



Dragonflies

Philip Corbet & Stephen Brooks



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Philip S. Corbet & Stephen J. Brooks



Editors

SARAH A. CORBET, ScD
PROF. Richard West, ScD, Frs, Fgs
DAVID STREETER, MBE, FIBIOL
JIM FLEGG, OBE, FIHORT
PROF. JONATHAN SILVERTOWN

The aim of this series is to interest the general reader in the wildlife of Britain by recapturing the enquiring spirit of the old naturalists. The editors believe that the natural pride of the British public in the native flora and fauna, to which must be added concern for their conservation, is best fostered by maintaining a high standard of accuracy combined with clarity of exposition in presenting the results of modern scientific research.

Dedicated with affection and gratitude to Sarah Jewell and Ann Brooks

DRAGONFLY

*Now let's have another try
To love the giant dragonfly.
Stand beside the peaceful water.
Next thing – a wispy, dry clatter
And he whizzes to a dead stop
In mid-air, and his eyes pop.
Snakey stripes, a snakey fright!
Does he sting? Does he bite?
Suddenly he's gone. Suddenly back. A
Scarey jumping cracker –
Here! Right here!
An inch from your ear!
Sizzling in the air
And giving you a stare
Out of the huge cockpit of his eyes-!
Now say: 'What a lovely surprise!'*

Ted Hughes

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FRONTISPIECE



FRONTISPIECE. Sequential digital still photography is a wonderful tool for tracking this male *Orthetrum cancellatum* as he flies by. The technique can be used to reveal the natural attitude of the wings, abdomen, head and legs while a dragonfly is in flight (Steve Cham).

Editors' Preface

DRAGONFLIES ARE OF particular interest to naturalists because they are lively, beautiful and interesting, and amenable to study without expensive equipment or laboratory facilities. Furthermore well illustrated field guides make it relatively easy to recognise the British species. An earlier *New Naturalist*, published in 1960, did much to bring the interest of dragonfly biology to the attention of naturalists, and to stimulate further research. Since then, dragonflies have become popular among both amateur naturalists and research workers; they have been transformed from an enigmatic group of minority interest to a focus of enthusiastic amateur study and exciting research on diverse aspects of ecology, behaviour and physiology. We now understand much more about what they do, and how and why they do it; so they deserve this completely new *New Naturalist*. Both of the authors have made major contributions to the study of British dragonflies, and have done much to encourage naturalists to appreciate them. Their book, illustrated with Robert Thompson's magnificent photographs, will enrich the study of dragonflies by the many naturalists who are already committed to this group, and will surely encourage new recruits to take up that interest.

In Memory of Philip S. Corbet 1929-2008

PHILIP CORBET WAS without doubt the world's foremost odonatologist and one who has had the greatest influence in the burgeoning interest in dragonflies for the past 50 years. With his Reading B.Sc dissertation and Cambridge Ph.D thesis he made the first strides in a monumental research career involving dragonflies.

His varied and distinguished appointments included research positions with the East African High Commission in Uganda; Director to the Research Institute, Canada Department of Agriculture; Professorships with the Universities of Waterloo (Canada) and Canterbury (NZ); Commonwealth Visiting Professor (University of Cambridge); and Professor, University of Dundee from which he retired in 1990 as Professor Emeritus.

Corbet's research interests emphasised periodicity, rhythmic behaviour and development in dragonflies and mosquitoes. These have been the co-ordinating strands in studies relating to taxonomy, morphology, life histories, arthropod-borne virus diseases, reproductive physiology, ecology of fishes and crocodiles, and arctic microclimates.

After retirement in 1990 he concentrated on the production of two major books: *Dragonflies: Behaviour and Ecology of Odonata*, published in 1999 is a definitive synthesis for which he was awarded the Neill Medal for Natural History by the Royal Society of Edinburgh. This masterly volume appeared in Japanese translation in 2006. This fine current *New Naturalist* with Steve Brooks is a fitting closure to an extraordinary career.

Philip Corbet's numerous awards include four higher doctorates: the Gold Medal for Outstanding Achievement from the Entomological Society of Canada, election to Fellowships of three prestigious societies, Honorary memberships to three national dragonfly societies; and he was elected to the Presidency of the Worldwide Dragonfly Association 2001-2003.

Michael J. Pa
Inaugural President
Worldwide Dragonfly Association
1998-2000

Preface by Former Keeper of Entomology, The Natural History Museum, London

FEW INSECT GROUPS command more awe or are more immediately recognisable to so many people as the dragonflies. They are a source of beauty and inspiration to all who take time to watch them. Their aerial skills and finely honed hunting abilities on the wing are second to none, yet these creatures retain many attributes that first evolved in recognisable ancestors more than 300 million years ago. Dragonflies tell us a great deal about what insects were like before the origin of flexing wings or complete metamorphosis, characters that foreshadowed the vast number of 'higher' insect species. Dragonflies are superb animals for the study of countless aspects of biology. Their aquatic larvae are important components of freshwater ecosystems and are indicators of water quality. Their territoriality and hunting skills make them excellent subjects for learning about animal behaviour. Their large size permits a much broader range of observations in the field than is possible for most other kinds of insects. Making these spectacular animals accessible to a wider audience is a worthy goal, and one fulfilled admirably by this volume.

There are no contemporary natural historians whom I admire more than Philip Corbet and Steve Brooks, nor any who are in a better position to have prepared this book. We are truly fortunate that they have combined their unmatched knowledge, experience and observational and writing skills to pull together such a wealth of material on British odonates. The book provides a wonderful foundation for anyone discovering the study of odonates for the first time or seeking to expand their knowledge by better understanding the breadth of dragonfly biology. The range of subject matter in this book is impressive, covering such diverse topics as habitats, populations, life history, parasitoids, feeding behaviour, seasonality, flight, sexual behaviour and maturation. This provides a firm foundation for in-depth studies of dragonflies in general and the British fauna in particular.

With this background and the authors' sound advice on how to locate, collect, photograph and identify British dragonflies, a spectacular world is opened to the interested observer. This constitutes one of the best introductions to odonatology available and will, I predict, contribute to the widening interest in dragonflies in Britain and the education of a new generation of both professional and amateur odonatologists who delight in the study of these most fascinating of creatures. As our environments continue to change rapidly in the decades ahead, a growing awareness and understanding of our dragonflies will prove essential to science and biological conservation. No one who would truly understand either insect evolution or the function of ecosystems associated with fresh waters can do so by ignoring the Odonata. The growth of expertise on any taxon depends heavily on access to reliable and inspiring literature; the dragonflies will profit immensely from just such a contribution from Corbet and Brooks.

Quentin D. Wheeler
Former Keeper of Entomology
The Natural History Museum
London

Authors' Foreword and Acknowledgements

DRAGONFLIES ARE THE largest, most conspicuous, flying insects one is liable to encounter in Britain in sunny weather. Because during their growth stages dragonflies live in water, the adults are usually encountered near ponds, lakes, streams or rivers, where they can often be seen engaging in elaborate aerobatics. Their vivid colours and aerial agility command, and hold, the attention of any observer. Except in highly specific situations, dragonflies are of no economic importance. Being generalised predators, both as larvae and as adults, they are unlikely ever to suppress the numbers of 'pest' organisms down to levels that meet human demands for health, profit or comfort: when one prey organism becomes too scarce to encounter readily, a dragonfly will simply switch its attention to another.

So why are so many people fascinated by dragonflies?

Perhaps the most convincing way to answer this question is to list some of the reasons why we, the authors, have become interested in these insects. An important reason, for any field naturalist, is that dragonflies are sufficiently large and conspicuous that one can often understand what they are doing; and, thanks to the great amount of research conducted by scientists on the behaviour of dragonflies, one can often interpret their actions in terms of their main adaptive needs, such as foraging (i.e. seeking prey) and reproducing. Moreover, for almost all the actions they perform, as larvae as well as adults, one can usually infer the significance of their behaviour in the context of the life history, which is steadily becoming better understood.

In Britain, compared with the continent of Europe, we have a marginal, impoverished fauna and flora. For example, Britain contains (as residents) only about 34 per cent (39/114) of the dragonfly species inhabiting the Continent. Having relatively few species can be an incentive to know them, to record them and to understand what influences their distribution in Britain. And there is the dragonfly life history, in which the larval and adult stages alternate between water and land in an impressive and hazardous transition: at the time of egg laying and then again at emergence (i.e. transformation from larva to adult). These are some of the objective reasons for our interest. Others, equally compelling though thoroughly subjective, lie in the excitement, admiration and awe that we experience whenever we encounter a dragonfly or learn of a newly discovered fact about the life history. We are not alone in our enthusiasm and affection for dragonflies. In addition to the British Dragonfly Society, with its 1,600 or so members, two well-subscribed international societies are devoted to the study of dragonflies, each producing a periodical containing scientific reports about dragonfly biology. Odonatology (the study of dragonflies) receives special mention in Chapter 1, and the history of odonatology in Britain is reviewed in Chapter 10.

This book is not a textbook on dragonflies; nor is it an identification manual. Useful literature of that kind is listed in Chapter 1. This book is about the natural history of dragonflies in Britain. (Our use of the terms 'Britain' and 'British Isles' is chosen for convenience only, and has no political connotation. We use these designations to denote the archipelago that comprises Britain and Ireland and associated islands.) Because our emphasis is on natural history, we have devoted little attention to the morphology or physiology of dragonflies, sources for which are listed in Chapter 1.

We hope that the information presented in this book will enhance the pleasure and inspiration that people derive from watching and studying dragonflies. We find dragonflies to be limitless sources of wonder and delight, and we regard it as a singular privilege to be able to share these sentiments

with others by writing about dragonfly natural history.

~~This book is intended for the informed enthusiast with a leaning towards natural history. In presenting it, we have four principal aims:~~

- to show or remind the reader what beautiful, elegant and superbly adapted animals dragonflies are, and to make the case for conservation of their species and their habitats;
- to enable the observer to understand better the biological significance of dragonfly behaviour;
- to help the reader place the ecology and behaviour of British species in the context of what is known about dragonfly biology worldwide, hoping that this broader perspective will illuminate understanding of the species in Britain; and
- to expose opportunities for further investigation that can be pursued without specialised equipment or facilities.

We have adopted certain conventions in the text. Specialised terms are italicised on first mention thus indicating that they have been defined in the Glossary on pages 373-381. Sources of information are cited in the text by superscript numbers. These correspond to abbreviated references, assembled under chapters in the section Endnotes on pages 382-394, and these in turn correspond to citations given in full in the Bibliography on pages 395-442. There are two indexes at the end of the book: one to authors cited in the text, and one to species, topics and people.

It is a pleasure for us to acknowledge help we have received during preparation of this book.

Our primary debt is to the many odonatologists whose careful (sometimes inspired!) observations, ideas and experiments have yielded the information from which our text is drawn. For the most part they are authors of publications, dating from the eighteenth century to recent times;¹ but a few are contemporaries who have devoted their time and expertise to constructive criticism of parts of the text. In this regard we make special mention of our colleagues Mike Parr (Chapters 1 and 7 and Appendix 2), Mike Siva-Jothy (Chapter 9) and Hansruedi Wildermuth (Chapters 3 and 5). We thank the compilers of *Odonatological Abstracts* (Bastiaan Kiauta) and the Odonatological Abstract Service (Martin Lindeboom and Martin Schorr) for the immensely valuable service they perform in enabling odonatologists to keep track of the many publications that appear annually. We are very grateful to Ann Brooks, Sally Corbet and Sarah Jewell for their valued comments on successive drafts of the text. We thank Robert Thompson for his generosity in allowing us to use a large number of his beautiful colour photographs, the inclusion of which greatly enhances the book's appearance. We are indebted also to Ann Brooks, Kevin Caley, Steve Cham, Zoë Greenwell, Ruary Mackenzie Dodds, Jürgen Ott and Hansruedi Wildermuth for allowing us to include photographs, the source of which is acknowledged in the captions.

We thank Faber and Faber for permission to reproduce the poem 'Dragonfly' by the former Poet Laureate, Ted Hughes.

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S.B. is grateful to the Trustees of The Natural History Museum for enabling him to work on this book in official time, and we both thank Professor Quentin Wheeler, former Keeper of Entomology at The Museum, for contributing a Preface.

During our pursuit of odonatology, and during the preparation of this book, we have enjoyed unfailing support from Ann Brooks and Sarah Jewell.

P.S.
S.
Crean Mill, St Buryan
Cornwall
and
The Natural History Museum
Cromwell Road, London
February 2000

CHAPTER 1

Introduction

DRAGONFLIES

AS AERIAL PREDATORS, adult dragonflies have few peers. Their extraordinary agility is unequalled among animals, except perhaps some of the smaller birds of prey, bats and bee-eaters; and they have an outstanding ability to detect the movement of small flying objects.

Dragonflies are robust insects comprising the order Odonata ('toothed ones'). Almost all species are aquatic in the larval (growth) stage and aerial as adults. In all but the first larval stage they are *obligate* predators, using powerful mandibles to masticate their prey. All odonate larvae catch their prey by explosive extension of a specialised lower lip (*labium*) (Fig. 60, p.115) derived from the fusion of the second maxillae. Among the senses used for prey detection, the *compound eyes* steadily acquire primacy during larval development. Concealment, immobility and occasionally rapid movement are among the attributes that make larvae effective predators of other, usually smaller, animals. Adults catch prey while on the wing and likewise masticate it using the mandibles. The compound eyes are well developed, especially in the adult.

In common with other morphologically generalised insects, dragonflies lack a pupal stage between larva and adult; the larva, though possessing rudimentary wings, otherwise broadly resembles the adult.

Odonata derive, with little structural change, from the Protodonata, an extinct order that flourished in the Upper Carboniferous, more than 300 million years ago. Those early dragonflies broadly resembled extant species but were much larger, having a wingspan of about 70 centimetres.¹ Some authorities attribute this gigantism to the higher concentrations of oxygen in the atmosphere at the time.² Together with their 'sister' group, the mayflies, or Ephemeroptera, Odonata, by direct lineage, are among the most ancient of flying insects surviving to the present day. Mayflies and dragonflies (together comprising the Palaeoptera) are believed to have shared a common ancestor that separated from the progenitors of all other winged insects (the Neoptera) early in the *evolution* of insect flight. Larvae of the extant Palaeoptera are almost all aquatic. Unfortunately, no fossil larvae of the early Palaeoptera have been found, so it is not known when larvae of Odonata became aquatic, although this may well have taken place during the Lower Permian.³

Today Odonata are to be found in every continent except Antarctica. In the northern hemisphere they occur from the equator to latitudinal tree line. About 6,000 species have been described, although the world fauna probably exceeds this number by several hundred. New species are being described at a steady rate, especially from tropical rainforest, where the diversity of species and suitable *habitats* is greatest. Because this *ecosystem* is being rapidly lost due to human impact, odonate taxonomists are aware that they are working against time to describe many species before they become extinct. The extent to which species and families of Odonata are endangered on a global scale is better known than for most other insect orders.⁴

We subscribe to the view that there are two extant suborders of Odonata: Zygoptera and Anisoptera. Some odonatologists recognise a third suborder, Anisozygoptera, but we share the

opinion⁵ that members of this third suborder occurred only during the Triassic, Jurassic and Cretaceous periods and so have been long extinct.⁶ Extant Zygoptera and Anisoptera are each represented by about 3,000 described species.

Adult Zygoptera ('similar wings') (Fig. 8, p.25), known as damselflies, are typically small and slender; the fore and hind wings are similar in shape and (except in Calopterygidae) are stalked (petiolate) at the base; the wing-loading and flight speed are low, the Zygoptera being 'forward-thrust fliers.'⁷ The larvae are slender and usually bear three conspicuous leaflike or sac-like appendages at the tip of the abdomen (Fig. 20, p.35). Inside the abdomen they lack recognisable gills and a muscular diaphragm. They swim by lateral movements of the abdomen, wriggling like a fish.

Adult Anisoptera ('dissimilar wings') (Fig. 30, p.50) are typically large and robust. Their wing-loading is high⁷ and they can fly rapidly and powerfully. In some, the base of the hind wing is much expanded, facilitating gliding and soaring, a modification found especially in species that habitually migrate. The larvae (Fig. 28, p.46) are robust and within the abdomen possess gills and a muscular diaphragm. The diaphragm plays a triple role: it controls pumping movements that generate inhalant and exhalant currents that ventilate the gills lining the rectum; it applies this capability in a more vigorous mode to enable a larva to swim by jet propulsion, as a means of escape; and it regulates the increase in blood pressure that enables the labium to project forwards suddenly when prey is being captured (Fig. 60, p.115). Larvae of Zygoptera can also project the labium abruptly, but do not employ a muscular diaphragm to do so.

The Zygoptera comprises 18 extant families and the Anisoptera comprises 12, one of which, the Epiophlebiidae, is assigned by some odonatologists to the suborder Anisozygoptera (see above).

ODONATOLOGY

Odonatology is the study of dragonflies with the explicit aim of learning about their biology and making the information so acquired generally available, in a formal way, through recognised channels. Practised for at least 250 years, odonatology has yielded a treasure house of fascinating information, many items of which have been acquired, serendipitously, by skilled observers. Such disparate facts, together with the products of observations and field experiments, provide the tesserae of a rich mosaic that await assembly and interpretation. Present and future odonatologists face the challenge of arranging and interpreting these tesserae so as to construct a coherent picture of dragonfly biology, and preferably one that will throw light on the paths along which evolution by *natural* selection has moulded the patterns of behaviour and ecology found in the order today. We hope that our treatment of this legacy of information constitutes a modest step towards this goal, especially as regards the British species.

The odonatologists, past and present, to whom we owe this legacy of facts (and hypotheses) have come from many walks of life (Chapter 10). Despite their varied backgrounds, they share certain attributes that have enabled them to contribute importantly to odonatology: enthusiasm and affection for Odonata; willingness to apply scientific rigour to their methods of study; and willingness to undergo the self-imposed discipline of communicating their findings to other odonatologists. We, their beneficiaries, are much in their debt, and are under obligation to maintain the rigour that is a feature of their work.

All odonatologists share a common, implicit, overriding objective: to increase the likelihood of the long-term survival of vigorous populations of dragonflies. Virtually all that is known about dragonflies, including the contents of this book, derives from the science of odonatology, practised

with the rigour that underpins all branches of biology. We have recently detected trends in human behaviour that may threaten the integrity and reputation of odonatology as a respected branch of science. Some involve the perceived propriety of collecting specimens for scientific study, a stance that can sometimes give rise to conflict. Odonatologists today have a responsibility to ensure that they prove worthy custodians of the legacy they have inherited from those practitioners who, by their dedication and skill, have made this science a respected and influential branch of biology. As practising odonatologists, we see ourselves as under obligation to try to improve the prospects for odonatology in Britain. Here we address two aspects of odonatology that could benefit from attention and reform. They relate, respectively, to nomenclature and collecting specimens.

NAMING DRAGONFLIES

Every species of dragonfly known to science has been assigned a scientific name according to the rules laid down by the International Commission for Zoological Nomenclature (Box 1). The official, required name of any dragonfly consists of four elements: genus, species, name of author of first published description and date of that description. To comply with the rules, the first (definitive) description should designate a type specimen (i.e. the specimen on which the description was based) and say where it has been deposited. The latter provision is mandatory and necessary because comparison with the type specimen is often the only way in which a future taxonomist can verify that a specimen of a species suspected of being undescribed is indeed new to science.

Following Carolus Linnaeus, who devised and established this binomial system of nomenclature for animals in 1758,⁸ all names of species follow a Latinate form which is used by zoologists internationally when referring to species.

In Britain, naturalists have long shown a tendency to assign English names to some of the more conspicuous and handsome insects (such as butterflies, moths and dragonflies). Unlike butterflies and moths, dragonflies have been given English names relatively recently, so some of the names appear contrived. Cynthia Longfield, in the first (1937) edition of her book,⁹ and in a successful attempt to make dragonflies more accessible to the non-specialist, gave each species of British dragonfly an English name. She was apparently unaware of the English names that had already been assigned to British dragonflies and which were revealed by Richard Gabb's examination of a collection in the Grosvenor Museum in Poynton, Cheshire.¹⁰ Her approach was to retain the scientific

BOX 1

SYSTEMATIC POSITION OF *ANAX IMPERATOR* LEACH, 1815, THE EMPEROR DRAGONFLY

Taxon	Name	Distinguishing attributes
Phylum	Arthropoda	Jointed, chitinous exoskeleton; jointed limbs.
Class	Insecta	Tripartite, segmented body; <i>thorax</i> bearing a pair of legs on each of its three segments.
Subclass	Exopterygota	Incomplete <i>metamorphosis</i> (i.e. no pupal stage).
Order	Odonata	Two pairs of long, membranous wings; larva typically aquatic; biting mouthparts in larva and adult; larva with specialised, protractible

labium.

Suborder	Anisoptera	Fore and hind wings differ in shape; larva has muscular diaphragm and gills inside abdomen.
Family	Aeshnidae	Diagnostic features of wing venation and shape.
Genus	<i>Anax</i>	Diagnostic features of body, especially colour pattern, and shape of abdominal appendages and <i>genitalia</i> .
Species	<i>imperator</i>	Diagnostic features of body, especially colour pattern, and shape of abdominal appendages and <i>genitalia</i> .
Authority	Leach	The authority who first described and named the species and designated the type specimen.
Date	1815	The year in which Leach's description of the species was first published, giving the location of the type specimen (which in this case has been lost).

generic name, so leaving no doubt about the genus to which the English name applied. Thus *Aeshna juncea* became the Common Aeshna, and *Sympetrum striolatum* became the Common Sympetrum. Since then the nomenclature has undergone several changes. In 1977 Cyril Hammond gave all generic names English equivalents.¹¹ As a result, *Aeshna juncea* became the Common Hawker and *Sympetrum striolatum* became the Common Darter. When some writers began to show originality in their use of English names, it became desirable to standardise the nomenclature and, beginning in 1991, the British Dragonfly Society (BDS) has listed in each issue of its journal the scientific name and its approved English equivalent for all species found in Britain. All these names, except that for *Gomphus vulgatissimus*, conform to those in Hammond's book and are accepted as definitive in English usage today, at least in Great Britain.

There have recently been two significant developments.

First, in their book on the dragonflies of Ireland, Brian Nelson and Robert Thompson introduced English names different from those in the BDS list for eight genera and 20 species, retaining the same names for only 14 species.¹² In the Irish list, *Calopteryx* becomes Jewelwing (instead of Demoiselle) and *Lestes* becomes Spreadwing (instead of Emerald Damselfly). These two generic names (and some others in the Irish list) conform with those approved for North American dragonflies in 1996 by the Dragonfly Society of the Americas (DSA),¹³ although the English names used for four genera (*Anax*, *Ischnura*, *Leucorrhinia* and *Sympetrum*) do not.

Second, in response to a perceived need, coupled with range expansions of European dragonflies into Britain (see Chapter 10), English names have been generated for Odonata of continental Europe for 29 species not on the British list.¹⁴ The names chosen have in general conformed with the system already in use by the BDS.

Two long-term goals among naturalists and odonatologists who wish to use English names must be to achieve quick recognition and to avoid ambiguity. As long as naturalists adhere to the names in the BDS list, it does not matter whether the English name or the scientific name is used, at least among odonatologists in Britain. However, it makes life much easier for non-British readers if odonatologists use the scientific names in their published work. Indeed it was to remove ambiguity deriving from the use of vernacular names that Linnaeus developed his system of nomenclature in the first place! We

hope that before long unanimity can be reached so that a list of vernacular equivalents can be agreed upon that applies to both Britain and Ireland. Such a list could with benefit conform closely to North American usage. In this book we use only scientific names throughout the text for the species of British dragonflies. In Appendix 1 we list the scientific names of all species found in Britain, together with their vernacular equivalents in Britain (excluding Ireland).

The position is less straightforward regarding the names of the suborders of Odonata. At some time, probably early in the nineteenth century, the English term 'damselfly' was adopted to denote a member of the suborder Zygoptera. This was unfortunate, because a corresponding English term for the suborder Anisoptera was not introduced at the same time. The precedent for the word 'damselfly' was probably the French 'demoiselle' which, according to Réaumur,¹⁵ was the vernacular name applied throughout France to *all* Odonata, not merely Zygoptera. By restricting this term to Zygoptera English-speaking odonatologists laid the foundation for the ambiguity we now address. After Réaumur, Fabricius (1745-1808), a pupil of Linnaeus, separated dragonflies from the Neuroptera (of Linnaeus), assigning them to the order Odonata in 1793.¹⁶ Much later, in 1853, Selys recognised and defined the suborders Zygoptera and Anisoptera.¹⁷ Because the term 'dragon fly' or 'dragonfly' had already been pre-empted to mean a member of the order Odonata, some English-speaking authors decided subsequently that an English term for Anisoptera was needed, but unfortunately a valuable opportunity was missed. Having decided to call Zygoptera 'damselflies', authors in North America¹⁸ and Britain⁹ chose to meet this need in several ways: by calling Anisoptera 'dragonflies proper'; by hyphenating the word 'dragonflies';¹⁹ or by using a lower-case initial letter (for 'dragonfly') to denote the suborder, and a capital initial letter to denote the order.^{20,21} Such suggestions have proved unworkable, partly because the initiators themselves sometimes failed to conform with the remedies they suggested! So the existing situation perpetuates an absurdity and stands in urgent need of reform.

German-speaking odonatologists have tackled this difficulty by calling Zygoptera 'Kleinlibellen' and Anisoptera 'Grosslibellen'. But for English-speaking odonatologists no such solution has been sought. Until a corresponding English name is adopted to denote Anisoptera, English-speaking odonatologists will continue to experience embarrassment, either by having repeatedly to explain in which sense they are using the term 'dragonfly' or by tolerating an ambiguity; and poor Linnaeus (or may suppose) will continue to turn in his grave. We believe that correction of this anomaly is long overdue and accordingly take this opportunity to recommend the following terminology for those who feel compelled to use an English name for Anisoptera. Thus we would have:

Odonata: dragonflies
Zygoptera: damselflies
Anisoptera: warriorflies.

We use this terminology in Appendix 1 but have no need to do so elsewhere in the text, where the terms 'Zygoptera' and 'Anisoptera' suffice.

COLLECTING DRAGONFLIES

There is a second respect in which the conduct of odonatology needs urgent attention.

As odonatology (or at least dragonfly watching) has grown in popularity for field naturalists and photographers, the ranks of dragonfly watchers have been enlarged (and enriched) by new enthusiasts many of whom have come to dragonflies after seeing them while out watching birds. Birdwatchers

typically claim that they do not need to capture a specimen to identify it reliably. Such an option is often unavailable to entomologists, including odonatologists, despite the fact that dragonflies have been nicknamed ‘the birdwatcher’s insect’.²² It is clearly understood among odonatologists that, to pursue their science with rigour, they sometimes need to capture and preserve a specimen and that, when this need arises, they *alone* (as odonatologists) should decide whether or not a specimen needs to be collected. The conduct of odonatology can be severely compromised if non-odonatologists try to prevent odonatologists from collecting specimens. It has happened recently that an odonatologist trying to collect a specimen for deposition in The Natural History Museum was obstructed, and subsequently abused, by self-appointed vigilantes who had chosen to intervene in the field.²³ We cannot emphasise strongly enough that such behaviour constitutes a severe threat to the future viability of odonatology – as a science – and so should be promptly and unequivocally denounced.²⁴

Odonatology is a science. Much of the information in this book would not exist had specimens of dragonflies not been collected and preserved for study. In the first place, as explained above, a species cannot be validly described and named unless represented by a designated type specimen. Furthermore, *voucher specimens* preserved for later study are essential for the pursuit of several branches of biology as well as for some aspects of conservation management and habitat protection. Appendix 2 explains further why voucher specimens are sometimes needed for the pursuit of odonatology.

No one, especially an odonatologist, likes to deprive a dragonfly of life. On the contrary, many odonatologists are deeply committed to conserving habitats on which the survival of dragonfly populations depends. Aware of their responsibility for the conduct of odonatology, and for its image, some odonatological societies have drawn up codes of conduct that apply to collecting. The most balanced, useful and comprehensive code known to us is included in Appendix 2.

THIS BOOK

The first book on dragonflies in the New Naturalist series, by Philip Corbet, Cynthia Longfield and Norman Moore, was published in 1960.²⁵ It was reprinted in 1985, in a paperback edition, but is now very difficult to obtain. It broke new ground in focusing on behaviour and ecology, but the information it contains has long been superseded. Since 1960 there have been massive advances in our knowledge and understanding of dragonfly biology. These have been reviewed, from a global perspective, in 1962, 1980 and 1999.²⁶

By far the most significant of these advances has been the discovery of *sperm displacement*.²⁷ This entails the dual function of the penis of the male dragonfly during copulation – as an organ for transferring sperm to the female and also as a device for removing or repositioning the sperm of rival males already in the female’s body. Sperm displacement has pervasive implications for almost every facet of dragonfly biology, and its discovery has revolutionised our perception of the evolutionary implications of reproductive behaviour of both sexes.²⁸ Almost every action associated with reproduction can now be understood better, and interpreted, in terms of the struggle between males and males, and between males and females, to secure parentage of offspring that themselves will compete successfully to leave vigorous descendants. An important part of this increased understanding is our interpretation of intramale contests during territorial activity. Noteworthy advances have been made in other fields of dragonfly biology, especially in larval ecology and behaviour; and we now have a much clearer understanding of the ways in which life cycles are regulated and are adapted to seasonal changes in the environment.

This book is about the natural history of dragonflies that inhabit Britain. Readers interested in the natural history of British species should be aware of several excellent books on western European dragonflies in French²⁹ and German.³⁰

After briefly describing dragonflies, as animals and insects, in this chapter, we introduce the British species in Chapter 2; and in Chapters 3 to 9 we explore each stage of the life history in detail, giving weight to behaviour and ecology. Although a great deal is known about the biology of dragonflies, many questions remain to be tackled, and we conclude each of Chapters 3 to 9 with suggestions for investigations that enthusiasts may wish to undertake. We recommend that, to save time and effort, would-be investigators consult the relevant literature before embarking on a project. To facilitate this we provide a Bibliography on pages 395-442 listing details of the literature sources cited under each topic in the text. In Chapter 10 we trace the development of odonatology in Britain, including the history and status of conservation – of dragonflies and their habitats – and the relevant, anticipated effects of prospective climate change. We do not provide scale bars on any of the photographs that appear in this book. Readers are referred to the books by Hammond³¹ and Brooks³² where measurements are given for adults and larvae of all British species. Certain terms italicised in the text are used in a specialised sense and are defined in the Glossary on pages 373-381.

Appendices comprise:

- 1) a checklist of species occurring in Britain, giving scientific names and their English (largely BDS) equivalents;
- 2) an introduction to the practice and philosophy of collecting specimens and advice for photographing dragonflies in the field;
- 3) the odonatological criteria according to which a site can qualify for designation as a Site of Special Scientific Interest (sssi) in Britain; and
- 4) maps showing the distribution in Britain of British dragonflies, categorised according to date.

LITERATURE

Until 1960, when the predecessor of this volume appeared,²⁵ books and monographs on British dragonflies were concerned primarily with identification – of adults, by Lucas³³ and Longfield³⁴ and of larvae by Lucas³⁵ and Gardner³⁶. The identification of larvae was placed on a firmer footing by Eric Gardner who reared and described many British species from egg to adult. The keys he produced³⁶ were reprinted in the New Naturalist book *Dragonflies*, published in 1960,²⁵ and in the book by Hammond in 1977 and 1983.³¹

Useful manuals exist for the identification of adults and larvae, for the Odonata of Britain (by Hammond, McGeeney, Miller and Brooks)³⁷ and Europe (by Askew),³⁸ and all except the book by Miller contain information about distribution. Miller's book also contains quality information about biology, especially behaviour. A publication focusing on distribution and conservation status and including summary information about the biology of each British species is the Atlas by Merritt, Moore and Eversham.³⁹

The lay reader interested in dragonflies on a global scale will be well served by recent books by Silsby⁴⁰ and Brooks.⁴¹ Both titles are liberally furnished with colour images and the former is unique in illustrating an example of an adult representing each of the 73 subfamilies of Odonata. Specialised information about the behaviour and ecology of Odonata as an order can be found in two books and a

article by Corbet.²⁶ The classic book *The Biology of Dragonflies*, by R.J. Tillyard, one of the giants of odonatology,⁴² was published in 1917.⁴³ It emphasised morphology and systematics; it is now long out of print and has become a collector's item. It is packed with information not easily found in modern publications. Fortunately, thanks to the initiative and industry of Richard Rowe, it is now available on the worldwide web.⁴⁴

The BDS, established in 1983, collates information about British Odonata, maintains a vigorous education programme and publishes the *Journal of the British Dragonfly Society*, featuring research reports about British species, as well as a bulletin, *Dragonfly News*, which gives details of field and indoor meetings. The BDS supports a standing committee, the Dragonfly Conservation Group, which *inter alia* advises statutory bodies on the conservation needs of dragonflies. There are now several books describing the dragonflies of different regions or counties in Britain (Box 2, p.14).

Two bodies serve odonatologists internationally: the Foundation Societas Internationalis Odonatologica publishes *Odonatologica* and *Notulae Odonatologicae*, and The Worldwide Dragonfly Association publishes *The International Journal of Odonatology* and the newsletter *Agrion*.

CHAPTER 2

The British Species

IDENTIFICATION OF SPECIES

DRAGONFLIES ARE A rewarding group to study because, unlike most insect groups, there are relatively few species to get to know; they are large and easy to find and, after some practice, many species can be identified in flight and from photographs. One of the most obvious features of a dragonfly is its large eyes. The dragonfly's world is a visual world. They recognise each other by sight, either by their striking colours or by their mode of flight and behaviour. And we too can hone our observational skills and soon learn to identify many species of dragonflies in the same way. Most species can be identified from their unique combination of markings, especially those on the abdomen. Many species are sexually dimorphic, that is the females and males of the same species have a different appearance (Figs 16 & 17, p.32). This means that twice as many types must be learnt, but also that it is often quite easy to tell the difference between males and females. For those species that are not sexually dimorphic, males can usually be recognised by the swelling under the base of the abdomen produced by the secondary genitalia, and females usually by the swelling or spike towards the tip of the abdomen formed by the *ovipositor*. Some species are very easy to recognise by their unique appearance. *Aeshna grandis* is the only British species of anisopteran to have amber-coloured wings. Others may require more detailed examination. For example, males of the *Coenagrion* species are identified by the shape of the small black marking on the top of the second abdominal segment. When viewed through binoculars, this marking is often visible, even on specimens several metres away. Some species can be identified reliably in the hand only by close examination of the anal appendages (e.g. *Lestes*, Corduliidae), or leg coloration and genitalia (e.g. *Sympetrum*) but, with experience, even species in these groups can often be identified without the need to net them. That said, it may be necessary to secure a voucher specimen (see Appendix 2). Sometimes visual, or even photographic, records are insufficient to permit secure identification, especially in species which differ in small subtleties of morphology.

Dragonfly larvae are much more difficult to identify than adults, especially in the early *stadia*. A few species have a characteristic appearance and can be identified in the field from the markings on the *caudal appendages* (*Pyrrhosoma nymphula*), the shape of the head (*Anax imperator*) or distinctive thoracic markings (*Cordulia aenea*). The number and shape of the abdominal spines can be a useful character for distinguishing species of Libellulidae, but these may be difficult to see if they are obscured by debris. Also, the extent of the development of these spines may depend on the presence of insectivorous fish. Other species can be distinguished only by close examination under a hand lens or a low-powered microscope. For example, most species of Aeshnidae differ in the shape and relative lengths of the caudal appendages (*epiprocts* and *paraprocts*) but these are too small to see clearly with the naked eye. The shape of the labium and arrangement of labial *setae* also provide important characters in many groups, but the setation may only be visible in dead or anaesthetised larvae. There are no known characters that will reliably distinguish the larvae of *Coenagrion puella* and *C. pulchellum* or *Sympetrum striolatum* and *S. sanguineum*. The *F-0 exuviae*, the shed skins of larvae left

on emergent plants after adults have emerged, of Anisoptera and Zygoptera are usually identifiable to species and provide the most reliable way of establishing which species are completing their life cycles at a particular site. However, the problems of identifying larvae should not be underestimated. The shape and appearance of the *caudal lamellae* of Zygoptera change greatly during development (Fig. 60, p.115), the number of labial setae can be highly variable and is not always diagnostic, and abdominal spines can be variably developed. There is still much work to be done to establish reliable characters for larval identification.

This book is not intended to be an identification guide. For this purpose, we refer you to other books which serve this function (Box 2). Instead, in this chapter, we review the broad distribution of dragonflies in Britain, and the factors thought to influence this, before describing the characteristics of each family that occurs in Britain.

BOX 2

SOME IDENTIFICATION GUIDES TO THE BRITISH SPECIES

- Brooks, S.J.** (Ed.) (1997) (4th revised edition, 2004). *Field guide to the dragonflies and damselflies of Great Britain and Ireland*. British Wildlife Publishing: Hook.
- Cham, S.** (2007). *Field guide to the larvae and exuviae of British dragonflies*. Volume 1: Dragonflies (Anisoptera). British Dragonfly Society.
- Cham, S.** (2008). *Field guide to the larvae and exuviae of British dragonflies*. Volume 2: Damselflies (Zygoptera). British Dragonfly Society.
- Hill, P. & Twist, C.** (1996). *Butterflies and dragonflies: a site guide*. Arlequin Press: Chelmsford.
- McGeeney, A.** (1986). *A complete guide to British Dragonflies*. Jonathan Cape: London.
- Miller, P.L.** (1995). *Dragonflies*. The Richmond Publishing Co. Ltd: Slough.
- Nelson, B. & Thompson, R.** (2004). *The natural history of Ireland's dragonflies*. The National Museums and Galleries of Northern Ireland: Belfast.
- Powell, D.** (1999). *Guide to the dragonflies of Great Britain*. Arlequin Press: Chelmsford.
- Hammond, C.O.** (1977) (1983, 2nd edition revised by R. Merritt). *The dragonflies of Great Britain and Ireland*. Harley Books: Colchester.
- Smallshire, D. & Swash, A.** (2004). *Britain's dragonflies*. WildGuides: Old Basing.

BOX 3

REGIONAL GUIDES TO BRITISH DRAGONFLIES

- Averill, M.** (1996). *The dragonflies of Worcestershire*. Mike Averill: Kidderminster.
- Belden, T.A.** (2004). *Dragonflies of Sussex*. Sussex Wildlife Trust: Chichester.
- Benton, E.** (1988). *The dragonflies of Essex*. Essex Field Club: London.
- Brook, J. & Brook, G.** (2001). *Dragonflies of Kent. An account of their biology, history and distribution*. Transactions of the Kent Field Club **16**: 1-115.
- Brownett, A.** (1996). *The dragonflies of Oxfordshire*. Brookside Books: Banbury.
- Cham, S.** (2004). *Dragonflies of Bedfordshire*. Bedfordshire Natural History Society: Bedford.

- Coker, S. & Fox, T.** (1985). *West Wales Dragonflies*. Mountain Books: Mountain.
- Collingwood, N.** (1997). *The dragonflies of Staffordshire*. Stoke-on-Trent City Museum and Art Gallery: Stoke-on-Trent.
- Dunn, R. & Budworth, D.** (2005). *Dragonflies in Derbyshire: status and distribution 1977-2000*. Derbyshire & Nottinghamshire Entomological Society: Derby.
- Follet, P.** (1996). *Dragonflies of Surrey*. Surrey Wildlife Atlas Series 2. Surrey Wildlife Trust: Woking.
- Gabb, R. & Kitching, D.** (1992). *The dragonflies and damselflies of Cheshire*. National Museums & Galleries on Merseyside: Liverpool.
- Garner, P.** (2005). *The dragonflies of Herefordshire*. Herefordshire Biological Records Centre: Hereford.
- Grover, S. & Ikin, H.** (1994). *Leicestershire dragonflies*. Leicestershire Museums: Leicester.
- Holland, S.** (1991). *Distribution of dragonflies in Gloucestershire*. Mrs Twissell: Cheltenham.
- Lockton, A.J.** (Ed.) (1996). *The dragonflies of Shropshire*. Wildscan Ecological Consultants on behalf of BIOS: Shrewsbury.
- Mendell, H.** (1993). *Suffolk dragonflies*. Suffolk Naturalists' Society: Ipswich.
- Prendergast, E.D.V.** (1991). *The dragonflies of Dorset*. Dorset Natural History and Archaeological Society: Dorchester.
- Randolph, S.** (1992). *Dragonflies of the Bristol region*. Bristol/Avon Regional Environmental Records Centre: Bristol.
- Saunders, J.W.** (1986). *Dragonflies of Pembrokeshire*. Pembrokeshire Coast National Park Authority: Pembrokeshire.
- Saville, B.** (Ed.) (1997). *Dragonflies of the Lothians*. Scottish Wildlife Trust: Edinburgh.
- Smout, A.-M. & Kinnear, P.** (1993). *Dragonflies of Fife: a provisional atlas*. Fife Nature: Glenrothes.
- Taverner, J., Cham, S. & Hold, A.** (2004). *The dragonflies of Hampshire*. Pisces Publications: Newbury.
- Taylor, P.** (2003). *Dragonflies of Norfolk*. Norfolk and Norwich Naturalists' Society: Norwich.
- Tyrell, M.** (2006). *The dragonflies of Northamptonshire*. Northants Dragonfly Group: Northampton.
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DISTRIBUTION OF DRAGONFLIES IN BRITAIN

The distribution maps shown in this book (Appendix 4) are based on records plotted at a resolution of 10 km². The records have been built up over a period of about 160 years. The latest maps which appear in Appendix 4 have been updated to the year 2006 and are based on 363,959 records from 48,881 sites. They represent a massive effort from the amateur Odonata recording community. While these maps provide a good idea of the broad distribution of the British species, areas of Scotland¹ and Ireland² remain less well covered than England and Wales. The maps may also provide a rather optimistic view of the status of the British species. The records are largely based on sightings of adults and no account is taken of numbers seen, whether or not the species were breeding at the place in which they were seen, whether these were one-off sightings or if the species has been recorded over a period of many years at the same site. It is also unclear from the maps how many sites are present within each 10-km square. A species may be recorded consistently from a particular 10-km square

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