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Review

A century on from *The Biology of Dragonflies* by Tillyard 1917: what have we learned since then?

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Abstract The field of odonatology has developed considerably during the past century. Three figures, namely E. Selys-Longchamps, R.J. Tillyard and P.S. Corbet, have undisputedly founded our current knowledge of odonatology and contributed massively to the understanding of systematics, biology, ecology and behaviour of odonates. The year 2017 will mark the 100th anniversary of Tillyard's *The Biology of Dragonflies*. We review the book and the author's life and contributions to Australian odonatology. We present an updated history of odonatology and highlight prominent advances in the field. The influence of the book on non-scientists is described. Future research in odonatology on aspects that have not been studied and others that need further investigations are discussed.

Key words Australian odonatology, biology, conservation, history, Odonata, systematics.

INTRODUCTION

The history of odonatology, entomologists and especially odonatologists may celebrate the 100th anniversary of one of the pioneer books in odonatology, *The Biology of Dragonflies* (Tillyard 1917a). This book is the first to compile detailed information on the morphology, anatomy, taxonomy and natural history of odonates and thus presents the foundation of the science of odonatology. It has deeply influenced the following generations of people and scientists in their perception of these insects and increased the desire among amateurs and researchers to explore their diversity, distribution, biology, behaviour and ecology (Corbet 1962, 1999; Córdoba-Aguilar 2008). Nowadays, odonates are widely recognised as excellent model organisms with which one can answer various questions related to demography (Cordero-Rivera & Stoks 2008), evolutionary biology (Johansson & Mikolajewski 2008; Stoks *et al.* 2008), community ecology (McPeek 2008) and conservation biology (Samways 2008).

Here, we present the following: (1) a short biography of Tillyard; (2) an overview of the book; (3) contribution of Tillyard to Australian odonatofauna; (4) a brief history of odonatology; (5) prominent advances in odonatology; (6) the influence of the book on non-scientists; and (7) future directions.

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SHORT BIOGRAPHY

Born on 31 January 1881 at Norwich, Norfolk, England, Robin John Tillyard (1881–1937) was a prominent naturalist; an entomologist with a deep interest in palaeontology. He was educated at Dover College and took up a scholarship to Queens' College Cambridge (BA, 1903; MA, 1907). Due to health problems, he migrated to Australia and taught mathematics and science at Sydney Grammar School in 1904–1913. He started publishing on odonates in 1905. His passion for studying insects and especially dragonflies led him to resign his position and study zoology at the University of Sydney. Successful in his studies, he earned a BSc in 1914 and a Doctorate in Science in 1917; the year during which he published *The Biology of Dragonflies* (Tillyard 1917a), a gold mine of information for subsequent odonatologists. He was a Macleay fellow in Zoology at the Linnean Society of New South Wales in 1915–1920 and Chief of the Biological Department of the Cawthron Institute in Nelson, New Zealand, in 1921–1928 where he wrote *The Insects of Australia and New Zealand* (Tillyard 1926), considered a seminal book in the history of Australian entomology. In 1928, he returned to Australia to set up the Division of Economic Entomology in the Council for Scientific Research. From 1924 to 1937, he published several papers in paleoentomology of Australia and the Elmo, Kansas Lower Permian fossil beds (Beckemeyer 2000). He died in 1937 at the age of 56 in a car accident in Australia. More information about the life of Robin John Tillyard can be found in Imms (1938), Evans (1963), Crosby (1977), Baker (2010), and Endersby & Fliedner (2015).

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Table 1 Chapters of *The Biology of Dragonflies* (Tillyard 1917)

Number	Title	Page
1	Introduction	1
2	The Imago - External Features and Skeleton	9
3	The Wings	38
4	The Larva or Nymph	67
5	The Alimentary and Excretory Systems	100
6	The Nervous System	120
7	The Sense Organs	137
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OVERVIEW OF THE BOOK

With 396 pages and 19 chapters (Table 1), Tillyard (1917a) established the fundamental biological knowledge of odonates based on his own research, with a particular emphasis on morphology, anatomy, taxonomy, embryology, ontogeny and phylogeny. A century later, no comparable endeavour on the biology of odonates has been published, as subsequent odonatologists did not thoroughly explore the biological aspect of odonates but used the book as basis to explore other aspects such as behaviour and ecology. Corbet (1999) stated 'The most comprehensive treatment of external and internal anatomy remains that of Tillyard (1917)'. This places the book as the definitive work on the biology of the insect group. The book contains 187 figures and 4 plates, two of which are coloured (e.g. Fig. 1a, b). The quality and precision of the sketches are astonishing, readily comparable with sketches made today in books and field guides using substantially advanced technology.

The first chapter is an introduction which takes the reader through the history of phylogeny of odonates, generalities on the habits and morphology of adults and larvae, and the position of the order in the Insecta. He started by acknowledging the work of marked odonatologists who contributed in the description of odonates in the 19th century, especially Baron Edmond de Selys-Longchamps and his disciples. The second chapter is devoted to the external features and exoskeleton of adults and gives detailed descriptions of the segmentation and appendages of the head, the thorax and the abdomen. Although the chapter places emphasis on the external anatomy, it also includes an internal view of the thorax and part of the abdomen. The third chapter focuses entirely on wings, probably because they formed the basis for Odonata classification. Here, Tillyard standardises the terminology for wing venation and presents seven figures and a plate (Fig. 1b) to illustrate the types of venation and shape diversity of different wing regions. He also writes about the wing development and phylogenetics. Chapter 4 is the second longest chapter and describes the development and the external anatomy of the larval stage. He starts by giving a description of egg hatching of odonates and describes larval growth by highlighting the morphological changes that take place during development. As in the discussion of adults, he gives detailed terminology of the various parts and segments of the larval body (head, thorax and abdomen). Tillyard made the distinction between two types of labial masks in odonates namely the *flat* and the *concave* (*spoon-shaped*) mask, and two types of dorsal appendages (*appendix dorsalis*), that is, the anal pyramid in anisopterans and caudal gills in zygopterans. The chapter ends with a description of the metamorphosis supplemented by an illustration of the different steps of the process in *Petalura gigantea*. This figure contains a controversy as it presents a hanging back emergence style (Fig. 2a) which does not correspond to the upright emergence style which seems to be the norm for the species (Fig. 2b; Baird 2013). So, either Tillyard used the species only for illustrative purpose to describe the metamorphosis in dragonflies or he observed an unusual behaviour for the species. The seven following chapters (Chapters 5–11), which represent one third of the book, are dedicated to the physiology of the group where he describes the alimentary and excretory systems, the nervous system, the sense organs, the circulatory system, the respiratory system, the body-wall and muscles and the reproductive system. The sketches that are presented in these chapters are accurate and reliable even today. Chapter 12 is about embryology and it presents the structure of the egg, embryonic development and the origin of the parts of the embryo. Chapter 13 is devoted to the coloration of odonates outlining the nature of colours, body, wing, larval coloration and colour dimorphism. Chapter 14 presents the classification of the order with 2 suborders, 5 families, 18 subfamilies and 26 tribes. In Chapter 15 (zoogeographical distribution), the odonatofauna of the six main zoogeographical regions is divided into palaeogenic, entogenic and ectogenic groups. Chapter 16 is entitled geological records and presents fossil records in the palaeozoic, mesozoic and tertiary. The author attempted to reconstruct the phylogeny of the order from the Carboniferous. Chapter 17 is on bionomics which is the only part of the book that treats natural history with some information on ecology and behaviour of odonates. Chapter 18 presents the British odonates with 42 species that Tillyard classified into 20 genera, 10 tribes, 9 subfamilies and 4 families. Chapter 19 is the last part of the book in which the author gives recommendations on how to collect and rear odonates and presents biological methods to manipulate and dissect specimens.

CONTRIBUTION OF TILLYARD TO AUSTRALIAN ODONATOLOGY

The Biology of Dragonflies benefited greatly from Tillyard's tremendous first-hand knowledge of the Australian fauna with species, genera, even families so different from other faunas much better known at his time. Whereas it is well-known that Tillyard introduced into science approximately as many Australian species as were previously known, considerably less attention is usually given to his taxonomic larval work that was crucial for

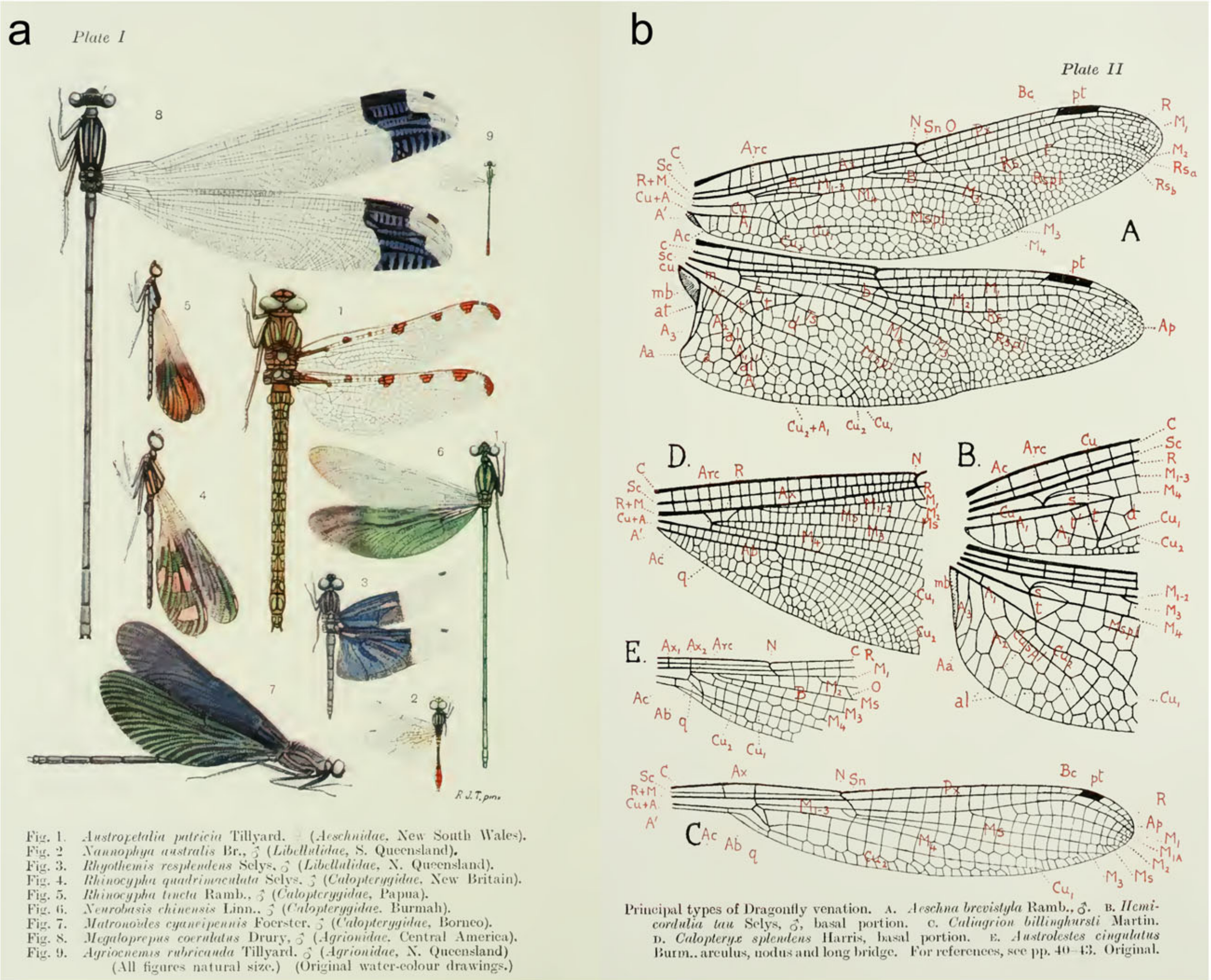

Fig. 1. (a) Plate 1 (frontispiece) of the book. Nine species are illustrated: 1. *Austropetalia patricia* Tillyard, 1910; 2. *Nannophya australis* Brauer, 1865; 3. *Rhyothemis resplendens* Selys, 1878, 4. *Rhinocypha quadrimaculata* Selys, 1853; 5. *Rhinocypha tincta* Rambur, 1842; 6. *Neurobasis chinensis* Linnaeus, 1758; 7. *Matronoides cyaneipennis* Foerster, 1897; 8. *Megaloprepus caerulatus* Drury, 1782; 9. *Agriocnemis rubricauda* Tillyard 1913. (b) Plate 2 of the book. The terminology of wing venation is given in detail for A. *Aeshna brevistyla* Ramb. male; B. *Hemicordulia tau* Selys male, basal portion; C. *Caliagrion billinghursti* Martin. D. *Calopteryx splendens* Harris, basal portion. E. *Austrolestes cingulatus* Burm., arculus, nodus and long bridge.

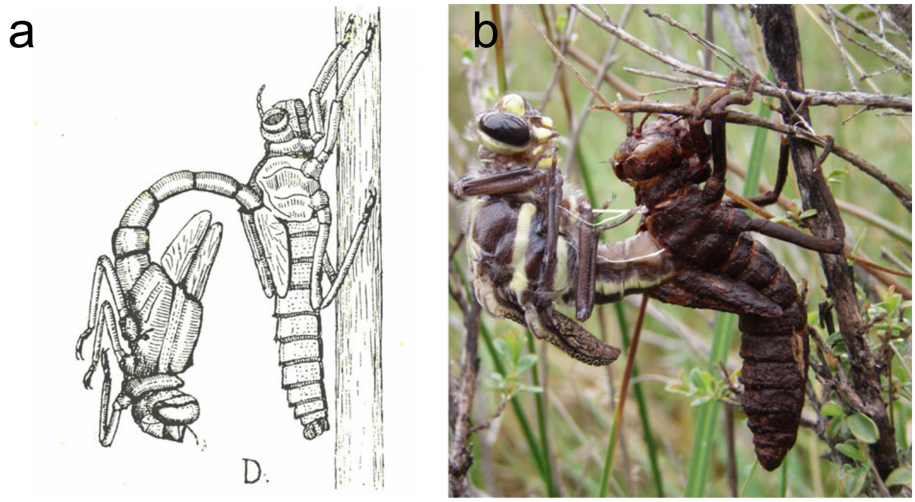

Fig. 2. Metamorphosis of *Petalura gigantea*. (a) Hanging back position emergence as illustrated by Tillyard (1917a), page 94, figure 43D; (b) upright emergence as described by Baird (2013).

Table 2 Australian larvae described by Tillyard. The reference Tillyard (1917a) in bold refers to his book *The Biology of Dragonflies*

Family	Species	References
Lestidae	*Austrolestes analis* (Rambur, 1842)	(Tillyard 1906, 1917a, 1932)
	Austrolestes cingulatus (Burmeister, 1839)	(Tillyard 1906, 1914, 1917a, 1917b, 1926)
	Austrolestes leda (Selys, 1862)	(Tillyard 1906, 1917a)
	Austrolestes psyche (Hagen, 1862)	(Tillyard 1917a, b)
Hemiphlebiidae	*Hemiphlebia mirabilis* (Selys, 1869)	(Tillyard 1928)
Synlestidae	*Synlestes weyersii* (Selys, 1869)	(Tillyard 1914, 1917a, 1917b, 1926)
Argiolestidae	*Austroargiolestes icteromelas* (Selys, 1862)	(Tillyard 1917a, 1917b, 1926, 1932), as *Argiolestes icteromelas*
	Griseargiolestes griseus (Hagen, 1862)	(Tillyard 1914, 1917a), as *Argiolestes griseus*
Lestoideidae	*Diphlebia lestoides* (Selys, 1853)	(Tillyard 1909b, 1912, 1915a, 1917a, 1926)
	Diphlebia nymphoides (Tillyard, 1912)	(Tillyard 1912)
Isostictidae	*Neosticta canescens* (Tillyard, 1913)	(Tillyard 1914, 1917a, b)
Coenagrionidae	*Argiocnemis rubescens* (Selys, 1877)	(Tillyard 1917a, b)
	Austroagrion watsoni (Lieftinck, 1982)	(Tillyard 1917b), as *A. cyane*
	Austrocnemis splendida (Martin, 1901)	(Tillyard 1917b)
	Caliagrion billinghursti (Martin, 1901)	(Tillyard 1914, 1917a, b, 1926)
	Ischnura aurora (Brauer, 1865)	(Tillyard 1917a)
	Ischnura heterosticta (Burmeister, 1839)	(Tillyard 1917a, b)
Austropetaliidae	*Austropetalia patricia* (Tillyard, 1910)	(Tillyard 1910c, 1917a, b, 1926)
Aeshnidae	*Anax papuensis* (Burmeister, 1839)	(Tillyard 1916a, b, 1917a; Tillyard 1932) as *Hemianax papuensis*
	Gynacantha dobsoni (Fraser, 1951)	(Tillyard 1916a, 1917a), as *G. rosenbergi*
	Dendroaeschna conspersa (Tillyard, 1907)	(Tillyard 1914, 1916a, b, 1917a)
	Austroaeschna obscura (Theischinger, 1982)	(Tillyard 1916a, b, 1917a) as *A. multipunctata*
	Austroaeschna parvistigma (Selys, 1883)	(Tillyard 1916a)
	Austroaeschna subapicalis (Theischinger, 1982)	(Tillyard 1916a), as *A. atrata*
	Austroaeschna unicornis (Martin, 1901)	(Tillyard 1916a), as *A. longissima*
	Austroaeschna pulchra (Tillyard, 1909)	(Tillyard 1916a), as *A. unicornis*
	Austrophlebia costalis (Tillyard, 1907)	(Tillyard 1916a)
	Notoaeschna geminata (Theischinger, 1982)	(Tillyard 1916a), as *N. sagittata*
	Telephlebia godeffroyi (Selys, 1883)	(Tillyard 1916a)
Gomphidae	*Ictinogomphus australis* (Selys, 1873)	(Tillyard 1917a), as *Ictinus australis*
	Antipodogomphus acolythus (Martin, 1901)	(Tillyard 1917a), as *Austrogomphus manifestus*
	Austrogomphus ochraceus (Selys, 1869)	(Tillyard 1916a, 1917a, 1926)
	Hemigomphus heteroclytus (Selys, 1854)	(Tillyard 1910c, 1914, 1916b, 1917a)
Petaluridae	*Petalura gigantea* (Leach, 1815)	(Tillyard 1909a, 1910c, 1911b, 1917a)
Synthemistidae	*Archaeosynthemis orientalis* (Tillyard, 1910)	(Tillyard 1910a, 1914, 1916b, 1917a), as *Synthemis macrostigma*
	Choristhemis flavoterminata (Martin, 1901)	(Tillyard 1910a)
	Eusynthemis tillyardi (Theischinger, 1995)	(Tillyard 1910c, 1916b), as *E. guttata*
	Parasynthemis regina (Selys, 1874)	(Tillyard 1910c), as *Synthemis regina*
	Synthemis eustalacta (Burmeister, 1839)	(Tillyard 1910c, 1917a, 1926)
Corduliidae	*Hemicordulia tau* (Selys, 1871)	(Tillyard 1914, 1915b, 1916b, 1917a, 1926; Tillyard 1932)
Libellulidae	*Diplacodes bipunctata* (Brauer, 1865)	(Tillyard 1917a, 1926)
	Diplacodes haematodes (Burmeister, 1839)	(Tillyard 1914, 1916b, 1917a)
	Nannophlebia risi (Tillyard, 1913)	(Tillyard 1913)
	Orthetrum caledonicum (Brauer, 1865)	(Tillyard 1916b, 1917a)
	Tramea loewii (Kaup, 1866)	(Tillyard 1917a, 1926)
Genera incertae sedis	*Cordulephya montana* (Tillyard, 1911)	(Tillyard 1911a, 1917a)
	Cordulephya pygmaea (Selys, 1870)	(Tillyard 1911a, 1914, 1916b, 1917a)
	Austrocordulia refracta (Tillyard, 1909)	(Tillyard 1910b, 1914, 1916b, 1917a)

As much as Tillyard's largely adult-based taxonomic studies of Australian dragonflies inspired, influenced and facilitated the work of subsequent generations of students of Australian dragonflies, his work on the larvae is the basis for all subsequent larval studies in Australia, and the reason why larval taxonomy of Australian dragonflies is in reasonable shape and now useful for diversity, environment, conservation and even climate change studies (e.g. Bush et al. 2013).

coordinating the wealth of biological and ecological traits and making them useful for systematics and phylogeny. Tillyard was the first to discover, breed out and describe the larvae of nearly 50 species of Australian dragonflies (Table 2). His descriptions were of a standard that makes them still very useful today. He used details of more than 30 of them in *The Biology of Dragonflies*.

Tillyard described 87 species and 21 genera from Australia. He also named Odonata from New Zealand, Fiji, and Papua New Guinea and, if ranks lower than species are included, 25 genera and 129 specific, subspecific or infrasubspecific taxa can be attributed to him. All but two of his genera (*Anacordulia* and *Notoneura*) are still recognised, as are 52 of his species

(40%). Thirty-seven (29%) of his species have been moved to another genus while 16 (12%) have fallen into junior synonymy. Twelve (9%) of his subspecies have been raised to full species status and two species have been relegated to subspecific status. Of the eleven subspecies, or varieties or races as Tillyard sometimes called them, not accounted for above, five are still recognised, albeit four in different genera; two are no longer considered as distinct subspecies, and four have disappeared from the modern literature.

Tillyard's taxonomic publishing career spanned the years 1906 to 1926 and is contained in 29 articles. Twenty-three of these were published in the *Proceedings of the Linnean Society of New South Wales*. The description of the New Zealand genus *Uropetala* was, understandably, published in the *Transactions of the Royal Society of New Zealand* and his work on Fiji specimens in *Transactions of the Royal Entomological Society London*. Tillyard rarely published jointly; two exceptions are with Herbert Campion in the *Journal of the Linnean Society (Zoology)* (Tillyard 1916a) and in Aeschnines, in 'Collections Zoologiques du Baron Edm. de Selys-Longchamps' Vol XIX which was edited by its prime author René Martin (Martin 1909).

It was very fortunate and a credit to Tillyard that some of his work on Australian dragonflies could be continued by the very prominent Australian J.A.L. Watson. Tillyard's descriptive efforts on the Australian dragonflies inspired and facilitated not only numerous detailed studies but also several comprehensive works on the fauna of this continent (e.g. Fraser 1960; Watson 1962; Watson 1991; Watson *et al.* 1991; Theischinger & Hawking 2006; Peters & Theischinger 2007; Theischinger & Endersby 2009) over more than a century. Seven regional taxa of the species group were dedicated to Tillyard by some of his colleagues over 90 years, from Martin (1906) to Theischinger (1995).

ETYMOLOGY USED BY TILLYARD

In the era of Tillyard's work, and earlier, it was rarely the practice to give the etymological derivation of the genus-group or species-group name. An exception which he sometimes used was to acknowledge a person after whom a species was named. Meanings of many of the names he proposed have to be deduced from likely Latin or Greek roots. Watson (1969) lists the location of primary type material, and designates lectotypes where necessary, for all Australasian dragonflies described by Tillyard. His paper serves as an excellent checklist to the dragonflies which Tillyard named. Tillyard (1916b) defines: 'The prefixes *Noto*- [Gr. Νότος = south wind] and *Austro*- [*L. australis* = southern] may conveniently be used to denote purely Australian genera'. Accordingly, he named nine genera with prefix *Austro*- and two with *Noto*-, 44% of his 25 genus names. A thorough treatment of the etymology of the dragonflies named by Tillyard is given by Endersby (2012).

If his 129 species-group names are categorised, eponyms (named after people) and colourings each number 25. Morphology is next with 24, and four others use the colour of a morphological character. Size or appearance account for another 8. There are 13 species which are toponyms (named after a place) in the broad sense with another 5 relating to a direction: eastern and western. Unlike his European predecessors, Tillyard had the privilege of seeing his specimens alive allowing him to name some for their behaviour (3) or their habitat or substrate on which they were commonly found (10). Describing colour, which can fade substantially in some museum specimens, also was made more definitive by reference to live specimens. That in total accounts for all but 12 of the specimens he named. [*Austrophya*] *mystica* still remains a puzzle, perhaps referring to the obliterated markings on the sole, aged and damaged female specimen. The remaining 11 species names recognize a relationship with other species.

Tillyard recognised the concepts of evolution and phylogeny, but perhaps not in a modern sense, even though he used the terms in some of his original descriptions. He defined '*Asthenogenesis* as the development of a successful line of descent by the adoption of weakness in structure'. The term is not in current use nor is it readily understood. Another early author interpreted it as meaning a reference to convergence through the loss of characters or neoteny. Tillyard writes of 'a specialized asthenogenetic offshoot from the main stock', 'one of the first asthenogenetic offshoots from that type' and 'a form *asthenogenetically intermediate* between the less-reduced *Lestes* and the more reduced *Protoneura*'. In another description, he suggests 'a more archaic form … has either evolved gradually from ..; a more useful form, or has arisen as a sudden mutation, or, possibly, as the direct inheritance of an acquired character, in the Lamarckian sense'.

HISTORY OF ODONATOLOGY

Updated history of odonatology

A detailed history of odonatology, modestly called 'A short history of odonatology', was published by Corbet (1991), in which he identifies six strands describing the progress of the field. Below, we summarise each strand and provide some updates corresponding to important events that took place after the publication of Corbet (1991).

The first one was named the exploring strand, and it refers to the period when attributes of odonates such as shape, mode of reproduction and development were recognised. During this period, there was no rational system for naming species. The span of this strand was not defined. The codifying strand starts in 1758 with the introduction of the binomial nomenclature by Linnaeus (1758) who described only 18 species that he placed in the genus *Libellula*. The number of described odonates increased during this period, especially with the descriptions of J. C. Fabricius who, by 1798, had a list of 69 species (Kirby 1901). Fabricius was the first to give to dragonflies a separate ordinal status with the name 'Odonata' in 1793. The classifying strand starts in 1820 and was founded by Baron Michel Edmond de Selys-Longchamps who realised that wing venation is a reliable trait for classification of several families of odonates. During his life, Selys described 700 species and established 134 valid genera (Wasscher & Dumont 2013). For more than a century and a half, wing venation was used as the key trait to classify families and genera. In fact, there have been many attempts to establish the phylogeny of odonates using morphological traits (Fraser 1957; Hennig 1969; Hennig *et al.* 1981; Pfau 1991; Trueman 1996). However, recent phylogenetic studies have shown morphology alone, even with extensive analyses (Rehn 2003), does not reflect the true phylogeny (Fleck 2004; Dijkstra & Vick 2006; Pilgrim & Von Dohlen 2007; Ware *et al.* 2007; Carle *et al.* 2008; Fleck *et al.* 2008) and can totally overlook cryptic species (Yong *et al.* 2014). For instance, wing venation is not a highly reliable trait because it evolved multiple times (Ware *et al.* 2007). After a long history of systematics, the classification of odonates has improved substantially by extensive phylogenetic studies (Ware *et al.* 2007; Fleck *et al.* 2008; Dijkstra *et al.* 2014). A decade ago, Trueman (2007) predicted that all major issues related to odonate classification worldwide will be resolved by 2017 and at most 2027. Although a lot has been done during the last decade, we probably need another decade to provide the definitive global phylogenetics of the order.

In the integrating strand (1913), odonatologists started to compile observations on ecology, behaviour and physiology of species. R. J Tillyard, named 'a giant' by Corbet (2003b) basically established this strand with his classic book '*The Biology of Dragonflies*' (Tillyard 1917a). Corbet is another important figure of this period who published a book (Corbet 1962) and a review (Corbet 1980) that encompass the biology, ecology and behaviour of odonates. In addition, two main books have been published during the past two decades (Corbet 1999; Córdoba-Aguilar 2008). First, *Dragonflies*: *Behaviour and Ecology of Odonata* (Corbet 1999) compiles information of all fields and treats all aspects of odonatology, except for morphology and physiology which have only been briefly discussed. It is probably the most used book by contemporary odonatologists. The second book is *Dragonflies and damselflies. Model Organisms for Ecological and Evolutionary Research* edited by Alex Cordoba-Aguilar and published in 2008, the same year in which Corbet passed away. The book contains 20 chapters written by many experts in Odonata research, encompassing reviews of modern studies in systematics, evolutionary biology, ecology, conservation biology and behaviour.

The intercommunicating strand which may be said to mainly start with the foundation of the Societas Internationalis Odonatologica (S.I.O.) in 1971 (Kiauta & Van Brink 1972) which launched the journal *Odonatologica* in 1972 whose aim is to promote and facilitate the international exchange of knowledge about odonates. In 1998, another major peer-reviewed journal named *International Journal of Odonatology* was founded. This quarterly journal promotes the publication of papers that address various subjects related to the study of odonates. In addition, regular national and international meetings are organised with the specific goal to provide a scientific forum and promote interactive exchange of ideas and results between scientists and amateurs. The International Congress of Odonatology is the largest meeting where odonatologists of different nations assemble to present projects related to the exploration and protection of the dragonflies of the world and their habitats.

The final conserving strand started with the formation of the Odonata specialist group within the IUCN in 1980 to determine conservation priorities for dragonflies and damselflies that ameliorate habitat degradation resulting from human activities (Moore 1982). Odonates have played an important role in systematic conservation planning (Prendergast *et al.* 1993), and their protection benefited many other invertebrates and vertebrates of freshwater ecosystem (Knight *et al.* 2005; Taylor 2006). It has been shown that dragonflies and damselflies are sensitive indicators of landscape change (Samways *et al.* 2005). Nowadays, the conservation of dragonflies and their habitats (Moore 1997) is established in many areas. Furthermore, the increased awareness about dragonflies and their conservation during the last decade has marked the contemporary development of this strand. Many scientist volunteers participate in data collection worldwide and contribute to the elaboration of databases of crucial importance to solve questions related to timely environmental issues and improve human well-being. Citizen science seems to go hand in hand with odonatology and is likely the future for improving our knowledge about dragonflies and damselflies of areas that have never been explored, synchronising sampling efforts at different parts of the world, and providing services that regular funding could not achieve.

A handy history of odonatology

The history of odonatology can be summarised in four eras: Selys era (systematics), Tillyard era (biology), Corbet era (behaviour and ecology) and blossoming era (volunteering, phylogenetics and climate change) (Fig. 3). Each era starts when its main contribution to odonatology was published, and stops when the subsequent significant contribution appeared. However, the influence of each era never stops since the advances of each era have built on the basic knowledge for subsequent eras and formed the current science of odonatology. The first three eras were named after scientists, but the fourth was not. It was called the blossoming era because it is characterised not only by an extraordinary increase in the popularity of odonates in scientific studies but also by the overwhelming contributions of volunteers and citizen scientists coming from different backgrounds. We have included the historical timeline of peer-reviewed journals that are still active today as well as regular scientific congresses. Finally, our representation is just a simplification and does not include the hundreds of field guides, atlases and red lists that are published frequently worldwide nor the hundreds of names of odonatologists who have made outstanding contributions to odonatology in particular and science in general.

PROMINENT ADVANCES IN ODONATOLOGY

During the past 50 years, there have been major advances in the knowledge of odonates in systematics but also in various biological, ecological and behavioural aspects. We present seven most significant findings that we believe Tillyard would love to see if he were still alive.

Phylogenetics has played a crucial role in the understanding of the evolutionary relationships among odonate species (Kambhampati & Charlton 1999; Artiss *et al.* 2001; Ware

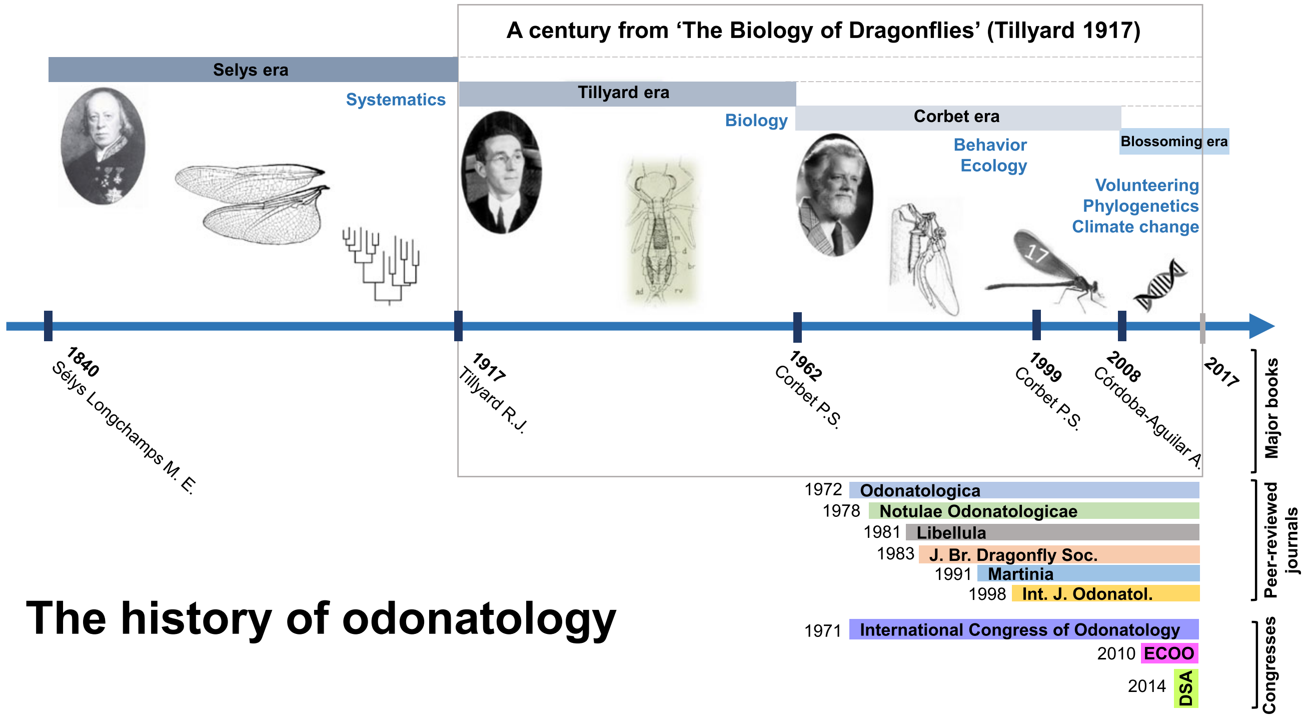

Fig. 3. A history of odonatology. Four main eras are defined: Selys era, Tillyard era, Corbet era and blossoming era. Although eras were limited in time in this representation, the dashed lines indicate that the influence of each era does not stop. Five major books are cited (de Selys-Longchamps 1840; Tillyard 1917; Corbet 1962, 1999; Córdoba-Aguilar 2008). Only peer-reviewed journals that are still active today are shown, among which *Odonatologica* and *International Journal of Odonatology* are the most popular. Two international congresses are noted. ECOO: European Congress on Odonatology; DSA: Dragonfly Society of America.

et al. 2007; Fleck *et al.* 2008; Dijkstra *et al.* 2014). The use of sequences of base pairs besides morphological traits like wing veins, aedeagus and colours to set a clear-cut phylogeny was certainly something that Tillyard would be delighted to use.

Odonate diversity on earth is estimated to be 7500 species (Clausnitzer *et al.* 2009). Recently, 60 new species were discovered in Africa, which represents the largest number of species to be named at once in 130 years (Dijkstra *et al.* 2015). Surprisingly, these species are far from being cryptic and can easily be identified with handy characters. This amazing discovery which motivated odonatologists worldwide indicates that more species are to be discovered, especially in areas where the risk of extinction is high.

Sperm displacement was first discovered by Waage (1979) in *Calopteryx maculata*. He noticed that the aedeagus of the damselfly possesses spines that remove sperm from female spermathecae with an efficiency of 99%. So a male removes sperm of previous mates before he transfers his own sperm. Since its discovery, sperm competition has been recorded in many other odonates (Miller & Miller 1981; Miller 1987; Cordero *et al.* 1995), and theories of co-evolution between the sexes were advanced, suggesting that the end result of such an elaborative shape of male penis is the ability of the females to store sperm from previous matings (Córdoba-Aguilar *et al.* 2003). The finding of Waage (1979) opened a new field of research on reproductive behaviour and sexual selection that has been explored thoroughly afterwards in other taxa (Simmons 2001).

Seasonal regulation is a topic that has received much attention during the past few decades. Odonates are of tropical origin and have successfully colonised temperate regions and adapted to seasonality. Seasonal regulation means that species and/or populations adjust their life history according to local environmental conditions (Pritchard 1982; Norling 1984), often imposed by latitude and elevation. Three types of odonate life cycle have been distinguished (Corbet 2003a). Spring species are those that spend the last winter before emergence as a final stadium (F-0) and consequently typically emerge synchronously and early. Summer species, on the other hand, spend the last winter in the stadium before F-0 and consequently emerge later asynchronously. Obligatory univoltine species have 1 year life cycle wherever they occur along the latitudinal or elevational gradient.

Thermoregulation strategies in odonates are among the most amazing in insects. Odonates thermoregulate to maintain their body temperature within the range that maximises their activity and fitness. For instance in Libellulidae, the posture of the body is dependent on the position of the sun so that individuals of some species may minimise or maximise their exposure according to their thermal needs (May 1976). Thermoregulation is mainly determined by climate, body size and behaviour (Corbet 1999). This aspect of odonatology has benefited mostly from the classic studies of O'Farrell A. F. (1964), Veron J. E. N. (1973, 1974) and May M. L. (May 1976, 1977, 1979).

Conservation biology of odonates has been recognised for a long time as a priority (Moore 1982) for many reasons such as their cosmopolitan distribution, their key trophic position within the food web (as predators and prey) and their excellent reliability in indicating water quality (Samways 2008). Odonates have played an important role in systematic conservation planning (Prendergast *et al.* 1993). The protection of dragonflies and damselflies benefits many other invertebrates and vertebrates of freshwater ecosystems.

The blossoming era is also a period that Tillyard would be amazed to witness. The increasing interest in dragonflies by scientists and amateurs has reached a point that has never been attained in the history of odonatology.

THE INFLUENCE OF THE BOOK ON NON-SCIENTISTS

Here, we report an anecdote which shows the importance of the book to the public. In the preface of the book, Tillyard wrote '*The MS. of this book was completed on March 19th, 1915…*' In March 2015, exactly 100 years to the month later, an amazing video that beautifully illustrates and animates several figures of the *The Biology of Dragonflies* was posted (access this video here: http://juliagoschke.com/2015/03/the-biology-of-dragonflies/). The artist, Julia Goschke, was contacted to enquire whether she knew about the author, the book or dragonflies. She answered: '*I'm just an illustrator and animator and I was inspired by the nice illustrations of this book. I just had the idea of making a piece of a dragonfly, because I like these animals*' (pers. comm.). As a matter of fact, it is easily detectable from her video that Ms. Goschke was not an entomologist since she included two figures of another insect taxon (Neuroptera) which do not belong to the book. Ms. Goschke was not aware of Tillyard's biography or when he completed his book. It was just a spontaneous inspiration that created an exceptional coincidence, showing that the book has not only inspired many scientists over the decades but also is still influencing non-scientists even today.

FUTURE DIRECTIONS

After 260 years of taxonomy of odonates, we are on the verge of completing the global phylogeny of one of the most ancient of winged insect groups (Grimaldi & Engel 2005). Some taxonomic issues and uncertainties have yet to be resolved, and a consensus for the reclassification must be attained before we witness this historical event. Since molecular results showed that wing venation is not a reliable criterion for classification, the next challenge is also to revise the taxonomy of fossil Odonata.

The priority for future research topics should include the understanding of geographic patterns of the dynamics of phenology and range distribution of odonates and the implication of climate change. Environmental factors that govern the direction and intensity of phenological response have to be investigated in detail to predict large scale changes in phenology and their consequences on the food web. Since odonates are predators and prey in both terrestrial and aquatic habitats, their phenological shift may lead to mistiming between trophic levels in terrestrial and aquatic system and local species extinction. Furthermore, the rapid range shift of different species of odonates to the north and higher elevations is alarming because of the lack of information about the potential community interactions between invaders and residents. Considerable efforts should be devoted to the taxonomy of tropical species, which have received much less attention than temperate species. Because tropical species are thought to be more vulnerable to warming than temperate species (Deutsch *et al.* 2008), many may go extinct before being discovered. Finally, habitat fragmentation and water pollution represent huge extinction forces that threaten species' persistence in various freshwater systems. Conservationists should develop a new practical theory that encompasses problem-orientated approaches rather than a fixed protocol for all species, taking into account the habitat, community (not a single species), sensitization and cultural background of local people.

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