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Dedicated to the memory of

JOHN WARD MAILLIARD, JR.

in appreciation of his long and faithful service as
a Trustee and as Chairman of the Board, of his
many benefactions to the Academy, and of
his stimulating faith in its future

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FOREWORD

This volume of essays has been prepared as part of the recognition of the Centennial of the California Academy of Sciences. In May, 1951, three members of the Council were authorized by the Trustees of the Academy to make plans for a volume of scientific papers appropriate to the occasion. After careful consideration the committee decided that a most appropriate central theme for the volume would be the historical treatment of biosystematics, using this term in the literal sense, namely, the systematic treatment of living things and with emphasis on developments since the founding of the Academy a century ago.

This theme appealed to the committee as especially appropriate since it was during this period, from the middle of the nineteenth to the middle of the twentieth century, that the basic principles underlying our present concepts and aims in the classification and systematic treatment of organisms were clearly enunciated and definitely accepted among biologists. The nineteenth century brought to biology two all-important contributions, Darwin's and Wallace's conception of organic evolution and Mendel's principles of heredity. Recognition of the doctrine of organic evolution led directly to the working concepts of the continuity of species and the transformation of old species into new ones. Recognition of the basic laws of heredity has led, in the twentieth century, to very great progress in the development of our concepts of the nature of the evolutionary processes.

It was inevitable that these tremendous forward steps should have a profound impact on the thinking and practices of those systematists who recognize the significance of the facts, not only of comparative morphology, but also of variation and heredity and of the contributory disciplines of cytogenetics, physiology, biochemistry, serology, biometry, ecology, and biogeography. Inevitable too was the apathy shown toward these epoch-making advances by many taxonomists who were content to pile up new names of species and genera without critical study of all available criteria of relationship, thus creating a maze of names rather than systematics. Although some taxonomists are still littering the waysides of biological literature with unnecessary names, there is a growing tendency among systematists to bring to bear upon problems of classification and nomenclature all of the various categories of evidence that are available in order that the decisions reached shall represent as nearly as possible the true state of nature. This modern viewpoint and aim is the culmination of many experiments in the systematic treatment of organisms prior to and extending throughout this "Darwinian" century.

It is only in recent decades, however, that the advantages of the many-sided attack on problems of relationship and phylogeny have been realized. Many obscure problems in the relationship of organisms have been cleared up by the evidence from cytology, genetics, and biochemistry, not to mention other contributory disciplines; and, in many instances, such evidence has resulted in radical changes in older taxonomic treatments. At the same time, it has been clearly

demonstrated that the evidence on relationship provided by the "newer" disciplines corroborates in the main the earlier systematic treatments that were devised by taxonomists who based their schemes primarily on comparative morphology. Certainly due credit should be given to the many "specimen taxonomists" who have labored through the centuries, often without fair recognition from other biologists and under great difficulties, in their conscientious efforts to bring hitherto unknown organisms into some sort of classificatory system. Without their invaluable services the general advance of biology would not have been possible.

Most of the essays in this volume attempt to review the progress made during the past century in the classification of organisms. The original plan of the volume included all the major groups of organisms. It was found impossible to achieve this degree of completeness; but except for a few gaps the earth's organic life is well represented and the committee consider it a great honor to be able to present to the biological world this series of authoritative historical reviews.

In the exploratory phase of plant and animal classification the services of field workers, especially of trained naturalists, are indispensable. Much of the activity of the California Academy of Sciences has been concerned with the collection and preservation of specimens. It seemed appropriate, therefore, that the first essay should deal with naturalists and the early days of the Academy. The following chapter presents a review of the beginnings of geodesy and astronomy in California because this Academy was so closely tied in with those events; and the third essay is a stimulating contribution by a philosophically minded biosystematist. Then follows the series of systematic reviews, together with four essays which do not treat of major groups of organisms—one on invertebrate paleontology, two on biogeography, and one on wildlife conservation. In all of these essays the disciplines represented are largely, but with some additions, those which have come within the purview of the California Academy of Sciences.

The committee are confident that this volume will long serve as a most valuable source book in the history of science.

ERNEST B. BABCOCK
J. WYATT DURHAM
GEORGE S. MYERS

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D. E. Kimmins outlined a program for a complete new catalogue and sought the collaboration of eighteen specialists and the loan of Ris's manuscript. A number of preliminary papers on nomenclature by Mr. Cowley were published but apparently World War II stopped further activity and the work has not, to my knowledge, been resumed.

EPHEMEROPTERA

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Of the estimated 2,000 or more species now known in the order Ephemeroptera, only a few more than a hundred—disposed among 11 genera of the family Ephemeridae—had been named in 1853. No one person, unless it be Pictet, had concentrated any great effort on the group. This is attested by the fact that about twenty-five writers had described species of mayflies, but of these, only Linnaeus, Say, Burmeister, Pictet, and Walker had described more than five species. The trend for nearly two decades remained one of merely describing new species, these new descriptions being primarily furnished by the neuropterists of the period. Genera were poorly delimited and unnatural, and only the European fauna had been investigated in any detail.

The Reverend Alfred E. Eaton must certainly be considered the father of the modern classification of the Ephemeroptera. After writing a number of small papers, he published in 1871 *A Monograph on the Ephemeridae,* which was succeeded a few years later by his monumental *A Revisional Monograph of the Recent Ephemeridae or Mayflies.* It was in this later publication that Eaton's genius for classification was brought to fruition. His division of the Ephemeridae into groups, series, and sections formed the basis of the modern classification. Eaton's concept of the genus was remarkably modern and he consistently designated genotypes throughout the order.

At the turn of the century, just before Eaton's attention was directed away from the mayflies, Dr. J. G. Needham, of Cornell University, started studying the American mayflies. In a series of papers that culminated in 1935 in the publication (with Traver, Hsu, *et al.*) of the book, *The Biology of Mayflies,* Dr. Needham and his students contributed immensely to all phases of mayfly study. At about the same time the eminent mayfly specialist, Dr. Georg Ulmer of Hamburg, Germany, started his study of the Ephemeroptera and subsequently published numerous papers on the world fauna. The publication of his *Übersicht über die Gattungen der Ephemeropteren, nebst Bemerkungen über einzelne Arten* was one of the true milestones in the literature of this order.

The French entomologist, J. A. Lestage, contributed about one hundred papers on mayflies. He had a keen interest in mayfly phylogeny and his endeavor knew no geographic boundaries. He is best known for his extensive work on the nymphs of Palearctic mayflies.

Drs. J. R. Traver, J. McDunnough, and H. T. Spieth have contributed extensively to the knowledge of American species. Dr. Traver is best known as the author of the systematic section of *The Biology of Mayflies*. Dr. McDunnough has described more North American species than any other person, and Dr. Spieth is well known for his phylogenetic studies.

The difficulties of collecting and preserving mayflies have resulted in important collections being established only by specialists in the group. A succession of specialists have built a fine collection in the British Museum (Natural History). Lestage's collection can now be found in the Institut Royal des Sciences Naturelles de Belgique, while it appears that Navás scattered his collection among many museums. Although Ulmer has an extensive personal collection, much of his work has been based on material from various European museums, especially the ones in Berlin and Hamburg. The collection established at the Museum of Comparative Zoology at Cambridge is rich in North American types, as are the Canadian National Collection and the Cornell University Collection.

The recognition of distinct groups within an ancient and apparently declining order such as the Ephemeroptera is not particularly difficult, but because the order is small there has been a continued reluctance to give familial rank to these groups. Such groups have consistently been utilized as the "working units" of the classification, even though they have been ranked as sections, tribes, subfamilies, or families. The history of the recognition of the various groups is relatively simple, but the story of the rank accorded such groups is indeed complex and often bewildering.

The division of the order Ephemeroptera into groups usually regarded as families at present started with Eaton's revisional monograph. Of his fourteen sections, twelve have been raised subsequently by various workers to the rank of family. Thus to Eaton's original arrangement can be traced the families Palingeniidae, Ephoridae (= Polymitarcidae), Ephemeridae, Potamanthidae, Leptophlebiidae, Ephemerellidae, Caenidae, Prosopistomatidae, Baetidae, Siphlonuridae, Baetiscidae, and Heptageniidae (= Ecdyonuridae).

In 1913 Bengtsson proposed that the genera *Ametropus* and *Metretopus* be considered as constituting a separate family, Ametropodidae, and in 1914 Georg Ulmer recognized the distinctness of, and named, the family Oligoneuriidae, a group formerly included in the Palingeniidae.

In the standard American work *The Biology of Mayflies,* Needham applied subfamily rank to the recognized families of European authors. The family Ephoridae (= Polymitarcidae) of the Europeans was divided into two subfamilies, Ephorinae and Campsurinae, the Ametropodidae divided into Ametropodinae and Metretopodinae, and a new subfamily Neoephemerinae, was proposed.

Balthasar (1937) removed *Arthroplea* from the Heptageniidae and placed it in a separate family, Arthropleidae. The soundness of such a move, however, remains to be proved. In the year 1938, Tshernova, and Motas and Baecsco independently proposed the family Behningiidae for the inclusion of the unusual genus *Behningia,* first described by Ulmer and later named by Lestage. The same year Lestage considered *Behningia* to be a member of the Oligoneuriidae and reduced Behningiidae to synonymy of Oligoneuriidae. Demoulin has recently reinstated, I believe correctly, this monotypic family. In 1938, Lestage

also proposed a new family, Siphloplectonidae, but in the writer's opinion the division is unnatural, and Siphloplectonidae is a synonym of Metretopodidae.

In his fine report on the mayflies of the Sunda Islands, Ulmer proposed a new subfamily of Siphlonuridae, Pseudoligoneuriinae, for *Pseudoligoneuria,* known only from an oligoneurid nymph whose incipient venation appears to be of the siphlonurid type. In 1943, Spieth transferred the subfamily to the Oligoneuriidae. Only three years before his death in 1945, Lestage proposed creation of the family Tricorythidae for a group of genera bearing remarkable convergent similarity to the Caenidae. The most recent proposed change in the classification is the relegation of Metretopodidae to a subfamily of the Siphlonuridae by Demoulin in 1952, but the desirability of such a move seems questionable.

The families have had a stable existence when compared to groupings above family level. As with the families there has been little agreement on the taxonomic level given such complexes of families. They have been ranked as groups, subfamilies, families, superfamilies, or suborders. Oddly enough, the great majority of all workers have regarded the mayflies as being of three great sections, although two, four, five, or six have been indicated by others. But there has been little agreement on the composition of these groups, and, with our present knowledge, stability is neither expected nor desired for some time to come.

As in most orders, the preponderance of the papers on Ephemeroptera has been dedicated to a limited area of the world, and thus, though there are great gaps in our knowledge, some areas have become well known. As is to be expected, the western Palearctic region is best known, as a result of many fine papers produced there by the numerous authorities. The eastern Palearctic region has been rather neglected by comparison. Except for studies of some of the Indian mayflies and the fine works by Ulmer on the Sunda Islands, the Oriental region also has been rather neglected. The Australian and New Zealand species have been reported upon by several competent specialists, but revisions are needed of this critical fauna. The mayflies of the Ethiopian and Neotropical regions are known chiefly from specimens that have come to the cabinets of European and American workers, but exceptional regional studies have been done on South Africa, Brazil, and Porto Rico.

The North American mayfly fauna is certainly one of the most extensively studied, but great geographical areas remain unworked. The first detailed study upon the mayfly fauna of any state was done by J. R. Traver in North Carolina, and other detailed studies have followed, the most notable being the recent reports on the Florida fauna by Berner and the Illinois form by Burks. Drs. McDunnough and Ide also have made extensive studies in certain parts of Canada.

Aside from the need for collecting and describing the mayfly fauna of the little known geographic areas of the earth and continuing the description of immature forms, there are many other fertile fields of study on this order of insects. Phylogenetic studies are most desirable. The present arrangement of families leaves much to be desired, and the grouping of families into larger groups is not satisfactory. Instead of confining studies by setting geographic boundaries, future workers will find it more productive to confine themselves to a systematic unit and ignore political subdivisions. Revisions of many genera are sorely needed; for example, I am aware of three congeneric species that are

now referred to three separate genera and I suspect that one or more species bears the alias of still a fourth genus. Distinct races exist within many species of mayflies and in some genera the problem of naming and making known these races and the causative factors of their formation and present distribution is very pressing. This inevitably leads to the problem of obtaining larger samples of specimens, topotypes of older species, and especially reared series. As representatives of an ancient group of insects that are, because of their short adult life and tendency to desiccation, seldom dispersed any great distance by air, mayflies are prime subjects for biogeographic studies. For those willing to meet the special problems of collecting and preserving the insects of this order, there is a promising field of research.

PLECOPTERA

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The history of our knowledge of the stoneflies is comparatively short. Not until late in the Middle Ages are they even modestly mentioned in the literature. Some authors of the sixteenth century dealt with them as *grosse Wassermücken* (big water flies). In 1603 in his *Theriotropheum Silesiae* Caspar Schwenckfeld described a perla as *Musca caudata.* Moufet in 1643 *(Insectorum sive Minimorum Animalium Theatrum)*, J. Johnston in 1653 (*Historia Naturalis de Insectis, Libri III*), and J. Wagner in 1680 (*Historia Naturalis Helvetiae Curiosa*) describe a *Musca aquatilis aestiva major* which is also a perla. In the literature of the eighteenth century, stoneflies were mentioned more often, but they had no name of their own until much later.

It is true that *Perla,* a name which has long been applied to a genus of well-known European stoneflies, appeared as early as 1602 in Aldrovandi's *De Animalibus Insectis Libri VII.* But it did not refer to a stonefly, for at that time perla was the common name for dragonflies, the larvae of which were known as *Libella fluviatilis.* Moufet (*op. cit.*) recognized the association between the larvae and the imagines and restricted the name *Libella* to Odonata. For some time *Libella* and *Perla* were used side by side (cf. Goedaert: *Historia Insectorum Generalis,* several editions), but in the eighteenth century we meet with *Libella* only. *Perla* disappeared as a generic name until it was revived by E. L. Geoffroy in 1762 (*Histoire abrégée des insectes*) and by Cuvier (1798), and P. A. Latreille (1802) made it the type of a section or family Perlariae among the Neuroptera.

Stoneflies were figured early. There is an excellent illustration of a perla in G. Hoefnagel's *Archetypa Studiaque* (1592) and *Diversae Insectorum volatilium* (1630). No text accompanies the figures.

The number of pre-Linnaean species of Plecoptera is very small and they cannot be identified with any certainty. Linnaeus and his pupils and the Lin-