mantis Traver and Edmunds, 1968
Centroptilum oreophilum Edmunds, 1954
Centroptilum selandorum Edmunds, 1954
Dactylobaetis anubis Traver and Edmunds, 1968
Dactylobaetis cayumba Traver and Edmunds, 1968
Dactylobaetis cepheus Traver and Edmunds, 1968
Dactylobaetis chiapas Traver and Edmunds, 1968
Dactylobaetis jenseni Traver and Edmunds, 1968
Dactylobaetis mexicanus Traver and Edmunds, 1968
Dactylobaetis musseri Traver and Edmunds, 1968

Table 1. (continued)

<i>Dactylobaetis penai</i> Traver and Edmunds, 1968
<i>Dactylobaetis phaedrus</i> Traver and Edmunds, 1968
<i>Dactylobaetis serapis</i> Traver and Edmunds, 1968
<i>Dactylobaetis warreni</i> Traver and Edmunds, 1968
<i>Dactylobaetis zenobia</i> Traver and Edmunds, 1968
<i>Dolania americana</i> Edmunds and Traver, 1959
<i>Epeorus margarita</i> Edmunds and Allen, 1964
<i>Ephemerella nadinae</i> McCafferty and Edmunds, 1973
<i>Ephemerella alleni</i> Jensen and Edmunds, 1966
<i>Ephemerella berneri</i> Allen and Edmunds, 1958
<i>Ephemerella cascadia</i> Allen and Edmunds, 1961
<i>Ephemerella coheri</i> Allen and Edmunds, 1963
<i>Ephemerella crenula</i> Allen and Edmunds, 1965
<i>Ephemerella gilliesi</i> Allen and Edmunds, 1963
<i>Ephemerella hecuba pacifica</i> Allen and Edmunds, 1959
<i>Ephemerella heterocaudata californica</i> Allen and Edmunds, 1961
<i>Ephemerella heterocaudata circia</i> Allen and Edmunds, 1961
<i>Ephemerella hispida</i> Allen and Edmunds, 1965
<i>Ephemerella lacustris</i> Allen and Edmunds, 1965
<i>Ephemerella nepalica</i> Allen and Edmunds, 1963
<i>Ephemerella orestes</i> Allen and Edmunds, 1961
<i>Ephemerella rossi</i> Allen and Edmunds, 1965
<i>Ephemerella simila</i> Allen and Edmunds, 1965
<i>Ephemerella traverae</i> Allen and Edmunds, 1963
<i>Ephemerella uenoi</i> Allen and Edmunds, 1963
<i>Ephemerella velmae</i> Allen and Edmunds, 1963
<i>Ephemerella verruca</i> Allen and Edmunds, 1965
<i>Ephemerellina crassi</i> Allen and Edmunds, 1963

Table 1. (continued)

<i>Fasciamirus rae</i> Peters, Peters and Edmunds, 1990
<i>Homoeoneuria dolani</i> Edmunds, Berner and Traver, 1958
<i>Hyrtanella christineae</i> Allen and Edmunds, 1976
<i>Isca janiceae</i> Peters and Edmunds, 1970
<i>Isca serendiba</i> Peters and Edmunds, 1970
<i>Kouma adusta</i> Peters, Peters and Edmunds 1990
<i>Kouma annulata</i> Peters, Peters and Edmunds, 1990
<i>Kouma aurata</i> Peters, Peters and Edmunds, 1990
<i>Kouma becki</i> Peters, Peters and Edmunds, 1990
<i>Lachlania powelli</i> Edmunds, 1951
<i>Lepegenia lineata</i> Peters, Peters and Edmunds, 1978
<i>Lepeorus goyi</i> Peters, Peters and Edmunds, 1978
<i>Lepeorus goyi australis</i> Peters, Peters and Edmunds, 1978
<i>Lepeorus calidus</i> Peters, Peters and Edmunds, 1978
<i>Lepeorus calidus notialis</i> Peters, Peters and Edmunds, 1978
<i>Lepeorus thierryi</i> Peters, Peters and Edmunds, 1978
<i>Microculus rossi</i> Edmunds, 1963
<i>Nesophlebia adusta</i> Peters and Edmunds, 1964
<i>Notobaetis penai</i> Morihara and Edmunds, 1980
<i>Simulacala massula</i> Peters, Peters and Edmunds, 1990
<i>Simulacala milleti</i> Peters, Peters and Edmunds, 1990
<i>Simulacala notialis</i> Peters, Peters and Edmunds, 1990
<i>Spinadis wallacei</i> Edmunds and Jensen, 1974
<i>Stygifloris sabahensis</i> Bae, McCafferty and Edmunds, 1990
<i>Sulawesi haema</i> Peters and Edmunds, 1990
<i>Thraulodes ephippiatus</i> Traver and Edmunds, 1967
<i>Thraulodes gonzalesi</i> Traver and Edmunds, 1967
<i>Thraulodes itatiajanus</i> Traver and Edmunds. 1967

Table 1. (continued)

Thraulodes lunatus Traver and Edmunds, 1967
Thraulodes osiris Traver and Edmunds, 1967
Thraulodes packeri Traver and Edmunds, 1967
Thraulodes papilionis Traver and Edmunds, 1967
Thraulodes regulus Traver and Edmunds, 1967
Thraulodes schlingeri Traver and Edmunds, 1967
Thraulodes spangleri Traver and Edmunds, 1967
Thraulodes ulmeri Edmunds, 1950
Thraulodes zonalis Traver and Edmunds, 1967

Table 2. George Edmunds' graduate and postdoctoral students of Ephemeroptera.

R.K. Allen, M.S. 1955, Ph.D. 1960, postdoctoral 1962-64
W.L. Peters, M.S. 1962, Ph.D. 1966
J.S. Packer, M.S. 1965
S.L. Jensen, M.S. 1966, Ph.D. 1972
R.W. Koss, Ph.D. 1969
W.P. McCafferty, M.A. 1969
S.H. Snow, M.S. 1970
A.F. Bednarik, postdoctoral 1971-72
M. Winokur, Ph.D. 1980
T. Fink, postdoctoral 1986-88

Table 3. Mayflies named after George Edmunds.

<i>Archobehningia edmundsi</i> Tshernova
<i>Baetodes edmundsi</i> Koss
<i>Brachycercus edmundsi</i> Soldán
<i>Edmundsius agilis</i> Day
<i>Edmundsula lotica</i> Sivaramakrishnan
<i>Ephemerella edmundsi</i> Allen
<i>Isonychia edmundsi</i> Kondratieff
<i>Jappa edmundsi</i> Skedros and Polhemus
<i>Misthodotes edmundsi</i> Carpenter
<i>Playtbaetis edmundsi</i> Müller-Liebenau
<i>Pseudocloeon edmundsi</i> Jensen
<i>Tricorythodes edmundsi</i> Allen
