AQUATIC INSECTS

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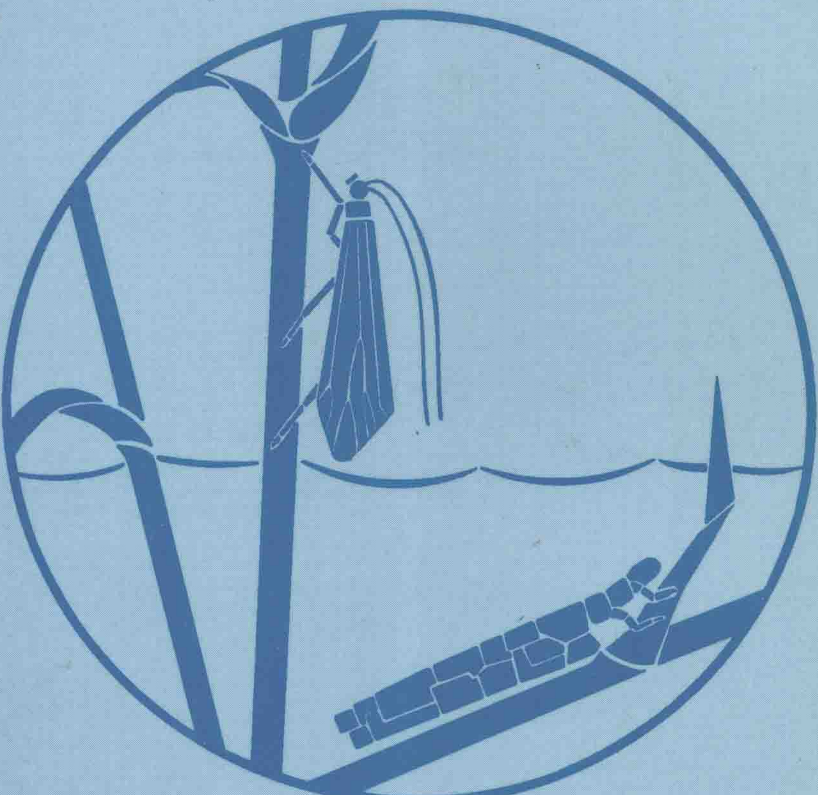

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AQUATIC INSECTS

This book is dedicated to our respective families:

Nancy, Sian, Owen and Bette Williams
and
Minnie and Gordon Feltmate

PREFACE

Study of aquatic insects has been proceeding for centuries, possibly millennia. Primitive man could hardly have failed to be aware of the adults of biting species, as early settlements were invariably close to water. Whether or not these humans made the connection between the immature stages in the water and the adults flying around them on land, however, is another matter. Claudius Aelianus (ca. 175 - 235 A.D.) recorded swarms of adult caddisflies over the River Astraeus in Macedonia and described the use of artificial flies to catch trout and grayling, a practice stemming from the time of the ancient Greeks and later documented in a more scientific manner by Dame Juliana Berners (1496).

Macan, in an early comprehensive review of the ecology of aquatic insects, in 1962, chose to organize the then known facts by insect order. This was despite it being "preferable to use principles or factors as the headings in an article on ecology" but was prudent, he felt, because "if these can be illustrated only by examples drawn from one group, discussion of them is necessarily one-sided and incomplete". To a certain extent, the imbalance in coverage of the different orders that Macan alluded to is still a reality. Taxonomically, although many groups are reasonably well known today, there are still many gaps in the study of immature and pupal stages (e.g. Coleoptera and Diptera) and still regions of the world where the faunas are poorly known and collected, e.g. central Africa and South America. Ecologically, the imbalance is just as evident even though the overall number of studies has increased almost exponentially (Fig. P.1). For a variety of reasons (personal preference, ease of study, importance to human health, funding opportunities, designated research/academic appointments, serendipity, etc.) some insect groups are still studied more than others. The Trichoptera, Ephemeroptera, Plecoptera and Diptera (especially black flies and mosquitoes) remain perennial "favourites" whereas relatively little is known of the ecology of the aquatic Coleoptera or Hemiptera.

In the past three decades, the study of aquatic insects has been revolutionized. Not only have pure research studies shown the pivotal role played by the larvae of aquatic species in the breakdown of terrestrial leaf litter and the pathways by which this plant energy is incorporated into the tissues of fishes, birds and other vertebrates but a host of more applied research has revealed the importance of aquatic insects in the spread of diseases, in the biological assessment of water quality, and in the reconstruction of past environments on earth. Most recently, aquatic insects are being used, increasingly, to test many elegant hypotheses in contemporary ecological theory.

The purpose of this book is to try to give the reader a taste of these exciting new findings in the study of aquatic entomology, together with some of the

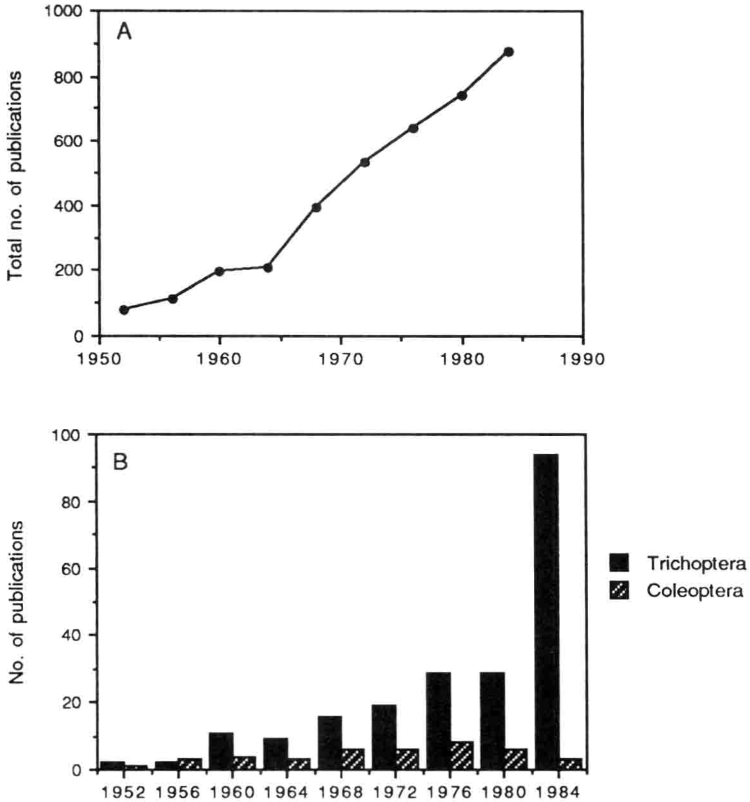

Fig. P.1 (A) Number of publications on the ecology of aquatic insects during the period 1952 - 1984; (B) Comparison of the number of publications on the ecology of the Trichoptera and aquatic Coleoptera over the same period (from the authors' own reference database).

basic background information necessary to comprehend them, and to provide references to more detailed studies in the primary literature. To these ends, coverage begins with an introduction to insects, in general, and designation of the aquatic groups. Chapter 2 characterizes each aquatic order by highlighting morphology, special features of development and differences in basic biology, and by comparing ancestry and the zoogeography of modern forms. Chapter 3 provides keys (to the ordinal level) for both mature and immature stages. Chapter 4 deals with aquatic insect habitats and the communities that they contain, and considers insect distribution at both the macro- and micro-level. Chapter 5 relates life history traits to habitat type and discusses the selection pressures at work. This is followed (Chapter 6) by coverage of the problems facing insects (which, originally, evolved on land) that live in water. Features of the population biology of aquatic insects are discussed (Chapter 7), with emphasis on dispersal and colonization patterns, population dynamics, coexistence and competition. Two chapters are devoted to trophic relationships, the first (Chapter 8) deals with the role of insects as processors and converters in aquatic food webs, and the second (Chapter 9) concentrates on predation and its consequences, especially the effects on species fitness. Experimental design and sampling methods are covered next (Chapter 10), as these often become pitfalls during quantitative studies, and holistic (field) versus reductionist (laboratory) approaches to experimental design are discussed for similar reasons. The final chapter (11) deals with the relationships between aquatic insects and mankind and discusses the former's role as biological indicators of degraded water quality, their importance to human health, the use of fossil insects as palaeoecological tools, and the development of artificial lures for angling.

This book could not have been completed without the valued assistance of several people. Foremost among these are Professors Nancy Williams and Noel Hynes who critically examined the entire text; Dr. Maurice Lock who provided a quiet oasis where (in the company of sheep) the senior author spent a sabbatical leave, writing; and Mrs. Judith Smith for her advice on the vagaries of Microsoft Word (or our interpretations of it). We are grateful also to all the authors who gave us permission to cite their published or unpublished works, but especially to Dr. Mike Lehane (Bangor), Dr. Lena Peterson (Lund), Prof. Rich Merritt (Michigan), Prof. Cal Fremling (Minnesota) and Prof. Doug Craig (Edmonton). The Natural Sciences and Engineering Research Council of Canada contributed funds to the project.

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FOREWORD

General books on aquatic insects have a long history, starting with Miall (1895). This dealt, as its title stated, with natural history, and because of that it had a great influence on me as a child thirty years after its first appearance. It was followed by a series of volumes in Europe and North America which dealt primarily with identification, and thus were of less interest to the general reader and the budding biologist. Details of these can be found in various chapters of Resh and Rosenberg (1984), where the history of the study is discussed among many other topics at a fairly high scientific level.

Then, during and after World War II, we started to get books that dealt again with natural history as well as identification, and I recall reading these avidly. I refer particularly to Wesenberg-Lund (1943) and Usinger (1956). The former dealt with the world literature, and in my enthusiasm to learn from it I acquired the ability to understand German, which my schooling had not given me. So books that inspire young people to follow scientific careers can have great value.

Since then many books and specialized treatises have appeared dealing with the aquatic fauna of various parts of the world, such as areas of Europe, Japan, New Zealand, Australia, West Africa and North America and several of them, most notably Merritt and Cummins (1978), incorporated information analogous to the natural history of Miall and Wesenberg-Lund but framed in modern ecological concepts. These are the handbooks of the professionals and although they are fascinating they are tough reading for the generalist.

In the present volume the authors have tried to produce a more general work that will give the interested reader an overall picture of what is going on in the study of aquatic insects, and how they have become important in this age of environmental concern. Indeed, aquatic insects feature nowadays in all kinds of research, be it toxicology, behaviour or general ecological theory. From being the mere interesting delight that was perceived by Miall they have become an important part of non-molecular biology, and this book serves as an introduction to them and their present-day status in science. I wish it success, and I think that Professor Miall would be happy with his intellectual descendants.

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H.B.N. Hynes
Waterloo, Ontario

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CONTENTS

1 INTRODUCTION

1.1 What is an insect?

Basically, an insect exhibits the following surface features: an external skeleton, or cuticle, made from chitin (a nitrogen-containing polysaccharide) and protein; a body divided into three sections (head, thorax and abdomen), although in the larvae of some forms the abdomen and thorax cannot be distinguished; three pairs of jointed legs attached to the underside of the thorax; a pair of antennae, usually a pair of compound eyes and up to three single eyes (ocelli) on the head; and, usually, one or two pairs of wings attached to the last two segments of the thorax. The abdomen generally lacks appendages, except for external genitalia and sensory cerci at the tip, but in the larvae of some aquatic forms there may be segmentally arranged gills. Excluding the areas around joints, the exoskeleton of most adult insects, together with that of many pupae and larvae, is hard. This hardness is due to sclerotization, a process by which the protein component of the cuticle is transformed into sclerotin, by the action of quinones. Cross-linkages are formed between the protein molecules which produce a substance of such strength that the mandibles of certain beetles are capable of biting through soft metals such as lead. Of these characteristics, probably the exoskeleton, six legs, and wings together with a crawling gait allow most lay people to recognize an insect. Scientists, however, are more precise and have painstakingly refined the study and definition of insects so that they may be distinguished from related animals such as spiders, crustaceans and centipedes.

Internally, the main body cavity is not the true coelom characteristic of other protostome coelomates (e.g. annelid worms and molluscs) but a system of large sinuses in the tissues (haemocoel) which are filled with blood. The latter contains a variety of amoebocytes and, depending on the species, the copper-based respiratory pigment haemocyanin or occasionally the iron-based pigment haemoglobin. The gut is divided into three regions. The large foregut and hindgut are lined with chitin, as they are derived from the ectoderm of the embryo, whereas the midgut is endodermal in origin and is frequently invaginated to increase its surface area for secretion and absorption. The central nervous system is concentrated in the head to form a brain (cephalization) but there are segmental ganglia located along the length of the ventral nerve chord. Respiration is accomplished by a system of air passages, the tracheae and the much smaller tracheoles, which communicate with the outside world via paired openings, or spiracles. These are located laterally, one pair per segment, on the last two thoracic and, usually, the first eight abdominal segments. Aquatic insects exhibit interesting adaptations of this system in order to allow them to breathe under water. Most insects are dioecious, that is they have separate sexes, and fertilization is internal. The gonads (ovaries or testes) are located in the abdomen and ducts from these open to the outside near its tip. The male duct opens ventrally on the 9th abdominal segment and is surrounded by a sperm-transfer organ, the aedeagus. The female duct generally opens on the ventral side of the 8th abdominal segment and, associated with it, may be structures used for sperm reception and storage, provision of nutrients and protective covers for the eggs, and glands that secrete adhesive material used for attaching the eggs to some substratum as they are laid.

Insects differ both in the degree of development completed prior to hatching and in the number of stages through which they pass prior to becoming adults. Growth typically follows a geometric progression and necessitates the entire exoskeleton being shed, periodically, so that a new, larger individual can be produced. The stages in the life cycle between these "moults" are known as *instars.*

1.2 The origin of insects

The fossil history of the arthropods can be traced back to the Early Cambrian Era (540 million years Before Present; Table 1.1) and indicates that the main groups and a number of subgroups were already in existence then. This early divergence, before the first known arthropods were fossilized, means that reconstruction of their early phylogeny is difficult. It is clear, however, that the arthropods themselves arose from primitive segmented worms (polychaetes) or from some common ancestor. Modern species from both groups show homologous features in terms of body segmentation, the central nervous system, embryonic development, and segmental appendages.

The Subphylum **Uniramia**, composed of the myriapods (centipedes and millipedes) and the hexapods, is thought to have evolved along a separate line from those leading to the chelicerates and the crustaceans with the bulk of its diversification taking place on land. A marine uniramian, *Aysheaia*, has been found, however, in the Burgess Shale of the mid-Cambrian (530 million years B.P.) (Whittington, 1978). The limbs and cuticle of *Aysheaia* are similar to the most likely ancestors of the Uniramia, the **Onychophora**, small, elongate, soft-bodied animals that today are restricted to damp terrestrial habitats in the tropics and southern hemisphere. The Onychophora, in turn, seem to have been derived from marine polychaete worms. Onychophorans exhibit many features in common with both segmented worms (Annelida) and arthropods and often have been likened to a missing link between these two phyla. Their phylogenetic status continues to be debated so that some workers consider them to be a separate phylum while others place them in a superclass within the Uniramia (Manton and Anderson, 1979). With the exception of the Onychophora, the oldest terrestrial fossil uniramians are myriapod-like animals from the Devonian

Table 1.1 Geological time scale together with major events in the evolution of the insects (based on Borror *et al.*, 1981; Geological Society of America, 1983).

Era	Millions of Years B.P. (beginning of period)	Periods Epochs	Event
Coenozoic	1.6	Quaternary	
		Pleistocene	First humans
	66.4	Tertiary	
		Pliocene	
		Miocene	Rise of modern insect genera
		Oligocene	
		Eocene	
		Palaeocene	
Mesozoic	144	Cretaceous	Most modern insect orders present; first flowering plants
	208	Jurassic	
	245	Triassic	Ephemeroptera & Odonata
Palaeozoic	286	Permian	Rise of most modern insect orders
	360	Carboniferous	First winged insects, most now extinct, e.g. Palaeodictyoptera
	408	Devonian	First insects (*Rhyniognatha*)
	438	Silurian	First land arthropods (scorpions & millipedes)
	505	Ordovician	First vertebrates
	570	Cambrian	First arthropods (marine)
Precambrian			Primitive invertebrates

(380 million years B.P.).

Until recently, all arthropods with six legs were classed as insects but it is now thought that the hexapod condition may well have evolved more than once from terrestrial myriapods. Current opinion proposes four classes of hexapod: **proturans**, minute animals living in moist soil or decaying plant matter; **collembolans**, or springtails, small animals similarly found in moist plant matter, under bark and in the soil but also on the surfaces of freshwater pools and along the shores of rivers, lakes and the sea; **diplurans**, small animals again found in a variety of damp places such as in rotting wood, under bark and stones, in the soil and in caves; and **insects**. The first three classes (sometimes collectively known as the Entognatha) differ from the insects primarily in terms of head structure. In the entognaths, the mandibles and maxillae are deeply recessed in pouches within the head capsule and articulate with it at only one point. During feeding, the tips protrude and their action reduces food pieces to very small particles that are then ingested. In insects, the mandibles articulate with the head capsule at two points. This enables the mandibles to move transversely, an action suitable for biting off and grinding particles of food (Daly *et al.*, 1978). Members of the different hexapod classes also differ in the ways in which they use their three pairs of legs: the Collembola can crawl but have become specialized in jumping through use of their unique ventral, forked structure, the furcula, combined with an ability to hold their bodies rigid; this contrasts with the marked flexibility of the trunk in the Protura and Diplura; whereas the insects (except the Thysanura) exhibit trunk stability through a plantigrade tarsus and a fixed sternal pleurite, which prevent rocking and provide the coxa with a firm base, attributes that contributed to the evolution of flight and the tremendous success and adaptive radiation of the group (Manton, 1979).

The earliest known hexapod is *Rhyniella praecursor*, a collembolan from the Lower Devonian of Scotland. However, as its morphological features show, this was already an advanced member of its class indicating that the transition from myriapod to hexapod must have occurred earlier. Another hexapod, *Rhyniognatha hirsti*, was contemporary with *Rhyniella* and probably represents the first known insect proper (?Ectognatha, possibly a small early progenitor of the mandibulate orthopteroids - Tillyard, 1928; Fig. 1.1).

In the Upper Carboniferous (290 million years B.P.) are remains of the palaeopterygote *Erasipteron larischi*, the neopterygote *Stygne roemeri* (an orthopteroid) and *Metropator pusillus* which may have been an oligoneopteran. Some ten orders of insect were evident by the close of the Carboniferous. These were still extant in the Permian (286 - 245 million years B.P.) and others appeared or firmly established themselves at this time (especially the neopterygote orders Orthoptera, Psocoptera, Hemiptera, Mecoptera and Coleoptera), coincident with the rapid development of land plants. By the end of the Permian the Palaeodictyoptera, the earliest known winged insects (belonging to the infraclass Palaeopterygota) and the possible ancestors of the Neopterygota, were extinct (Fig. 1.2). It is likely that primitive mayflies (Ephemeroptera) were