Kleber Del-Claro · Rhainer Guillermo
Editors

Aquatic Insects

Behavior and Ecology

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Preface

In our current environmental scenario, it is a matter of the utmost importance to highlight the loss of freshwater habitats. Notwithstanding, aquatic insects have taken the role of ambassadors with the mission to show us how anthropogenic impacts have been depleting freshwater reserves worldwide. Although several aquatic insect orders have been intensively studied for decades, most groups lack crucial biological information required for species conservation and for the maintenance of ecological communities and processes they are part of. For instance, their behavior, natural history, general biology, and ecology are underexplored, mostly in the tropics.

This book offers us the opportunity to look to the future and address important gaps in knowledge and research. The aim here was to provide an overview and appraise the behavior and ecology of aquatic insects under a multidisciplinary approach, as a way to address the neglected dimensions of their complex biodiversity. We expect that each chapter serves not only as a tool for current research but also as an inspiration for undergraduate and graduate students. We urge young scientists to pursue their career researching the myriad of themes and areas of interest we outline here.

This extensive set of work produced by several renowned and young scientists would not have been possible without the priceless support of universities, research institutes, state financial agencies for science, and a long list of teachers, advisors, students, and support staff.

We are most grateful to our families, friends, and colleagues that made this work possible and embarked with us in this endeavor.

This book is dedicated to every person who believes in science as a way to have a better world.

Uberlândia, Minas Gerais, Brazil — Kleber Del-Claro
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Chapter 1
Aquatic Insects: Why It Is Important to Dedicate Our Time on Their Study?

Kleber Del-Claro

Abstract Evolution begets diversity, and insects are the most diverse organisms in the history of life, so insects should provide profound insight into evolution. Insects are considered keystone species because loss of their critical ecological functions (e.g., pollinators; seed dispersers; predators; and parasitoids) could lead to collapse of the wider ecosystem. Indeed, insects dominate freshwater aquatic systems, but in general we know very few about the biology and natural history of these organisms. Here, we present a good set of basic data and knowledge in ecology, natural history, and behavior of this unknown fauna. Our hope is that it encourages young researchers to investigate basic aspects of the life history of aquatic insects, mainly in tropical systems.

Keywords Biology · Behavior · Behavioral ecology · Ecological networks · Wetlands

The diversity of life is one of the most astonishing aspects of our planet. Organisms are spread from the highest mountains to the deepest oceans of the Earth. They are under the bark of trees and inside flowers, in deep soil, in air, and even in frozen lakes. How many are they? How long will they stay as they are, or will evolve? Or disappear like so many others?

In a more recent and conservative perspective we suspect that there are more than 8.7 million (±1.3 million SE) eukaryotic species globally (Mora et al. 2011). But these numbers can be higher, as some researchers suggest that only to arthropods we could have between 5 and 10 million species (Ødegarrd 2000), perhaps 30 million (Erwin 1991). Regarding insects, the estimations vary from a minimum of 1 to possibly more than 5 million species (Scheffers et al. 2012), in a conservative approach. The unique real consensus is that we do not know the majority of species; 86% of existing organisms on continental environments and 91% of species in the ocean

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still await description (Mora et al. 2011). If they need description and basic taxonomic studies, then what we know about their behavior, ecology, and natural history? Indeed, very little.

I was a naturalist for my whole life, roaming around tropical forests, savannas, high mountains, and margins of rivers and lakes. When asked by a student about "what that insect does for a living?" my most common answer, after some general comment, is "but … indeed, in this specific case, it is a very interesting question! Why you do not study it?" This is particularly real in relation to aquatic insects, mainly in the tropics, where their diversity is absurdly high and most species are unknown. A book like this has as objective to stimulate young biologists to go deep in the water exploring these amazing creatures' life histories.

Evolution begets diversity, and insects are the most diverse organisms in the history of life, so insects should provide profound insight into evolution (Grimaldi and Engel 2005). The vast majority of known insects are among the most conspicuous creatures, like the flying butterflies, beetles, wasps, and bees, that call our attention for beauty and also for agronomic, economic, or sanitary reasons. Insects may dominate food chains and food webs in a wide aspect being essentials in (a) nutrient recycling and soil turnover, like ecosystem engineers; (b) plant propagation, including pollination and seed dispersal; (c) control of plant community composition and structure, via herbivory; (d) base of food chain, serving as food for insectivorous animals; and (e) regulation of animal community structure, via predation, parasitism, or like a vector of several diseases (Fig. 1.1). Thus "Some insects are considered *keystone species* because loss of their critical ecological functions (e.g. pollinators; seed dispersers; predators and parasitoids) could lead to collapse of the wider ecosystem" (Gullan and Cranston 2014). Despite this clear importance of insects, even in the twenty-first century we still need to harp on the same string: the vast majority of our knowledge on insects is based on the most visible, beautiful, or important animals to man's health, economy, or their ecological services. What can we say about the immense hidden insect fauna? The "Darwin's entangled bank" was buried in the ground or dipped in lakes, ponds, streams, and rivers.

All inland water bodies (rivers, streams, or lakes) support a biological community. Invertebrates (insects, crustaceans, and nematodes) provide the highest levels of biomass, production, and number of individuals in freshwater communities. Indeed, insects dominate freshwater aquatic systems. However, in general we know more about the biology and natural history of the few vertebrate species (mainly fishes and birds) in any inland aquatic system than of the whole community of invertebrates that structure all the bottom-up process in these complex ecological networks. We cannot neglect the immense and extremely important set of knowledge we have produced on aquatic insects' biology, physiology, taxonomy, environmental monitoring, and general zoology (e.g., Grimaldi and Engel 2005; Gullan and Cranston 2014). But to the major orders of insects that are almost exclusively aquatic in their immature stages, the Ephemeroptera (mayflies), Odonata (damselflies and dragonflies), Plecoptera (stoneflies), and Trichoptera (caddisflies), we know in fact little about their life histories, ecology, and behavior. It is surprising

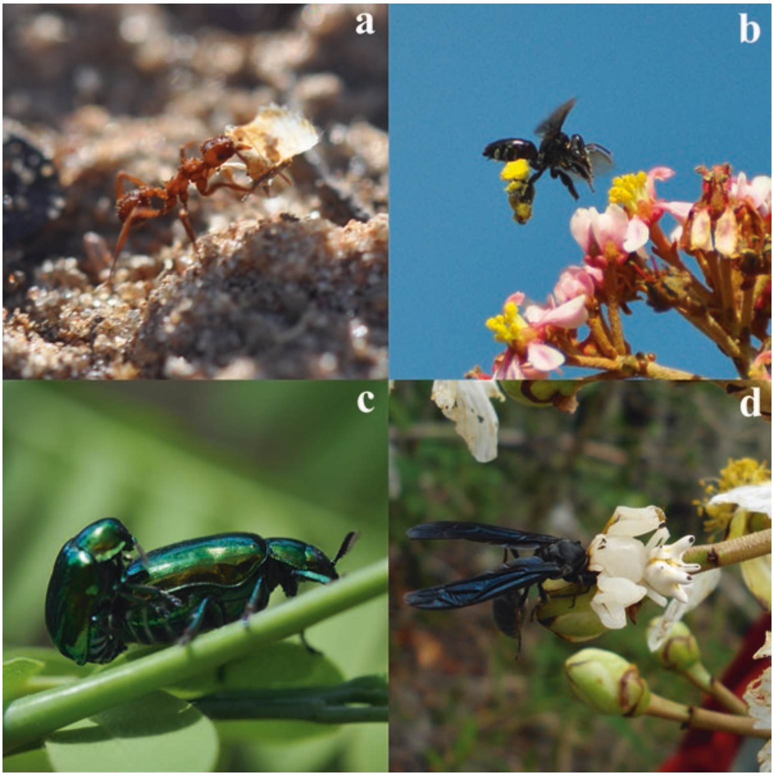

Fig. 1.1 Insects are the most diverse organisms in the history of life, so insects can act as ecosystem engineers (**a**) modifying the environment like the ants *Pogonomyrmex naegeli* that revolve soil and also prey on or disperse seeds. Their activities, like pollination by bees (**b**) and herbivory by beetles (**c**), shape plant community composition and structure. Serving as food for insectivorous animals, like *Epicadus heterogaster* (**d**), a crab spider that prey on pollinators while hidden in flowers, insects also interfere in the whole animal community directly or indirectly

that it also occurs to adults of the most species of Odonata, animals commonly conspicuous, very attractive for their beauty (Fig. 1.2).

I am an ethologist, and to me it is incomprehensible to how to think about the preservation of these amazing species, without thinking about how they relate each other, and how each behavioral decision of one impacts reproduction, life, and death of others. We need to know details of life histories and behavior, to understand the ecological interactions and the network behind the Darwin's entangled bank.

The study of ecological networks is derived from graph theory to investigate the structure and shape of ecological interactions around the world. Nowadays, it is incontestable that graph theory brings enormous advances to the knowledge of ecological interactions modifying the manner we look to the tree of life (Del-Claro et al. 2018). Thus, to indeed understand the dynamic of aquatic ecological networks, we need to know deeply the set of interconnected biotic interactions. The sum of

Fig. 1.2 *Argia angelae* (Odonata: Coenagrionidae), example of a very flashy group of aquatic insects on which we have relatively little knowledge

this knowledge, that conducts us to understand like conserve and/or recover the severely endangered freshwater systems, has its basis in basic biology, natural history, and behavior.

Thus, the aim of our book is to present a good set of basic data and knowledge in ecology, natural history, and behavior of this unknown fauna. Our hope is that it encourages young researchers to investigate basic aspects of the life history of these insects, mainly in tropical systems. It is imperative, especially in endangered biomes like the tropical savanna of South America and Africa, where species are quickly disappearing due to the expansion of human activities on natural areas. See what WWF says about Cerrado, the Brazilian savanna, in a recent publication titled "The Big Five of the Cerrado":

"*Imagine a place where there are over 11,000 species of plants and the fauna is as diverse as the flora. The Cerrado harbours 837 species of birds, 120 reptiles, 150 amphibians, 1,200 fish, 90,000 insects and 199 mammals. Together, they account for 5% of the world's species and 30% of Brazil's biodiversity. … Less than 10% of the Cerrado is covered by protected areas, and less than 3% of its area is strictly protected, putting various animals at risk of extinction.*"

(https://www.wwf.org.br/informacoes/english/?50242/The-Big-Five-of-the-Cerrado).

This text is about the five big mammals of Cerrado, the maned wolf, the giant anteater, the jaguar, the tapir, and the giant armadillo. Nevertheless, in just one small pound in central Brazil, a Vereda (palm swamp communities, Fig. 1.3) surrounded by tropical savanna, only 5 km far from the borders of a big city (population of ~750,000), we recorded at least 31 damselflies and dragonflies species of 5 different

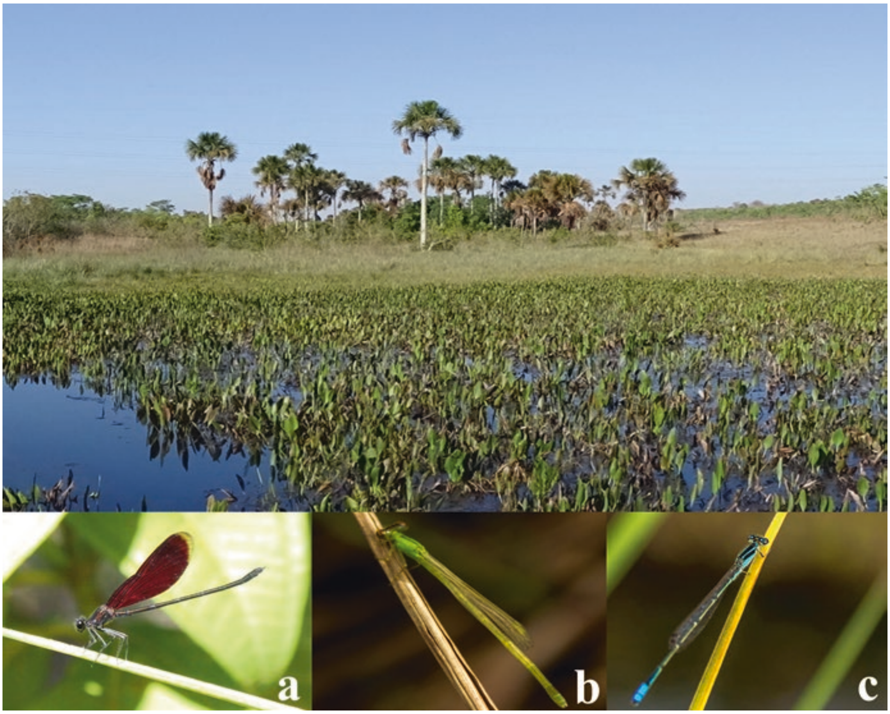

Fig. 1.3 In a single Vereda, a palm swamp environment, in central Brazil we can find an enormous and unknown diversity of aquatic insects. Of damselflies, like *Mnesarete pudica* (**a**), *Ischnura capreolus* (**b**), and *Acanthagrion truncatum* (**c**), we do not know anything about the life underwater and know very little about their adult life

families and 21 genera (Vilela et al. 2016), some possibly endemic, and some new species. Our knowledge on this fauna is still poor, and areas like that are in general located in private country clubs and small farms. Being so, these areas are subject to real estate speculation, or risk being used for agricultural purposes; in any case they are in evident risk of extinction.

The study of behavior, or in simple words "what an animal does or does not do" (Del-Claro 2010), is not only a basic tool to better explore and know the ecology and the outcomes of interactions involving animals, like aquatic insects. It is also a tool to present amazing and surprising strategies of animals in their constant fight for survival and reproduction, in a captivating manner to the general public. Behavior is not only a source of knowledge; it's also a way to make people fall in love with nature. For example, Vilela et al. (2017) studying the tropical tiger damselfly, *Tigriagrion aurantinigrum*, combining techniques of computer sciences with basic observations of animal behavior and behavioral ecology, showed that the species replaced direct and physical conflict with the use of visual signals to solve territorial contests. The authors demonstrated that winner males have more orange-yellow patches in their frontal head than the losers, and that threat displays are more efficient to win contests than physical conflict. This study confirms the importance of coloration patters in Odonata and the importance of these insects as models in the study of animal visual communication. There are several other studies, just as much or even more interesting to the general public, that need better scientific divulgation.

Then, in our search of a way to stimulate more people, mainly young biologists, to dedicate their time on the study of aquatic insects, we edited this book that presents in few chapters a general vision of ecology and behavior of aquatic insects, beginning with basic knowledge and finishing with possible future applications. Thus, after this introduction, the second chapter, headed by Ricardo Koroiva and Mateus Pepinelli, will show how aquatic insects have successfully achieved a global distribution, with an extraordinary capacity of survival in the most distinct conditions. Considering the breadth of the subject, this chapter aims to show some of the factors related to the distribution of aquatic insects, illustrating the main habitats used by the main orders. But not only distribution, but also dispersal, is one of the fundamental processes that influence the ability of organisms to reach suitable habitats, to find mates, and to avoid potentially disastrous disturbances. In the third chapter, Michael L. May brightly discusses fascinating questions related to aquatic insects' dispersal capabilities and its implications. In the two following chapters, headed by Rhainer Guillermo and an enthusiastic group of young researchers, the abiotic (Vinicius Marques Lopez, Aurélio Fajar Tonetto) and biotic factors (Gabriela C. Mendes, Guilherme Gonzaga da Silva, Leonardo Samuel Ricioli) that influence the interactions and success of aquatic insects, depending on its biology and behavior, are explored. These chapters shape an interesting background for beginners in this research field.

Communication is imperative to the evolutionary success of any organism. In the sixth chapter, J. Manuel Tierno de Figueroa, Julio M. Luzón-Ortega, and Manuel Jesús López-Rodríguez use the mating behavior of stoneflies to show us how vibrational signals can be produced by drumming, rubbing, tremulation, or a combination of these methods, and are species specific; therefore, they can be used as a method to confirm/infer phylogenies or define species. Following the line of communication and visual perception, our colleagues Manuela Rebora, Gianandrea Salerno, and Silvana Piersanti give us an excellent contribution. In their chapter titled "Aquatic Insect Sensilla: Morphology and Function," they teach us how insect success is directly related to their ability to respond quickly to external and internal cues, thanks to a great variety of sensory systems, able to evolve over a relatively short time.

The sensory and communication abilities open a new window to aquatic insects, the habitat contestation, and the defense of territories. Gregory F. Grether after providing a brief introduction to territoriality in general in his chapter reviewed the taxonomic distribution and types of territoriality reported in aquatic insects, before delving into more theoretical topics. This was extremely well done, offering some general advice for studying territoriality and concluding by identifying areas where more research is needed. For example, what is the importance of communication to the sex of aquatic insects? Bright colors associated to face-to-face displays exhibited by males can communicate strong, ability, dominance to females and result in success? Our colleagues, Diogo Silva Vilela and Iago Sanmartín-Villar, revised the communication aspects involved in the reproductive behavior and sexual selection among aquatic insects. In one of the best illustrated chapters, the authors lecture about it in a so clear manner that any college student will be able to comprehend the text completely. This presentation opens space for a deeper analysis, which was done in sequence by Adolfo Cordero-Rivera and Anais Rivas-Torres. According to them, "the field of sexual selection has been historically dominated by a stereotyped view of the sexual roles, with competing males and selective females, but in recent decades there has been a paradigm switch, with the emergence and dominance of the concept of sexual conflict." In an amazing chapter these colleagues stressed the hypothesis that "the dimensional structure of the habitat will affect the intensity of sexual conflict over mating rate, copulation duration and postcopulatory guarding." To achieve their objective, authors illustrate the text with wonderful examples in which behavior, basic biology, and ecology are fundamental to our understanding of what is going on.

Animals live to survive, grow up, and reproduce; they evolved distinct mechanisms and features to have success in this process, which in the endgame may also be needed to protect their best chance for eternity: the progeny. In the book sequence, parental care is discussed among aquatic insects, having as model the giant water bugs (Belostomatidae). Our colleagues Shin-ya Ohba, José Ricardo I. Ribeiro, and Melania Santer revel how behavioral ecology may be important providing basic tools to enable us to study parental care as it deserves, with experimentation. This chapter is finalized in a very stimulating manner, presenting plausible directions that must be followed. One of these directions calls attention to unknown fauna underwater, unexpected life forms that we can find especially in tropical systems. Vanessa Stefani and her scientific initiation students Iasmim De-Freitas and Julia De Agostini presented us an amazing case. Although most Lepidoptera are exclusively terrestrial there are some lineages associated with the aquatic environment. Little is known about aspects of the biology and life history of its representatives, leading to a gap in scientific knowledge. In this chapter, possible evolutionary paths explored which aquatic lepidopteran larvae had to live in aquatic environments, and the authors examine the incipient studies that address life aspects of these extraordinary animals.

The three final chapters of the book are more applied and point to us future directions. Not only the very preserved and untouched natural areas are under our sights and deserve our attention, but also study and preservation of aquatic insects. In the urban environment, our colleagues Javier Muzón, Lía S. Ramos, and Alejandro del Palacio show that "aquatic insects, as key components of urban wetlands, are critically impacted by human environmental changes and practices. The main threats are those derived from the loss, replacement or fragmentation of natural habitats, ecosystem homogenization, and the modification of hydrological, sedimentological and thermal wetland characteristics, due to the surrounding urban matrix." Therefore, this chapter will focus on the importance of insect knowledge as indicators of environmental health in urban wetlands, and the promotion of the citizen science to improve their conservation. Thinking in the same direction, Drielly da Silveira Queiroga, Renan Fernandes Moura, and Jessica Ware bring us an excellent new look over aquatic environments in their chapter “Genetic Connectivity in Conservation of Freshwater Insects.” The authors will show us in this amazing chapter that “rich biodiversity is fundamental for the balance and stability of ecosystems, providing vital ecosystem services such as climate regulation. Although aquatic environments are essential to human health, they are often the most exploited environments. Many aquatic insects may increase or decrease their abundance in response to environmental disturbances; these species are known bioindicators and may be used to evaluate environmental quality of an aquatic ecosystem. Thus, it is imperative to preserve bioindicators as they can alert us before degradation becomes large enough to extinguish ecologically important species. To best determine which species require the most attention, many scientists have turned to genetic tools to identify genetically diverse populations and their relative genetic connectivity: the exchange of genetic material among populations of the same species, enabling the maintenance of genetic diversity.”

We decided to close the book, with a futuristic chapter that very competently Stanislav N. Gorb and Elena V. Gorb produced to us. In this awesome chapter the authors demonstrate how the knowledge of basic biology, morphology, and behavior can help humans solve contemporary problems. “Aquatic insects, due to their aquatic or amphibiotic habit, evolved many particularly interesting functional solutions, which are of special interest for biomimetics. Understanding functional principles of insect materials, structures, sensors, actuators, locomotion patterns, control systems, and behavior is of major scientific interest, since we can learn about their functional principles and biological role. On the other hand, this knowledge is also highly relevant for technical applications. One of the greatest challenges for today’s engineering science is miniaturization.” I am sure that this chapter will call attention of a broad and diverse audience.

I am a beginner in the study of aquatic insects and this book was a challenge to me: to produce a piece of art supported in the shoulders of others, lovers of aquatic insects: people devoted to give part of their time in this wonderful planet to protect, to preserve, and to recover the unknown fauna that can maintain our survival as a species.

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Chapter 2
Distribution and Habitats of Aquatic Insects

Ricardo Koroiva and Mateus Pepinelli

Abstract Understanding how communities, populations, and species are organized and distributed is one of the main objectives of ecology. Aquatic insects are composed of several orders of diverse groups found in many different types of aquatic (and semiaquatic) habitats. From the highest water trickles to the largest rivers and deepest lakes, aquatic insects have successfully achieved a global distribution, with an extraordinary capacity of survival in the most distinct conditions. Considering the breadth of the subject, this chapter aims to show some of the factors related to the distribution of aquatic insects, illustrating the main habitats used by the main orders.

Keywords Biodiversity · Spatial factors · Lentic-lotic · Saltwater · Environments inhabited

2.1 Introduction

Any place that has freshwater is likely to harbor aquatic insects. Although they represent about 6% of all insect diversity (Dijkstra et al. 2014), they are the dominant organisms in aquatic ecosystems and are defined by species that spend part of their life cycle or all development in the water. Such organisms show a varied range of metabolic and morphological adaptations, allowing them to occupy virtually any kind of aquatic freshwater habitat, including high-salinity water bodies and streams and lakes that freeze during winter. The distribution of aquatic insects is driven by several factors acting in different scales, beyond the lotic versus lentic or permanent versus temporary freshwater binary views. Nonetheless, there is one aquatic

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ecosystem that insects didn't successfully colonize, the oceans, having only relatively few species adapted to live in marine water (Springer 2009).

Several factors influence the distribution of aquatic insects. On a large scale, historical processes and climate are considered the main factors. Over the last decades, studies have shown that, at local scales, variables such as substrate heterogeneity, land use, abiotic components, aquatic flora, and water current velocity are important factors determining communities. Some of these variables are related to the structure of the watershed, ecosystem differences, and microhabitats. Although recent studies have shown that variables at multiple scales can substantially affect aquatic insects' community structuring, local scale variables have been suggested as the most important drivers of aquatic insects' distribution and diversity, due to the action of filters on trait composition of communities (Bae et al. 2011; Tolonen et al. 2016).

The close association between different orders of aquatic insects and aquatic environments is reflected in several adaptations developed for life on water, including a wide range of physiological and structural solutions (physiological and morphological traits) used by the many aquatic groups to colonize different water systems. The results are dramatic new ways to breathe, move, find mates, acquire food, etc.

Considering the complexity of factors related to the distribution of aquatic insects, in this chapter, we provide an overview of the main aspects that affect their distribution and some of the most common habitats used by them. First, we indicate how large and local scale factors play important roles in determining their distribution. Then, we present some freshwater systems (water bodies) with examples of groups with peculiar adaptations to the various habitats explored. In this way, we intend to illustrate the variety of environments inhabited by aquatic insects and how they overcome the challenges of living in water.

2.2 Question of Scale

The processes that determine diversity are scale dependent and, therefore, it is crucial to examine the relative roles of factors at multiple scales (Poff 1997). As stated by Tolonen et al. (2016), for some life-history traits of benthic macroinvertebrates, the importance of environmental factors that vary at large spatial scales could be more pronounced than the importance of local environmental variables. In a large-scale view, historical factors, such as speciation, extinction, dispersion, and climatic factors, such as temperature and precipitation, are important in structuring species pools, acting over traits and filtering species. Zooming into the spatial scale of environmental filters, factors such as river basin features, and more localized abiotic and biotic conditions, are some of the main factors influencing the assemblages. Altogether, these filters determine the diversity, composition, and functional taxonomic variability of the assemblages through the characteristics of each species. Thus, only species with adequate characteristics are able to overcome the challenges presented by filters at each scale (Heino 2009).

2.2.1 Large Scale

The influence of historical effects in determining the distribution of aquatic insects on a large scale is directly related to the historical and current development of natural environments. Geological processes such as the formation of mountains and the continental drift have been some of the factors associated with large-scale distributions of aquatic insects (Grimaldi and Engel 2005). Probably, the earliest example of how large-scale continental processes (Wegener 1922) shaped the distribution of aquatic insects came from a monograph published in 1966 by the Swedish entomologist Lars Brundin, who studied the transantarctic relationships of chironomid midges (Brundin 1966).

More recent examples are exemplified from a study on the spring brook headwater-specific caddisflies (Trichoptera), of the genus *Palaeagapetus* Ulmer. Using a molecular approach, the authors showed how the genetic structure of *Palaeagapetus* clearly reflects the separation of eastern and western Japan in the Fossa Magna region (Tojo et al. 2017). All nine species of *Palaeagapetus* caddisflies belong to two major clades, whose geographic boundaries are in the center of the Japanese Islands (i.e., center of Honshu), corresponding to the westernmost side of Fossa Magna, the Itoigawa-Shizuoka Tectonic Line.

While continental drift was responsible to separate several clades of animals and plants, it was the climatic conditions that shaped and are still a strong mechanism shaping distribution. Temperature and precipitation, for example, strongly influence river ecosystems. As evidenced by Poff et al. (2010), water temperature, annual thermal regime, and precipitation regulate the growth of aquatic insects and the structure and function of the flow in aquatic environments, which directly and indirectly regulate many aspects of the aquatic community, including its composition.

Critical changes introduced by climate events promote impacts on the water quality and on the physical habitats in water ecosystems. The increase in air temperature, for example, leads to other changes such as alterations in rainfall cycles, increase of water temperature, shifting habitat dynamics, affecting species with weak adaptability (Sáinz-Bariáin et al. 2016). These changes influence the phenology, distribution, composition, and dynamics of aquatic communities, providing a broad subject for ecological studies.

Recent studies suggest that, as a result of global warming caused by human activities, the freshwater biodiversity is declining at much higher rates than the most affected terrestrial ecosystems, because the increase of temperature can promote habitat reduction and physiological changes for several aquatic insects (Fenoglio et al. 2010). Even long-term climate cycles of natural conditions such as El Niño and La Niña can dramatically alter aquatic communities. These cycles are characterized by complex weather patterns, such as the change in temperature and the amount of precipitation. For aquatic insects, studying the effects of this type of phenomenon has served as an indicator of how directional changes in global temperature will affect species distribution, and studies have predicted that many aquatic insects are vulnerable to extreme changes over different scenarios (Kingsolver et al. 2011; Shah et al. 2017).

Finally, large-scale variables have their share influencing aquatic insect distribution; however the local scale ones have been suggested as the most important drivers of aquatic insect distribution and diversity, both in terms of explaining variability in community composition and those that act directly on the organisms (Tornwall et al. 2017).

2.2.2 Local Scale

Decreasing the spatial scale, factors such as watershed abiotic and biotic conditions are the environmental filters determining the assemblages, by filtering the organisms based on their functional attributes (Poff 1997). According to recent metacommunity studies, dispersal is an important mechanism structuring aquatic insect communities and it varies according to the type of water body and the dispersal capacity of the insects in question; however, environmental factors usually overlap with spatial factors (Heino et al. 2015). Several authors have shown broad categorizations of local factors related to community structuring, and here we list five of the most important, substrate heterogeneity, land use, abiotic factors, aquatic flora, and water current velocity.

2.2.2.1 Substrate Heterogeneity

The characteristic and composition of the bed substrate are of extreme importance especially in lotic environments, since they are the primary components determining which groups of insects are able to live and assess the resources. The colonization of insects on aquatic substrates is influenced by substrate heterogeneity and complexity, such as interstitial spaces, surface complexity, different types of sediment, and presence of organic matter from the riparian vegetation. Heterogeneous and complex substrates harbor higher density and richness of aquatic insects than homogenous do, because it provides more hiding places, creates different current flow speed, and provides substrates for egg deposition, protection from predators, and greater availability of food (e.g., Brown 2003, Barnes et al. 2013 but see Palmer et al. 2010). For example, aquatic detritivores can be affected when their food supply is either buried under sediments or diluted by increased inorganic sediment load. For the family Chironomidae, higher substrate heterogeneity promotes higher diversity of microhabitats and usually harbors greater number of species and guilds (Gurski et al. 2014).

2.2.2.2 Land Use

Closely associated with bed composition, land use has recently been considered one of the main factors driving environmental changes in aquatic systems, because the impacts almost always result in structurally simplified habitats. Changes of land cover may increase the surface runoff rates, as well as the amount of sediment and nutrient inflow (Kasangki et al. 2008). The conversion of forest areas reduces the entry of allochthonous material into headstreams, reducing the abundance of species associated with leaves and woods (Valente-Neto et al. 2015).

In forested streams, terrestrial detritus is an important resource for the aquatic food web; therefore the dependence on their input directly influences the composition of aquatic insects (Minshall 1978; Power et al. 2013). Summarily, species composition can be considered the best predictor for severe alterations of land use in the insect community (see Siegloch et al. 2014; Gimenez et al. 2015). In lentic environments, the effects of forest removal are expected to be of a lower magnitude, considering that these systems are already open to sunlight and the influence of allochthonous material is low (Richardson 2008). However, studies have shown that concentrations of nutrients and other components are positively correlated with the nature of the environment modification. For example, agropastoral activities have been related to nutrient enrichment (Abell et al. 2011) and increasing the abundance of some aquatic insects such as chironomids (Blumenshine et al. 1997).

2.2.2.3 Aquatic Vegetation

The presence of vegetation inside a water course also greatly affects the environment and the fauna. The so-called aquatic macrophytes are plants that require a water environment to complete all or most of their life cycle. They can be classified as emergent, floating, or submerged plants; are present in both lotic and lentic environments; and play a key role in structuring communities not only of aquatic insects but also of fish and other organisms. In temperate shallow lakes, for example, these plant communities are probably the most important group that affect whole lake ecosystems (Scheffer 2004). Also, in the situation of degradation of riparian vegetation, the presence of macrophytes can provide an important alternative food source, and sustain in-stream productivity and, consequently, faunal biodiversity (Paice et al. 2017). In northern lakes, macrophytes play an important role in structuring littoral macroinvertebrate communities (Heino 2013), because they alter the dynamics of nutrients, dissolved organic and inorganic carbon, oxygen, pH, sediment quality, etc., having been recognized as “biological engineers” to aid in restoring water quality (Byers et al. 2006).

For many aquatic insect groups, the food availability, both directly in the form of fresh and detrital material, structural habitat, and refuge against predation (Heck and Crowder 1991; Bell et al. 2013) increase the density and richness of aquatic insect species on macrophyte vegetation, when compared to areas without this resource. Also, studies such as that of Gonçalves Jr. et al. (2004) demonstrate the ability of different species of macrophytes to support different aquatic insects, considering that the chemical composition of the macrophyte detritus strongly influences the decay rate, while degradative ecological succession is the driving force of the invertebrate community.

2.2.2.4 Abiotic and Environmental Variables

Other important geomorphological factors related to the ecology of aquatic insects are the abiotic and environmental variables of the water body, such as water temperature, pH, salinity, and oxygen concentration. They directly affect the tolerance limits of organisms and consequently the distributional range of species (Death and Winterbourn 1995). Water temperature is considered one of the most important environmental factors, because if affects the aquatic insect growth. The "optimum thermal regime" (Vannote and Sweeney 1980), the temperature in which optimal growth, reproduction, and other measures of fitness are greatest (Dallas and Day 2004), and "thermal tolerance range," the range over which a species may survive, allow us to understand diverse biological aspects of the species as well as their fundamental niches, geographical distribution, and evolutionary dynamics.

The relation between thermal limits and evolution led to the development of different biogeographic hypotheses such as the climate variability hypothesis proposed by Janzen (1967), which predicts that more variable climates select for organisms with broader thermal tolerances, whereas less variable (stable) climates select for narrower thermal tolerance. Recent studies (e.g., Shah et al. 2017) have corroborated this hypothesis for aquatic insects, but also need to take into consideration altitudinal factors. Like terrestrial insects, many aquatic species have adapted to extreme temperature conditions, such as a *Tanytarsus* van der Wulp species present in hot springs (<34 ° C) in California (Lamberti and Resh 1985), as well as the survival of long periods of freezing as for some chironomids capable of maintaining activities even at −16 °C (Paterson 1971; Kohshima 1984).

Directly related to water temperature, the concentration of oxygen is another important and limiting factor. The sensitivity of aquatic insects to oxygen depletion is characterized by both the oxygen concentration in the water and the respiration capacity. The concentration of oxygen in natural environments varies with other biotic factors, such as effects of microbial respiration in eutrophic environments, and abiotic factors, like water temperature and current velocity. Anthropic influence can affect both the biotic, with the addition of nutrients, and abiotic equilibrium, changing water temperatures, reducing the concentration of dissolved oxygen, etc. For example, some cold-water lotic mayflies and stoneflies cannot tolerate dissolved oxygen concentrations below 8.0 mg/L (e.g., *Epeorus sylvicola* (Pictet) and *Baetis alpinus* (Pictet); Barton and Taylor 1994), as they possess gill membranes, require high concentrations of oxygen, and display specialized behaviors for greater diffusion of oxygen (Genkai-Kato et al. 2000). On the other hand, some aquatic insect species such as *Chironomus* Meigen species, are practically not dependent on the dissolved oxygen content of the water and can live where the oxygen is nearly zero at all times (Shobanov 2001) and other dipterans, such as mosquito larvae (Culicidae), have respiratory syphons that enable them to use atmospheric oxygen, and are thus adapted to live in poor water quality conditions (Chipps et al. 2006).

Besides the function of gas diffusion, gill membranes present in some orders, like Odonata and Ephemeroptera, have an important role in ion exchange. For insects without gills, other epithelial membranes on the surface of the body, or spe-

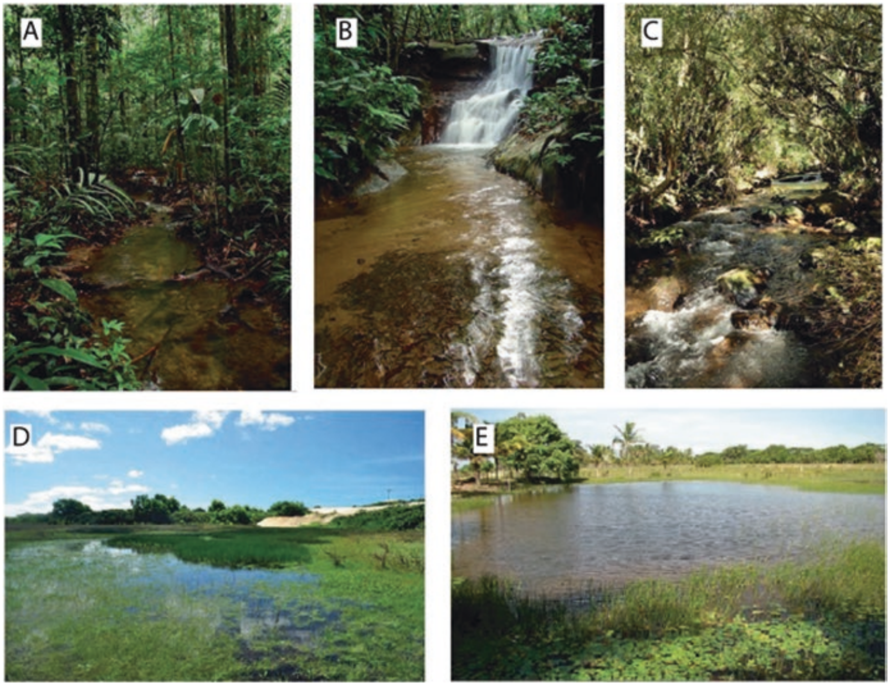

Fig. 2.1 Lotic and lentic environments. (**a**) Stream with predominance of roots. (**b**) Stream flowing over rock slab (in the background), sandy sediment (center), and foliage (foreground). (**c**) Rapid creek water. (**d**) Lake densely covered by hydrophytes. (**e**) Small lake. Modified from Salles and Ferreira-Júnior (2014). Reprinted with permission from Insetos aquáticos na Amazônia Brasileira: taxonomia, biologia e ecologia, edited by Hamada, N.; Nessimian J.L.; Querino, R. © 2014. Published by Editora do INPA

cialized structures, are responsible for the ion transport. The salinity of the environment, especially Na and Cl ions, is essential for maintaining hormone-signaling pathways, generating electrical cell potentials, and regulating bodily fluids. However, the physiological limitations of osmotic control in high concentrations of salinity (>35 ppt) limit the presence of aquatic insects in this condition. A broad review about ion diffusion such as sodium, potassium, calcium, magnesium, chlorine, bicarbonate, and sulfate in aquatic insects is revealed by Griffith (2017).

Finally, current velocity is considered the most important factor in structuring the community of aquatic environments. The division into standing (lentic) and fluvial (lotic) waters represents the two major ways used to classify water bodies, despite the wide range of aquatic systems for both environments (see Fig. 2.1). Water flow has a wide influence acting on both biotic (e.g., vegetation composition) and abiotic (e.g., pH, water oxygenation) elements, changing key conditions for community structuring. Although many groups occur in both environments (for instance the presence of pool areas in lotic environments), the current velocity strongly determines the ecological distribution of the species, especially because of its relation with morphological and behavioral adaptations.

2.3 Environments Inhabited

Considering the differences between lotic and lentic environments, the analysis of the composition and distribution of the species allows us to investigate how each environment acts in the characterization of its community. However, far beyond rivers and lakes, aquatic insects can be found in virtually any freshwater habitat worldwide. In this topic, we present different types of water bodies and peculiarities about morphological traits related to the success of aquatic insects in colonizing these environments.

2.3.1 Rivers and Streams

Defined by limnologists as lotic environments, rivers and streams share the same function of carrying flowing water back to the oceans, differing only on their sizes. Classification systems such as the Strahler stream order (Strahler 1952), where numbers are used to define stream size based on a hierarchy of tributaries, or how the tributaries coalesce together to form a bigger stream, allow an efficient and visual classification. Order numbers may range from 1 (a stream without any tributaries) to 12 (Amazon River in its mouth), being the vast majority of streams from first through third order, also called headwater streams.

Considering this classification, Vannote et al. (1980) in his River Continuum Concept (RCC) used flow order (Fig. 2.2), energy sources and nutrients, and food webs to characterize the community of aquatic insects. In a river system flowing through a forested region, the headwaters (orders 1–3) are heavily shaded where algae growth is limited by light. According to Vannote et al. (1980), in this region it is expected the predominance of shredders, a functional feeding group, or organisms that feed of large-sized organic matter such as animal carcasses, leaves, and woody debris, also called coarse particulate organic matter (CPOM) (Cummins 2016). In spite of remembering that functional feeding groups are not an immutable classification, common shredding invertebrate taxa are found among Ephemeroptera (mayflies), Plecoptera (stoneflies), Diptera (true flies and midges), and Trichoptera (caddisflies) (Merritt and Cummins 1996).

Increasing the order flows (orders 4–6), an increase in the diversity of both vegetation and insect species is expected since the tributaries are wider and less shaded, generating a high diversity of macrohabitats to be explored. Primary production levels increase in response to the increase of light, along with the production of periphyton and the consumption of fine particulate organic matter (FPOM). Functional groups such as grazers and collectors increase in abundance and this section is characterized by the greater diversity of groups such as predators, shredders, collectors, and grazers with predominant occurrence of Ephemeroptera (mayflies), Plecoptera (stoneflies), and Diptera (true flies and midges) (Allan 1996).

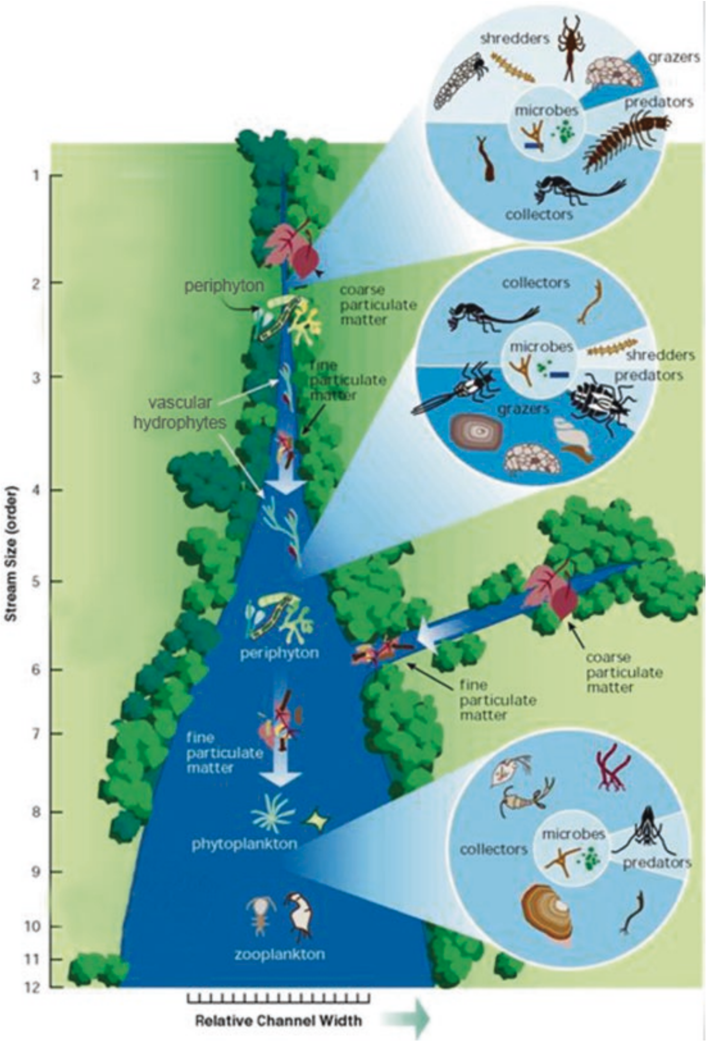

Fig. 2.2 The river continuum concept by Vannote et al. (1980). The proportion of invertebrate feed groups corresponds to changes of environmental conditions in the structure of the river basin (Figure taken from USDA 2001). Reprinted with permission from Stream Corridor Restoration: Principles, Processes, and Practices, edited by Federal Interagency Stream Restoration Working Group. © 1998. Published by USDA. In addition, reprinted with permission from Canadian Science Publishing (Vannote et al. 1980), © 1980

Finally, the rivers of higher orders are too wide to be dependent on allochthonous material and too deep so that the production of algae in the bed is not preponderant. Thus, organic inputs of the floodplain with both phytoplankton and zooplankton production play an important role in structuring the community, with the domain of collectors, such as chironomids and mayflies (Battle et al. 2007; Masson et al. 2010).

Despite the broad characterization, the applicability of the River Continuum Concept has limitations because it is a model that considers a perennial flow and absence of changes in riparian vegetation. As it is well known, streams and rivers from the different biogeographic realms have different structures and face different seasonal climatic variations (Vinson and Hawkins 2003), factors that are not included in the RCC model. Even within these limitations, the RCC has served as a useful conceptual model and has stimulated research on aquatic community characterization to date (see Xenopoulos et al. 2017).

In recent decades, the traditional linear conceptual models of aquatic ecosystems, such as RCC, have been replaced by a view that considers the role of the spatial structure of river networks in determining diversity patterns (Siqueira et al. 2014). Dendritic networks (so-called river networks) are structural and functional backbones of river basins, which can be viewed as rooted trees formed by fluvial erosion over a drainage basin (Balister et al. 2018). As evidenced by Tonkin et al. (2018), the organization of the dendritic network and the unidirectional physical flows can exert strong controls on the consequent distribution of biodiversity, depending on species traits which influences the dispersion and the ability to survival (see more in next subtopic). In this sense, studies of metacommunities have deepened with the understanding of how local and regional factors act in the distribution of species and, as already mentioned, local environmental factors tend to overlap with spatial factors in structuring insect communities in lotic environments (Heino et al. 2017, but see about very small spatial scales in Grönroos et al. 2013).

2.3.1.1 Life in Running Waters

Several morphological adaptations have evolved for living under the influence of streamflow, especially ones related to breathing, acquiring food, and locomoting underwater. The dorsoventral flattening is a classic example of adaptation for living under fast currents, because it is a hydrodynamic shape that provides the animals the perfect balance of surface contact with the substratum, water drag, and lift that they need to be able to live close to the surface layer. Dorsoventral flattening is well expressed in a number of mayflies (e.g., Heptageniidae, Ephemerellidae) and stonefly nymphs (e.g., Perlidae), reaching its highest degree in water-penny larvae (Psephenidae). Other animals developed innovative mechanisms and behaviors for anchoring in rapid waters, such as suction cups (Blephariceridae), hooks and grapples (Simuliidae, Fig. 2.3), and architectural cases and shelters (different families of Trichoptera and some Chironomidae).

Despite the fact that most of rivers and streams have well-oxygenated water, stream-dwelling insects are at least as well provided with respiratory apparatus as are the inhabitants of ponds (Hynes 1970).

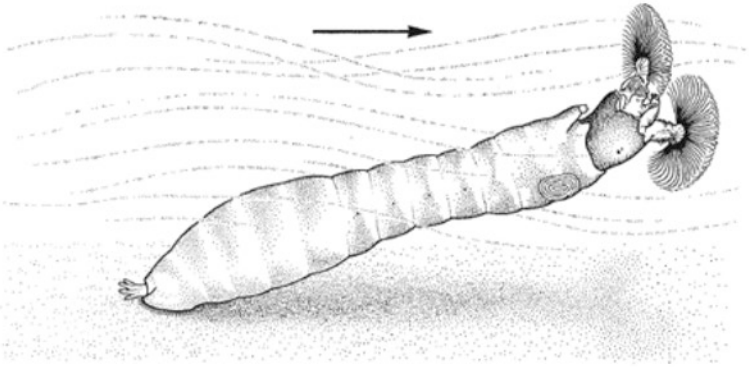

Fig. 2.3 Black fly larvae live exclusively in running waters. Larvae anchor themselves to the substrate by means of a posterior circlet of hooks embedded in a dab of silk. Food particles borne in the water current are captured by the cephalic fans (Gullan and Cranston 2014). Arrow indicates the direction of flow. Reprinted with permission from John Wiley and Sons: The Insects: An Outline of Entomology, edited by P. J. Gullan and P. S. Cranston. © 2014. Published by Springer Publishing Company. In addition, modified and reprinted with permission from Cambridge University Press (Currie 1986), © 1986

2.3.2 Intermittent Streams

In many regions of the world, streams can dry out seasonally, occasionally, or even for several years. In these environments, aquatic insects can take refuge in moist cracks within the bed, under leaves, barks, or stones, to wait for the water to return (Boulton and Lake 2008; Chester and Robson 2011). Despite the great diversity, most species can be classified as "facultative" because they are present in both perennial and intermittent streams. One of the few species that have been preferentially related to non-perennial streams are larvae of arrowhead spiketail (*Cordulegaster obliqua* (Say); Odonata: Cordulegastridae) (Santos and Stevenson 2011). Other species go rapidly throughout their life cycles and disperse as adults before drying is completed, such as have been speculated for the pupae of *Rhyacophila grandis* Banks (Trichoptera: Rhyacophilidae) (London 2017), and there are cases where there is a substantial exchange of individuals between temporary or ephemeral flows and near-permanent waters (Godoy et al. 2016).

2.3.3 Lakes and Ponds

Also called as lentic environments, lakes and ponds are widely distributed in all continents. In broad characterization, most lakes have at least one natural outflow in the form of a river or stream, which maintain the average level by allowing the drainage of excess water. However, some remain as closed bodies of water, such as lakes formed in volcano craters, and lose water solely by evaporation or underground seepage or both. The difference between lakes and ponds is mostly related to their sizes, but the thresholds are yet debatable. There are several distinct types of lakes, and a landmark study is provided by Hutchinson (1957).

Lakes provide habitats for many aquatic insect groups, some specialized in standing water such as the Chaoboridae and Corethrellidae flies, in which their larvae are able to move and migrate in the water column. Other groups such as some coleopterans and heteropterans can also move in the water column. However, because they need to obtain air from the atmosphere for breathing, they are always visiting the water surface or living in regions with aquatic vegetation. In general, insects in lentic environments are concentrated mainly near the shores of the lake (the littoral zone), where the water is relatively shallow and lush vegetation may be present.

The vertical component (depth) of the lake creates several effects. Deep lakes typically have strong temperature gradients associated with reduction on the concentrations of dissolved oxygen as you dive. The deep zone of a lake is typically a homogeneous habitat where only a handful of taxa are able to thrive, as some very characteristic genera of chironomids such as *Chironomus*. These genera have evolved the presence of high hemoglobin concentration in the hemolymph, and can obtain carbon derived from methane, both examples of adaptations for living in this type of habitat (van der Valk 2012).

Other important factor associated with spatial structuring of aquatic insects in lakes and ponds is the dispersal ability of terrestrial forms. Recent studies (e.g., Hill et al. 2017) have shown that for lentic and temporary environments, weak dispersers generally showed less environmental control and more spatial structuring, while strong dispersers, such as most aquatic insects, showed greater environmental control and no significant spatial structuring (Heino et al. 2015). However, other studies have shown different results, without any significant spatial and environmental structuring in aquatic small organisms (e.g., Nabout et al. 2009).

2.3.4 Wetland, Temporary Ponds, Madicolous Habitats, and Human-Made Environments

Despite being a single word, wetlands represent a complex of ecosystems that are related to flooded lands or areas that have soil saturated with moisture (Fig. 2.4). This definition includes lands covered by water, either salty or fresh, marshes, rock pools, edge of a lake or ocean, delta at the mouth of the river, peatlands, freshwater swamps, and mangroves.

Among the diverse of wetland environments, extreme conditions of low oxygen concentration, low nutrient richness, and high salinity affect the structuring of communities. However, most of the main orders are present, such as Diptera—Chironomidae (Armitage et al. 1995; Batzer and Sharitz 2007), Ephydridae, etc.; Heteroptera—Corixidae, etc.; Coleoptera—Dytiscidae, Hydrophilidae, etc.; Odonata; and Ephemeroptera. Batzer and Ruhí (2013) found that the Chironomidae

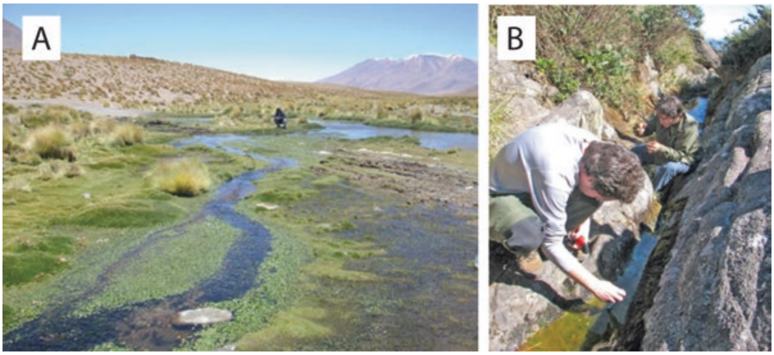

Fig. 2.4 Flooded areas in Bolivia (**a**) and rock pools in Brazil (**b**)

(midges) and Dytiscidae (predaceous diving beetles) were the only families that were virtually ubiquitous across the 447 wetlands they studied. Corixidae (water boatmen) and Hydrophilidae (water scavenger beetles) occurred in most (>50%) of the wetlands. A large revision of over 25 families of aquatic insects can be found in Batzer and Boix (2016).

Another type of freshwater habitat that has been shown to have a great diversity of aquatic insects is the madicolous habitats. They are characterized by a thin layer of water temporarily or permanently flowing over rocky surfaces. Such habitats harbor a rich fauna of aquatic, semiaquatic, and terrestrial organisms, some of which are rare or even endemic, living exclusively in this biotope, and termed eumadicolous fauna (Vaillant 1956). For example, Sinclair and Marshall (1987) listed 13 eumadicolous species from southern Ontario, including 12 dipteran (Tipulidae, Psychodidae, Thaumaleidae, Ceratopogonidae, Stratiomyidae, and Dolichopodidae species) and 1 Trichoptera species (Hydroptilidae). Shimabukuro et al. (2015) listed 20 higher taxa (families or order) of insects from madicolous habitats in Brazilian mountains.

Despite these records, it is a fact that those habitats have remained historically understudied. As evidenced for rock pools (Jocque et al. 2010), large wetlands (see Keleher and Sada 2012), and madicolous habitats in mountainous regions (Shimabukuro et al. 2015), these environments are unique habitats housing a high diversity of specialist and endemic species and therefore contribute substantially to regional diversity.

Under the pressure of evaporation, temporary pools are another important environment explored by aquatic insects. They include any habitat that has intermittently standing water and which, once flooded, retains water long enough for some species to complete the aquatic phases of their life cycle ignoring the size and time of resilience of these pools. It might include temporary lakes, temporary ponds, and environments created by humans.

As evidenced by Wiggins (2004), many species have adapted to life in temporary freshwater ponds, and at least two advantages can be recognized by the colonization of this environment: firstly, the rare presence of fish species, considered the main predators of aquatic insects. Other predatory insects such as water bugs, beetles, and dragonfly nymphs that are also less diverse and abundant in this type of habitat. The second advantage is due to the nutrition and growth of the species. In general, temporary pools have their food web based mainly on detritus which, differently from submerged environments, tends to present a phase of degradation in the air. This period causes the debris to be degraded faster and to have higher protein concentration, especially by the colonization of fungi.

A classic example of organisms present in temporary pools in the northern hemisphere is certain species of the caddisfly family Limnephilidae (Wiggins 2004). These species, such as *Limnephilus indivisus* Walker, present several adaptations for survival such as suspension of ovarian development by late summer and eggs wrapped with thick gelatinous mucopolysaccharide matrix, which allows resistance to dissection for months. In this way, oviposition has become independent of water, allowing these species to lay eggs in temporary pools after surface water has been depleted.

Finally, human-made environments, artificial containers (Fig. 2.5), should not be overlooked. Broadly, urbanization has led to an increase in the number of man-made containers, including water storage systems for human use (e.g., water boxes) and urban waste (e.g., tires and unloaded bottles). In forest environments, artificial containers often attract the same fauna as natural systems, while in open environments many species may not tolerate the abiotic conditions found (e.g., high temperature) being common the presence of generalist species like *Culex* Linnaeus mosquitoes (Kling et al. 2007; Yee and Yee 2007).

Species of medical importance often exhibit a wide survival capacity and are well adapted to extreme conditions. As summarized by Manguin and Boëte (2011), three major biological characteristics are found among the most invasive mosquito species: (1) close association with humans, (2) egg resistance to desiccation (genus *Aedes* Meigen), and (3) small larval habitats such as a wide variety of water-holding containers among which man-made ones are suitable. Thus, the proximity to humans and the use of artificial containers have allowed an assistance to transport of most of mosquito invasions as well as their maintenance in urbanized areas. Lloyd (2003) brought to attention the need of eliminating artificial containers in urban environments to tackle diseases associate with its inhabitants.

2.3.5 Phytotelma and Water-Filled Tree Holes

Phytotelma and water-filled tree holes also provide an environment for the development of a diverse community (Fig. 2.6). Tanks of bromeliads, carnivorous plants, tree holes filled with water, bamboo internodes, and axillary waters collected by leaves, bracts, or petals are water reservoirs formed from parts of living plants capable of being inhabited by aquatic insects, while water collection cavities are formed in the fallen parts of plants.

Fig. 2.5 *Aedes albopictus* (Skuse) breeding sites. Examples include (**a**) metal containers, (**b**) terrarium, (**c**) stone holes, (**d**) ceramic vessels, (**e**) plastic containers, (**f**) gutters, (**g**) used tire dumps, (**h**) surface accumulated water, (**i**) disposable containers, (**j**) parking poundings, (**k**) flowerpot trays, and (**l**) metal containers. Reprinted with permission from Elsevier (Bonizzoni et al. 2013), © 2013

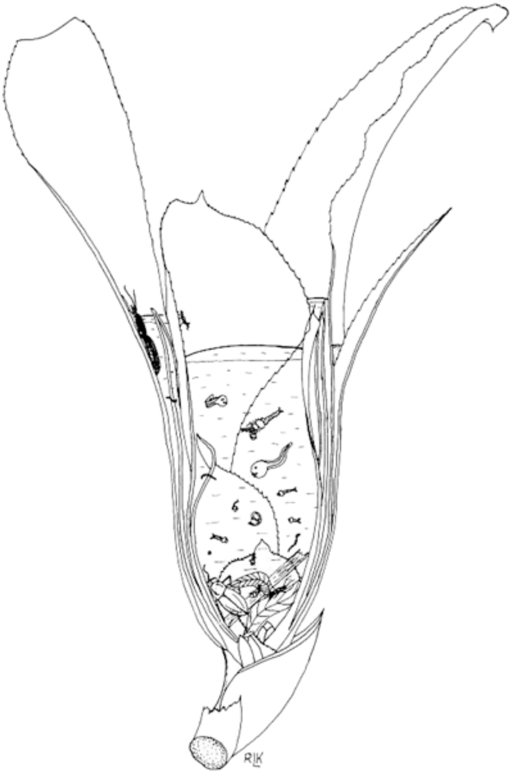

Fig. 2.6 Cut-away schematic of a community in a tank bromeliad (composite) (figure taken from Kitching 2009). Reprinted with permission from Food Webs and Container Habitats. The Natural History and Ecology of Phytotelmata, edited by R. L. Kitching, © 2009. Published by Cambridge University Press

There are at least 1500 species of plants, belonging to 29 families, which have been recorded as phytotelmic environments. There are records of over 70 families and 11 orders of insects inhabiting those habitats, with Diptera being the most abundant order (Greeney 2001) with over 20 families occuring in these habitats (Williams 2006). Like artificial containers, natural containers such as phytotelma may play an important role in the presence of insects of medical importance, but factors such as competition and predation affect the abundance of their inhabitants (Zahouli et al. 2017).

Among symbolic species that have their development associated with phytothelmic habitats, we highlight the dragonflies of the family Pseudostigmatidae. Hypoxia conditions and pH variation are some of the factors that their larvae had to overcome to colonize this type of environment. Behavioral differences among larvae provide additional evidence that species of Pseudostigmatidae have adapted and specialized for either tree holes or bromeliads, but not both. For example, larvae of the *Megaloprepus* Rambur species and some *Mecistogaster* Rambur species rarely leave its tree hole breeding site (Fig. 2.7), whereas larvae of *Mecistogaster modesta* Selys, a species of bromeliad odonate, usually crawl out of the plant seeking better and bigger habitats as they grow (Fincke 1998).

2.3.6 Marine Environments

Undoubtedly, the greatest diversity of aquatic insects occurs in continental freshwaters; however, there are a few groups that have also successfully colonized marine environments. They are mostly considered semiaquatic or live in the region between tides (intertidal). Among the main representatives are Diptera, Hemiptera, and Coleoptera. One of the most iconic examples of intertidal insects is the caddisflies of the Chathamiidae family. Present in Oceania, the larvae live in intertidal pools and build cases from algae (usually *Corallina* Linnaeus spp) and shell or sand (Cowley 1978). In this peculiar family, the species *Philanisus plebeius* Walker lay the eggs within the coelom of the starfish *Patiriella regularis* (Verrill), where they develop until they are released as first instar larvae (Winterbourn and Anderson 1980).

Few species are truly marine. *Pontomyia* Edwards, an exclusive genus of flightless chironomid insect, are rarely observed on the ocean surface (Fig. 2.8). As a form of adaptation, the females had extreme body reduction, having lost the wings and the legs, and reduced the head and the thorax, becoming animals similar to worms. Their males have highly reduced and modified wings, and have lost the power to fly, but they walk on the surface of the sea for displacement. Another iconic group in marine environments is the water striders in the genus *Halobates* Eschscholtz. Although most *Halobates* species are coastal and associated with mangroves or other vegetation, at least one species is completely oceanic (Andersen and Cheng 2004).

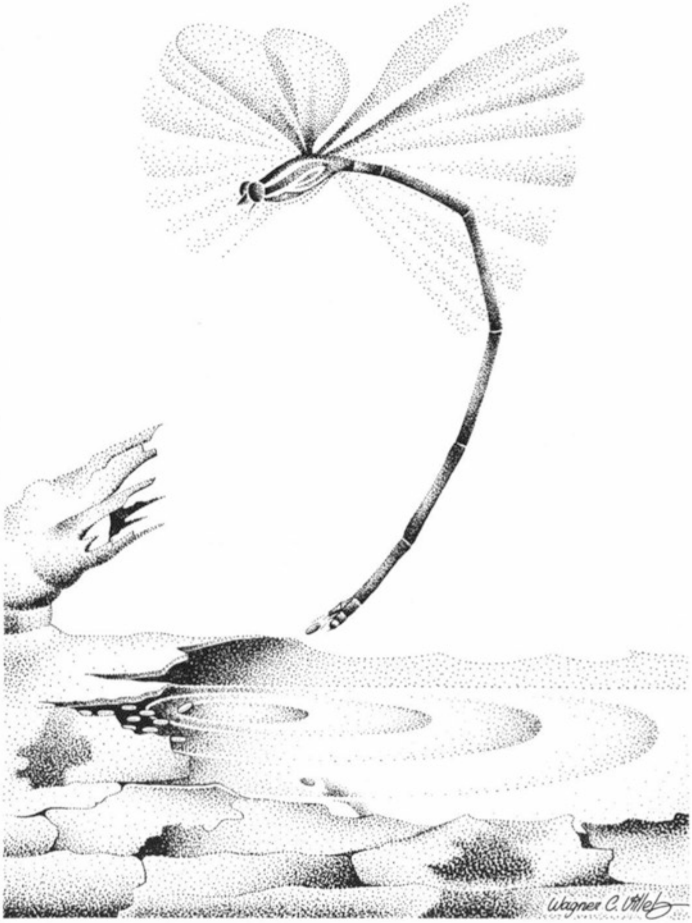

Fig. 2.7 Artistic view of a female *Mecistogaster* sp. throwing eggs in the water contained in a tree hole. The proportions of the insect to the fallen trunk and its hole were purposely modified. Reprinted with permission from Osmylus Scientific Publishers (Machado and Martinez 1982), © 1982

Here we presented an introduction to the main factors influencing the distribution of aquatic insects and its most common water habitats. Considering that the topics covered in this chapter are vast, from spatial spread to diversity, from habitats to aquatic insect adaptations, they will percolate through all the following chapters, with particular emphasis in the next two chapters looking into dispersal and the role of abiotic factors (Chap. 3 and Chap. 4).

Fig. 2.8 (**a**) *Pontomyia oceana* Tokunaga masses at Turquoise Bay, Ningaloo Reef, in the Indian Ocean. (**b**) Male and (**c**) female specimen of *P. oceana*. Reprinted with permission from Springer Nature (Bessey and Cresswell 2016), © 2016

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Chapter 3
Dispersal by Aquatic Insects

Michael L. May

Abstract All habitats change over time, so most organisms must resist unfavorable conditions or disperse to more favorable localities. Typically, aquatic habitats are relatively short lived because of drying or infilling. Aquatic insects, then, often have adaptations for effective dispersal, sometimes over long distances and most often by flight. This chapter examines some of the environmental drivers and organismal responses that affect the nature of dispersal. These include consideration of how different habitats affect dispersal, especially some differences between lentic and lotic habitats. Dispersal characteristics may also have major effects on genetic structure of populations. Both selective forces and proximate cues affect when insects disperse and when and where they colonize new habitats; availability of space, presence of predators, and availability of food may all play a role, depending on species and circumstances. Adaptations for dispersal include, in addition to active flight, behaviors that promote passive movement by wind, dispersal polymorphism (i.e., changes in body structure, such as wing development, that enhance dispersal, usually hormonally controlled and incurring some cost in fecundity), increased body size, and timing of diapause and reproduction. In a few species dispersal extends to migrations of hundreds of kilometers and may have important seasonal effects on habitats of origin and of destination. Dispersal is also integral to the concept of metapopulations and in fact may be a major driver of community composition and dynamics. Simultaneous dispersal of very large insect populations can have an important effect on nutrient and energy flow to and from communities. Finally, dispersal may be a critical determinant of whether and how aquatic insects respond to climate warming.

Keywords Geographic range · Use of habitat · Habitat template · Community dynamics · Climate warming

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3.1 Introduction

Dispersal is one of the fundamental processes that influences the ability of organisms to reach suitable habitats, to find mates, and to avoid potentially disastrous disturbances. It can also have major effects on geographic range, genetic structure of populations, population persistence, and movement of energy and nutrients. Because the habitats of aquatic species are physically relatively well defined and cover broad ranges of size, permanence, and faunal complexity and because it is often relatively easy to maintain small populations and communities in the laboratory or under seminatural conditions they lend themselves to many sorts of observational and manipulative studies that are more difficult in many other animals. My hope is that this chapter will make clear some of the fascinating questions that have been and can be addressed using aquatic and semiaquatic insects as subjects.

3.2 The Evolution of Dispersal by Flight

The evolution of wings was the sine qua non of most insect dispersal, and one of the great morphological innovations of Metazoa—the first wings on earth. A brief discussion of that landmark therefore seems appropriate, especially since aquatic insects may have been the first to evolve proto-wings. For many years, most entomologists subscribed to the idea that insect wings developed from paranotal lobes, flattened extensions of the thoracic terga, and present on many Paleozoic insect fossils (Snodgrass 1935). The work of Kukalová-Peck (1978, 1983), however, based on detailed analysis of fossil morphology, turned the focus to aquatic taxa. She argued that wings originated as outgrowths of the insect pleura, possibly as modifications of movable gill covers that were found on the thoracic and abdominal segments of aquatic Paleozoic insect nymphs and that have a pattern similar to the inferred plesiomorphic pattern of veins in the wings. Although modifications of her scheme have been proposed (Trueman 1990; Elias-Neto and Belles 2016; Linz and Tomoyasu 2018), the main features seem likely to endure. Marden and Kramer (1994) suggested that the behavior like that of brachypterous stoneflies skimming across the water surface might have been a predecessor of flight, implying that flight may actually have originated in aquatic insects (but see Dudley et al. 2007). Wings then enabled insects to reach and exploit almost every nonmarine habitat on earth.

3.3 The Habitat Template

No habitat is perfectly stable, although change may occur at timescales ranging from hours to millennia. All eventually change owing to physical and/or biological processes, including human disturbance. Consequently, most organisms must be able to evade or resist unfavorable conditions. Aquatic insects, especially those inhabiting temporary ponds or pools, may resist periodic drought by, e.g., burrowing into mud or sheltering under vegetation or stones as adults or (rarely) larvae, diapausing in a drought-resistant form, or entering a terrestrial adult life stage (Batzer and Wissinger 1996). Most, however, have at some time in their life cycle the capacity to move from their area of birth or current residence to another, more suitable area. Many species that inhabit seasonal ponds and wetlands develop rapidly, with the resulting adults flying to permanent waters where they pass the dry season, in some cases reproducing there and in others returning to temporary waters for reproduction (Batzer and Resh 1992; Batzer and Wissinger 1996; Saijo 2001). Other insects may pass the dry season as adults in reproductive diapause (Corbet 1999). This movement from their birthplace or place of initial reproduction to other locations is dispersal, the subject of this chapter.

Dispersal of aquatic insects is not usually observed directly, and almost never from departure to arrival at a new habitat patch. Most often it is inferred from changes in populations in response to seasonal or other environmental changes. Sometimes direct observation of important portions of the dispersal process is possible and very useful, however. This is usually most feasible with large, diurnal species such as dragonflies (e.g., Russell et al. 1998; Wikelski et al. 2006; Anderson 2009; May 2013) or in cases of unusual dispersing swarms of smaller insects (e.g., Stevens et al. 2007). Mark-recapture methods have sometimes been useful, notably by using fluorescent powders to mark mosquitoes (e.g., Service 1993; Epopa et al. 2017; this technique does not allow discrimination of individuals) or paint marks or numbers on wings of Odonata (e.g., Michiels and Dhondt 1991) and on several species of water striders (Gerridae; Ditrich 2016), corixid bugs (water boatmen; Boda and Csabai 2009), and dytiscids (predaceous diving beetles. Davy-Bowker 2002). Medeiros et al. (2017) marked large numbers of the mosquitoes, *Culex quinquefasciatus and Aedes albopictus*, by adding small amounts of $^{15}KNO_3$ or ^{14}C-glucose to water in plastic tubs colonized by wild mosquitoes. Using light traps for recapture, they determined that *C. quinquefasciatus* females seeking oviposition sites often dispersed 1–2 km from the marking site while females of *A. albopictus* seldom went further than 300 m. Thus, despite the limitations of all mark-recapture techniques, a great deal has been learned through careful observation and experiment with both undisturbed and manipulated populations.

In general, dispersal increases in frequency and importance as habitat stability declines and habitat isolation increases (Southwood 1962). Some aquatic habitats are effectively permanent, including large, deep lakes, e.g., L. Baikal, estimated to be 20–25 million years old (Wikipedia 2018a), and a few river channels (Wikipedia 2018b; even if these estimates are correct, however, the habitats in these rivers have probably changed radically over the millennia). The vast majority of aquatic environments are of relatively short duration, and many still waters, such as shallow lakes, ponds, and wetlands, are seasonal or sometimes dry for several years at a time. Datry et al. (2014) estimated that ca. 30% of the total length of rivers globally are intermittent. Thus many aquatic habitats are relatively unstable and isolated from similar habitats by environments that are unsuitable for aquatic insects. Some aquatic species can survive desiccation in a state of diapause, commonly as eggs (e.g., Williams 1996; Corbet 1999), but for many dispersal is an essential, often urgent, adaptation that affects individual fitness, population and metapopulation dynamics, and community composition and persistence.

Intermittent rivers notwithstanding, still, or lentic, waters are much more likely to desiccate or suffer from other catastrophic events at relatively frequent intervals and will eventually be obliterated by sediment infilling. Moreover, lentic habitats are generally less interconnected than are lotic (running) waters, which normally are continuous with other streams and river systems. For that reason, insects of lentic waters are expected to have greater powers of dispersal than lotic species. Despite the difficulty of observing dispersal directly because of the small size of most insects and the difficulty of marking and recapturing large numbers, this expectation is supported indirectly by numerous studies.

For example, Arribas et al. (2012) studied sister species pairs of hydrophilids (water scavenger beetles) and showed that the member of each pair that lives in ponds had a substantially larger geographic ranges and longer wings than their stream-dwelling relative, both of which suggested greater powers of dispersal. Ribera and Vogler (2000) found that other aquatic beetles from lentic habitats had on average considerably larger ranges than lotic species in the Iberian Peninsula. On a wider geographic scale, Ribera et al. (2003) showed a similar difference, as well as higher species turnover, among lotic species throughout Europe. These differences were also present in each of the four independent beetle clades. Hof et al. (2008) presented evidence that in freshwater animals generally, not only insects, lotic species richness in Europe declines steadily with latitude, suggesting poor dispersal from southern Pleistocene refugia from glaciation, while lentic species richness showed a maximum at intermediate latitudes, and β-diversity (a measure of species turnover) was greater at any latitude for lotic than for lentic species, suggesting less mixing of populations among the former. Hof et al. (2012), using more detailed information on the European ranges of Odonata, found that lentic species usually occupy more of the projected suitable range, based on climatic characteristics, than do lotic species, again suggesting that the former disperse more readily into areas made suitable by a warming climate. Finally, many species of southern European Odonata have recently expanded their range northward, probably in response to climate warming, but this effect has been much stronger in lentic than in lotic species (Grewe et al. 2013). All these studies, however, measured presumed indicators of dispersal rather than dispersal directly, and comparable data apparently are not available from other continents.

Perhaps the most persuasive evidence of the correlation of range size with dispersal capacity is that of McCauley et al. (2014) for North American Libellulidae. These authors used data from McCauley (2007) on observed dispersal distance and rate from natural source populations to initially uninhabited artificial ponds. This was used along with two measures of niche breadth and several other variables as possible factors that might explain range in multiple regressions; only dispersal and niche breadth had significant effects, positive in both cases, on range size, which was extracted for each species from the web site, OdonataCentral (https://www.odonatacentral.org/) as of 2007.

Another indicator of the relative degree of dispersal is the genetic structure of populations. In species with high rates of dispersal, populations should experience a high level of genetic exchange, whereas if dispersal rates are low populations are more isolated and genetic differentiation among populations should be higher. This is commonly expressed in terms of F_{ST} (Wright 1951), which is a measure of the relative extent of genetic variation among subpopulations; the value ranges from 0, if the entire population is randomly mixed, to 1 if all variation is between, rather than within, subpopulations. Since the advent of allozyme frequency analysis, and especially of DNA sequence analysis, population structure of many organisms has been measured in this way. For example, Marten et al. (2006) compiled F_{ST} values for European aquatic molluscs, crustaceans, and insects. In all three cases, lotic species had, on average, significantly higher F_{ST}s. As might be expected, average F_{ST} values were lower in insects generally than in the other organisms, since among these only insects can fly.

On the other hand, such broad generalizations may obscure a great deal of variation within and overlap among habitat types. Short and Caterina (2009), e.g., demonstrated that three largely sympatric, lotic beetles in southern California diverge markedly in genetic and phylogeographic population structure and corresponding variation in inferred population connectivity. They varied from practically unstructured, implying almost complete mixing throughout the entire population, to having an extremely close correlation of haplotype with geographic origin, thus presumably very little movement away from their place of origin. Likewise, Phillipsen et al. (2015) compared population genetic structure in three lotic species, *Abedus herberti* (a flightless bug), a stonefly, *Mesocapnia arizonensis* (males brachypterous, females fly), and *Boreonectes aequinoctialis* (a strong-flying beetle). All three showed precisely the genetic pattern that was predicted: *A. herberti* had high mean and variance in genetic distance among populations, and no indication that this was affected by geographic distance (i.e., almost no genetic mixing among its isolated populations); *Boreonectes* had very low mean and variance of genetic distance, and again no effect of geographic distance (populations all very similar because of great dispersal ability and intermixing); and in *Mesocapnia* the mean and variance increased smoothly with distance (i.e., so-called isolation by distance, consistent with intermediate dispersal; Fig. 3.1). Thus, while the broad patterns found by Marten et al. (2006) are probably correct, many individual exceptions surely exist.

Although streams are typically more stable than lentic waters, organisms in streams that dry up partly or entirely face many of the same problems as those of still waters. In some cases residual pools remain throughout the dry season and can provide refuges for at least some stream inhabitants, and a few species may shelter in the hyporheic zone (Stubbington 2012), but others must either disperse to running streams or diapause in a drought-resistant form (e.g., Corbet 1999; Garcia and Hagen 1987). A form of disturbance peculiar to streams is the occurrence of spates, or sudden floods may displace organisms far downstream. These may be avoided by movement into the hyporheic region, which seems to be a more common and

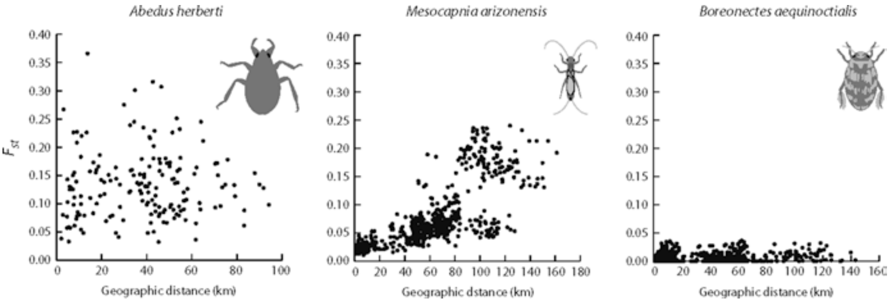

Fig. 3.1 Relationships between genetic distance (Fst) and geographic distance in three species of desert insects from the southwestern USA. The pattern for *Abedus herberti* shows highly variable genetic distance with virtually no relationship to distances between populations, suggesting that there is very little genetic exchange even between nearby populations. In *Mesocapnia arizonensis* nearby populations are more similar genetically than are distant populations, i.e., isolation by distance. *Boreonectes aequinoctialis* populations are all closely similar in genetic characteristics irrespective of distance between them, indicating that the regional population is essentially panmictic. Figure from Phillipsen et al. (2015), used with permission

successful strategy in the face of spates than in drought (Stubbington 2012), by sheltering under rocks or other in-stream objects, or, especially in univoltine species, by timing adult eclosion for the end of the dry season, so that most larvae have exited the stream just before the onset of flooding (Corbet 1999; Lytle 2008; pers. obs. 1994). In addition, many very small larvae may disperse short distances into the hyporheic zone, possibly to avoid predators as well as physical stresses (Mugnai et al. 2014; Williams 1981).

Lotic organisms also face another challenge that has received a great deal of attention over the years. Because of the persistent downhill flow of water in streams, their insect inhabitants, as well as other aquatic organisms, will tend to be displaced downstream; this is known as drift and has been documented in a number of lotic systems (e.g., Waters 1972). Thus headwater streams apparently would be depleted of aquatic fauna in the absence of substantial compensatory upstream movement. This process was first described explicitly by Müller (1954, 1982), who called it the “colonization cycle” (also known as “drift compensation” or “the drift paradox”). Müller presented data in support of his ideas, but subsequent tests of the phenomenon have been inconclusive; one study using stable isotope labeling with ^{15}N strongly supported the pattern of drift and return in arctic mayflies (Hershey et al. 1993), and Coutant (2008) used a similar technique to recover caddisflies up to 16 km upstream from a source of effluent of ^{65}Zn, but Briers et al. (2004), using ^{15}N as a label, showed little indication of preferential upstream movement in stoneflies in Wales. Several studies using malaise traps or sticky traps along a stream have obtained equivocal results (e.g., Svensson 1974; Bird and Hynes 1981; Williams and Williams 1993; Macneale et al. 2004; Winterbourn et al. 2007).

Anholt (1995) was probably the first to suggest that “drift compensation” by mass upstream movements of adults may be unnecessary if repopulation is density dependent; that is, under reasonable assumptions, if drift depletes larval populations upstream it is likely that the offspring of only a few adult pairs or gravid females can replenish the population, since few existing larvae will be present to compete with the newly colonizing individuals. This basic idea has been refined (Pachepsky et al. 2005; Mazzucco et al. 2015) and appears to provide a reasonable mechanism for maintenance of upstream populations, but without accurate measurements of insect movements it is difficult to verify in detail. It is also possible in some cases that movement of aquatic larvae, by swimming or crawling upstream, might partly reverse the effects of drift, and significant upstream crawling has been reported (Elliot 1971; Hershey et al. 1993; Williams and Williams 1993), although most investigators have found this to be of much less importance than adult flight (e.g., Graham et al. 2017). Humphries and Ruxton (2002), however, modified Anholt's model to show that, under some reasonable assumptions about population size and persistence, upstream crawling of less than 1 m might be sufficient to compensate for drift without reliance on adult flight. Substantial upstream crawling by larvae can occur (Graham et al. 2017) and may even facilitate independent habitat selection by larvae. Galatowitsch and Batzer (2011) observed large numbers of mayfly larvae moving upstream against strong currents into floodplain wetland, where they enjoyed faster growth than in the adjacent river channel.

Another fraught issue in the study of dispersal of insects in lotic habitats is the extent of overland movement away from natal streams that might indicate dispersal to separate streams or watersheds. It is clear that many insects do move along streams or stream valleys (e.g., Bogan and Boersma 2012). Most studies using passive traps have concluded that lateral movement away from streams is small, often less than 100 m (e.g., Collier and Smith 1998; Griffith et al. 1998; Briers et al. 2002; Petersen et al. 1999). In contrast, some genetic studies suggest substantial gene flow among separate watersheds at distances of up to tens or even hundreds of kilometers (Wilcock et al. 2003, 2007; Chaput-Bardy et al. 2008; Hughes et al. 2011). A possible reconciliation of these results is suggested by Didham et al. (2012), who placed arrays of passive interception traps at standardized distances from several streams, both at ground level and in the canopy of adjacent forest fragments approximately 15 m above ground. They collected more than three times as many adult aquatic insects in the canopy as at ground level, including at more than 1 km (the greatest distance of trap placement) from the nearest stream, although with some differences among taxa. Thus the apparent discrepancy between trapping and genetic results may stem, at least in part, from trapping schemes that failed to collect a majority of dispersing adults because traps were only placed at ground level.

Somewhat counterintuitively, several studies have demonstrated appreciably greater genetic uniformity across catchment basins than among reaches within streams (Bunn and Hughes 1997; Schmidt et al. 1995; Miller et al. 2002; Hughes et al. 2011). This could be explained by the so-called "patchy recruitment hypothesis" (Bunn and Hughes 1997). If each section of stream is colonized by offspring of only a few individual insects, then the allele complement in different reaches may differ strongly simply by the accident of which females oviposited there. If, at the same time, there is ample mixing of populations across catchments, the genetic profile of each catchment, which would include many individual reaches, should be similar to others in the region. This pattern may be common in many situations, although it seems less likely in taxa that emerge synchronously and oviposit quickly thereafter (Bunn and Hughes 1997) or that maintain large populations in very stable habitats (e.g., Krosch et al. 2011). Another pattern shown by some populations of insects confined to headwater streams, especially in mountains, is that populations in different catchments are more closely related to others on the same mountain than to lower portions of the same catchment. This suggests that such species are limited, possibly by temperature and stream gradient, to the uppermost reaches of streams but can disperse overland to nearby headwaters of other systems originating on the same mountaintop (Finn et al. 2007). Hughes et al. (2009) summarize the characteristics and predictions of these and several other models of genetic exchange.

3.4 Cues for Dispersal and Colonization

Given that dispersal allows organisms to anticipate and avoid deterioration of their habitat, what are the indicators of decline, currently or in the near future? Besides leaving a deteriorating habitat, dispersing individuals must locate and, often, assess the suitability of a new locale. This section examines some of the known solutions to these exigencies.

3.4.1 Initiation of Dispersal

Few experiments have addressed the direct effects of drying of water bodies on insect dispersal. Boersma and Lytle (2014) placed individuals of the giant water bug, *Abedus herberti*, which occurs in intermittent streams in the southwestern USA, into small tanks either with or without water and lined with screening so the insects could escape. These were placed into larger outer tanks that contained water. After 24 h, ten times as many bugs had left the dry small tanks as the small tanks with water. Velasco and Millan (1998) studied one hydrophilid and two dytiscid beetles and a corixid bug (water boatman), also from intermittent streams, and found that two of the beetles and the corixid left their aquaria if the water temperature was raised to about 40 °C. In addition, they found that, when they placed individuals of the same species in aquaria with different depths of water, from 10 cm deep to entirely dry, all of the beetles flew or crawled out of the aquaria when the depth was 1 cm or less; the corixid did not respond to water depth. In each replicate, 5–10 individuals of a single species were placed in the same aquarium, irrespective of depth, so it is possible that the beetles were responding to crowding rather than to water depth per se (Boersma et al. 2014). *Rhantus* spp. (Dytiscidae), which live primarily in temporary seepage pools, also respond to crowding with escape behavior (which would lead to dispersal), and to high temperature and to unsuitable substrate (smooth glass bottom in experimental containers; Smith 1973). Drummond et al. (2015) observed assemblages of insects in natural scour pools during progressive drying; emergence rates of most, but not all, taxa increased as drying progressed. Some larval mosquitoes from temporary pools accelerate development in response to drying (Chodorowski 1969; Schäfer and Lundström 2006); Chodorowski (1969) also observed slowing of development when pools were diluted with rainwater. On the other hand, De Block and Stoks (2005) found that damselfly larvae (*Lestes viridis*) from temporary ponds actually developed more slowly and emerged later than controls as water volume was reduced in outdoor tubs, although individuals that hatched late in the season did accelerate development (and see Johansson and Rowe 1999). The authors suggested that in this case crowding increased competition for food, which made rapid growth impossible. Jannot (2009) showed that development time in the caddisfly, *Limnephilus indivisus,* was unaffected by water depth but female size at eclosion was reduced. Some *Asynarchus* caddisfly larvae, which live in high-altitude snowmelt basins, become aggressive toward and may cannibalize conspecifics in response to high temperature, crowding, and lowered water level; this behavior may accelerate pupation and allow for successful dispersal by the resulting adults (Lund et al. 2016). Based on statistical analysis of field trap catches, Klečka (2008) concluded that dytiscids, hydrophilids, and scirtids (marsh beetles) in the Czech Republic made more dispersal flights when water in occupied pools was low. Finally, Lytle et al. (2008) observed large numbers of adult water beetles and dragonfly larvae displaying uncharacteristic positive rheotaxis and crawling upstream in a desert stream just ahead of the receding waterline of a drying stream reach.

An excess of water, at least in lotic habitats, can be nearly as harmful as the absence of water. Particularly in arid regions subject to occasional heavy rains, spates may represent a substantial danger to aquatic organisms, and several taxa, especially Hemiptera and Coleoptera, in the arid American southwest climb out the stream bed in response to rainfall and escape the danger of flash floods (Lytle 1999, 2001; Lytle and Smith 2004). Alternatively, some insects may time adult eclosion to just precede the onset of rains, thus avoiding spates (Lytle and Smith 2004). A number of other stimuli can induce dispersal, and their effect may depend in part on the phenotype of the dispersing insect.

One might imagine that the presence of predators would promote dispersal, but this has not often been demonstrated. The clearest evidence of a direct effect on dispersal behavior is probably the work of McCauley and Rowe (2010) and Baines et al. (2015, 2018) on the backswimmer, *Notonecta undulata*, in mesocosms (water-filled cattle tanks). In the first of these studies, the authors showed that in the presence of predators (caged fish that could not actually reach the insects), *Notonecta* dispersal increased dramatically in the presence of one fish, but there was no significant additional effect of adding a second fish. If one or more *Notonecta* were deliberately fed to the fish, however, there was a sharp increase in dispersal that increased further as additional *Notonecta* were eaten; therefore, these insects are sensitive not only to the presence of predators but also to some signal that conspecifics were consumed. The experiments of Baines et al. examined the effects of predators in combination with body condition adjusted by pre-experimental feeding regime (Baines et al. 2015), or conspecific density and predation (Baines et al. 2018). In the first experiment, emigration was higher in the presence of caged fish, irrespective of body condition. Better-conditioned bugs initially emigrated more rapidly than those in poorer condition, but the effect declined over time so the difference was marginal for the entire experiment. In the later study emigration increased across three levels of increasing density. Predation significantly increased emigration only at medium density for reasons that were not clear. Dispersal was also positively correlated with beetle density in dytiscids (Yee et al. 2009). Plant density was also manipulated and had a significant but small negative influence on dispersal.

The effect of predators on dispersal of mayfly (*Baetis* spp.) larvae has been investigated extensively by Peckarsky and her colleagues. *Baetis* usually coexist with insectivorous trout in mountain streams and in fact maintain higher densities in streams with trout than without (Peckarsky et al. 2011). They feed by drifting with the current until they encounter rocks with good patches of benthic algae, so they drift more in streams with less food available (Hernandez and Peckarsky 2014). Peckarsky and McIntosh (1998) placed larvae in one of the four mesocosms with flowing water and stones with roughly uniform growths of algae: (1) exposed to water dripping from a tank containing trout, (2) trout odor and predaceous stonefly larvae with mandibles glued so they could not prey on the mayflies, (3) stonefly larvae and odorless water, and (4) odorless water and no stoneflies. All *Baetis* were predominantly active at night, but fish odor reduced drifting sharply during the night. The presence of stoneflies increased crawling during the day in the absence of fish odor and drifting at night with or without fish odor. Thus fish tended to reduce dispersal while the presence of stoneflies increased dispersal even in the absence of actual predation (Peckarsky et al. 2008; Peckarsky et al. 2011). Wooster and Sih (1995) review earlier work on the effects of predators on drift in stream insects.

Because dispersal is a crucial part of the adaptation of an animal's life cycle to its environment, it must be coordinated with other facets of the life cycle, e.g., adult eclosion and timing of reproduction. Photoperiod supplies a cue that triggers many events in the lives of insects. Apparently no evidence has demonstrated a direct effect of photoperiod on dispersal, but certainly events that are closely coordinated with dispersal are strongly influenced by photoperiod. Lytle (2002, 2008) showed how photoperiodically controlled metamorphosis allows insects to time their adult eclosion, and thus their dispersal from the stream, before flooding is likely to occur. The trichopteran, *Phylloicus aeneus*, probably uses just such a strategy (Lytle 2002). In addition, photoperiod controls development of either winged or wingless forms in at least some wing-polymorphic species (Harrison 1980; Zera and Denno 1997), which clearly has profound effects on dispersal ability. Among related species, aptery is often more common in those that occupy more permanent habitats (e.g., Ditrich et al. 2008).

3.4.2 Colonization of New Habitats

Dispersal, i.e., moving away from a now or soon-to-be unsuitable place, also implies colonization, the occupation of a new and presumably more suitable environmental patch. How, then, do insects find appropriate habitats? At least part of the answer for aquatic species is by detection of polarized light reflected from water surfaces, a phenomenon demonstrated by Horváth and his associates (Bernath, et al. 2001; Horváth 1995a, b; Horváth and Kriska 2008). Several researchers have taken advantage of this phenomenon by using other polarizing surfaces, such as black plastic, as a means of attracting and collecting insects for study (e.g., Boda and Csabai 2009); this also explains the strange propensity for dragonflies to attempt oviposition on black gravestones and on the surface of cars (Horváth et al. 2007; Wildermuth and Horváth 2005).

More than likely some insects use other visual, tactile, or chemical cues to locate appropriate habitat, but few of these have been identified. Some aquatic insects can detect the presence of underwater predators without direct contact. Blaustein et al. (2004) showed that mosquitoes, *Culiseta longiareolata*, whose larvae are highly vulnerable to predation by notonectids (backswimmers), avoid ovipositing in artificial or natural pools containing *Notonecta*, apparently responding to chemical cues; midges, *Chironomus riparius*, have much less vulnerable larvae and do not avoid *Notonecta*. *Culiseta longiareolata* females also avoid laying eggs in pools containing a larva of the dragonfly, *Anax imperator* (Stav et al. 1999). Mosquitoes also apparently respond to other chemical and physical cues. Among tree hole-breeding mosquitoes in Florida, USA, drought-susceptible species chose more permanent holes that are larger and lower, with larger, more vertical openings, and contain darker water with higher conductivity, pH, and tannin-lignin content (Bradshaw and Holzapfel 1988). In coastal NSW, Australia, Mokany and Mokany (2006) studied larvae of *Ochlerotatus notoscriptus*, a relatively drought-resistant species, and the more drought-susceptible *Anopheles annulipes*, in small mesocosms with filtered pond water concentrated by evaporation by fivefold; mesocosms were filled with either 2 L or 4 L of either dilute or concentrated water. Larvae of *A. annulipes* were consistently recruited to higher volume containers, regardless of concentration, while *O. notoscriptus* favored higher concentration containers, regardless of volume. Thus *O. notoscriptus*, at least, responded to water chemistry.

Resetarits and Silberbush (2016) found that two species of *Culex* mosquitoes also avoid fish predators in arrays, each consisting of nine mesocosms constructed from plastic pools. In each array, the pools (“patches”) were arranged into three groups of three (“localities”). One locality contained no patches with fish, one a single patch with fish, and one two patches with fish. In this configuration, female mosquitoes exhibited a phenomenon called “compression” by these authors (Fig. 3.2). Mosquitoes laid fewer eggs in patches containing fish than in fish-free patches, but also laid fewer eggs in fish-free patches in localities also containing one and still fewer in those containing two patches with fish. That is, female mosquitoes were sensitive not only to the condition of individual patches but also to their

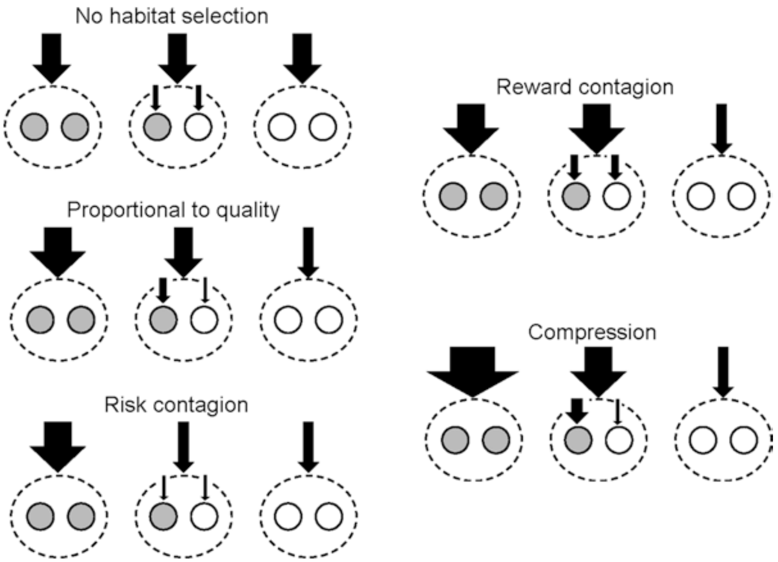

Fig. 3.2 Schematic illustration of effects of locality (dashed ovals) and patch (small circles) quality on colonization by dytiscid and hydrophilid beetles. Filled circles are patches of higher quality, e.g., lacking predators or with higher food quality, than open circles. Widths of vertical arrows are proportional to the number of beetles colonizing each locality or patch. Modified from Pintar and Resetarits (2017a), used with permission

context, i.e., the condition of each locality, so that more eggs were "compressed" into localities entirely without fish.

Similar experiments on dytiscid and hydrophilid beetles and some aquatic Hemiptera have examined several different contrasts among patches. Binkley and Resetarits (2007), e.g., found that these taxa were dramatically more likely to colonize mesocosms under an open tree canopy than under a closed canopy. The beetles also detected and avoided fish in mesocosms and even discriminated among fish species in a pattern that reflected the degree of threat they posed (Resetarits and Pintar 2016). Resetarits and Binkley (2009, 2013, 2014) arranged localities with variable numbers of patches (cattle tanks) with and without fish, resulting in three patch types: (1) fish free and distant from any fish-containing patches, (2) with fish, and (3) without fish but adjacent to patches with fish ("fish-associated" patches). In fish-free localities the number of colonists did not differ significantly among patches. Patches without fish always had more beetles than patches with fish, and the difference increased as the number of patches per locality increased, although the fish could not reach the beetles. Fish-associated patches had intermediate numbers. The difference in colonists between fish-free localities and localities with fish increased with locality size, even though the ratio of patches with and without fish was always 1:1 in mixed localities; beetles apparently perceived increasing rather than constant risk as the number of patches with fish increased ("spatial risk contagion"; Resetarits et al. 2005; Fig. 3.2). This response might lead to underutilization of some suitable natural habitats.

Vonesh et al. (2009) also reported that caged fish reduced the abundance and altered the composition of colonizing insects (mostly Diptera in their case). Subsequent exposure of the colonized containers to uncaged fish reduced abundance further due to predation. However, tanks that were fish free during the colonization phase still had more insects after actual predation than did the fish-associated tanks. Thus, differences in dispersal behavior can have long-lasting effects on community composition despite exposure to predators. Kraus and Vonesh (2010) showed that in their system the avoidance of fish by dytiscids was not strong if other colonizing species were allowed to accumulate but was much stronger if earlier colonizers were removed periodically. Hydrophylids and mosquitoes strongly avoided fish under all conditions, but, surprisingly, chironomid midges preferred to oviposit with fish, possibly because fish usually eliminate many invertebrate predators. Thus the responses of insect colonists may depend on subtle differences in patch characteristics. The presence of predators may also have other effects on life history and morphology, such as causing earlier metamorphosis, and, consequently, smaller size at metamorphosis, or development of defensive spines (Benard 2004).

The presence of food may also influence colonization of new habitat patches. Pintar and Resetarits (2017a, b, c) studied colonization by dytiscids (predators) or hydrophilids (predators as larvae, scavengers as adults). Hydrophilids preferred hardwood litter initially but later favored pools with pine needles, presumably due to changes in zooplankton composition. Dytiscids showed no significant preference. Individual species of both families mostly followed the same patterns, so the change among hydrophilids was not primarily due to species turnover. In separate experiments, dytiscids, but not hydrophilids, responded markedly to removal or addition of zooplankton to half the mesocosm containers (Pintar and Resetarits 2017b).

Aquatic beetles are subject to spatial contagion and compression in response to variation in resource level (Pintar and Resetarits 2017a). Beetles were as strongly attracted to localities with one high and one low resource patch as they were to localities with two high patches, and in the former case they compressed into the high-quality patch. As expected, localities with two low patches were less attractive. Finally, Pintar et al. (2018) compared the effects of three levels of predatory fish combined with three nutrient levels (i.e., nine possible combinations). In all cases they found that the presence of predators depressed colonization but, in these circumstances, the effect of nutrient level was not significant for any one species of beetle, although it was significant for all beetles taken together. They also counted egg rafts of *Culex* mosquitoes, which responded to both nutrients and presence of predators. Overall, they concluded that predators had a stronger effect than nutrient level on immigration. The giant water bug, *Lethocerus deyrollei*, however, emigrates more readily if deprived of food (Ohba and Takagi 2005).

3.4.3 Timing of Dispersal

The daily and seasonal peaks of dispersal may be responses to specific environmental cues, although this has received less attention than the questions of whether and where to disperse. As seen in the next section, seasonal timing is often a crucial adaptation for dispersal, especially when the latter is necessary to avoid seasonally unfavorable conditions. The timing of dispersal, however, may also serve more quotidian ends and may respond to several immediate cues. In some cases, as with many Odonata, adult emergence occurs at night or near dawn and is followed by dispersal away from the natal site as soon as hardening of the exoskeleton allows for flight (e.g., Corbet 1957; Michiels and Dhondt 1991; Geenen et al. 2000). This probably reduces predation and also spares the still rather fragile new adults from attack and injury by mating attempts from mature conspecific males at the water before their muscles are fully developed and their exoskeleton is fully hardened.

In other insects various physical cues may stimulate and assist dispersal. These are summarized exhaustively by Johnson (1961). More recently Boda, Csabai, and colleagues in Hungary have investigated conditions favoring or inhibiting dispersal by aquatic beetles and bugs. One important factor is wind. Dispersal flights were most common at wind speeds of <6 km h^{-1} and was completely inhibited by wind speeds of >12 km h^{-1} (Bota and Csabai 2005). Csabai et al. (2012) found that most of species of Coleoptera and Hemiptera flew during one or more of three distinguishable daily intervals: mid-morning, near noon, or at nightfall. In the spring, however, a few species flew throughout the day, and a number of others had different activity patterns in different seasons. Nearly all had a distinct seasonal peak, although relatively few were confined strictly to a single season. The authors concluded that the seasonal variation was driven by changes in air temperature in relation to the minimum temperature for flight and the (higher) minimum for mass dispersal although they did not report measurements of minimum or routine body temperatures. Certainly, however, wind and temperature are likely to have marked effects on dispersal in these and other insects.

3.5 Adaptations for Dispersal

The division between this section and the last is somewhat artificial. Clearly the responses to the various "cues" that stimulate dispersal and colonization ordinarily are adaptive, so I have made some arbitrary decisions about how to allocate information to one or the other topic. Here we will be concerned with characteristics that have evolved to favor successful dispersal rather than the circumstances that dictate when and where dispersal begins or ends. However, the sources of many cues for dispersal and colonization, such as food sources or presence of predators in a habitat patch, are the immediate result of features that make avoidance or exploitation of those patches adaptive, as shown clearly in the preceding discussion.

3.5.1 Passive and Active Dispersal

An important distinction is that between passive and active dispersers, i.e., between those that are propelled entirely by wind or water or that attach themselves to other animals, and those that move primarily under their own power. Most insects, because they can fly, fall into the latter category. Nevertheless, a number of insects, especially small Diptera, including mosquitoes, ceratopogonid midges, and blackflies, are dispersed by wind (Elbers et al. 2015; Jones et al. 1999; Service 1980). Japanese encephalitis is thought to have been introduced to Australia by wind-blown *Culex* mosquitoes from Papua New Guinea (Chapman et al. 2003), and genetic analysis suggested a panmictic population of these mosquitoes throughout western PNG and the Australian Cape York Peninsula. So-called aerial plankton—small organisms that are transported passively by winds, usually at hundreds to thousands of meters altitude—includes small insects of many orders, including a number of aquatic groups (Compton 2002). *Ischnura aurora*, a tiny zygopteran, also probably migrates passively on the wind while teneral (Rowe 1978). All these insects have little control of their direction except during takeoff and landing, and their movements may not always be either intentional or adaptive.

Of course not all insects are airborne dispersers. Many aquatic insects can walk or swim for some distance to reach emergence sites, escape drying habitats (Lytle et al. 2008), or compensate for downstream drift (as discussed above). Among terrestrial species nymphs of some locusts (Acrididae) and Mormon crickets (Tettigoniidae), e.g., walk for long distances to find food (Reynolds et al. 2014). In many Lepidoptera first instar caterpillars “balloon” by spinning out long silk threads that catch the wind. Some small Hemiptera nymphs can position themselves at the edge of leaves to launch themselves into the wind (Washburn and Washburn 1984). These methods are mostly unavailable to aquatic insects, however. Several semi-aquatic insects and Collembola are also propelled by wind or currents on the surface of water, and this may effect successful dispersal but probably is often maladaptive (Reynolds et al. 2014). One known case of adaptive dispersal in this manner is that of the aphid, *Pemphigus trehernei*, for which the sea aster, a plant of tidal salt marshes, is secondary host. First instar larvae are initially photopositive and crawl to and walk on the soil surface until they encounter the incoming tide. They are small enough to remain on the surface due to surface tension and often are blown along the surface by wind until they reach their host, at which time they become photonegative and descend through cracks in the soil to the aster roots where they feed (Foster and Treherne 1978).

Darwin (1859) famously observed that newly hatched larval snails readily attached themselves to a duck’s feet. He conclude that small aquatic animals might easily be dispersed on the feet and legs of water birds, and this has been confirmed in a number of cases for some small crustaceans and other zooplankton (Figuerola and Green 2002). Desiccation is a danger in such circumstances, but it should be possible for desiccation-resistant resting stages, including diapausing insect eggs. Apparently, though, this has never been definitely confirmed for insects.

3.5.2 Dispersal Polymorphism

A dramatic example of adaptive morphology is that of dispersal polymorphism, in which some individuals are adapted for dispersal and have fully developed wings while others do not disperse and usually have reduced or absent wings (brachyptery or aptery). For non-dispersing individuals there can be a considerable advantage to reduced or absent wings and flight muscles because in most insects these structures represent a considerable investment of energy and material, which may slow development and reduce fecundity compared to individuals without them (Harrison 1980; Zera 1984; Zera and Denno 1997).

Among aquatic taxa, this has been studied extensively in Gerridae, or water striders (summarized by Vepsäläinen 1978). Wing development varies among species, often geographically within species, and often between diapausing (usually wintering as inactive adults) and non-diapausing (summer, actively breeding) generations. Some species of *Gerris* are not dimorphic at all, while in others the diapause generation is long-winged, since they need to find sheltered sites for diapause and then return to habitats suitable for reproduction. The non-diapause generation generally does not disperse, sacrificing the ability for higher fecundity. In some species, populations in certain areas retain functional wings in summer, perhaps to avoid drying of their habitat. In some species dimorphism is seasonal, as described above, and probably is controlled by photoperiod, while in others dimorphism is genetically determined. Several other combinations of diapause and wing development have been identified. Zera et al. (1983) found in the North American genus *Limnoporus* that both genetic factors and photoperiod affect wing development, with short and declining photoperiod favoring production of long-winged morphs. Harada and Nishimoto (2007) reported that in *Aquarius paludum*, adults held under a long-day photoperiod regime and fed daily quickly broke reproductive diapause and matured ovaries while also histolyzing their flight muscle; others on the same photoperiod but fed only once every 3 days remained in diapause and retained functional flight muscles and their ability to disperse by flight. Thus the underfed individuals could disperse and possibly colonize a more favorable patch, while those with ample food diverted resources to gamete production and were ready to reproduce in situ (see Dingle and Arora 1973 for a more detailed study of a similar phenomenon in terrestrial bugs).

In the closely related and ecologically similar family Veliidae (riffle bugs), somewhat similar patterns are found (Ditrich 2016; Ditrich et al. 2008). As an interesting aside, at least one species of *Velia* is mostly flightless and is dispersed overland by walking (Ditrich and Papáček 2009).

A diverse group of other aquatic taxa also exhibits flight polymorphism. These include at least one mayfly (Ruffieux et al. 1998), a number of stoneflies (Brittain 1990; Lillehammer 1985; Zwick 2000), several Hemiptera in addition to gerrids and veliids especially corixids and notonectids (Young 1965; Baines et al. 2018), a few Trichoptera (Giudicelli and Botosaneanu 1999), and a few Diptera (Byers 1969;

Berendonk and Bonsall 2002). Whether reduced wings and/or flight muscles are genetically determined or induced by environmental circumstances is mostly unknown. The selective pressures that might lead to this condition may include the trade-off between flight and rate of development, fecundity, or longevity, or they could be in response to the danger of being permanently transported away from suitable habitat (Bilton 1994), as might be the case for species living on oceanic islands (e.g., Short and Liebherr 2007); these authors questioned the "island effect" as an explanation in this case, however, as did Roff (1990) more generally.

One other taxon deserves brief mention here. Although not truly aquatic, several species of planthoppers in the family Delphacidae are restricted to intertidal salt marshes. These were extensively studied by Denno and his collaborators (Denno and Roderick 1990) and subsequently reviewed in a broader context by Zera and Denno (1997). This is one of the most thorough studies of flight polymorphism to date, including ecological, physiological, and evolutionary aspects such as the close correlation of brachyptery with stable habitats. This correlation is also supported by Roff (1990) based on data from a very wide array of aquatic and terrestrial insects.

Aside from physical polymorphism, more subtle changes in the flight system affect dispersal. Dispersal behavior is usually accompanied by hormonal and other physiological changes. Modulation of juvenile hormone (JH) is probably the most pervasive of these. JH probably plays a major role in determining whether individuals develop normal or reduced wings, as well as muscle histolysis, although ecdysone, the molting hormone, is also important. The interplay of these hormones also largely controls the ultimate body size of individuals. In addition, a suite of hormones, most prominently adipokinetic hormone (AkH), but also including octopamine, regulate the deposition and mobilization of fat and the relative utilization of fat, carbohydrate, and, in some taxa, amino acids as fuel for energy metabolism. Fat is the normal fuel for all but very-short-range dispersers because it contains the largest amount of metabolic energy per unit mass (Dingle 2014).

Body size is influenced by many selective and life history factors (e.g., Peters 1986), but requirements for dispersal are often among these. Although not thoroughly investigated, a number of instances are known in which dispersers are larger on average than non-dispersers (reviewed by Benard and McCauley 2008). These include several cases among Odonata (e.g., Angelibert and Giani 2003; Conrad et al. 2002; Anholt 1990; and Michiels and Dhondt 1991). Roff (1991) found similar relationships in intraspecific comparisons. Larger body size may benefit active migrants because the mass-specific metabolic cost of flight tends to be smaller at larger body size. Flight speed and hence the ability to control flight direction at higher wind velocity are usually greater. Larger size might also tend to increase fecundity and make successful colonization of new habitats more likely. On the other hand, Thompson (1991) found no size difference among resident and dispersing individuals of a coenagrionid damselfly. McCauley (2005, 2010) also very carefully investigated males of two species of libellulid Anisoptera, *Leucorrhinia intacta* and *Pachydiplax longipennis*, both of which are highly territorial and aggressive, dispersing from permanent to recently refilled temporary ponds. In both cases, dispersing males were smaller than non-dispersers. The large males dominated smaller ones in territorial interactions, and the latter may disperse because of their greater difficulty in establishing new territories at the occupied ponds.

Since variation in body size does not necessarily prevent dispersal, it is often said to influence the propensity to disperse, i.e., a behavioral effect rather than a physical barrier to dispersal like aptery. Another such adaptation is subtle variation in wing size or shape. For example, Rundle et al. (2007) found that in *Enallagma* damselflies in North America wing length was positively correlated with range size, even when controlling for body length. In three species of *Libellula* dragonflies McCauley (2013) showed that two species with a broader habitat range and that dispersed further and more frequently had larger wings with a higher aspect ratio than a third species that had a narrow habitat range and was less dispersive. Suarez-Tovar and Sarmiento (2016) found that, when corrected for phylogenetic relatedness, migratory South American Libellulidae had larger and more deeply corrugated wings and a more expanded hindwing anal lobe than in nonmigratory species. In Swedish mayflies and stoneflies wing length was positively correlated with range size and in mayflies also with occupancy (the proportion of sampled sites actually occupied by a species) (Malmqvist 2000), and a similar, although not entirely consistent, correlation with habitat predictability occurs in chironomids (McLachlan 1985). Adaptive changes in dispersal propensity need not depend only on morphological features—physiology and behavior are clearly involved and may be of greater importance. Iversen et al. (2017), e.g., argued that the difference in flight tendency and distance in two genera of dytiscids are purely behavioral, since the wings and flight muscles remained intact in both.

McPeek (1989) found that larvae of two species of *Enallagma* damselflies only inhabit permanent lakes with predatory fish (which usually extirpate large invertebrates) and two others occur only in fishless lakes, dominated by invertebrate predators and generally less permanent than fish lakes. One species, *E. ebrium*, mostly inhabited “winterkill” lakes, which normally have fish but where winter oxygen levels may drop below lethal levels for fish, allowing large invertebrate predators to take over. *Enallagma ebrium* can coexist with fish but not with invertebrate predators, so adults disperse temporarily to lakes with fish only. The four species that coexist only with fish or with predatory invertebrates but not both are very philopatric. *Enallagma ebrium*, however, is adapted to lakes in which predator populations change radically and thus is much less philopatric. McCauley (2006), in another mesocosm experiment, showed that connectivity to other tanks explained a high proportion of the species richness of Odonata adults, and a still higher proportion of larvae, in the focal tank. The identities of adults seen nearby natural habitats and fields without cattle tanks were also extremely similar to those of adults and larvae at or within the tanks, suggesting that no physical barriers to dispersal existed. McCauley concluded that dispersal behavior alone limited colonization and largely determined community composition of these odonates.

3.5.3 Diapause, Reproduction, and Dispersal

As suggested in several examples already described, diapause, reproduction, and dispersal, with or without morphological changes, are intimately coordinated (Southwood 1962). The case of *Aquarius paludum* females (Harada and Nishimoto 2007) was described above. Other examples include several Odonata. In Japan, most *Sympetrum frequens* disperse from emergence sites in lowlands, often rice paddies, into highland areas during the summer, where they undergo partial reproductive diapause, although gametes slowly mature and mature coloration develops (Corbet 1999, pp. 390–394; Ueda 1988), and a very similar phenomenon occurs in *Sympetrum meridionale*, *S. striolatum*, and *Aeshna mixta* in Algeria (Samraoui et al. 1998). In many tropical dragonflies in areas with a distinct dry season, prereproductive adults may move from bodies of water where they reproduce into forest where they remain in reproductive diapause, often until the onset of rains, then quickly mature gametes, and develop mature coloration (Corbet 1999, pp. 261–262; pers. obs. 1974, 1994).

Because dispersal and diapause are intimately related, it may be difficult to distinguish independent environmental conditions that induce the two states, and in fact the cues may be the same. It is commonly assumed that photoperiod usually affects both, and Goehring and Oberhauser (2002) showed that in Monarch butterflies diapause induction and readiness to migrate are closely parallel. In other cases, it has been implicitly assumed that one effect of diapause induction (and sometimes also termination) is to initiate migration (Saunders 2010), but I know of no comparable studies on aquatic insects.

The close connection among dispersal, diapause, and reproduction led Johnson (1969) to propose the “oogenesis-flight syndrome,” that is, female insects have hypertrophied fat bodies and maintain their gametes in an immature state until dispersal is accomplished, after which JH titer increases, mature eggs develop, and oviposition ensues. This should allow them to begin dispersal with maximum energy stores and possibly reduced flight costs, and arrive at their destination with maximal reproductive value. This syndrome does apply to many dispersing insects. Rankin (1978) showed that in the large milkweed bug, *Oncopeltus fasciatus*, migration is stimulated by an intermediate level of JH and maturation of gametes by a high level. Instances of oogenesis-flight syndrome have not been studied in detail in aquatic insects but seem likely in the hydrophilid, *Helophorus brevipalpis* (Landin 1980), and dytiscids in the genus *Graphoderus* (Iversen et al. 2017). There is also good evidence for the syndrome in belostomatid bugs (Cullen 1969; Lytle and Smith 2004), and it is likely in Gerridae and probably numerous other taxa, although its hormonal control has not been shown definitively in either aquatic Hemiptera or Coleoptera. On the other hand, it certainly is absent, or present in abbreviated form, in some migrating dragonflies. These normally begin migration when sexually immature (Corbet 1999, pp. 395–396), but they mature gametes and may mate and oviposit long before reaching their final destinations (May and Matthews 2008; May 2013; May et al. 2017).

3.6 Long-Distance Migration

Many authors have used the terms migration and dispersal interchangeably or ambiguously (Johnson 1969, pp. 3–8). Here, I consider migration to be a category of dispersal, more or less equivalent to Corbet's (1999, p. 394) interhabitat displacement, that is, usually a movement over multiple tens to hundreds of kilometers. Typically it entails a later return to the original habitat, although, in insects, not usually by the same individuals that migrated initially. Among terrestrial insects, this would include the famous migrations of monarch (e.g., Agrawal 2017) and painted lady butterflies (Stefanescu et al. 2012), the bug, *Oncopeltus fasciatus* (e.g., Dingle 1996), or plague locusts such as *Schistocerca gregaria* (Rainey 1951, 1976). Only a few aquatic insects, notably Anisoptera, undertake similar migrations under their own power, although a number of taxa may be dispersed passively for long distances, as noted above. Kennedy (1985) defined migration in behavioral terms as "… persistent and straightened-out movement effected by the animal's own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station-keeping responses, but promotes their eventual disinhibition and recurrence." This is still a useful and insightful definition and is widely used, although it does not include purely passive dispersal (but does include, e.g., cases in which insects actively fly high into the air so as to become entrained in air currents—a "vehicle"—which thereafter carry them passively). It also does not depend on any particular adaptive advantage accruing or even require that dispersal be adaptive, although Kennedy certainly recognized the advantages and trade-offs involved.

Although butterflies, locusts, and dragonflies perform the most visually spectacular migrations, recent attention has been focused on vast migrations at hundreds of meters aloft by a variety of smaller insects at night across Britain and northern Europe (Hu et al. 2016). These fly well above their flight boundary layer (Taylor 1958), so they depend largely on the wind for propulsion and have been shown to actively seek out altitudes where wind direction matches their intended flight direction. They have been studied partly by aerial sampling e.g., (Chapman et al. 2004) but mainly by upward-looking radar that reveals patterns, velocities, and even headings, of insects as small as 10 mg. Upwards of 3×10^{12} insects (including many <10 mg, estimated from high-altitude net captures) may pass over southern Britain during the autumn, always on northerly winds. The smallest species are carried passively, but even slightly larger insects can modify their course by shifting their heading if wind is not blowing within 20° of the preferred flight direction (Chapman et al. 2015). The vast majority of these are terrestrial species, although a small number of aquatic insects—Corixidae, Dytiscidae, and Hydrophilidae—are included. These flights illustrate, however, the extent and importance of long-distance insect migration.

Odonata are probably the most flight-worthy of aquatic or semiaquatic insects and rank high among all insects. Several species are known to make long migrations, in at least two cases over thousands of kilometers. Although they do fly under their own power, they also depend, at least to some extent, on favorable wind for propulsion. One species that has been studied extensively, *Pantala flavescens* (the "Wandering Glider" or "Globetrotter"), has been shown to fly some 500–1000 km from India to the Maldives archipelago and thence on to east and southeast Africa, a total distance of around 3500 km (Anderson 2009). Based on observations in the Maldives and literature reports from southern India and east to southeast Africa, Anderson inferred that *P. flavescens* adults emerging in India during late summer fly southwest at high altitude on winds associated with the Intertropical Convergence Zone (ITCZ) to Africa. Corbet (1962) noted that adults are at various latitudes in Africa in synchrony with the ITCZ, and they may breed continuously within the continent. During the northern spring, however, a strong westerly upper air current, the Somali Jet, develops off the Horn of Africa and blows across the Arabian Sea and northern Indian Ocean, also bringing moisture that helps initiate the southwest monsoon in south Asia. This jet probably enables a reverse movement of *P. flavescens* back to northern India. Hobson et al. (2012), using stable hydrogen isotope ratios in wing samples of *P. flavescens*, showed that the most probable origin of specimens collected on the Maldives in October was in northeasternmost India, Nepal, and Bangladesh. This confirms Anderson's proposed route from India to the Maldives and is strongly supportive of a circuit very much as he suggested.

Pantala mostly breed in ephemeral pools created by rains along the ITCZ and consequently have very rapid larval development (Corbet 1999, p. 227). It is very likely that they never diapause as larvae and are obligate migrants in most places where they occur. Some other migrant odonates may diapause as larvae and thus could have two options for surviving conditions unsuitable for development. The common North American migrant, *Anax junius* (Fig. 3.3), is one such species. It has

Fig. 3.3 Photograph of male *Anax junius* in flight, as during migration. Used with permission of the photographer, Dennis R. Paulson

attracted attention since the nineteenth century because of its sometimes spectacular mass migrations (Russell et al. 1998). It was long thought (Trottier 1971) that two temporally separate cohorts exist, one emerging in early summer and breeding in the neighborhood of its natal site, and the other emerging in late summer and migrating south. Freeland et al. (2003) showed that migrant and nonmigrant individuals could not be distinguished genetically. Thereafter Matthews (2007a) and Hobson et al. (2012), again using stable hydrogen isotopes, confirmed that late summer-autumn migrants collected in Texas and Mexico had very likely emerged in the northern USA or southernmost Canada. Matthews (2007a) also found that *A. junius* population show very little genetic differentiation across their entire eastern North American range. Stable isotope studies indicate, as expected, that individuals collected in the northern USA in early spring emerged far to the south (Matthews 2007a; Macfarland K, pers. comm. 2015). Most recently May et al. (2017) examined developmental phenology of *A. junius* at several sites in the eastern USA. Two emergence groups of larvae could usually be distinguished, but they overlapped broadly both in larval size and adult emergence, making genetic differentiation unlikely. Larval growth and timing of eclosion suggest that the early emerging group are largely individuals that overwintered as late instar diapausing larvae and probably will lay eggs locally, most of which will hatch as larvae that again overwinter in diapause. Late emerging adults are thought to be the offspring of adults that migrated from the south and laid eggs in early spring. The resulting larvae develop directly, emerging in late summer or autumn, and migrate south. However, because of the genetic evidence already cited and the broad overlap of larval size groups and adult emergence, it is probable that the timing of emergence and hence the likelihood of migration are determined by the effect of some environmental cues such as photoperiod on early larval instars (Matthews 2007b). Other known but less studied migrants among Odonata include *Aeshna mixta, Anax ephippiger, A. parthenope, Libellula quadrimaculata, Pantala hymenaea, Rhionaeschna bonariensis, Tramea lacerata*, and several species of *Sympetrum*, among others (Corbet 1999).

Long-distance migrants are likely to face some challenges that are absent or much less acute for insects that disperse short distances. One of these may be the necessity for navigation over hundreds of kilometers—the mere fact that it is far away makes a remote habitat patch harder to find than a comparable nearby patch. Presumably these and other long-distance migrants recognize suitable habitat using cues similar to those already described after arrival in the appropriate region, although it is not always clear how they recognize the latter. In the case of *Anax junius*, and probably some other migrants, migrating adults may mate and oviposit several times before reaching their final destination (May and Matthews 2008; May 2013).

Monarch butterflies have been studied extensively and have a complex, multifaceted navigation system (Reppert et al. 2016; Shlizerman et al. 2016) that allows individuals from all over the eastern USA to find a few patches of forest in a limited area in the mountains of Mexico. Comparable information is not available for any aquatic insect. On the other hand, most migrants are much less constrained than Monarchs as to their destination. May and Matthews (2008) suggested that *A. junius* might find suitable habitats, because the latter are quite widespread, simply by orienting very generally southward and avoiding dangerous areas such as open sea. It seems unlikely that *Anax* navigation is quite that simple, since they do preferentially fly when tailwinds are available (Wikelski et al. 2006) and may follow landmarks such as roadways (pers. obs. 1992). Other migrants have also been observed flying along river courses (Dumont and Hinnekint 1973) and probably dry wadis in the northern Sahara (Dumont and Desmet 1990).

In the case of ITCZ migrants or others that rely mostly on flying downwind to more favorable regions, usually where sustained rainy periods are starting, navigation problems are considerably less, since they need, for the most part, simply to maintain a flight heading that takes best advantage of the wind. Recognition of suitable habitat may also be simplified, because the downwind flight automatically brings them to areas where suitable pools are available, although they must still, of course, recognize specific sites for reproduction. Also, most, and probably all, animals that migrate by flight depend to a significant degree on wind to assist and guide their flight. For example, visible migration of *Anax junius* usually takes advantage of northerly winds associated with cold fronts that appear to stimulate flight and typically also strongly influence its direction (e.g., Russell et al. 1998; Wikelski et al. 2006). During fall migration, dragonflies, like many birds, take advantage of updrafts over mountain ridges to reduce flight cost and gain altitude.

The stimuli that prompt Odonata to begin or end migration are not well known but are more likely to be related primarily to seasonal changes and weather than immediate responses to predation, competition, or food supply because predation probably is often more intense during migration than during other periods (Nicoletti 1997), and long-distance migration is generally initiated before food availability deteriorates. Some other migrants such as *Oncopeltus* may respond to restriction of their food supply (Dingle 1968). Among so-called obligate migrants (Corbet 1999, pp. 408–418), migration may be initiated endogenously shortly after the teneral period (i.e., as soon as the cuticle has become sufficiently hardened); this appears to be the case in many Odonata, in which dispersal begins shortly after adult emergence with the so-called maiden flight (Corbet 1957). Alternatively, in ITCZ migrants it could be triggered by the onset or the cessation of rains or in response to habitat drying. In North America southward migration often is associated with cold fronts (Russell et al. 1998; Wikelski et al. 2006). As suggested above for *A. junius*, photoperiod might trigger developmental processes that determine whether eclosing individuals are prone to migrate or not. In principle, photoperiod might directly inhibit or stimulate migratory behavior, as it does in birds (Dingle 1996, 2014). In addition, conditions that prompt shorter dispersal episodes, described above (e.g., drying of natal ponds, crowding, high or low temperature, food supply, or availability of local oviposition sites), may stimulate or modulate long-distance migration in some species (Johnson 1969, pp. 203–239). Regardless of the specifics, it is likely that bouts of migration alternate with intervals of maintenance behavior such as feeding, probably at least in part because of reciprocal inhibition of flight and maintenance; for example, at the beginning of migratory flight, stimuli that would ordinarily elicit feeding are inhibited, but as flight is prolonged, feeding stimuli become more salient and eventually inhibit flight, and vice versa. This general pattern was first described by Kennedy (1961, 1985) in "migrating" aphids, but it appears to apply to many migratory organisms (e.g., Wikelski et al. 2006). The separation of migration and maintenance activity is not absolute, however, as I have watched migrating dragonflies divert from their flight path to grasp prey, albeit much less frequently than during nonmigratory feeding aggregations (Russell et al. 1998).

3.7 Population, Community, and Ecosystem Consequences

3.7.1 Metapopulations

We often think of populations and communities as existing as isolated and self-contained entities (Forbes 1887). Many organisms, however, exist not in isolated populations but rather in groups of subpopulations, each within a restricted area (a "patch"), so that population dynamics of these subpopulations may strongly influence one another. They may, e.g., experience fairly frequent stochastic extinctions within a patch but with the possibility of "rescue" by dispersal from other nearby patches. This led Levins (1969) to propose the concept of a metapopulation, i.e., a group of these interacting populations, and to analyze how their dynamics might differ from those of larger but more remote populations. These ideas have been tested, modified, and expanded by a number of authors (e.g., Hanski 1998; Bohonak and Jenkins 2003), for instance by explicitly incorporating variation in patch characteristics and isolation; by allowing for priority effects, including local adaptation, that may give initial colonizers an advantage in exploiting the patch; or by considering assemblages of species within patches (a metacommunity; Wilson 1992; Hanski 1998). These metapopulation models seem particularly appropriate for understanding the dynamics of small ponds scattered through a landscape, isolated from one another by variable stretches of terrestrial habitat. The general concept has also been modified (Hanski 2001) to include circumstances similar to those envisaged by MacArthur and Wilson (1967), with a single large and relatively stable population, e.g., in a lake, with a number of smaller ponds nearby containing populations that might show local adaptation or even become extinct but could be rescued by dispersal from the lake; the large, stable population would presumably be little changed. Metapopulation analyses have also been extended to include population along different reaches in a single stream catchment (Fagan 2002; Downes and Reich 2008). There is general agreement that the model is applicable to many organisms and that interchange among subpopulations can stabilize the wider population of a species, depending on the size, number, and connectivity (i.e., the ease of moving among subpopulations).

A number of studies described above, including most mesocosm experiments in which initial conditions are very similar among widely separated patches, probably fit the assumptions of metapopulation models reasonably well, although few, if any, have continued long enough to observe extinction and rescue. Nevertheless, they do illustrate that dispersal ability can have an important influence on population and community dynamics. For example, McCauley (2006) showed that dispersal was probably the primary determinant of species richness of Odonata larvae in tanks placed at varying differences from source populations of adult odonates, and in fact the more distant tanks contained, for the most part, a nested subset of the species found in the closer tanks. Most of the experiments of Resetarits and colleagues, cited above (pp. 11–13), directly show the effects of dispersal and colonization but not subsequent population and community development, because colonizing insects were completely removed each week. Recruitment varied among treatments, often among taxa, over time, and in response to conditions in neighboring patches, e.g., presence of predators. All these effects were dependent on dispersal followed by acceptance or rejection of patches at close range and made large differences in the sizes of populations and community composition. A frequent assumption in modeling dispersal in metacommunities is either that (1) dispersal is random and selection of dispersing organisms occurs after entering a habitat patch, e.g., by competition or predation, or (2) populations are philopatric, i.e., they rarely disperse from their natal patch (McPeek 1989). Resetarits et al. (2005) argued that nonrandom dispersal and subsequent individual habitat selection (IHS) based on perceived patch quality are likely to be frequent, and they showed experimentally that this, rather than random dispersal or philopatry, is the rule among water beetles (Binckley and Resetarits 2005; Resetarits and Binckley 2013). In turn, habitat selection makes possible the phenomena of compression and contagion, discussed above. These authors argue that IHS is likely to provide a better description than truly random dispersal of population changes and species assembly for many active dispersers. Philopatry may be common principally among species inhabiting extremely stable habitats, perhaps including large, deep lakes, or organisms that cannot detect potential predators in a new habitat, as may be the case for many adult Odonata in habitats with larval predators (McPeek 1989; pers. obs.).

3.7.2 Dispersal and Genetic Change

Dispersal may also influence species characteristics or speciation since it strongly affects the extent of genetic interchange among (sub)populations. In general it is assumed that greater dispersal results in more gene exchange and thus increases the genetic similarity among populations and reduces the opportunity for speciation. Bohonak (1999) found a general, albeit weak, tendency for this to be true in a wide variety of animals. It is particularly evident in very mobile and widespread taxa like the dragonflies, *Anax junius* (Matthews 2007a) and *Pantala flavescens*, which Troast et al. (2016) suggested may be panmictic throughout its nearly global range (but see Pfeiler and Markow 2017). Several possible mechanisms, however, could alter this outcome. Rapid population growth and local adaptation (De Meester et al. 2002) or low dispersal rates (Bohonak and Jenkins 2003) might make it difficult for genes from individuals dispersing from outside to invade an existing population, thus increasing the likelihood of divergence of populations, and possibly speciation. On the other hand, if dispersal leads to a suitable patch with few or no conspecifics or allows the disperser to successfully establish itself in an occupied patch, new alleles will be introduced that may, if they spread initially, result in an altered genetic landscape within that patch. Finally, if dispersal propensity is contingent on properties of dispersing individuals (e.g., body size) or of their natal patch (e.g., crowding), the chances are increased of the same contingent behavior being spread (Arendt 2015).

3.7.3 Dispersal and Community Dynamics

Dispersal might be important in determining community composition and dynamics even in the absence of niche-based interactions such as competition or predation. Hubbell (2001) introduced the so-called neutral theory of biodiversity, which suggests that similar organisms' coexistence does not depend on differences in niche, but rather that they enter a community via dispersal until resource availability is limiting and then are extirpated or fail to invade purely by chance. In such a case, the existing assemblage of species depends largely on their probability of immigrating into the community. A likely example applying to aquatic insects is a study by Siepielski et al. (2010), who investigated *Enallagma* damselfly larvae that coexist with fish. These clearly occupy a different niche than their congeners that cannot coexist with fish, as well as non-congeneric Odonata, but among themselves they are ecologically extremely similar. Siepielski et al. compared growth and mortality of seven species of *Enallagma* larvae, with special emphasis on two species, across a range of primary production, macrophyte abundance and diversity (as refugia for the larvae), and abundance and diversity of potential predators. They found that the species appeared to be ecologically equivalent, i.e., to share a single niche. This led to the conclusion that coexistence of these species depended on stochastic immigration and local extinction. It should be borne in mind, however, that dispersal is assumed to be stochastic here, but this is rarely known to be the case. Other studies have suggested that adaptations to particular aquatic niches are, in some habitats, the principal determinants of insect distribution (e.g., Heino and Mykrä 2008).

Immigration may increase intraspecific competition for resources and for mates (if the sex ratio of the newcomers is not 1:1), while emigration could have the reverse effects, and might also ameliorate the effects of kin selection, if this exists. Profound effects on other organisms occupying the patch could occur. In fish-free bodies of water, the top predators are often dragonfly or dytiscid and hydrophilid larvae. If large numbers of these insects invade a habitat where none or only a few lived before, it is conceivable that they could seriously compete with native species or decimate their prey, with effects throughout the food web. This has never been investigated, but would surely be worth examining. Conversely, if their progeny later leave the habitat, as probably occurs in long-distance migrants, a substantial relaxation of competition or predator pressure, or a reduction of food resources, might occur. The potential for nutrient and energy transfer by migrating insects in general is quite large. Hu et al. (2016) estimated that the nocturnal fall migration of insect over England transports as much as 5.78×10^{12} Joules of energy, 100,000 kg of nitrogen, and 10,000 kg of phosphorus annually. Over the long term quantities transferred southward are very close to those transferred northward in spring, but in some years amounts are markedly unbalanced, resulting in substantial net movement of nutrients and energy in one direction or the other.

3.7.4 Dispersal and Nutrient Subsidies

Although little is known about the effects of mass long-distance migration of aquatic insects on the ecosystems they enter or leave, the effects of nutrient and energy flux from aquatic to terrestrial habitats have been studied rather extensively on a smaller scale and can be impressive (reviewed by Polis et al. 1997; also more briefly by Schindler and Smits 2016). It must be said at the outset that energy and nutrient subsidies are nearly always greater from terrestrial to aquatic systems than vice versa, simply because of gravity—mineral nutrients either in solution or as suspended material, and carbon and energy from detritus and dissolved organic solids, are all brought in by runoff from the surrounding land. In many headwater streams energy from this source substantially outstrips in-stream primary production (Fisher and Likens 1973). Nevertheless, the energy and nutrients from the bodies of dispersing insects can provide a substantial subsidy downstream or to nearby terrestrial habitats. Among the more impressive reported instances are at Lake Mỳvatn (Lake of Midges) in Iceland, where huge numbers of midges emerge in summer. Dreyer et al. (2015) estimated that some 290 kg ha^{-1} yr^{-1} of midges were deposited within 450 m of the lake edge (mostly within the nearest 100 m) during the most prolific of 4 years of study, although the amount was less than 10% of this during the least prolific year. This was equivalent to about 10 kg N ha^{-1} yr^{-1} and 1 kg P ha^{-1} yr^{-1} during the best year. Thus the nutrient subsidy was very significant, at least during good midge years.

Jackson and Fisher (1986) measured production of aquatic insects in Sycamore Creek, Arizona, during April to November, spread over part of two calendar years. In-stream secondary productivity was about 1200 kg ha^{-1} yr^{-1} and biomass of emerged insects was 230 kg ha^{-1} yr^{-1}, i.e., similar to the Lake Mỳvatn values, although in a starkly different habitat. Both of these results are unusually high for productivity of aquatic insects, but they illustrate the potential for nutrient transfer as a result of dispersal away from the immediate site of emergence. Paetzold et al. (2006) artificially subsidized small plots along a stream with about 75 mg day^{-1} of dried aquatic insects, i.e., approximately 3 kg N ha^{-1} yr^{-1}, assuming that the insects were ca. 10% N (Fagan et al. 2002), and recorded slightly more than twice the abundance of aquatic arthropods in the enriched plots as in control plots. Thus the natural subsidies at Lake Mỳvatn and Sycamore Creek cold have quite a significant effect on the later abundance of aquatic insects.

Export of insect biomass from aquatic habitats may also have marked effects on predators of flying adults of aquatic insects. For example, Fukui et al. (2006) used netting to prevent emergence of insects along a 1.2 km reach of a forest stream in Japan and measured bat foraging activity along that reach and an undisturbed adjacent control reach. They found that bat activity was dramatically reduced along the experimental reach compared to the control reach in May and June; thereafter, the abundance of aquatic adults decreased in both reaches while flying terrestrial insects increased throughout, and bat foraging increased, apparently because bats then depended on terrestrial prey.

3.7.5 Dispersal and Climate Warming

As the most recent report of the IPCC (2018) makes clear, climate warming is proceeding rapidly and is likely to continue for some time even under the most optimistic scenarios. These changes already are affecting aquatic insects. For many this means that to avoid extinction, they must quickly evolve resistance to the rapidly changing conditions or be able to disperse to more a favorable climate; in other cases, northward expansion may enable species to exploit otherwise suitable habitats from which they had been excluded by low temperature. Indications that this has happened during and since postglacial warming (Grewe et al. 2013) and probably still is occurring (Hof et al. 2012) have already been cited. Additional studies, especially in the UK, suggest that the pace of northward expansion has accelerated in recent decades. Hickling et al. (2006) showed that the northern limit of the ranges of both aquatic bugs and Odonata on average moved northwards about 75 km from 1970 to 2000 and 1960 to 1996, respectively. Hassall and Thompson (2008), in a general review of effects of climate change in UK Odonata, reported that emergence periods have shifted to earlier dates in many species, an ability that might improve their success if moving north but is complicated by its interaction with photoperiod as well as temperature. Considerable anecdotal evidence suggests that some tropical and subtropical odonate species have expanded their ranges northward (e.g., Paulson 2011), although this has not yet been supported by formal studies. Odonata are, among aquatic taxa, among the best adapted for dispersal, but they are also relatively easily detected and identified. It is likely that members of other orders have also moved northward.

Hering et al. (2009) estimated the sensitivity of European Trichoptera to climate change, based on current habitat requirements. Perhaps counterintuitively, they predicted that southern taxa would probably be more vulnerable to adverse effects of warming. Southern species lived in more restricted habitats and had smaller ranges, probably because they occupied areas south of the limit of Pleistocene glaciation and had been present in their current ranges for longer and become more specialized. These authors also, as expected (e.g., Laurance et al. 2011), found that high-altitude species are at rather high risk. Similarly, De Knijf et al. (2011) estimated that the range of two boreo-alpine *Somatochlora* dragonflies in the mountains of

Romania were predicted to be forced upward by at least 200 m and thus to lose ca. 40% of their current range by a temperature increase of 1.5 C. *Epiophlebia laidlawi*, a relict odonate from the Himalayas, is predicted to lose around 60% of its current potential range by 2050 under even a moderate warming regime (Shah et al. 2012).

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Chapter 4
Effects of Abiotic Factors and Ecogeographic Patterns on the Ecology, Distribution, and Behavior of Aquatic Insects

Vinicius Marques Lopez, Aurélio Fajar Tonetto, Ricardo Cardoso Leite, and Rhainer Guillermo

Abstract Aquatic insects are inserted in a physical and chemical world with a wide range of challenges that selected a myriad of adaptations and strategies throughout their evolutionary history. Mayflies, stoneflies, dragonflies, and many other insects inhabit both still and running waters, freshwater, and brackish waters; hence, they must deal with temperature regimes, variations on habitat complexity, and water chemical composition on a daily basis. All these environmental features determine not only how aquatic insects behave and occupy microhabitats in a stream or pond, but also define species distribution at macroscale. Here, in this chapter we attempt to show how this fascinating water world influences the lives of aquatic insects and their distribution across space.

Keywords Environment · Habitat · Microhabitat · Heterogeneity · Complexity · Hydraulics · Temperature

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4.1 Introduction

Freshwater environments are highly heterogeneous and widely distributed across the land. Water bodies are characterized by not only extremely variable chemical composition, but also physical components. For instance, rocks, sand grains, plants, and other types of substrates altogether make part of the physical environment that insects must interact with in freshwater systems. Hydrodynamics, habitat complexity, and visual background are then strong forces that aquatic insects are well adapted to. Here, we attempt to show how abiotic factors may play a remarkable role on the ecology, behavior, and distribution of aquatic insects. First, we present a brief revision of ecogeographic patterns that encompass a variety of climatic variables to predict species occurrence and distribution at macroscales. Further, we explore how water temperature, chemical composition, altitude, hydrodynamics, and other factors affect behavioral and physiological adaptations of aquatic insects at meso and microscales. To better illustrate the role of such abiotic factors, we present a selection of examples that we hope to instigate interest in this fascinating aquatic world of insects.

4.1.1 Ecogeographic Patterns and World Climate

Over the last few centuries, one of the major goals in biological sciences is to understand macroecological patterns. In this sense, scientists established ecogeographic rules, which attempt to link phenotypic variations in populations/communities to climatic and biogeographic gradients. For example, several factors can drive the variations in body coloration exhibited by taxa of the same clade such as temperature, humidity, latitude, and altitude (Chown and Gaston 2010; Cooper 2010; Shelomi 2012; Zeuss et al. 2014). Body size and coloration are usually specific traits that influence aquatic insects' behavior and ecology, predicting sexual selection, predation regimes, and population dynamics. Therefore, ecogeographic rules are crucial for the comprehension of how climatic and geographical features influence aquatic insects' ecology and behavior, habitat occupancy, niches, and species distribution.

There are many ecogeographic rules (Gaston et al. 2008), however, here we propose a brief review regarding aquatic insects. It is important that readers know that biological rules do not apply to all groups of organisms. Biological rules have been proposed by noted biologists such as Lamarck, Humboldt, Darwin and Haeckel, and they must consider the probabilistic factor of the question addressed. This exemplifies the difficulty of creating universal laws in the biological sciences, because of the probabilistic and causal characteristic of biological phenomena, being one of the primordial differences of Biology in relation to Exact Sciences (Mayr 1996).

4.1.1.1 Thermal Melanism Hypothesis

The thermal melanism hypothesis (TMH) usually applies to ectothermic animals and predicts that individuals with darker coat or tegument are more effective in converting solar radiation to heat (Watt 1968). Thus, darker animals would have greater thermoregulatory advantages in cold environments, because they may become active before lighter morphotypes. For example, in some groups of European dragonflies, the predominant selective pressure for the evolution of body coloration is thermoregulation (Fig. 4.1, Zeuss et al. 2014).

Comparing the North American dragonfly assemblies with the European ones, Pinkert et al. (2017) have reported that darker colorations occur in dragonflies from regions with cold climates, and species with brighter body coloration are more common in regions with warmer climates. These studies corroborate others that show the relationship between coloration and distribution in odonates on all continents (see Hassall and Thompson 2008). Although data suggest a general pattern, supporting the TMH as a central predictor of coloration, idiosyncratic features in the

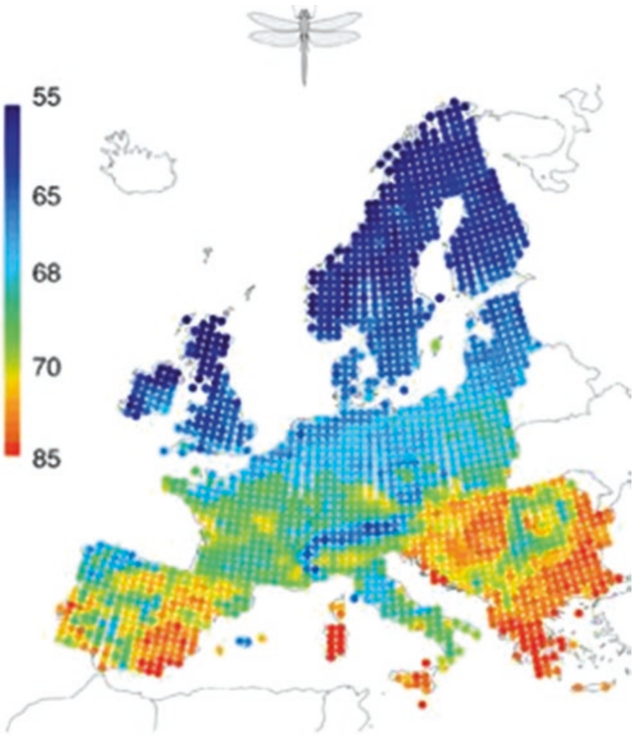

Fig. 4.1 Average color values across species on a scale from 0 (black) to 255 (white). Red indicates light-colored Odonata assemblages and blue indicates dark-colored assemblages ($n = 1845$). There is a decrease from assemblages dominated by light-colored species in the south to assemblages dominated by dark-colored species in the north. Adapted from Zeuss et al. (2014)

evolutionary history of taxonomic clades, such as sexual selection, resistance to diseases, or even pleiotropic genes, may be the main drivers for these phenotypes (Roulin 2016). Studies on TMH could have implications for predicting the effects of climatic change and can assist in species conservation, since environmental changes can alter species distribution and assembly structure (Deutsch et al. 2008; Dillon et al. 2010; Pateman et al. 2012; Zeuss et al. 2014).

4.1.1.2 Bergmann's Rule and the Temperature–Size Rule

Bergmann (1847) described a relationship between latitude and body size and proposed an intraspecific phenomenon where larger endothermic species can be found at higher latitudes (Bergmann 1847; Mayr 1956). However, some changes have been proposed to describe the observed patterns (mainly in ectotherms). For example, there is a strong positive correlation between latitude and body size in the damselfly *Erythromma viridulum* Charpentier (Odonata: Coenagrionidae), which is consistent with Bergmann's rule (Hassall et al. 2014).

Body size is a very important feature indeed, influencing a wide variety of important parameters to organisms (Roff et al. 2006; De Biee et al. 2012). Although this characteristic can be influenced by a variety of factors (e.g., genetic and environmental; see also Shelomi 2012), there may be a significant relationship between temperature and body size in aquatic arthropods—the "temperature–size rule" (TSR) (Horne et al. 2015). The TSR proposes that individuals that developed at colder temperatures exhibit larger body sizes than individuals that developed at warmer temperatures (Atkinson 1994). The TSR is diffused among ectotherms (Horne et al. 2015) and is often confused with Bergmann's rule, because there is a strong correlation between latitude and temperature.

The aquatic taxa may have a stronger negative TS response than terrestrial taxa, and they follow the "size-temperature" rule in over 90% of cases. In Diptera, species with aquatic larval phases had a TS negative response more expressive than other taxa. In *Calopteryx maculata* (Palisot de Beauvois) (Odonata: Calopterygidae), the TSR also explains body size range in part of the species distribution (Hassall 2013). Forster et al. (2012), in a meta-analysis, proposed that oxygen supply plays a central role in explaining the "size-temperature" responses in ectotherms, with the response of aquatic organisms being ten times higher than terrestrial organisms. Hence, oxygen gradients in space are probably one of the main factors of response to TSR in aquatic insects (Forster et al. 2012).

4.1.1.3 Other Possibilities

Some other hypotheses are proposed to explain the distribution of aquatic insect species. For instance, eco-morphology (Wainwright and Reilly 1994) may explain the distribution of an endemic fauna of New Zealand stoneflies (106 species/21 genera). They are distributed over a wide altitudinal gradient (0–2000 m), with a great variety of phenotypes, such as the reduced-wing (26 spp.) and the winged (80 spp.) forms. In this group, there is a significant correlation between altitude and body size for brachypterous taxa, but the same correlation could not be found for winged taxa (McCulloch and Waters 2018). These results suggest that morphology and altitude may interfere in the predictions made by ecogeographic rules, since the maintenance of traits related to flight represents an evolutionary constraint on body size (McCulloch and Waters 2018).

Finally, the ecophysiological hypothesis (EH) may also explain the distribution of aquatic insects at local and regional scales (De Marco Júnior et al. 2015). The EH suggests that the organization of the metacommunities of dragonflies and damselflies of small-to-medium tropical streams is related to the degree of sunlight availability, thermoregulatory characteristics, and body size of each species. In other words, environmental filters (e.g., narrow streams) can differentially select certain odonate taxonomic groups (Zygoptera and Anisoptera). For example, anisopteran abundance and species richness may increase with channel width, while zygopteran abundance usually decreases (De Marco Júnior et al. 2015). This effect is theoretically based on the thermoregulatory strategies of each taxon. Ectothermic species are expected to exhibit heliothermic behavior and perch on sunny spots to achieve optimal body temperature, while endothermic species adopt a “flier” strategy and keep constant flight activity (De Marco Júnior et al. 2015).

4.1.2 Temperature

Temperature regimes may determine aquatic insect distribution at macroscale, but it also varies spatially according to position in water bodies, mostly regarding depth and distance to banks. Several studies have shown the importance of diel temperature regimes for aquatic insects. For instance, hyporheic waters provide more constant thermal conditions than surface waters. Such variation in water temperature is an abiotic factor that has a predominant effect, mainly, on aquatic eggs and larvae.

Water temperature plays a crucial role in larval development and growth. For example, 90% hatching success was recorded for *Lestagella penicillata* (Barnard) (Ephemeroptera: Teloganodidae) eggs in the 10, 15, and 20 °C (Ross-Gillespie et al. 2018). Larval development rates in odonates are progressively faster at higher temperatures (Lutz 1968; Mendonça et al. 2018). Adult mayflies of *Cloeon dipterum* (L) (Ephemeroptera: Baetidae) become smaller as temperature warms, because warming temperature causes development rates to increase proportionately faster than growth rate (Sweeney et al. 2018).

Aquatic insects may encounter a wide range of thermal conditions when moving in a water body, when facing seasonal changes and throughout a single day; hence, they must develop mechanisms to adapt to these fluctuations and to extreme climatic changes. As an example, a recently discovered stonefly species was found living under ice in Patagonia, Argentina (Pablo Pessacq personal communication). In winter, some aquatic insects (e.g., many chironomids) build cocoons to suspend metabolism and development (Lencioni et al. 2015). Some other aquatic insects have striking adaptations to cope with heat and cold. Temperature may impact oxygen concentration in plastrons and ultimately affect the metabolism and activity of aquatic insects (Jones et al. 2018). Diving beetles, for example, have hollow setae on the elytra that interconnect with the tracheal system. This way, beetles are able to extract oxygen directly from the water. In this case, hypoxia may reduce heat tolerance. Consequently, diving beetle species with higher densities of structures have high cold tolerance, but reduced heat tolerance (Verberk et al. 2018).

As other examples, caddisfly shredders' leaf-breakdown and survival rates are affected by warming temperature (Martins et al. 2017). Crawling water beetles (Coleoptera: Haliplidae) stay submerged for shorter durations in response to both increasing water temperature and decreasing dissolved oxygen (Banks et al. 2018). Temperature may also influence predator-prey dynamics. Temperature influenced larvae of *Anisops sardea* Herrich-Schäffer (Hemiptera: Notonectidae) in the predation of *Anopheles stephensi* Liston (Diptera: Culicidae), the most common malarial vector in Southeast Asia (Mondal et al. 2017). Through a laboratory bioassay, Mondal et al. (2017) suggest that the rate of prey consumption was positively related to the increase in temperature. Finally, the timing and duration of emergence in aquatic insects involve responses to temperature, often interacting with photoperiod (e.g., Norling 2018).

4.1.3 Light Environment and Turbidity

Solar irradiance may be a key factor determining habitat occupancy, thermoregulation, voltinism, and sexual behavior in some aquatic insects. Characteristics of the thermal environment, as discussed in this chapter, and selection of locations for behavioral displays and territory defense may present conflicting interests, generating trade-offs. For example, male calopterygid damselflies defend sunny spots along streams, which females visit to mate and oviposit. In this case, the light environment may increase recognition by potential mates and increase detection by predators (e.g., Endler 1991; Kemp et al. 2018). Understanding patterns of habitat/microhabitat use can provide good insights into their ecological drivers and, in this context, top predators such as dragonflies and damselflies are good tools for these studies.

Many studies report the importance of the thermal and light environments for Odonata, as aspects of microhabitat luminosity have been reported by researchers as factors predictive of species occurrence. In forestall environments, for example, light may become a limiting factor. Riparian shading has a crucial role in tropical and subtropical streams, refraining the explosive growths of aquatic and semiaquatic plants, and algae, while creating a high allochthonous influx of organic matter, mainly from decaying leaves. In the tropics, these habitats support diverse and well-adapted endemic aquatic insects. For instance, mayflies and other larvae seek shelter and hide under leaves, which also act as a foraging site (Fig. 4.2a), and there are some shade-seeking adult Odonata that prefer to inhabit dark habitats in forests

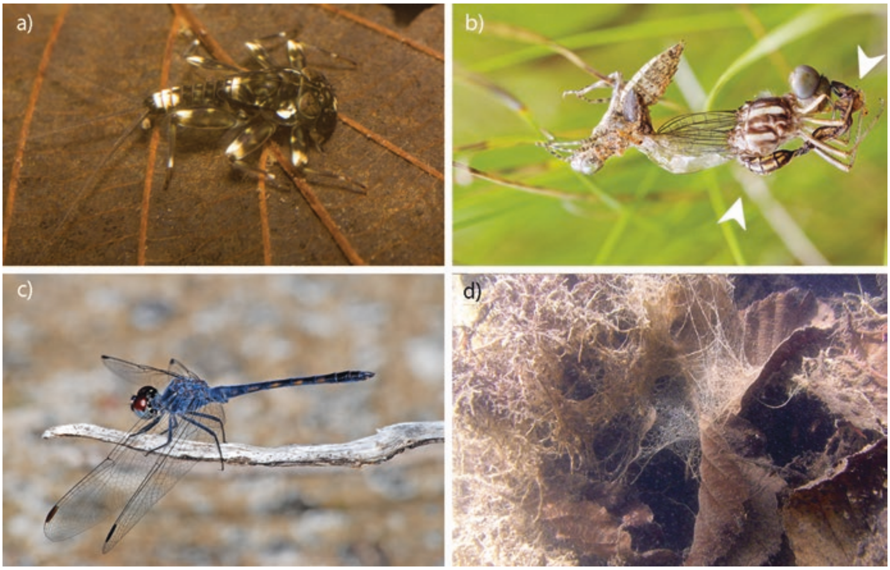

Fig. 4.2 Mayflies may hide under leaves, seeking shelter (**a**). The abiotic factors can affect the development and emergence of aquatic insects; for example, this unsuccessful emergence attempt by libellulid dragonfly in the Neotropical savannah, being eaten by ants (white arrowheads) (**b**). *Erythrodiplax berenice* (Drury) (Odonata: Libellulidae) is known to oviposit in brackish waters (**c**). Net-spinning caddisflies may act as environmental engineers and create complex habitats (**d**). Photos by Adolfo Cordero (**a**, **b**, **d**) and Dennis Paulson (**c**)

when adults (Henry et al. 2017) or larval forms that hide in darker substrates (Tavares et al. 2018), showing the importance of absence of light or dim light for some taxa.

Some other taxa exhibit positive phototropism. Stoneflies, caddisflies, aquatic Lepidoptera, Coleoptera, Hemiptera, and others exhibit this behavior that, in the natural environment, favors adults during mate searching. However, the same insects are attracted to artificial light and light traps. Consequently, the tendency of some aquatic insects to confuse certain colored or polarizing structures with the water surface is quite common. For instance, it is known that dragonflies find water bodies due to polarization of light. Many aquatic insects that are attracted to horizontally polarized light sources are also attracted to unpolarized UV blacklight (Nowinszky 2003). Cars, for example, are visual deceptions to aquatic insects, solely explained by the reflection–polarizational characteristics of the car paintwork (Kriska et al. 2006). In this context, light act as an evolutionary and sensorial trap. This can cause high mortality rates and select insects that are not attracted to light, affecting normal sexual behavior.

Finally, photoperiod has a remarkable effect on larval development and adult behavior. For instance, odonate larvae may exhibit synchronous development that depends on photoperiod (Norling 2018). In mayflies, photoperiod may affect size at emergence and survival (Corkum and Hanes 1992). Turbidity, which relates to the aquatic light environment, is also an important regulatory factor for aquatic insects. Particularly, turbidity may be one major factor determining the occurrence of dragonflies in water bodies (Klein et al. 2018). Nevertheless, turbidity may be related to water flow, suspended sediment, and temperature, which might be more important for aquatic larvae than the light environment. For example, turbidity due to suspended sediments may affect leaf shredding by caddisflies, and hence suppress processing of organic matter (Hornig and Brusven 1986).

4.1.4 Water Chemical Composition

Water is an effective medium of dissolved chemicals and thus generates many different gradients in freshwater habitats, e.g., pH, dissolved oxygen, and particles from headwaters to river mouths, or salinity degrees from freshwater to marine. The chemical composition of water bodies is another environmental trait that predicts the occurrence and behavior of aquatic insects. Salt, ion concentration, and conductivity may have an impact on osmotic regulation and select for species that tolerate certain ranges of water chemical composition.

Several chemical components and abiotic factors are widely recognized by their influence on the composition of aquatic insect communities. Even small variations in these environmental characteristics can exert direct changes in microhabitat conditions and, consequently, influence habitat occupancy and colonization. For instance, abiotic factors such as pH, electrical conductivity, dissolved oxygen, total dissolved solids, and oxidation reduction potential influence richness, abundance, and composition of Odonata species (see Table 4.1, Mendes et al. 2018). All these features of water composition may affect larval development and growth, for example, resulting in death during emergence (Fig. 4.2b).

In this context, salinization of water bodies is currently one of the problems that deeply concerns scientists (Cañedo-Argüelles et al. 2013; Kefford et al. 2016). Salinization has been reported in all inhabited continents and is mainly associated with human activities. In the short term, the results of this imbalance may be a reduction in the number of species and changes in community composition and ecosystem processes (see Kefford et al. 2016 for review). In a climate change scenario and growing demand for water, studies on behavioral adaptations and on how aquatic insects respond to changing conductivity regimes may help to elucidate the real impact of this phenomenon worldwide.

In fact, salinity is important for metabolic functions, and may even increase the richness of tolerant insect species (Kefford et al. 2011; Kefford et al. 2016). However, the richness of groups such as Trichoptera, Ephemeroptera, and Plecoptera diminishes with increased salinity (Kefford et al. 2011). Other taxa exhibit variable sensitivities, such as Diptera, Odonata, Coleoptera, and Hemiptera (Kay et al. 2001; Kefford et al. 2012; Cañedo-Argüelles et al. 2013). Nevertheless, in naturally saline streams, Diptera, Heteroptera, and Coleoptera seem to be the most diverse groups (Millán et al. 2011).

Table 4.1 Table illustrating the relationship between assemblages of Odonata, Anisoptera, and Zygoptera and abiotic factors. Results from Mendes et al. (2018) through the MDRM and PCA analyses

Assemblage	Variable	Df	Sum of squares	Mean squares	F model	R^2	Pr ($>F$)
Odonata	pH	1	0.378	0.378	1.183	0.032	0.265
	DO	1	0.349	0.349	1.091	0.030	0.339
	HII	1	0.558	0.558	1.746	0.047	0.058
	ORP	1	0.574	0.574	1.795	0.049	0.049[a]
	Residuals	31	9.905	0.320	–	0.842	–
	Total	35	11.763	–	–	1.000	–
Zygoptera	pH	1	0.160	0.160	15	0.014	0.852
	DO	1	0.466	0.465	–	0.039	0.209
	HII	1	0.506	0.506	–	0.043	0.165
	ORP	1	0.331	0.331	–	0.028	0.444
	Residuals	31	10.323	0.333	2	0.876	–
	Total	35	11.786	–	2	1.000	–
Anisoptera	pH	1	0.008	0.008	20.902	0.054	<0.01[a]
	DO	1	0.120	0.120	303.442	0.777	<0.01[b]
	HII	1	0.012	0.012	29.178	0.075	<0.01[a]
	ORP	1	0.002	0.002	5.890	0.015	0.01[a]
	Residuals	31	0.012	0.000	–	0.079	–
	Total	35	0.155	–	–	1.000	–

Abbreviations: *DO* dissolved oxygen, *ORP* oxidation reduction potential, *HII* habitat integrity index

[a] The test was significant ($p < 0.05$), but with a very low power of explanation

[b] The test was significant ($p < 0.05$), with a high power of explanation ($R^2 = 0.777$). Adapted from Mendes et al. 2018

It is axiomatic that insects are the most dominant group of invertebrates in lotic habitats, but the evolutionary history of each group may limit their adaptive capacity to environmental changes, such as increased salinity. Several taxa inhabit saline or marine habitats. For example, marine thysanurans comprise an abundant group in the ocean shore; some caddisflies tolerate high salt concentrations, such as *Philanisus plebeius* Walker (Trichoptera: Chathamiidae), a sea algae eater that builds its case with silk and sand grains (Leader and Bedford 1979); *Halobates* (Hemiptera: Gerridae) are wingless hemipterans that skim the water surface of the sea (Cheng 1985); *Erythrodiplax berenice* (Drury) (Odonata: Libellulidae) oviposits on the sea shore and marshes and larvae are adapted to a wide range of salinity (Fig. 4.2c, Dunson 1980); *Hexagenia limbata* (Serville) (Ephemeroptera: Ephemeridae) nymphs can survive elevated salinity (Chadwick and Feminella 2001). Adaptations include, for example, folding of osmoregulatory cell membranes in the tracheal gills of stonefly nymphs (Kapoor 1978).

The diversity of Ephemeroptera is also negatively affected by pH (Sutcliffe and Carrick 1973; O'Halloran et al. 2008). Despite apparently unfavorable conditions, some specialists do thrive in acidic waters (e.g., a few Odonata, Juen and De Marco

Jr 2011). Furthermore, aquatic insect biology is influenced by other factors such as organic matter input (in autochthonous and allochthonous environments); concentration of phosphorus, nitrogen, and carbon; and dissolved oxygen and conductivity, which may constrain development and growth (e.g., Johnson et al. 2015).

4.1.5 Habitat Complexity

Environments are heterogeneous and vary in complexity and visual and structural characteristics of the habitat that affect biological and behavioral aspects of organisms and interfere with predator-prey dynamics (Xiao et al. 2016). Complex habitats may provide shelter and conditions for camouflage, making it difficult to locate prey (Merilaita 2003) and reduce the risk of predation. However, structural complexity also provides structures such as perches and shelters that increase predation rates of sit-and-wait predators, such as odonate larvae (Klecka and Boukal 2014). Some aquatic insects, such as web-spinning caddisflies, act as ecosystem engineers, creating a complex habitat for themselves and other organisms (Fig. 4.2d). Background visual complexity can determine the distribution of predators and prey; for example, larvae of *Acanthagrion lancea* Selys (Odonata: Coenagrionidae) have preference for more complex backgrounds (Tavares et al. 2018).

4.1.6 Hydraulics and Substrate Roughness

Hydraulics and hydrodynamics influence the spatial and temporal distribution of insects in stream habitats, where features of flow physically constrain habitat occupancy by benthic organisms. Hence, insects must deal with substrate heterogeneity to achieve the best suitable places for growth and development. All these features, mostly related to unidirectional flow, affect whole communities by displacing organisms, resources, and sediments. Indeed, the disturbance of water flow is a dominant organizing factor in stream ecology (Resh et al. 1988; Gordon et al. 2004). Water movement comprises a very complex system that combines fluid transportation from upstream to downstream (longitudinally), from bank to bank (laterally), and from bottom to surface (vertically), while the whole system varies temporally (Ward 1989).

These would be all the dimensions of water flux to be considered if streams ran in smooth and regular channels. However, real water bodies present substrate heterogeneity and variances in the channel topography. There are changes in depth and in water velocity in each narrowing or widening of a creek to adapt the flow to the streambed shape. As the water accelerates or decelerates by diverting from solid structures of the substrate, it creates the turbulent flow that is the remarkable characteristic of lotic systems. Given this physical complexity of the fluid medium, the hydraulic features are predictors for the aquatic assemblage's establishment (Brooks et al. 2005; Biggs et al. 2005; Graba et al. 2013) because successful attachment and colonization in this environment are determined by the relationship between water flow and substrate structure (Ditsche-Kuru et al. 2010; Ditsche et al. 2014; Biggs and Hickey 1994). To better understand how hydrodynamics mold the aquatic insects' world, it is important to look at different spatial scales.

Starting from the mesohabitats, which are represented by the riffles and pools, it is easy to recognize that a very-high-speed flow between two rocks represents a physical barrier to insects that live on each stone. Now, looking to the microscale level, it is possible for insects to survive in these environments positioning themselves in shelters. These small zones of slow water created by the interaction between the substrate roughness and the turbulent flow itself are the key factors to keep the diversity in fast waters. In fact, hydrodynamic laws state that the layer of water just above a rough substrate has a speed close to zero, and the water surface has the maximum speed. The rougher the substrate, the thicker is this slow water layer. Hence, the aquatic insects exhibit numerous types of behaviors regarding their feeding, dispersal, or reproduction modes (Merritt and Cummins 1996), as a way to deal with substrate heterogeneity and water flow to achieve the best suitable places for the best ecological fitness. These complex and dynamic variations of water flow influence larval behavior and, thus, drive the variation of community structure in freshwater habitats.

Historically, the literature focuses on physical factors to explain the variation of fauna distribution in a range of spatial scales. Variations in the macrohabitat level occur mainly due to hydrological and geomorphological factors (Sheldon and Walker 1998). In mesohabitats, the highlight goes for the longitudinal gradients in the water flow, particle size, and hydraulic variables (Growns and Davis 1994; Downes and Hindell 2000). In smaller scales, species microdistribution is correlated with hydrodynamics, depth, substrate features, or combinations of these elements (Davis and Barmuta 1989). Today, we have a better comprehension that all these scales are important for studies on aquatic insects; however, in a recent past, most studies addressed the effect of abiotic factors at macroscales only. A common point of view in the study of stream aquatic macroinvertebrates, illustrated by the review made by Cooper et al. (1998), considered that scales smaller than the section did not need to be considered for faunistic and ecological studies in different water bodies or different drainage basins because they have a low interference at the larger scales. While the scientific community was focused on the larger scales, significant variability was observed in the fauna of aquatic insects between stretches of streams of the same order, between sections of the same stretch, between riffles of the same section, and between groups of rocks of the same riffles (Downes et al. 1998).

Larger scales studies are important for obvious reasons that we showed previously in this chapter; nevertheless, we also highlight the importance of studying aquatic insect communities at smaller scales. In mesohabitat scale, the contrast between riffles and pools caught the attention of curious minds that asked how these organisms could handle with these two different worlds that coexist at such a small distance. Several studies have shown that insects exhibit a great variability in habitat occupancy regarding faster waters in riffles and sluggish flows in ponds (e.g., Roque and Trivinho-Strixino 2001; Crisci-Bispo et al. 2007). Indeed, there is a high number of species and even higher taxonomical categories recognized as riffle inhabitants, such as dipterans *Simulium incrustatum* Lutz (Diptera: Simuliidae), *Leptohyphes* spp. (Ephemeroptera: Leptohyphidae), *Parametriocnemus* sp. (Diptera: Chironomidae), *Lopescladius* sp. (Chironomidae), *Farrodes* spp. (Leptophlebiidae), *Rheotanytarsus* sp. (Chironomidae), diamphipnoid and eustheniid stoneflies, and polythorid and calopterygid damselflies.

Pools dominated by sand as the main substrate provide no shelter for predators and are mainly inhabited by small dipterans (e.g., Chironomidae) and larger insects that can burrow (e.g., some Gomphidae, Odonata). Furthermore, higher richness and abundance in riffles seem to be a general pattern in tropical streams (Logan and Brooker 1983; Brown and Brussock 1991; Baptista et al. 2001; Silveira et al. 2006), and the substrate composition is related to this. Riffles are typically composed by rocky streambed while pools exhibit leaves, sediment, and organic matter in addition to stones. These substrate features are often perceived as a major factor contributing to the distribution of many invertebrates (Merritt and Cummins 1996; Taniguchi and Tokeshi 2004).

Mesohabitat studies have improved our knowledge on stream ecology and suggest that some questions on insect distribution can be answered only at microscale level. The variation of substrate shape exerts a great influence on stream benthic communities. Different surface irregularities such as roughness, pits, crevices, and macrophytes have been considered determinant habitat components that may explain richness and abundance of freshwater invertebrates (Downes et al. 1995, 1998). In order to evaluate substrate heterogeneity that occurs in both mesoscale and microscale, the concept of microhabitat architecture can be very useful. This concept was approached unpretentiously in the work of Robson (1996), who suggested its use to avoid possible confusion in experimental descriptions, such as using the terms complexity and heterogeneity to characterize the substrate. According to the author, habitat architecture can be represented by different dimensions such as substrate type, texture, and peculiar characteristics such as cracks and presence of vegetation.

Here, we approach this concept to the niche theory (Hutchinson 1957), using the multiple dimensions that can be attributed to habitat architecture to characterize the conditions and resources available in each microhabitat. Considering the lotic environment and insect behavior and ecology, we can define three basic dimensions of microhabitat architecture: (a) instability of the environment—representing the hydraulic forces acting on individuals; (b) potential refugia—a three-dimensional composition of the substrate; and (c) food availability in the environment. To represent these dimensions and to work at microscale, we have a challenge: we must adopt metrics consistent with the microscale, and the collection of aquatic organisms must also be adjusted to the reality of the microhabitat.

Taniguchi and Tokeshi (2004) developed a creative and elegant method to assess substrate complexity. In terms of fractal geometry, they modelled the structural pattern of microhabitat architecture focusing on surface features. The authors found that the number of species and invertebrate density were scaled positively with complexity levels. For instance, more complex surfaces provide more refuge areas because the irregularities may change the flow pattern. Furthermore, insect body size tends to decrease in function of increasing complexity, since shelters tend to become smaller. In other words, the size of refuges matches the organism's size (Bergey 1999; Tokeshi 1994).

In a way, the use of fractal geometry allowed us to assess the complexity of the substrate, but other complex factors, such as microhabitat hydrodynamics and biodiversity itself, cannot be represented satisfactorily by simplified measures. In this regard, water flow in a streambed can be considered a complex variable. Heterogeneity of surface architectures can change flow profiles and associated drag forces, turbulence, gravity, and viscosity. Hence, one small patch may exhibit several different hydraulic conditions. Therefore, there are so many dimensions of water flow to describe the stream dwellers that there is a shortfall on measures that represent all water flow complexity. Nevertheless, there are a few classic measures that together help with the description of microhabitat architecture.

One of them is the Reynolds number: a dimensionless coefficient used to characterize different flow regimes over a specific surface and describe whether the mean flow is laminar or turbulent (Davis and Barmuta 1989). Brooks et al. (2005) found that Reynolds number explained more the spatial variation of richness and abundance of invertebrates than other hydraulic variables. They found that most species preferred the areas of riffles with the lowest turbulence close to the streambed, highlighting the microhabitat architecture importance. Probably, this condition provides a friendlier boundary layer (distance between free water flow and substratum surface), where metabolic requirements are more easily accomplished (e.g., acquisition of oxygen). Additionally, insects also seek a place to stay without constantly fighting the current; in fact, most riffle species live under the rocks most of the time and go to the upper part to feed. In this context, a flattened and streamline body seems to be typical for many insects. For instance, many mayflies and stoneflies have legs positioned laterally reducing drag and providing better attachment (Merritt and Cummins 1996).

As streams are highly heterogenous, it is highly expected to find a very complex gradient of hydraulic conditions even in a small scale. Insects deal with these hydraulic factors all the time to experience the best ecological fitness possible. However, all these conditions change through time (Gordon et al. 2004). Specially in tropical regions, it is possible to distinguish rainy and drought periods. Seasonal variation of flow affects invertebrates through hydrological alterations influencing dispersal, attachment, and resource acquisition, and also changing abiotic factors like temperature (increasing with low flow) and dissolved oxygen (reducing with low flow) (Sharpe and Downes 2006; Brooks and Haeusler 2016). Brooks and Haeusler (2016) suggested that during a low-flow period faster waters can act as a refuge habitat for filter feeders. Thus, during droughts these insects track local velocity conditions to obtain enough resources and resist extended low-flow periods. On the other hand, gill-respiring invertebrates (e.g., Ephemeroptera, Plecoptera, Zygoptera) seem to be less influenced by low flows since they can rhythmically beat their gills to control oxygen uptake.

However, the relationship between stream invertebrates and hydraulics is also species specific. There are many obligates, facultative, or flow avoiders among macroinvertebrates, and it seems to be related to functional groups. For example, filterers prefer more turbulence and shear velocities where they can constantly receive supplies from the rapid flow, while shredders occur on slower waters with lower shear velocities and Froude number (related to depth and gravitational forces) containing detrital material (Growns and Davis 1994). Moreover, the morphology of the insect gills seems to be associated to water velocity. Species with higher gill morphological complexity tend to be pond dwellers, while aquatic insects with simpler gill structures inhabit faster waters at microscale (Tonetto et al. 2018). Nevertheless, this relationship seems to vanish when water velocities are analyzed at mesoscale (Fig. 4.3). Thus, the attributes of a species are expected to respond consistently along specific environmental gradients (Brooks and Haeusler 2016), and it is reasonable to note that a combination of body plan, behavior to obtain resources, and hydraulic conditions strongly influence the spatial distribution of the species in stream habitats.

All these environmental features of water bodies can be condensed in the River Continuum Concept (RCC, Vannote et al. 1980). The RCC is a model that relates all the physical parameters described above, e.g., channel width, water depth, slope angle, flow velocity, and sediment load, to explain the variation of biological communities and their distribution along stream and river patches. For instance, headwaters and low-order streams have a large input of allochthonous plant material, which favors the occurrence of shredders, such as caddisflies. Middle patches of a stream have a larger concentration of autochthonous material and particulate matter that favors collectors and gazers, while further stream patches have more fine particulate matter that favors collector-filterers. Therefore, here we suggest that macroecological processes that are inherent to the RCC are also intrinsically related to meso and mesohabitat characteristics, in a wider scenario that predicts the behavioral (e.g., habitat selection, resource exploration), functional (e.g., shredders, grazers, collectors, filterers, and predators), and ecological (e.g., population dynamics and assemblage composition) traits of insect communities.

4.1.7 Drought

Temporary water bodies are home to many aquatic insects. These species tend to have fast development and explosive synchronic mating events. For instance, when water levels decline, caddisflies may use conspecific density as a cue to adjust behavior and development in the face of habitat drying. Since early drying is a constraint for population stability in temporary habitats (Lund et al. 2016), aquatic insects must be well adapted to hydric stress. The larvae of *Neohermes filicornis* (Banks) (Megaloptera: Corydalidae) actively burrow into the dry substrates after draught (Cover et al. 2015).

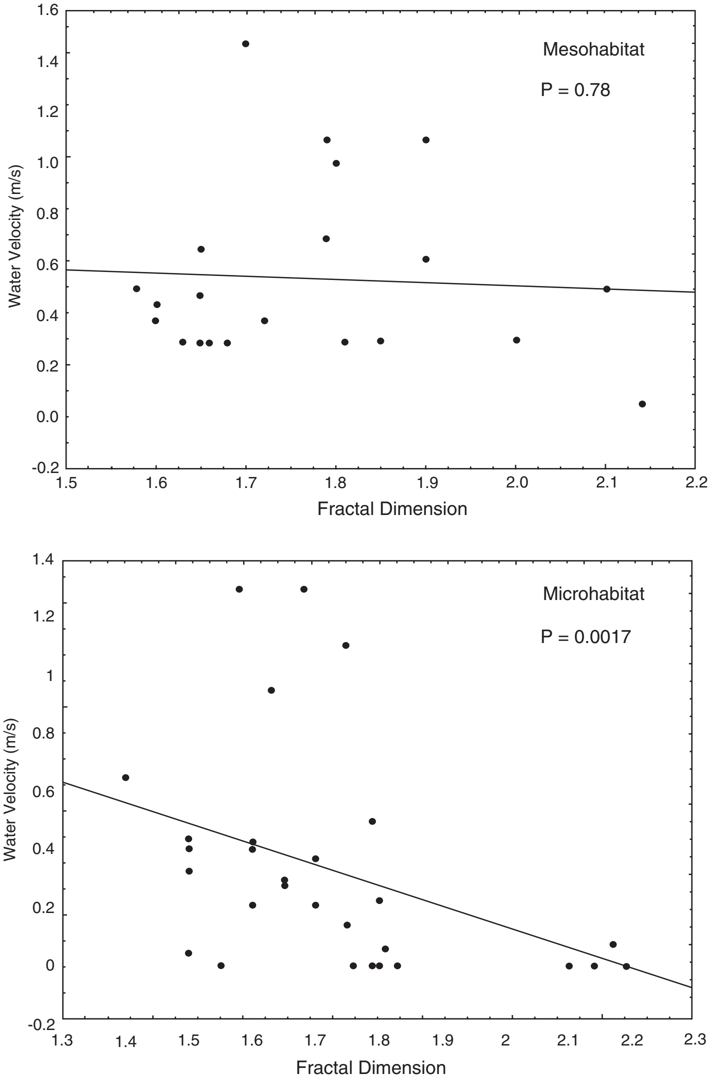

Fig. 4.3 The relationship between the fractal complexity of aquatic insect gills and water velocity at meso- and microscales (from Tonetto et al. 2018)

4.1.8 Altitude

As previously shown in this chapter, the aquatic insect community may be under selective pressures of temperature and hydraulics. In water bodies located at high altitudes, there is a great number of endemic lineages and species constrained by adaptations to alpine environments. Historically, the negative correlation between diversity along increasing altitudinal gradients is widely recognized (Vinson and

Hawkins 2003), mainly its influence on aquatic fauna (Godoy et al. 2017). However, no general rule was observed in aquatic insects. The richness differences along the altitudinal gradients appear to be singularities of the taxa. In other words, diversity is highest in higher latitudes for: Odonata; lower for Plecoptera-Ephemeroptera; and not significant for Simullidae and Trichoptera (Vinson and Hawkins 2003; McCreadie et al. 2018). The main constraints are lower temperature and higher slopes, besides the autochthonous food resources that form the basis for high-altitude trophic webs, while there is a shift towards allochthonous aquatic systems at lower elevations (Atkinson et al. 2018).

4.1.9 Concluding Remarks

Here, we have described and explored several ecogeographical rules and abiotic factors that interact to regulate ecological processes at macro-, meso-, and microscales. Understanding how such factors function to shape the diversity of aquatic insects and to determine their occurrence and distribution is crucial to conserve species and freshwater resources. Which ecogeographical model is most appropriate or which abiotic factor is more important in a given situation depends on the particular taxon and objectives of the study in question. We finally suggest that future studies should focus on understanding how these rules and factors select different behavioral and physiological adaptations. These approaches have been widely neglected or vilipended in studies on aquatic insects; however, this kind of study is strikingly necessary since they involve dimensions that create and maintain biodiversity.

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Chapter 5
The Biotic Environment: Multiple Interactions in an Aquatic World

Gabriela C. Mendes, Guilherme Gonzaga da Silva, Leonardo Samuel Ricioli, and Rhainer Guillermo

Abstract The distribution and diversity of aquatic insects is a result of their interactions with the environment and other organisms. Right from the egg to larval and adult stages, insects must deal with a great biodiversity of natural enemies and mutualists. Such relationships evolved for millions of years in such a way that aquatic insects developed behavioral, ecological, and evolutionary strategies to cope with predation, parasitism, and competition. In the same way, they have joined forces with other organisms to solve problems, such as the interaction with gut bacteria to digest cellulose. These strategies and selective forces not only predict behavior and occurrence of aquatic insects, but also shape their diversity, community structures, and population dynamics. In this chapter, we sought to bring to the reader a useful source of information and a background for future studies. Although our current knowledge on species interactions in freshwater habitats allows us to discuss several topics, there is an open field of possibilities and gaps to be addressed in future research.

Keywords Ecological interactions · Biotic factors · Aquatic animals · Trophic webs · Networks · Trophic cascades

5.1 Introduction

The freshwater environment is a rich amalgam of functional groups. Several taxa are parasites, predators, parasitoids, or prey of aquatic insects, and aquatic insects themselves make part of an extensive interaction network that harbors terrestrial, aquatic, and semiaquatic organisms. Here, in this chapter, we attempt to cover most of this biodiversity and give an insight into the evolution of behavioral strategies

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adopted by aquatic insects in their interactions with the biotic environment. This issue is extremely relevant, mainly considering the current perspective in which biodiversity must embrace the enormous richness present in biotic interactions, encompassing life histories, biology, and behavior of related species (Del-Claro and Torezan-Silingardi 2012). Therefore, we must consider that the outcomes of each interaction vary depending on proximal (internal factors) and distal (environmental, external factors) biotic changes that may modify the character of each interaction (e.g., Del-Claro et al. 2016).

Interactions between aquatic insects and other organisms will vary, depending on the context, like any other type of interaction. Hence, the outcomes of each interaction can change from positive to neutral or negative according to variations that may depend (e.g., prey abundance) or not on density (e.g., seasonal plant phenology). Thus, aquatic insects may present harmonic (e.g., commensalism, facilitation, and mutualisms) or disharmonic interactions (e.g., predation, herbivory, competition, exploitation, and parasitism), several of them subject to spatial and/or temporal variation. Predation and parasitism (including herbivory) are deleterious relationships that act as selective pressures on aquatic insects, which have developed strategies and behaviors to prey and to avoid predation, and to parasitize and to avoid parasitism. Competition and exploitation may be intra- and interspecific, where individuals compete for sites, mates, and resources. These negative relationships often force selection to favor strategies that increase fitness of those who are better competitors in specific habitats. Finally, commensals, facilitation between sympatric species, and mutualisms are rarely documented when researchers focus on aquatic insects, but here we show some interesting cases and suggest future approaches that will bring light towards such interactions in freshwater trophic cascades.

5.1.1 Predation

Selective pressures from predation may directly affect population dynamics, species distribution, and occurrence in natural environments. The presence of predators in the habitat interferes with prey survival in a direct and lethal way, through consumption, or indirectly by causing behavioral modifications on prey due to predation risk (Hoverman et al. 2005), the nonlethal effects that reduce reproductive success. Studies on invertebrates, fish, and amphibians have shown that nonlethal effects may be even larger than lethal effects in determining behavior, condition, density, and distribution of animals over a range of trophic levels (Luttbeg and Kerby 2005). Ultimately, predator presence can alter the distribution of threat-sensitive aquatic insects, interfering with the choice of a patch, its size, or the connectivity between two or more occupied patches (Resetarits Jr and Binckley 2009). For instance, in heterogeneous habitats, prey select patches with the highest expected fitness in order to maximize growth and minimize predation risk (Lima and Dill 1990). As an example, stonefly predators may force changes in behavior and habitat occupation by mayflies (Peckarsky 1980; Peckarsky and

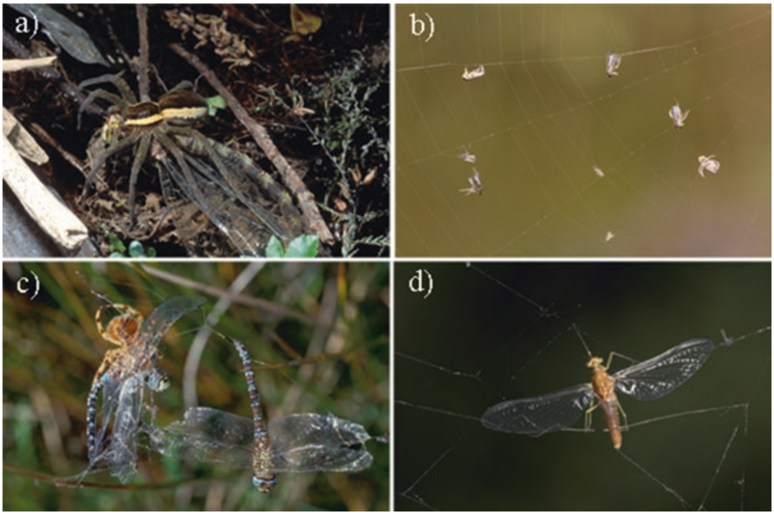

Fig. 5.1 A pisaurid spider preying on a male *Boyeria irene (Fonscolombe)* (Odonata: Aeshnidae) (**a**); corixids, dragonflies, and mayflies caught on spider webs (**b**–**d**). Photographs by Adolfo Cordero Rivera

Dodson 1980) and affect benthic communities and ecological processes through consuming and scaring prey (Majdi et al. 2015).

Aquatic insects may constitute a great portion of a predator's diet. For instance, the presence of aquatic insects in riparian environments can contribute to a great amount of all the energy requirements of spiders (Fig. 5.1, Sanzone et al. 2003). This contribution may be significant for *Bembidion* Latreille and *Nebria* Latr. carabid beetles that depend entirely on the consumption of such prey (Paetzold et al. 2005). A significant part of fish diet is also composed by aquatic insects—mayflies are among the preferred food items of many species, along with caddisflies and stoneflies (Allan 1995; Nair et al. 2015). Other predators rely on aquatic insects to complement their diet, such as amphibians, birds, lizards, bats, and other arthropods (Nakano and Murakami 2001; Sabo et al. 2002; Hering and Plachter 1997). Humans also consume aquatic insects, mainly in China, Mexico, Colombia, Thailand, Indonesia, Japan, Australia, and Africa (Williams and Williams 2017). Aquatic insects must even face predation from plants. The plant *Utricularia australis* R. Brown (Lentibulariaceae) has water-filled bladders that function as a suction trap for aquatic prey, such as damselflies, mayflies, and dipterans (Martens and Grabow 2011). In soils especially poor in N, many carnivorous plants use insect bodies as a source of N, and damselflies are commonly found as prey of species like *Drosera* L. (Droseraceae), very common plant in the borders of ponds, for example at the South American savannas.

In response to such a great biodiversity of predators, and consequent multitude of predatory tactics, aquatic insects have developed strategies to avoid predation. Insects with complex life cycles, such as most aquatic insects, can exhibit different antipredatory behaviors at various stages of life. In insects with an aquatic larval stage, the recognition of predator cues can induce ovipositing females to choose habitats with a low risk of predation to increase offspring success (Andrade et al. 2017). For example, female *Culex* L. *(Diptera: Culicidae)* mosquitoes select water bodies that are relatively free of predators (Silberbush and Resetarits Jr 2017). In some cases, the ability to distinguish environments occurs through the recognition of kairomones released by fish that feed on larvae (Eveland et al. 2016), which act as chemical cues of predation risk. Waterborne fish cues may also provoke inducible defense on mayflies. *Drunella* Needham nymphs that developed in streams with fish had significantly longer caudal filaments and lower mortality when exposed to predation by trout than those mayflies that developed in fishless streams (Dahl and Peckarsky 2002). Mayflies often use the cerci to detect disturbances in the water and detect predators; however, they may also be used to deflect predators. For example, mayfly nymphs adopt a "scorpion posture" and avoid predation from stoneflies (Peckarsky 1987).

This recognition of predatory signals decreases the costs of avoiding predators and can occur visually, chemically, or through the recognition of species-specific signals (Sih 1982). A recent study also showed that mosquito larvae can identify water vibrations from predatory dragonfly larvae and reduce foraging activity (Roberts 2017). The presence or absence of antipredatory behavior may also affect prey community composition. For example, the swimming larvae of the libellulid dragonfly *Leucorrhinia dubia* VD Lind. are more vulnerable to attack by predatory fish than the larvae of *Libellula quadrimaculata* L. and *Orthetrum coerulescens* (Fabricius) that feint death when a predator approaches (Henrikson 1988), affecting species composition and distribution in odonate communities.

Predation risk may select and change foraging behavior, induce morphological defenses, and affect emergence time and rates of aquatic insects (Benard 2004). For instance, some aquatic insects have developed behaviors to avoid attacks from predators. When facing a predator, water striders adjust the angulation of their legs as they push the surface of the water to make a great escape jump, increasing their chances of surviving an attack (Yang et al. 2016). Odonate larvae also have behavioral adaptations to increase their chances against predators. Aeshnid larvae use water jet propulsion as way of locomotion, when water is expelled by the anal region. When there is an encounter with a predator, larvae can rapidly burst their way out of danger (Corbet 1999).

The intensity of predator-prey interactions is relatively stable, and defensive strategies can be permanent in these environments. However, there are cases where environments are extremely heterogeneous or unstable and subject to change over short periods of time. In these cases, the prey may develop inducible antipredator responses. For example, the nymphs of some dragonflies have spines as defenses against their predators (Johansson and Samuelsson 1994), sharp protrusions used to pierce those who try to devour them. Larvae of *L. dubia* develop different sizes of spines, depending on the presence or absence of the predators (Johansson 2002). Larvae exposed to the presence of predatory fish have developed longer spines than nymphs under low predation risk—this phenomenon is called "inducible defense." Inducible defense strategies are advantageous due to the energy saved by avoiding unnecessary production of defensive characters in the absence of predators (Auld and Relyea 2011), which could decrease the net gain of individuals (DeWitt 1998).

Caddisfly larvae case design and predator-avoidance behavior may affect the vulnerability to predators (Nislow and Molles Jr 1993; Wissinger et al. 2006). Trichopteran larvae may also exhibit glands that secrete defensive exudates that inhibit predators from approaching (Duffield et al. 1977). Stoneflies may exhibit autohemorrhage at the intersegmental membranes of the coaxial and tibiofemoral joints of the legs when subjected to traumatizing stimuli, a defense against predators, mainly ants and fish (Benfield 1974; Moore and Williams 1990). Moreover, this behavior creates a sound that may delay the attack from vertebrate predators (Benfield 1974). Stonefly larvae may also be aggressive towards each other, causing spacing and decreasing predation risk as well (Moore and Williams 1990).

Antipredatory behavior of *Anax junius* Drury (Odonata: Aeshnidae) larvae varies according to developmental stage, where older larvae are successful in escaping predatory tadpoles, while only 12.5% of the young achieve the same result, showing that ontogeny may represent a vulnerability for young larvae (Hopkins et al. 2011). The larvae of mosquitoes that occupy environments with water accumulated on epiphytic plants (as is the case of bromeliads) are exposed to predation by tadpoles, as demonstrated by Salinas et al. (2018), who evaluated the predatory capacity and rate of predation of tadpoles *Phyllodytes luteolus* (Wied) (Anura: Hylidae) feeding on mosquito larvae. This study also suggests strong evidence of the relationship between body size and stage of development and predatory efficacy of tadpoles, demonstrating that the risk of predation may also change according to the level of predator development. Although aquatic insects are small in size and serve as prey to many taxa, a great part of freshwater biodiversity is composed of predatory insects.

5.1.1.1 Predatory Aquatic Insects

Many aquatic insects are important predators in trophic networks that connect water and land. This is the case of dragonflies that are top predators when aquatic larvae, and predators of remarkable aerial abilities that prey on other insects when adults. Dragonflies are often generalists, attacking every prey with certain size that moves. Giant water bugs, *Belostoma* Latreille (Heteroptera: Belostomatidae), are sit-and-wait predators that feed on fish, amphibians, snails, and other aquatic insects (Menke 1979). These animals use their raptorial legs to capture their prey and pierce it to inject toxins and digestive enzymes that cause prey paralysis and necrosis (Swart and Felgenhauer 2003). However, other taxa are specialists, such as diving beetles (Coleoptera: Dytiscidae) that are often specialized in certain prey. For instance, many larval insects are adapted to prey on mosquito larvae. In some cases, they can be even more specialized. *Hyphydrus japonicus* Sharp (Dytiscidae: Hydroporinae), have adapted mandibles and a projection on the head to open the valves of seed shrimps and gain access to the prey within (Hayashi and Ohba 2018). Helicopter damselflies (Odonata: Pseudostigmatinae) glean spiders from their webs or steal wrapped prey from the web (Fincke 1984; Ingley et al. 2012). Some

Heptageniidae (Ephemeroptera) are collectors (gathers) and some species are even predators (engulfers) (e.g., Soluk and Clifford 1985).

Top predators in freshwater habitats, such as dragonflies, diving beetles, water bugs, water striders, some stoneflies, and even chironomids, compose one of the most striking selective forces acting on communities' structuring, affecting prey behavior, life history, and population dynamics (Chase 1999; Babbitt and Jordan 1996; Kehr and Schnack 1991). For example, trophic cascades that occur when predators reduce prey abundance, indirectly impacting lower trophic levels, may regulate species interactions that include aquatic insects. In an elegant study, Knight et al. (2005) showed that ponds with fish may reduce larval dragonfly abundances, hence fewer adult dragonflies hunting for prey in the air. Consequently, pollinators were benefited and plants near ponds with fish received more pollinator visits than plants near ponds without fish. Finally, freshwater predators may be a driving force for community species composition by acting as selective filters. Dragonfly larvae prey on water boatman (Hemiptera: Corixidae), especially on small species like *Trichocorixa* Kirkaldy; hence, larger species occupy water bodies with odonates, while *Trichocorixa* colonizes dragonfly-free brackish waters (Coccia et al. 2014).

5.1.2 Parasitism

Parasites and parasitoids may also have striking impacts on the ecology of aquatic insects, at individual, population, and community levels. Such interactions may affect insects directly, by decreasing individual fitness, or indirectly, by changing population densities, species interactions, and behavior (Kohler 2008). An impressive variety of parasites and parasitoids inhabit riparian environments and rely on aquatic insects as hosts. Consequently, aquatic insects have their fitness impacted, which may decrease interspecific competition and ultimately benefit species coexistence. Nevertheless, intraspecific competition may favor those individuals that are able to defend themselves against parasites, by adopting strategies or exhibiting good immunocompetence. With few exceptions, aquatic insects regularly need to face attacks from Microsporidia, Nematoda, Nematomorpha, Gregarina, Trematoda, Diptera, Hymenoptera, and Acari (Poulin and Morand 2000).

Trematodes search for intermediate insect hosts after development in a mollusk, until infecting the definitive host, usually a vertebrate (Chae et al. 2000; Esch et al. 2002). These parasites can infect aquatic insects and alter their behavior. For instance, larvae of *Aedes aegypti (Linnaeus in Hasselquist)* that are heavily infected with metacercariae are less active and spend more time at the water surface. As a result, host behavior manipulation facilitates predation or accidental ingestion by aquatic vertebrates, the final host (Poulin 1995).

Females of *Forcipomyia* Meigen (Diptera: Ceratopogonidae) are ectoparasites of flying insects (Fig. 5.2a). In odonates, for example, female midges attach to the host exoskeleton to feed on their hemolymph. *Forcipomyia paludis* (Macfie) firmly attaches to the main veins at the wing base of odonates (Wildermuth and Martens 2007). Another midge species, *F.* (*Pterobosca*) *incubans Macfie*, was recorded parasitizing

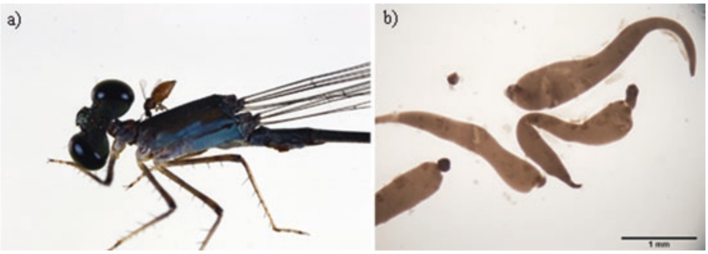

Fig. 5.2 A female *Forcipomyia* midge biting the thorax of a male *Epipleoneura tariana* Machado (Odonata: Protoneurniae) in the Brazilian Amazon (**a**) and gregarines infecting the gut of a *Polythore gigantea* (Selys) (Odonata: Polythoridae) (**b**). Photographs by Adolfo Cordero Rivera

Fig. 5.3 Water mites infecting a dragonfly *Sympetrum sanguineum* (Müller) (Odonata: Libellulidae) (**a**) and a diving beetle (*Dytiscus* L.) (**b**). Scanning electron microscopy micrographs showing the mite larvae attached to a damselfly's exoskeleton (*Ischnura graellsii* Rambur) (**c**) and a detached one (**d**). Photographs by Adolfo Cordero Rivera

wings of several odonate species throughout the neotropics (Guillermo-Ferreira and Vilela 2013). While some parasites may infect hosts in specific developmental stages, others do not have this restriction. This is the case of gregarines (Fig. 5.2b), which may infect aquatic insects at any stage of their development (González-Tokman et al. 2011). When infecting dragonflies, gregarines may cause metabolic syndromes and obesity in the host, decreasing activity and causing alterations in performance of flight muscles (Schilder and Marden 2007).

Water mites can also infect adults of aquatic insects (Fig. 5.3), usually attaching to the ventral part of the body (Böttger 1976). Most water mites act as predators of chironomid larvae in lotic habitats. In lentic environments, it is common to find water mites acting as predators of eggs and as ectoparasites, attached to aquatic insects (Proctor and Pritchard 1989), such as Coleoptera, Odonata, Plecoptera, Diptera and Trichoptera. *Hydrachna globosa* (De Geer) larvae, for example, swim around on the water surface until they find a host, *Nepa rubra* L. and *Ranatra linearis* (L.) (Böttger 1972). As an outcome of the infection, insects may have lower longevity, fecundity, and survival (Smith 1988), because the infection may compromise the ability to respond to parasites and pathogens in subsequent infections (Honkavaara et al. 2009). When odonates are parasitized by water mites, they suffer with increased wing load, thus decreasing flight distance and dispersal, resulting in increased predation (Marden 1989). Moreover, mites can cause damage to flight muscles, result in less symmetric wings, and reduce fat content (i.e., energy reserves), which potentially affects odonate dispersal, foraging rates, and mate acquisition (Stechmann 1978; Smith 1988; Stoks and Córdoba-Aguilar 2012).

Nematodes and horsehair worms (Nematomorpha) (Fig. 5.4a) infect some species of mayflies, caddisflies, stoneflies, corixids, black flies, and beetle larvae (White 1969; Grabner 2017). In nematodes that infect multiple hosts, the parasite frequently changes the intermediate host behavior to facilitate transference to the final host. For example, odonates may act as paratenic hosts of nematodes that parasitize freshwater turtles (Wiles and Bolek 2015). Even humans may be part of complex parasitic nematode cycles, where human consumption of odonate larvae may lead to infection (Corbet 1999). Consequently, the aquatic insect may exhibit altered behaviors that facilitate transmission. When mayflies *Baetis bicaudatus* Dodds (Ephemeroptera: Baetidae) are infected by parasites, they are preferentially attacked by their stonefly predator (Vance and Peckarsky 1997), as a result of pathological side effects.

Parasite transmission is utterly linked to parasite fitness; hence, in order to get to its final host, a parasite needs to adopt strategies to facilitate infection. Some parasites of hematophagous insects do it by enhancing sensibility of their hosts to odor cues (Rossignol et al. 1986). When infected, *Anopheles gambiae Giles*—a common vector of *Plasmodium falciparum*, a parasite that causes human malaria—were significantly more attracted to a substrate emanating human odor than noninfected ones. This occurs because the parasite enhanced mosquito olfactory sensibility to humans, augmenting infection chances (Smallegange et al. 2013). Females of *A. gambiae* also increase the feeding frequency when parasitized and take larger blood

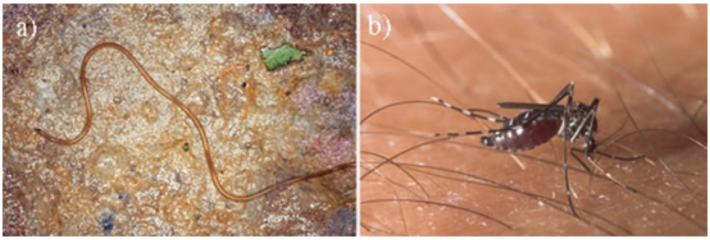

Fig. 5.4 A gordiid horsehair worm (Nematomorpha) (**a**). Some larval forms of these worms infect aquatic insects. *Aedes albopictus* (Skuse) (Diptera: Culicidae), vector of the yellow fever virus, dengue fever, and Chikungunya fever, having a blood meal (**b**). Photographs by Adolfo Cordero Rivera

meals than uninfected females. Malaria parasites may decrease risky behaviors of their hosts during pre-infectious phase, such as blood feeding, but this behavior resumes when the parasite is ready to be transferred to its final host (Schwartz and Koella 2001; Anderson et al. 1999; Koella et al. 2002).

Leishmania also manipulates its host behavior. Sand flies infected with the parasite present altered behavior, depending on the parasite developmental stage. When the parasite is infectious, it manipulates sand fly behavior, enhancing biting persistence, thus enhancing host infection (Rogers and Bates 2007). Parasitized sand flies fed on multiple hosts much more frequently than non-parasitized sand flies, augmenting infection chances (Ready 2008). *Leishmania* also produces a mucin-like gel in the sand fly gut that blocks its mouthparts, causing regurgitation during blood feeding. This effect enhances parasite transmission during feeding (Rogers 2012).

Viruses can also manipulate the host behavior. La Crosse virus (LACV) depressed blood meal size in *Aedes albopictus* (Skuse) (Fig. 5.4b) and *Ae. triseriatus (Say)*, making them more avid to feed again. In this way, infected mosquitoes feed more frequently, enhancing horizontal transmission (Jackson et al. 2012). In females, LACV increased sexual activity, and infected females mated significantly more than noninfected ones (Gabitzsch et al. 2006), although it is still not clear if this is a host response to infection, or if it benefits the parasite fitness. Viruses may also alter the host locomotion behavior: in *Ae. aegypti*, parasitized mosquitoes presented higher activity levels (Lima-Camara et al. 2011).

All aquatic Hymenoptera are parasitoids of aquatic invertebrates. They search for insect immature stages, mostly eggs and larvae of Coleoptera, Diptera, Hemiptera, Lepidoptera, Odonata, and Megaloptera. At least one-third of the hymenopteran parasitoid species can be found in lotic environments, while all the other species are associated with lentic habitats (Bennett 2007). Some pompilid wasps may also hunt adult semiaquatic spiders (Shimizu 1992). Most hosts are herbivore insects associated with aquatic plants (Feitosa et al. 2016; Kula et al. 2017). While most terrestrial plants produce volatile organic compounds in response to herbivory to attract natural enemies of herbivores (Turlings and Erb 2018), some aquatic parasitoids search for hosts in a random pattern, apparently not using chemical cues produced by the host insect or plant. The female of *Apsilops japonicus* Yoshida et al. (Hymenoptera: Ichneumonidae), for example, needs to probe underwater petioles of the yellow water lily *Nuphar* Sibth. & Sm. one by one to find the host pupae *Neoschoenobia testacealis Hampson* (Lepidoptera: Crambidae) (Hirayama et al. 2014). *Caraphractus cinctus* Walker (Hymenoptera: Mymaridae) parasitizes eggs of diving beetles (Dytiscidae). Males usually emerge first, and search for host eggs and wait for females to emerge and mate. This wasp is able to swim using their wings and live for about 15 days, sometimes completely submerged (Jackson 1966). The Trichogrammatidae egg parasitoid *Pseudoligosita longifrangiata* (Viggiani) finds the host plant *Tonina fluviatilis* Aubl. (Eriocaulaceae) and searches for *Argia insipida* Hagen in Selys (Odonata, Coenagrionidae) eggs underwater (Querino and Hamada 2009). *Anagrus obscurus* (Hymenoptera: Mymaridae) parasitizes eggs of *Calopteryx haemorrhoidalis* (Vander Linden) and *Platycnemis pennipes* (Pallas) (Odonata: Calopterygidae: Platycnemididae)

(Santolamazza et al. 2011). Many aquatic Hymenoptera have adaptations like dense pubescence and elongated strongly curved claws that seem to be adaptive to live underwater (Bennett 2007). The ectoparasitoid genus *Agriotypus* Haliday exhibits a unique pupal respiratory filament to breathe after death of its hosts, caddisfly pupae (Elliott 1982).

5.1.2.1 Response to Parasitism

Since pathogens and parasites are widespread in the water column, aquatic insects are able to use some sort of ability to detect parasitoids and adopt spatial avoidance strategies to evade them. Detection of parasitoid signals may trigger responses such as evasive or aggressive behaviors in hosts (Gross 1993). Volatile cues, along with visual, tactile cues such as nonvolatile chemicals and waterborne cues such as vibrations and chemicals, could be detected by potential hosts that may change their behavior to evade parasitoidism (Hirayama and Kasuya 2015). The detection of chemical compounds, called necromones, produced by dead or infected animals, may trigger behavioral responses to avoid affected habitats or food sources and infected mates, conspecifics, and prey (Behringer et al. 2018). Females of *Ae. aegypti* avoid oviposition in water containing or that previously contained larvae parasitized by *Plagiorchis elegans* (Rudolphi) (Trematoda: Plagiorchiidae), which suggests a response to chemical signals produced by the parasitic infection (Lowenberger and Rau 1994). In high parasitoid wasp densities, which represents a higher parasitism risk, female water striders *Aquarius paludum insularis* (Motschulsky) (Heteroptera: Gerridae) tend to increase oviposition depth (Hirayama and Kasuya 2009).

Ultimately, adult and larval forms of aquatic insects must have well-adapted immunological responses to parasites. However, the response to infection can be dependent on resource allocation and adopted behavioral strategies, which may be sex dependent. There is a delicate balance between energetic investment in defense against pathogens and reproductive traits, causing a sex-biased difference favoring females (Stoehr and Kokko 2006; Klein and Flanagan 2016). For example, male odonates tend to allocate more resources to mating success than to defense against parasites, which cause higher infection levels and lower survival rates than females (Córdoba-Aguilar and Munguía-Steyer 2013).

5.1.3 Competition

Competition occurs when individuals must share resources. In freshwater environments, such resources are often related to microhabitat occupancy, oviposition sites, and food exploration. These interactions are crucial for the maintenance of biodiversity, since sympatric species must develop ways to live in equilibrium or exclude each other. Competition may also occur between individuals of the same species;

however, this topic will be better addressed in another chapter of this book. Here, we exemplify the most striking relationship between sympatric species; for instance, mosquitoes that live in phytotelmata are good models for studies on interspecific competition because several species are sympatric, at least in the larval stage, and directly compete for resources. Yee and Skiff (2014) carried out a study to determine potential ecological effects of *Culex coronator* (Dyar and Knab) (Diptera: Culicidae) on other container-dwelling mosquitoes. In this study, larvae of *Ae. albopictus* (Skuse) and *C. quinquefasciatus* (Say) (Diptera: Culicidae) were placed with *C. coronator* in three different resource scenarios. Survival rates, male and female body mass, and development time were impacted by interspecific competition. Female mass reduction may directly affect egg production, and hence mating and oviposition.

Competition can be so intensive that results in cannibalism (Fig. 5.5a). Eating conspecifics is a behavior that usually is expressed in stressful situations, such as in high population densities and reduced resources. The cannibal benefits not just from nutritional input, but also by attenuating competition in the future (Fincke 1994). Consequently, cannibalism aids populations to endure stressful situations (Parajulee and Phillips 1995). In well-delimited habitats, such as phytotelmata and ponds, the effects of cannibalism can be well studied. The larval *Megaloprepus coerulatus* Drury (Odonata: Pseudostigmatinae) live in water-filled tree holes where, independently of prey availability, larger larvae regularly prey on smaller conspecifics. In this case, cannibalism is the major cause of mortality in the first life stages (Fincke 1994).

Intraguild predation (IGP) occurs when individuals of one species prey on other species that use similar resources, reducing potential competition (Fig. 5.5b). IGP also has an important role in poor nutrient habitats, as seen in the caddisfly *Asynarchus nigriculus* (Banks). These trichopterans live in subalpine wetlands, in temporary ponds, and present intraguild predation and cannibalism independent of conspecific or heterospecific density, taking advantage of a head start in development that propitiates larger body sizes (Wissinger et al. 1996). In temporary ponds, ephemeral habitats, individuals have to emerge fast, hence, animals are much more aggressive than heterospecifics that live in other habitats. Caddisflies

Fig. 5.5 Cannibalism in *Homeoura* Kennedy (Odonata: Coenagrionidae) in Peru (**a**) and a case of intraguild predation by *Gomphus pulchellus* Selys (Odonata: Gomphidae) devouring a male *Ceriagrion tenellum* (De Villiers) (Odonata: Coenagrionidae) (**b**). Photographs by Adolfo Cordero Rivera

from permanent wetlands were much less aggressive than caddisflies from temporary ponds, suggesting that IGP can play an important role in complementing the detritivores diet. Predating other insects of the same guild leads to earlier emergence, something important for an animal that lives in unpredictable habitats (Wissinger et al. 2004).

5.1.4 Harmonic Interactions

Aquatic insects can take a hike on other organisms and can be used as phoretic transports by others. Chironomids are known to adhere to other aquatic insects such as Megaloptera, dragonflies, black flies, stoneflies, damselflies, mayflies, belostomatids, and naucorids, and also hydrozoans, fish, and gastropods (Roque et al. 2004; Boonsoong 2016). Some are even known to associate with freshwater sponges (Fusari et al. 2014). Such associations can result in mutualistic interactions, for instance, *Cricotopus nostocicola* (Wirth) (Diptera: Chironomidae) and *Nostoc parmelioides* Kützing (Cyanobacteria) are involved in a mutualistic relationship. The chironomid benefits from eating the mutualist cells, and *Nostoc* colonies that contain mosquito larvae are larger and present higher photosynthetic rates (Ward et al. 1985).

Ecological facilitation may occur when shredders live in sympatry (Bronstein 2009). This type of interaction benefits at least one species and cause harm to neither. When sympatry, shredder caddisflies facilitate food acquisition towards other species. As a result, there may be positive effects on emergence rate, wing length, and biomass, resulting in higher survival and fecundity of one caddisfly (Westveer et al. 2018). Rarely, other mutualistic relationships, such as pollination, are recorded for aquatic insects. For example, some stoneflies visit flowers and are known to act as facultative pollinators (Wong Sato and Kato 2017).

Some aquatic insects rely on the association with plants for growth and survival. Several species use macrophytes as oviposition sites and shelter for larvae. Water scorpions (Hemiptera: Nepidae), naucorids, odonate larvae and diving beetles actively occupy and seek shelter in macrophyte leaves and roots and use them as perch to stalk prey (Fig. 5.6). Other aquatic insects depend on plants for camouflage, or to defend a territory when adults. Evidence suggests, for example, that some damselfly species may exhibit preference and site fidelity in relation to the species of plant on the environment (Guillermo-Ferreira and Del-Claro 2011). Caddisfly larvae use leaves and plant material to build their cases, and some aquatic Lepidoptera have a close relationship with macroalgae that are cultivated in their silk cocoons.

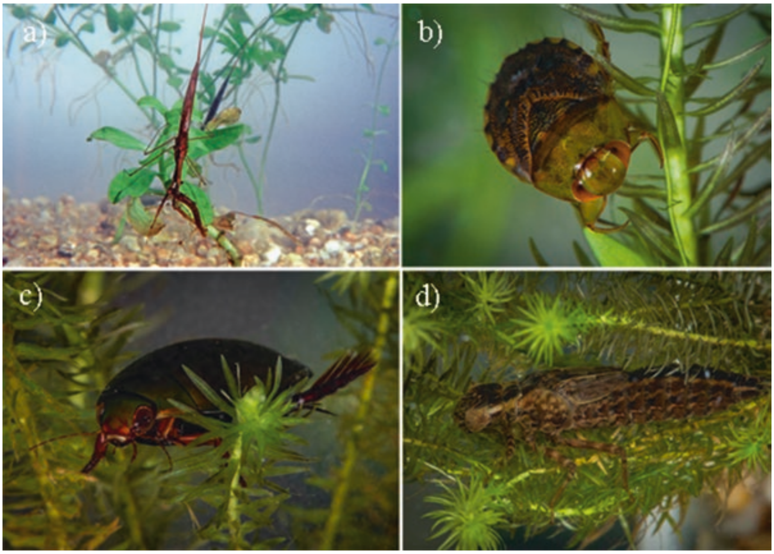

Fig. 5.6 Predatory aquatic insects usually seek shelter in macrophytes and use the perch to stalk prey, for example, water scorpions *Ranatra linearis* (Hemiptera: Nepidae) (**a**), creeping water bugs (Hemiptera: Naucoridae) (**b**), diving beetles (Coleoptera: Dytiscidae) (**c**), and dragonfly larvae (Odonata: Aeshnidae). Photographs (**a**) by Adolfo Cordero Rivera and (**b–d**) by Frederico Salles

5.1.5 Bacteria

Bacterial activities are essential to nutrient cycles on ecosystems and for the maintenance of food web dynamics (Baines and Pace 1991; Elser et al. 2000; Godwin et al. 2017). Some of the most commonly found species in lakes and rivers are Proteobacteria, Cyanobacteria, Actinobacteria, Verrucomicrobia, and Cytophaga-Flavobacterium-Bacteroides groups (Zwart et al. 2002). These organisms degrade the organic matter dissolved in the water and directly affect the entire trophic networks (Logue et al. 2016). For example, most aquatic bacteria constitute an important element of freshwater biofilms, consisting in a matrix that may be formed by communities of prokaryotic and eukaryotic organisms that grow on rock surfaces (Zancarini et al. 2017) and plants (Marsollier et al. 2004). Some mayflies are scrapers and feed on the biofilm on rock surfaces. Chironomid larvae feed directly upon bacteria that degrade methane (Kiyashko et al. 2004), and some species of leaf shredders depend on bacterial enzymes acquired through ingestion of detritus or produced by endobiont bacteria that live in their guts (Sinsabaugh et al. 1985).

Aside from decomposition agents, some bacteria are in fact pathogenic and widespread among freshwater environments. The proteobacteria *Wolbachia* Hertig and Wolbach, an obligate intracellular parasite whose incidence in aquatic insects was subject to recent surveys, is found in 52% of the species. Ephemeroptera, Plecoptera, and Trichoptera have the lowest incidence of infection, while infection prevalence is higher in Diptera, Hemiptera, Odonata, and Coleoptera (Sazama et al. 2017). Some strains of *Wolbachia* are vital in mutualistic associations, where the growth and nutrition of the host are dependent on B vitamins provided by these endosymbionts, but most strains are facultative or parasitic associates (Nikoh et al. 2014). Certain strains of this bacteria, for example, have strong deleterious effects or additive effects on egg production and viability, survival, adult body size, and fecundity, and seem to be transmitted to offspring whenever the female is infected (e.g., gut bacteria—Coon et al. 2016; Axford et al. 2016).

5.1.6 Fungi

There are also interactions between sympatric aquatic insects and fungi. For instance, fungi greatly contribute to the growth of caddisfly larvae (Chung and Suberkropp 2009). Symbiotic fungi (Trichomycetes) are found in the guts of aquatic insect larvae, such as shredder caddisflies that need this association to break leaf material (Ferrington Jr et al. 2005). The interaction between shredders, fungi, and bacteria involved in the breakdown of leaf litter is widely recognized, especially involving aquatic hyphomycetes colonizing leaf material (for reviews, see Cummins and Klug 1979; Bärlocher 1985; Anderson and Cargill 1987). Some studies have shown that fungal colonization on leaves can affect the food choice and growth of shredders by changing the palatability and the nutritional quality of leaves (Suberkropp 1992). Fungi can even play a greater role than bacteria in the food choice of shredders. For example, *Pycnopsyche* Banks caddisflies exhibit a greater preference for fungal-colonized than for bacterial-colonized leaf material (Mackay and Kalff 1973). Leaf material colonized by fungi is a high-quality food resource and contributes to the growth of *Pycnopsyche* caddisflies (Chung and Suberkropp 2009). Limnephilid caddisfly larvae may even exhibit preference for leaves colonized by two specific fungi, when leaves that were individually colonized by ten different fungal species were offered to larvae, showing that shredders can even discriminate among different fungal species (Arsuffi and Suberkropp 1988).

Nevertheless, fungi can also act as natural enemies. *Lagenidium giganteum* Couch is commercially produced as a control agent of mosquitoes (Scholte et al. 2004). *Ophiocordyceps odonatae* (Kobayasi) and *Hymenostilbe odonatae* Kobayasi are known as entomopathogenic fungi that affect dragonflies (Ke and Ju 2015). Therefore, freshwater communities could face large-scale effects caused by fungal infections, which are major regulators of population dynamics (Kohler and Hoiland 2001). For instance, the dominant caddisfly *Glossosoma nigrior* Banks outcompetes other grazers and filterers, except when microsporidian outbreaks affect *G. nigrior* populations (Kohler and Wiley 1997).

5.1.7 Herbivory

Herbivory is the "ingestion of living plant tissue from algae or vascular plants" (Cummins 1973). Shredder herbivores feed on living tissues of rooted plants, producing holes in leaves (Cummins 2016). Examples of shredders are beetles (Coleoptera), aquatic moths (Lepidoptera), and some representatives of Diptera and Trichoptera (Merritt et al. 1996). Aquatic insects that feed on algae and associated material on surfaces where the periphyton accumulates are called scrapers. This is the case of Leptophlebiidae and Heptageniidae mayfly nymphs (Cummins 2016). To feed on surfaces, these insects need to maintain their position in the stream, and have adaptations for this purpose, such structures to attach to the substrate (Cummins 2016).

Aquatic insects may also form galls and induce overgrowth of plant tissue by chemical compounds found in salivary and oviposition fluids (Bartlett and Connor 2014). Among the few records of aquatic insects forming galls in aquatic plants, there are chironomids in Podostemaceae macrophytes (Jäger-Zürn et al. 2013), and gall midges (Cecidomyiidae: Diptera) were found inducing galls in rhizomes of Erichhornia azurea (Sw.) Kunth (Ponteridaceae) (Peláez-Rodriguez et al. 2003; Urso-Guimarães et al. 2014). Larvae of some species of chironomids burrow their way inside the host plant while feeding, mining the tissue and using cavities as shelter to complete development (McGaha 1952).

5.1.8 Concluding Remarks

Freshwater ecosystems harbor an extraordinarily rich and sensitive biota that depend on ecological interactions to thrive. Here in this chapter, we sought to show part of this biodiversity and to give an insight into how ecological interactions may shape aquatic insect assemblages. The great majority of the 126,000 species of freshwater animals are insects (60.4%) (Balian et al. 2008); however, the study of biodiversity lacks even the most basic data on this group (see Cardoso et al. 2011 for an overview). Acquiring knowledge on different species or phylogenetic lineages is a fundamental step in documenting biodiversity, mainly by understanding the behavioral, ecological, and evolutionary processes associated with diversity patterns and consequently support conservation strategies. Finally, we suggest that future studies should address the ecological and evolutionary patterns of interaction networks involving tropical aquatic insects to unravel the driving forces of their evolution and distribution.

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Chapter 6
Drumming for Love: Mating Behavior in Stoneflies

J. Manuel Tierno de Figueroa, Julio M. Luzón-Ortega, and Manuel Jesús López-Rodríguez

Abstract This chapter describes the current knowledge on the mating behavior of stoneflies (Insecta, Plecoptera). Arctoperlarian stoneflies use intersexual vibrational communication as a mechanism for encountering mates and pair forming, acting as a reproductive isolation mechanism. These vibrational signals can be produced by drumming, rubbing, tremulation, or a combination of these methods and are species specific; therefore, they can be used as a method to confirm/infer phylogenies or define species. Of particular interest is our understanding of their evolution from ancestral to derived models. Currently, the vibrational signals of approximately 200 species, mainly from North America, Europe, and, of less concern, Asia, have been described. For those species that do not use vibrational communication (principally Antarctoperlaria) or that occur in particular habitats where it is not effective, other mate-encountering mechanisms are discussed. In relation to non-vibrational mate-encountering mechanisms, some studies seem to show that certain substrates could act as encounter sites by aggregating sexes, both for Arctoperlaria and Antarctoperlaria. Finally, other reproductive behaviors, such as mating (sperm transmission, female stimulation, etc.), formation of mating balls, or mate-guarding strategies (both contact and noncontact guarding mechanisms), are also addressed.

Keywords Plecoptera · Vibrational communication · Encounter sites · Reproductive strategies · Mate guarding

In stoneflies (order Plecoptera), most biological studies have focused on nymphs because this life stage is much longer than the adult stage. Nevertheless, although the adult biology of stoneflies, and particularly their reproductive behavior, has been scarcely studied (except perhaps their employment of intersexual vibrational

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communication, which has received greater attention in the last decades), we now know that they exhibit complex strategies to facilitate mate encounters, mate evaluation, copulation, mate guarding, etc., making its study a bewitching topic of research. In this chapter, we try to elaborate on a brief compilation of the extant knowledge.

6.1 Vibrational Communication

Vibrational communication seems to be a very ancient system in animals; it is probably the primary channel of communication in some groups and is ubiquitous in arthropods and vertebrates (Hill 2008; Cocroft et al. 2014). Although sound communication has been well studied in many animals, vibrational communication using low-frequency, substrate-borne vibrations has been considerably less explored, despite its importance (Stewart 1997; Cocroft et al. 2014). In fact, many insect groups communicate by means of the production and reception of vibrational signals through solid substrates, and this is particularly the case in some aquatic insects, such as Plecoptera, Trichoptera, Megaloptera, and Neuroptera Sisyridae (e.g., Rupprecht 1968, 1975; Stewart 1997). However, among insects, it is in stoneflies (Plecoptera), particularly Arctoperlaria, where this communication system has evolved into its most complex form as a mechanism for mate encounter and pair forming (Stewart 1997, 2001). Nonetheless, among stoneflies, vibrational communication is unknown in Antarctoperlaria and has not been reported in Arctoperlaria that inhabit the Southern Hemisphere (Notonemuridae and part of Perlidae), in either Scopuridae or Styloperlidae families (Stewart 2001; Boumans and Johnsen 2015; DeWalt et al. 2015).

In Plecoptera, this communication system was first quantified by Rupprecht (1965, 1968), but as compiled by Rupprecht (1968) it was known in the nineteenth century (Newport 1851) and had been reported in the second half of the nineteenth century and first half of the twentieth century by authors such as Hagen (1877), MacNamara (1926), and Gaunitz (1935). Since then, the vibrational signals of approximately 200 species have been described, mainly in North America, Europe, and, to a lesser extent, Asia (Boumans and Johnsen 2015, DeWalt et al. 2015, updated data).

Stoneflies produce vibrational signals by drumming, rubbing, tremulation, or a combination of these methods (Stewart 1997). Drumming, or percussion, consisting of tapping (beating) on substrates with the ventral portion of the abdomen or some kind of specialized structure on it (such as ventral lobes, hammers, knobs, or vesicles, Fig. 6.1), is the most widely employed signaling method among stoneflies (Stewart 1997). It was Rupprecht (1976) who first demonstrated, by means of observational and experimental studies, that hammers and vesicles were used for drumming, acting in the production, internal monitoring, and control of the signals (in Abbott and Stewart 1997). A complete review of the evolutionary relationships between these structures and the vibrational communication behaviors can be found in Stewart and Maketon (1991). Rubbing consists of scraping the specialized

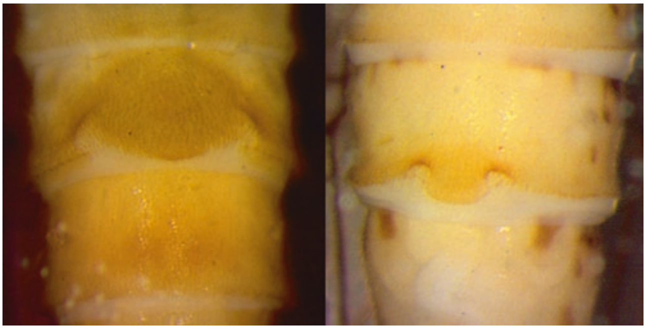

Fig. 6.1 Ventral view of the male abdomen of *Hemimelaena flaviventris* (left) and *Isoperla morenica* (right) showing the lobe

abdominal structure on a substrate, producing a more continuous vibration. According to Stewart (1997), rubbing is an “abdominal-substrate stridulation”. Finally, tremulation involves rocking (jerking) the abdomen or entire body and transmitting the resulting vibrations into a solid substrate through the legs. Examples of species that produce signals by drumming can be found in all Plecoptera families in which vibrational signals have been described (Stewart 1997), e.g., males and females of *Perla marginata* (Rupprecht 1965), *Isoperla phalerata* (Szczytko and Stewart 1979), and *Protonemura meyeri* (Tierno de Figueroa et al. 2014). Rubbing signals, reported in Perlidae, Perlodidae, and Peltoperlidae (DeWalt et al. 2015), are produced by some species, such as the males of *Peltoperla tarteri* (Maketon and Stewart 1988), *Flavoperla hagiensis* (formerly *Gibosia hagiensis*) (Hanada and Maruyama 2001), and *Isoperla bipartita* (Tierno de Figueroa and Luzón-Ortega 2002). Some species produce their signals through a combination of rubbing and tapping (drumming), such as the male of *Peltoperla arcuata* (Maketon and Stewart 1988) or the female of *Isoperla bipartita* (Tierno de Figueroa and Luzón-Ortega 2002). Tremulation in stoneflies was described by Rupprecht (1981) and, until now, had only been described in a few Chloroperlidae species, such as *Siphonoperla torrentium, Siphonoperla montana*, and *Suwalia pallidula* (Rupprecht 1981; Alexander and Stewart 1997).

Adult stoneflies (as some other arthropods, e.g., Bradbury and Vehrencamp 2011) can communicate by introducing waves into plant tissues (or other substrates able to transmit waves), and receivers that are some distance away from the sender can detect these waves as they pass under their feet when they are stationary. In fact, Rupprecht (1968) proved, through experiments in which he eliminated or stimulated certain parts of the body, that the subgenual organs [specialized chordotonal or scolopophorous organs in the proximal part of the tibiae (Chapman 1998) and one of the possible sense organs for vibrational reception] are the perceiving sense organs in stoneflies. Detailed explanations on the mechanistic basis of signal detection and transmission and other aspects of vibrational communication in insects can be found in Chapman (1998), Bradbury and Vehrencamp (2011), and, particularly, Hill (2008) and Cocroft et al. (2014).

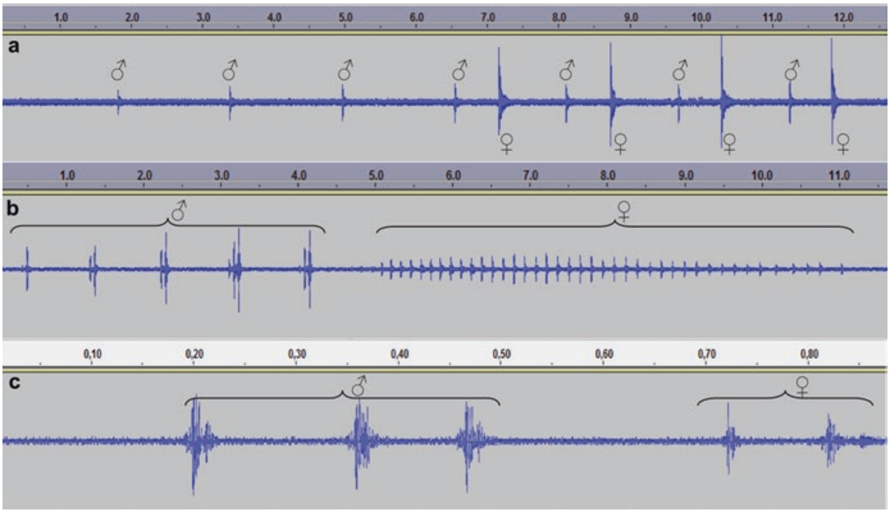

Fig. 6.2 Oscillograms showing duets of (**a**) *Capnioneura mitis* (fam. Capniidae), (**b**) *Protonemura meyeri* (fam. Nemouridae), and (**c**) *Hemimelaena flaviventris* (fam. Perlodidae). Time (horizontal axis) in seconds. Images obtained using Audacity v1.2.6 software (Free Software Foundation, Boston, MA, USA)

The signal is usually initiated by the male ("call") and followed by the female ("answer"), but in some species a three-way signal (male-female-male) is produced (the last signal of the male is called the "reply"). It is accepted that only virgin females produce vibrational signals (Rupprecht 1968, 1969). Duets (Fig. 6.2) are typically repeated sequences of two-way or three-way conversations, or symphonies of grouped calls interspersed by grouped answers (Stewart and Sandberg 2006). Exceptionally, females can produce signals when males are not present (Maketon and Stewart 1988; Tierno de Figueroa et al. 2014), and, therefore, the female signal can also be considered a call and not only an answer, as usually pointed out in stoneflies. Female signals are usually short [even composed by only one beat, as in *Hansonoperla appalachia* and *Perlinella drymo* (Zeigler and Stewart 1977) or *Guadalgenus franzi* (Tierno de Figueroa et al. 2002)] and less complex than male signals, but the female signals of some Perlidae (Stewart and Sandberg 2006) and Nemouridae (Luzón-Ortega and Tierno de Figueroa 2003; Tierno de Figueroa et al. 2014) are composed of a high number of beats, and cases like that of *Isoperla bipartita* female, which has a signal composed of a beat and a rub (Tierno de Figueroa and Luzón-Ortega 2002) and that of *Suwallia pallidula*, in which the female answers the male's tremulation by tremulating (Stewart and Sandberg 2006), among others, are exceptional. The generally higher complexity of male signals could be a consequence of intrasexual competition and intersexual conflict, the latter when part of male signal mimics the female answer (Boumans and Johnsen 2015).

Vibrational signals produced by stoneflies can be as simple as a two-beat signal, such as the one described in the male of *Guadalgenus franzi* by Tierno de Figueroa

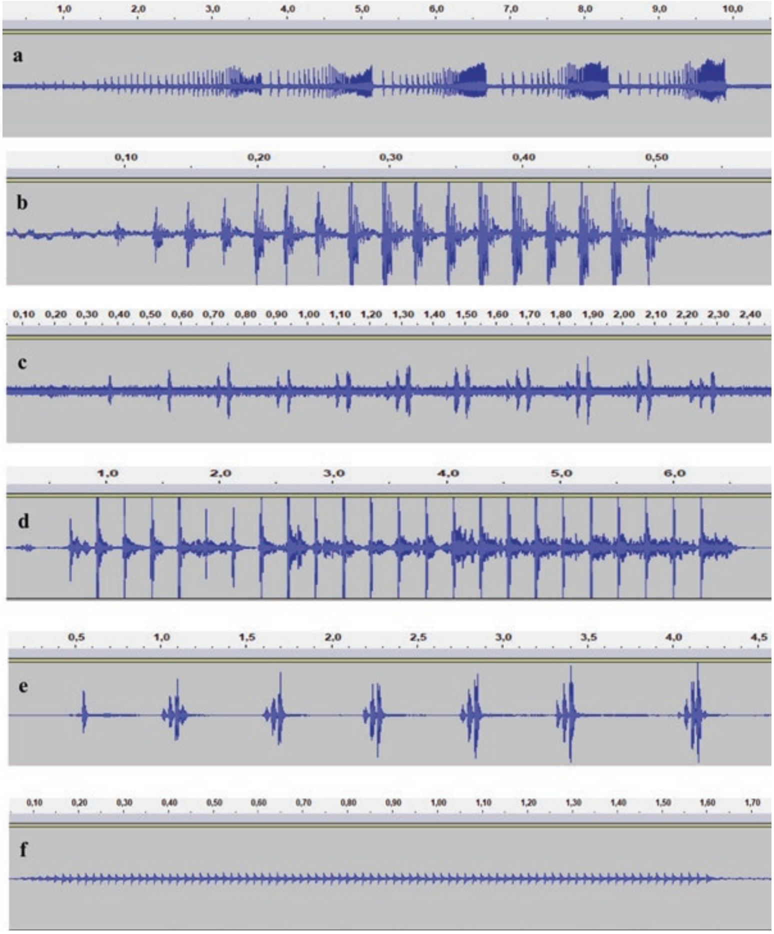

Fig. 6.3 Oscillograms of the male vibrational signals of (**a**) *Isoperla nevada* (fam. Perlodidae), (**b**) *Eoperla ochracea* (fam. Perlidae), (**c**) *Tyrrhenoleuctra minuta* (fam. Leuctridae), (**d**) *Capnioneura libera* (fam. Capniidae), (**e**) *Protonemura meyeri* (fam. Nemouridae), and (**f**) *Rhabdiopteryx thienemanni* (fam. Taeniopterygidae). Time (horizontal axis) in seconds. Images obtained using Audacity v1.2.6 software (Free Software Foundation, Boston, MA, USA)

et al. (2002), or as complex as the one composed of diphasic sequences with its first sequence being different from the following ones (e.g., the male of *Isoperla nevada,* Tierno de Figueroa and Sánchez-Ortega 1999) or the one that involves different call production methods (e.g., *Peltoperla arcuata,* Maketon and Stewart 1988, as reported above) (Fig. 6.3). Understanding the evolution of these signals within Plecoptera from ancestral to complex derived models is of particular interest. According to Maketon and Stewart (1988), the ancestral method of signal production was percussion, and those ancestral signals were monophasic repetitions of evenly spaced beats. Increasingly complex signals were favored by natural selection, allowing for greater communication efficiency for pair encounters and, possibly, male fitness evaluation and mate selection. The complexity of signals may have evolved through changes in the rhythmic patterning of signals or patterns of male-female duets, more sophisticated signal production methods (sometimes related to the specialized coevolution of ventral abdominal structures in males), and possibly the use of selected natural substrates for signal transmission (Stewart 1997, 2001, 2009; Stewart and Sandberg 2006). As an example, Fig. 6.4 shows the possible theoretical evolution of vibrational call complexity in the Southern Iberian Perlodidae (from Tierno de Figueroa et al. 2002, 2009, updated with data from Tierno de Figueroa et al. 2011a, 2013, and unpublished data on a Spanish population of *Perlodes microcephalus*), following the evolutionary paradigm proposed by Stewart (2001) and Stewart and Sandberg (2006). According to Fig. 6.4, natural selection would have acted in favor of derivation from an ancestral, monophasic call to new signals with different numbers (higher or lower) of beats, distinct interbeat intervals (often phased and/or grouped to form sequences), or different methods of call production (such as rubbing) (Tierno de Figueroa et al. 2002). In a recent paper, Boumans and Johnsen (2015) proposed that much of the complexity in stonefly duetting could be explained by male competition and pre-copulatory mate guarding with part of the male signal mimicking or masking the female answer.

The stonefly vibrational signals are genetically programmed and species specific, which make them potentially useful lines of evidence for resolving systematic questions and inferring phylogenies within the order (Maketon and Stewart 1984a, b; Stewart and Zeigler 1984b). Therefore, the role of these signals as reproductive isolation mechanisms in Plecoptera has been stressed many times, and they have thus been repeatedly used to solve systematic questions and clarify the taxonomic status of some taxa (e.g., Berthélemy 1979b; Szczytko and Stewart 1979; Tierno de Figueroa and Sánchez-Ortega 1999), sometimes supported by molecular data (e.g., Tierno de Figueroa et al. 2011a; Murányi et al. 2014).

Rupprecht (1969, 1983) noted that sympatric species of *Isoperla* showed more different call models than the allopatric species. The great diversity of calls sometimes detected among closely related species, which mostly coexist in common areas and have very similar flight periods, may be, in part, the result of selective pressures that favor such diversification and avoid erroneous mating (acting, therefore, as a mechanism of prezygotic reproductive isolation) (e.g., Tierno de Figueroa et al. 2002, 2009 for Plecoptera, Matthews and Matthews 2010 for insects in general). This affirmation was pointed out in a recent study, in which Tierno de Figueroa et al. (2011b) analyzed the drumming signals of the four species of *Capnioneura* present in Southern Spain. The call patterns were homogeneous among the four species, only differing in mean interbeat intervals [in fact, in stoneflies, the ability of an unmated female to recognize a signal from a male of the same species appears to be mainly based on the interbeat intervals (Stewart and Zeigler 1984a, Zeigler and Stewart 1985b) and/or, of lesser concern, intersequence intervals, as seems to occur in at least some *Protonemura* species (Tierno de Figueroa et al. 2014), or other parameters (Stewart and Maketon 1990, see below)]. Although the four species have overlapping flight periods, coexistence in the same area has only been reported in *C. mitis* and

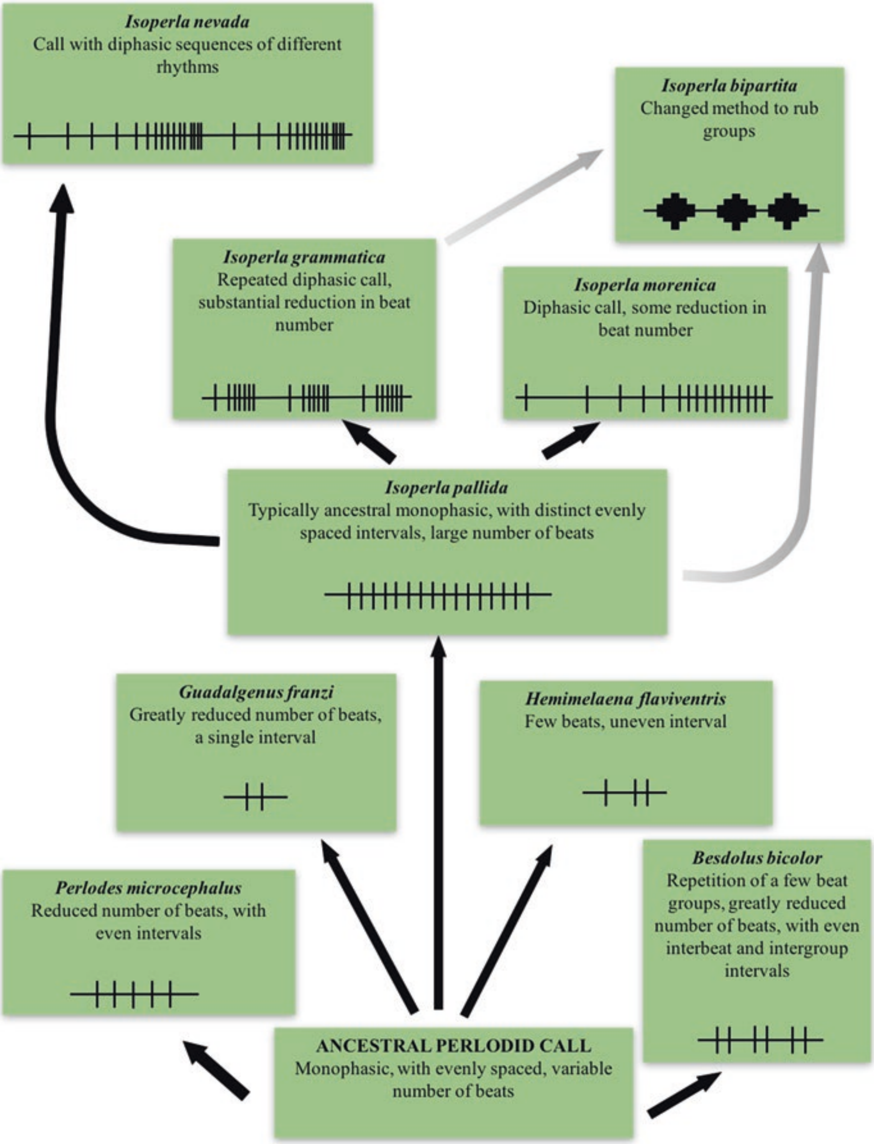

Fig. 6.4 Possible evolution of vibrational call complexity in Southern Iberian Perlodidae (modified from Tierno de Figueroa et al. (2002, 2009) and updated with data from Tierno de Figueroa et al. (2011a, 2013) and unpublished data on the drumming call of a Spanish population of *Perlodes microcephalus*). As the drumming call of the Andalusian population of *Perlodes microcephalus* has not been yet recorded, unpublished data on a *Perlodes microcephalus* population from Central Spain has been used. Gray arrows indicate alternative possibilities

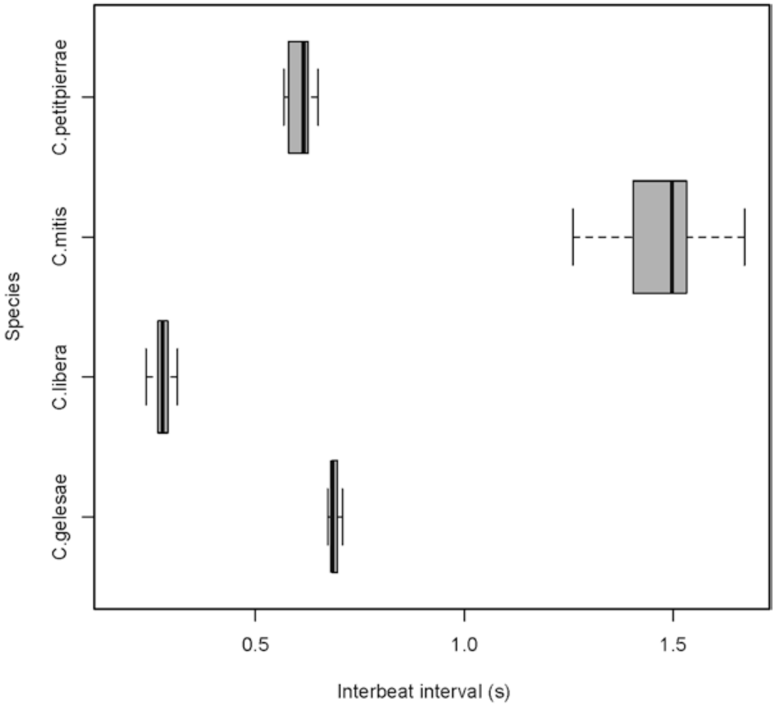

Fig. 6.5 Graphical comparison of interbeat intervals of four Iberian *Capnioneura* species: *C. gelesae*, *C. libera*, *C. petitpierreae* and *C. mitis* (modified from Tierno de Figueroa et al. 2011b). Boxes represent the interquartile range (IQR), whiskers represent data within the 1.5·IQR, and the middle line is the median of the dataset

C. petitpierreae, on the one hand, and *C. mitis* and *C. libera*, on the other. As seen in Fig. 6.5, drumming calls were more different in species that coexist than in those that do not, supporting the hypothesis that stonefly drumming can play an important role as a reproductive isolating mechanism. Nonetheless, cases of hybridization (Hanson 1960) and mitochondrial introgression (Boumans and Tierno de Figueroa 2016) have been detected in stoneflies.

Despite being species specific, the existence of dialects among populations inside the same species has been reported in stoneflies, such as *Diura bicaudata*, which was the first known case of dialects in vibrational signals among insects (Rupprecht 1972). It is also known that temperature can affect the beat rate (and consequently the duration of interbeat intervals) of drumming signals in stoneflies (e.g., Zeigler and Stewart 1977), but females respond to male calls registered at temperatures similar to those where the female is (in Zwick 1980). This coincides with what has been pointed out in a spider species, in which each female appeared to prefer vibrational signals from males that were produced at her current ambient temperature (Shimizu and Barth 1996, in Hill 2008). Experimental studies (with modified computer-simulated male calls) have proven that the female answer depends on (1) a minimum threshold of number of beats or rubs, (2) a discriminative range of interbeat intervals, and (3) other specific parameters, such as general patterns of signals (with sequences, phases, etc.) (Stewart and Maketon 1990). Finally, and despite the short life span of adult stoneflies, age-related effects on drumming have also been described (Maketon and Stewart 1984a; Zeigler and Stewart 1985a), with decreasing numbers of calls per hour in older individuals and no effect on the signal structure. As reported by Zeigler and Stewart (1985a), those differences could be related to age and/or differences in nutritional state.

It was Rupprecht (1968) who first reported that mate encounter is favored by the establishment of a duet between a male and female. Therefore, when a female answers the male's call, he can become oriented by the intensity of the signal. The importance of drumming in mate locating and male searching behavior has been experimentally studied on artificial and natural substrates (Abbott and Stewart 1993; Alexander and Stewart 1996b), and these studies have demonstrated that males could integrate the information received from the answer of the female to correct wrong turns and reinforce correct turns toward her. The ability of certain stoneflies, particularly *Isoperla*, to effectively transmit their drumming signals in the presence of streamside extraneous noises, including rushing water, has been shown as well (Szczytko and Stewart 1979), and experiments with *Perlinella drymo* have demonstrated that signals can be transmitted and received even at a distance of 8 m through a wooden substrate (Stewart and Zeigler 1984b). It has also been reported that the female of *Pteronarcella badia* can discern the fitness of particular males that duet with her by measuring the time required for them to find her, and, if the time requirement is not met, she leaves her position (Abbott and Stewart 1993, in Stewart 1997).

6.2 Encounter Sites

It has been repeatedly pointed out that adults of some species of stoneflies show clear preferences for particular substrates (Zwick 1980) where they aggregate (Fig. 6.6). As vibrational communication is only effective on resonant substrates, and males and females need to be relatively close for the correct signal transmission, the aggregation of individuals at particular sites is an important prerequisite for duet formation (Stewart 1994, 1997). In fact, encounter sites acting as aggregation mechanisms for mating have been described as important events during the imaginal life of Plecoptera (Stewart 1994), as well as of other insects (Parker 1978). These aggregation sites in stoneflies (encounter sites sensu Stewart 1994) can be a consequence of the selection of particular places for emergence by nymphs or the active search for places by adults, mainly through visual patterns, either for reproductive purposes or for places to obtain food or protection (Stewart 1994; Tierno de Figueroa et al. 2000b). Nonetheless, as pointed out by Stewart (1994), some encounter sites, such as bridges, may be such because they are structures that intercept stoneflies when flying or walking.

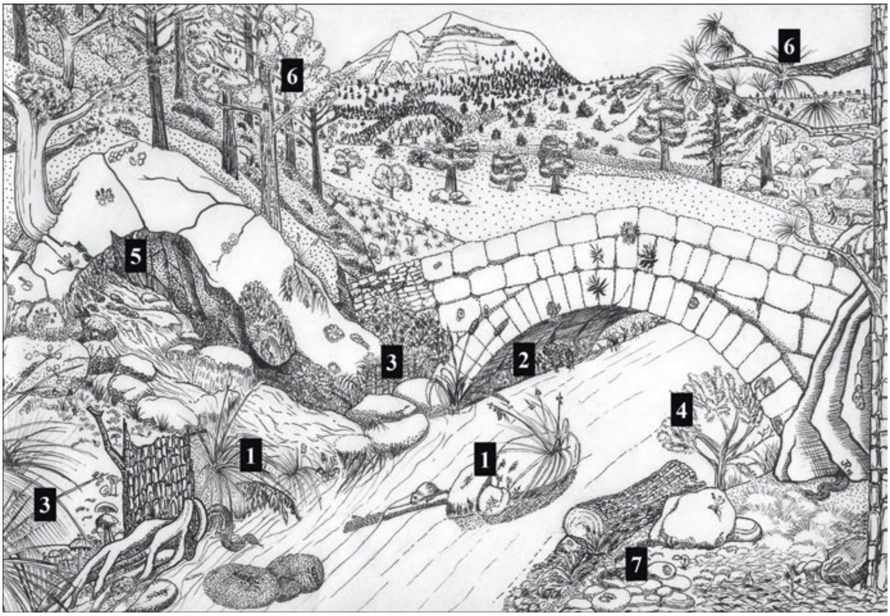

Fig. 6.6 Drawing illustrating a representation of the main aggregation sites of some stonefly species from the Southern Iberian Peninsula based on the authors' observations (this is a hypothetical river putting together species from different areas). *1 Dinocras cephalotes*, *2 Protonemura alcazaba*, *3 Isoperla nevada*, *4 Guadalgenus franzi*, *5 Protonemura gevi*, *6 Capnioneura mitis*, *7 Tyrrhenoleuctra minuta*

Some studies seem to show that emergence substrates could act as encounter sites to aggregate sexes. Alexander and Stewart (1996a), Hanada et al. (1997), and Jáimez-Cuéllar and Tierno de Figueroa (2005) studied three stonefly species, *Claassenia sabulosa*, *Microperla brevicauda*, and *Dinocras cephalotes*, respectively, and concluded that emergence sites seemed to function as encounter sites for mating in these species, in which both sexes were able to mate relatively soon after emergence (additionally, *C. sabulosa* and *D. cephalotes* males are brachypterous and, consequently, have a low dispersal ability). In *D. cephalotes*, Jáimez-Cuéllar and Tierno de Figueroa (2005) found that in the different selected emergence substrates, alternative strategies could be employed to maximize the mating encounter effectiveness, including emerging in stream stones, which favors random mate encounters because of the small surface but renders it difficult due to the ineffectiveness of drumming transmission (and enemy exposure is high), and riparian vegetation, where drumming calls can be transmitted without difficulty, but its greater surface area makes random encounters difficult.

In many cases, stoneflies must actively move to encounter sites, directly or previously aggregating at feeding sites after a postemergence maturation toward mating conditions (Stewart 1994). It is known that many stoneflies need a period of egg maturation (Hynes 1976; Zwick 1980), and adult feeding is also very important for most species (Hynes 1976; Rupprecht 1990; Zwick 1990), except for those with the largest sizes (Tierno de Figueroa and Fochetti 2001; Fenoglio and Tierno de Figueroa 2003).

The existence of encounter sites where individuals of both sexes can aggregate for mating is particularly important in stoneflies from the Southern Hemisphere, which do not produce vibrational signals, and for other species that inhabit particular habitats. Some of these encounter sites could be places where individuals go initially with another aim, such as feeding (Stewart 1994). On the other hand, Stewart (2001) hypothesized that those stoneflies could exhibit particular aggregation behaviors using very specific encounter sites, as well as employ other intersexual communication channels (visual, olfactory, etc.) that are useful for encountering a mate (in Stewart and Sandberg 2006). In this sense, Andersson (1986) experimentally tested the role of pheromones in mate location in the Arctoperlarian *Isoperla grammatica* and concluded that they did not play a significant function in this behavior [although this species employs drumming signals (Rupprecht 1969)]. Nonetheless, Rebora et al. (2016), based on an ultrastructural investigation on the Arctoperlarian *Dinocras cephalotes*, suggested that stonefly antennae were rich in sensilla of different kinds, opening new perspectives into the study of the behavior of these insects during their adult stages, and Abbott and Stewart (1993) pointed out that in *Pteronarcella badia*, when close, males find females by tactile contact. A further electrophysiological study of Rebora et al. (2017) in males and females of *D. cephalotes* demonstrated that they could perceive olfactory cues through their antennae and hypothesized an involvement of the sense of smell in finding the encounter sites.

Although adult behavior data of Southern Hemisphere stoneflies are scarce, Hynes (1974) pointed out that species in different families of Australian Antarctoperlaria fly or climb to tall trees, bushes, or tree ferns. These places probably act as aggregation and encounter sites, and perhaps as feeding places. In relation to the latter, Smith and Collier (2000) pointed out that some adult gripopterygid stoneflies from New Zealand moved toward riparian vegetation to feed after emergence.

As reported by López-Rodríguez and Tierno de Figueroa (2012), the exclusively cavernicolous species *Protonemura gevi* (Fig. 6.7) seems to rely mainly on aggregation sites to maximize pair encounters, considering that, opposite to other epigean species of the genus (Tierno de Figueroa et al. 2014), this species does not seem to produce drumming signals and, even if it could produce them, the substrate inside the cave would not transmit the vibrations. Moreover, the total absence of light is also an important problem for mate searching; therefore, cues other than visual must be implicated in aggregation at particular places. In relation to this, the study of the antennal sensilla of this and two other *Protonemura* species (Piersanti et al. 2017) showed that no differences existed in the types and morphologies of antennal sensilla among the species, but antennae had a wide variety and quantity of sensilla that could help in mate encounter, wherever the habitat.

Another particular species is the wingless stonefly, *Capnia lacustra,* which only inhabits the deep waters in Lake Tahoe associated with *Chara* sp. (Caires et al. 2016).

Fig. 6.7 Male of *Protonemura gevi* in its natural habitat

This is the only known species of this order of insects that does not emerge from the water for mating and laying eggs (Jewett 1963), but unfortunately the knowledge on its mate-encountering behavior is scarce.

6.3 Mating and Mate Guarding

While intersexual vibrational communication has been widely studied in stoneflies, other important aspects of their reproductive biology, such as other strategies for mate finding, copulation, displacement attempts during copulation, and mate guarding, have received scarce attention (e.g., Brinck 1956; Stewart 1994; Alexander and Stewart 1996a; Tierno de Figueroa 2003).

It is known that in some species individuals can mate soon after emergence, while others need a period of a few to several days before mating (Khoo 1964; Hynes 1976; Zwick 1980). Although other factors can also be involved, the degree of gamete development at the moment of emergence could influence how much time is needed. Thereby, some species of stoneflies emerge with mature eggs and can oviposit hours after emergence, while others need to complete egg maturation during the adult stage (Zwick 1980). Similarly, Fausto et al. (2002) observed that in the testes of adults of two species of Perloidea with a large size and long life cycles and that do not feed during the imaginal stage, the spermatogenetic process is complete, and follicular cysts contain only spermatozoa ready to enter into the ducts (as previously reported by other authors, such as Matthey and Aubert 1946), while in some smaller Perloidea species with univoltine life cycles and in which adults actively feed during the adult stage different stages of spermatogenesis can be observed in their follicular cysts.

Although the emergence period (and consequently the flight period) of males and females is almost identical, a protandry (i.e., males emerging earlier than females) has been detected many times in stoneflies with seasonal life cycles that inhabit temperate and cold areas (e.g., Hynes 1976; Zwick 1990; Tierno de Figueroa et al. 2003). A possible advantage of this protandry is that males could search and occupy potential encounter sites while waiting for female emergence (Alexander and Stewart 1996a), enhancing their reproductive success in relation to the fact that females usually mate only once and then become non-receptive, while males can mate many times (in Tierno de Figueroa et al. 2003). Nevertheless, the fact that females copulate several times may be more common than previously reported in the literature (e.g., Brinck 1949; Stewart et al. 1969; Luzón-Ortega and Tierno de Figueroa 2003; Tierno de Figueroa 2003), as discussed below. In a study on *Agnetina capitata*, Moreira and Peckarsky (1994) pointed out that, while females are mature soon after they become adults, the maximum activity and quality of male drumming calls occur some days after emergence, coinciding with the delay observed between male and female emergence. Tierno de Figueroa et al. (2003) studied and quantified the degree of protandry of 11 species with different flight period models. Although all species exhibited a positive protandry value, it was less pronounced in species with very extended flight periods, on the one hand, and particularly brief flight periods or highly concentrated flight maximums, on the other. This is because, in the first case, protandry does not bring benefits, considering that there would be a continuous availability of young females, and in the second displaced flight periods could hinder encounters between the sexes. These authors also obtained that the degree of protandry did not correlate with the degree of sexual dimorphism in size, contradicting the theoretical prediction in other insect orders that dimorphism is positively correlated with protandry and showing that more pronounced protandry is not simply a physiological consequence of differential growth between sexes.

The mating of stoneflies occurs on the substrate (stones, branches, etc.) when males and females meet, and while vibrational signals are very useful for mate encounters they are not an indispensable prerequisite for mating, even in species that employ this communication system (Berthélemy 1979a; Alexander and Stewart 1996a; Tierno de Figueroa et al. 1998, 2000a). Brinck (1956) and Zwick (1973), among a few others, carried out comprehensive studies in stoneflies that related the morphology and anatomy of the reproductive system to copulation. Despite the great extant diversity of stonefly genitalia, particularly the structures involved in sperm transmission (Brinck 1956), the approach and initiation of copulation are very similar in all studied species (e.g., Wu 1923; Frison 1929, 1935; Stewart et al. 1969; Benedetto 1970; Burkantis and Peckarsky 1985; Tierno de Figueroa et al. 2000a; Yoshimura et al. 2003). When a male and a female meet (under conditions of light or darkness, depending on the pattern of diel activity of each species), the male tries to mount the female's back. Some authors (e.g., Khoo 1964; Rupprecht 1968; Zeigler 1990; Tierno de Figueroa 2003) have observed that non-receptive females escape or raise their abdomen or wings to avoid male copulation attempts. If the female is receptive to copulation, the male mounts her and bends his abdomen in an S-shape under the female's abdomen, allowing the contact of his copulatory organ

Fig. 6.8 *Perla* sp. mating

with the female genital opening (Fig. 6.8). Sperm transference in stoneflies can occur through spermatophores (in Antarctoperlaria and some Arctoperlaria such as *Pteronarcys reticulata*, *P. sachalina*, and several Taeniopterygidae) or free sperm (direct semen transfer) (in most Arctoperlaria) (Zwick 2000; Madsen and Aagaard 2016). Stewart and Stark (1977) described a particular external sperm transference in *Hydroperla crosbyi,* consisting of an active aspiration of sperm by the female (by means of telescoping contractions of the abdomen's apical segments) from an external pocket (a cuplike depression formed by the male's epiproct around the female's genital opening) where the sperm was previously deposited and after a cercal brushing or tapping by the male on the female. During the copulation, the stonefly male mounts the female, adopting different positions ranging from parallel (e.g., *Leuctra hippopus* or *Isoperla nevada*) to X-shaped (e.g., *Capnioneura mitis*), passing for V-shaped, more or less oblique (e.g., *Isoperla morenica*, formerly included in *I. curtata*) (Brinck 1956; Tierno de Figueroa 1998; Tierno de Figueroa et al. 2000a).

Some authors (Brinck 1949; Stewart et al. 1969; Benedetto 1970; Tierno de Figueroa 1998; Tierno de Figueroa et al. 1998, 2000a), studying species from Europe, North America, and South America, pointed out the existence of tactile contacts between sexes during copulation, consisting of the male rubbing its mouthparts on the female pronotum or both partners touching each other with the antennae. These contacts have been interpreted as possible tactile stimulation, but they could also be a way of obtaining information about the partner. As noted by Rebora et al. (2016), the presence of olfactory sensilla, gustatory sensilla, and mechanoreceptors in the antennae could play an important role in mate recognition and evaluation. Moreover, it has been reported in some stonefly species that males begin to actively drum just after mating (Brinck 1949). Particularly, in *Isoperla morenica*, formerly included in *Isoperla curtata*, Tierno de Figueroa et al. (2000a) detected this action in all cases in which mating occurred, and they proposed that this behavior could be useful for the female's evaluation of males in terms of cryptic female choice (Eberhard 1997), especially considering that females of this species usually re-mate with other males. Conversely, Zeigler (1990), based on the scarce receptivity of the females of the species that he studied to re-mate or answer male drumming calls, along with their short adult life span and the fact that they probably require mating only once for fertilization of most or all their eggs, suggested that females are probably poorly selective. More studies in different stonefly species are necessary to evaluate the importance of the selectivity of the females in this order of insects.

In the studied stonefly species, males were not selective and, despite having some inactive periods, tried to mate with as many females as possible. In fact, males trying to mate with females of a different species, other males, dead females, or even mature nymphs near emergence have been repeatedly observed in Plecoptera, both in nature and in the laboratory (e.g., Brinck 1949; Khoo 1964; Zeigler 1990; Tierno de Figueroa 1998), as well as in other insects (Thornhill and Alcock 1983). According to Zeigler (1990), this lack of selectivity could be related to the low male investment in sperm transmission (only 1.12% of the body weight of the species he studied, *Pteronarcella badia*). In this sense, it would be expected that males that produce spermatophores were more selective than those that do not, but this hypothesis should be tested in stoneflies.

The time that the couple stays in the mating position is very variable among species (as well as within some species), ranging from just 1 min to several hours or even days (e.g., Brinck 1949; Khoo 1964; Benedetto 1970; Berthélemy 1979a; Alexander and Stewart 1996a; Tierno de Figueroa et al. 2000a; Luzón-Ortega and Tierno de Figueroa 2003; Tierno de Figueroa 2003), and, as reported by most of these authors, long periods in the mating position could correspond with a post-copulatory mate-guarding mechanism (Parker 1970; Thornhill and Alcock 1983). In fact, when a male leaves after mating, the female is susceptible to being fertilized by a new male that could displace the sperm of the first (Zeigler 1991). In relation to this, cases of males attempting to displace other males that are in the mating position are frequently reported, but such attempts are usually unsuccessful (Zeigler 1991; Alexander and Stewart 1996a; Tierno de Figueroa et al. 1998, 2000a; Tierno de Figueroa 2003). Furthermore, Zeigler (1991) observed that couples of *Pteronarcella badia* remained in mating positions for considerably more time when other individuals were present and pointed out that, while his observations were incomplete, they suggested mate guarding by the male during copulation. Afterwards, Tierno de Figueroa (2003) statistically demonstrated that in *Leuctra fusca*, the duration of the male in the mating position is longer when other males interfere, trying to displace him and, from research on this and other species (*Leuctra andalusiaca*, *Capnioneura mitis*, and *Isoperla nevada*), obtained results that seem to support the idea that natural selection has favored a contact mate-guarding mechanism (consisting of long periods in the mating position or the possibility to prolong mating when displacement attempts occur) in males whose females are occasionally polyandric but not in those whose females copulate only once (Tierno de Figueroa 2003; Tierno de Figueroa et al. 2009). In addition to the previously

Fig. 6.9 Mating balls of *Dinocras cephalotes* (left) and *Hemimelaena flaviventris* (right)

referred contact-guarding type, post-copulatory, noncontact guarding mechanisms have also been reported in stoneflies, such as the existence of sperm plugs to prevent subsequent inseminations (Berthélemy 1979a; Zwick 1990).

Finally, another mating strategy displayed by stoneflies is the formation of mating balls, i.e., when some males simultaneously attempt copulation with one female, and they pile onto and around her forming a ball (Tierno de Figueroa et al. 2006). Mating balls have been described in the stoneflies, *Dinocras cephalotes* and *Hemimelaena flaviventris* (Fig. 6.9), and they were previously known in other animal groups, particularly in colubrids and anurans, which share some characteristics, such as the nonexistence of male-male combat, high population density in a relatively concentrated reproductive period, tendency to aggregate, and females that are larger than males (Tierno de Figueroa et al. 2006), suggesting that the same strategy has evolved through convergence in phylogenetically distant groups (Tierno de Figueroa et al. 2009).

6.4 Conclusions

Stoneflies exhibit a wide array of complex behaviors of intersexual communication, mate encountering and copulation, as well as mate guarding, which we have just begun to understand. In fact, as can be concluded after reading this chapter, most of the extant information (except that regarding vibrational communication) comes from the study of one or a few species. Therefore, we only know the tip of the iceberg. We hope that future research focuses on this interesting topic and that our knowledge on these insects continues to increase.

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Chapter 7
Aquatic Insect Sensilla: Morphology and Function

Manuela Rebora, Gianandrea Salerno, and Silvana Piersanti

Abstract Insect extraordinary evolutionary success is due to different reasons among which their ability to receive and respond to a great variety of sensory cues thanks to their developed sense organs encompassing a high number of diversified sensilla, mainly located on their antennae. The successful invasion of lotic and lentic freshwaters by terrestrial insect required physiological constraints also regarding sensory systems. This chapter reviews the present knowledge about antennal sensory equipment in adult and aquatic stages of Ephemeroptera, Odonata, Plecoptera and Trichoptera. These insect orders have aquatic larval stages well adapted to this environment, while they move to the terrestrial habitat as adults. To be able to receive sensory cues in two very different biotopes during the young and the adult stage is a fundamental prerequisite for these insects. The data reported are mainly based on morphological investigations under scanning and transmission electron microscope (SEM, TEM), and behavioural and electrophysiological investigations (the latter available only for Odonata and Plecoptera). The chapter considers separately the main sensory capacities located on the antennae in the above-reported aquatic insect orders, in particular mechanoreception, chemoreception, thermo-hygroreception and their modifications from the aquatic to the adult stage.

Keywords Antennae · Mayflies · Dragonflies · Stoneflies · Caddisflies

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7.1 Introduction

Different factors contributed to make insects the most evolutionarily successful group of organisms on Earth. One of them is probably the ability to respond quickly to external and internal cues, thanks to a great variety of sensory systems able to evolve over relatively short time (Gullan and Cranston 2006).

Insects rely mainly on compound eyes for photoreception while the other senses are located inside special organs defined sensilla constituted of a cuticular and a cellular component. The latter is composed of modified epidermal cells, called auxiliary cells, and bipolar sensory neurons enveloped by a dendrite sheath. Thanks to a specialised sensory cuticle, sensilla can capture specific types of signals, such as mechanical and chemical cues, and convert them into changes in action potentials, which are then carried by sensory neurons to the brain where the information is integrated (primary and secondary pathways). We can distinguish mechanoreceptors, chemoreceptors and thermo-hygroreceptors on the basis of their internal and external morphological and molecular organisation reflecting a different sensory role. Sensilla with pores (multiporous, uniporous) generally serve as chemosensilla, whereas sensilla associated with touch-, thermo- and hygroreception are predominantly aporous (Fig. 7.1). Sensilla can be named after the structure of their cuticular parts (Schneider 1964; Zacharuk 1985), and we can distinguish trichoid sensilla with a long thin hair; chaetic sensilla with a long thick hair; basiconic sensilla with a usually shorter hair and a thin cuticle; styloconic sensilla showing a wide stylus bearing an apical sensory cone; coeloconic sensilla with a short peg-like structure usually situated in a pit; and placoid sensilla situated in a plate-like cuticular structure (Fig. 7.2) (Zacharuk 1985; Hallberg and Hansson 1999).

Nearly 100,000 species from 12 insect orders spend one or more life stages in freshwater (Dijkstra et al. 2014). In consideration that all aquatic insect groups are the result of the invasion of freshwaters by terrestrial groups, adaptation to life in running (lotic) and standing (lentic) water bodies requires interesting physiological constraints, not only about thermo- and osmoregulation, respiration, feeding and locomotion but also regarding sensory systems.

In consideration that antennae are the main insect sensory organs for intra- and interspecific communication and for the detection of environmental cues, the aim of this chapter is to review the present knowledge about antennal sensory equipment in adult and aquatic stages of Ephemeroptera, Odonata, Plecoptera and Trichoptera. These orders (together with Megaloptera, a very small insect order here disregarded) are considered purely aquatic insects because they are almost exclusively restricted to freshwater by an aquatic larval stage showing a closed tracheal system with gills, in agreement with a well-developed adaptation to this environment, while they move to the terrestrial habitat as adults. To be able to receive sensory cues in two biotopes during the young and the adult stage is a fundamental prerequisite for these insects. During metamorphosis (incomplete in Ephemeroptera, Odonata and Plecoptera, complete in Trichoptera), the insect nervous system must change to accommodate the sensory requirements of the new environment.

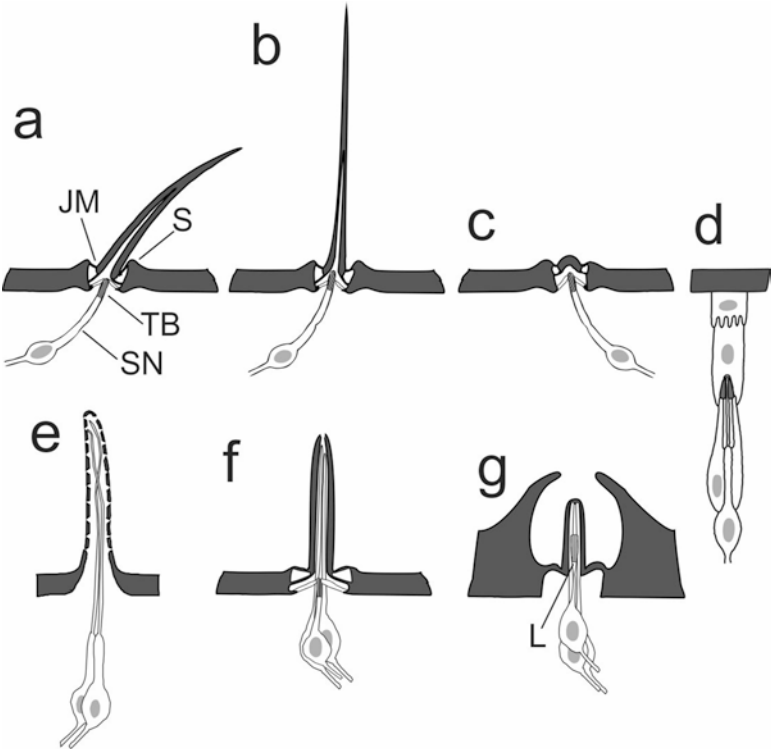

Fig. 7.1 External and internal morphology of mechanoreceptors (**a**–**d**), chemoreceptors (**e**, **f**) and thermo-hygroreceptors (**g**). Chemoreceptors can be multiporous olfactory sensilla (**e**) or uniporous gustatory sensilla (**f**) whereas mechanoreceptors (**a**–**d**) and thermo- and hygroreceptors (**g**) are predominantly aporous. A bipolar sensory neuron/s (SN) innervates each sensillum. Cuticular mechanoreceptors can be hairs (**a**, **b**), campaniform sensilla (**c**) or chordotonal organs (**d**). Hairs can be functionally divided into bristles (**a**) and filiform hairs (**b**). Note that in mechanoreceptors the sensory cuticle (typically a hair) is connected via an elastic “joint membrane” (JM) to a circular or oval socket (S) in the body cuticle. The sensory neuron ends at the base of the sensory cuticle and contains tightly packed microtubules constituting a distal structure called the tubular body (TB). Gustatory sensilla typically have a mechanosensory neuron ending at the base of the sensillum while the remaining sensory cells reach the terminal pore. In olfactory sensilla the sensory neurons enter the sensory cuticle reaching the apical region of the hair. Thermo-hygroreceptors are typically located inside cuticle invaginations, and have inflexible socket and a dendritic sheath connected with the sensory cuticle; thermoreceptive unit typically differentiates lamellae (L) in the outer dendritic segment

Although the morphology of antennae varies greatly among insects, they are composed of three basic segments including scape, pedicel and a sub-segmented flagellum. Traditionally, Ephemeroptera and Odonata have been classified as Paleoptera (old wings), while Plecoptera and Trichoptera belong to Neoptera (new wings). In particular, Plecoptera are basal Neoptera, while Trichoptera have a strongly supported sister taxon relationship with Lepidoptera (moths and butterflies)

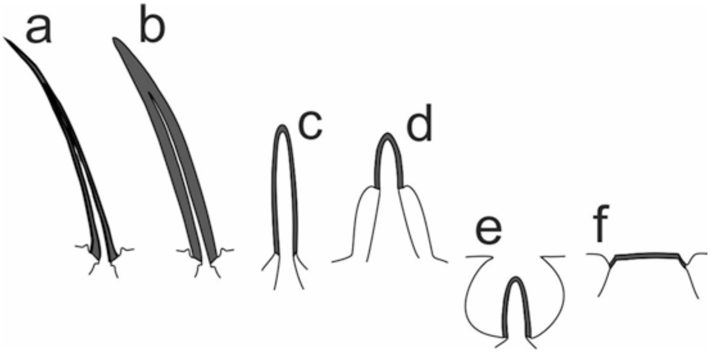

Fig. 7.2 Sensilla categorisation on the basis of their cuticular parts; we can distinguish trichoid sensilla with a long thin hair (**a**); sensilla chaetica with a long thick hair (**b**); basiconic sensilla with a usually shorter hair and a thin cuticle (**c**); styloconic sensilla showing a wide stylus bearing an apical sensory cone (**d**); coeloconic sensilla with a short peg-like structure usually situated in a pit (**e**); placoid sensilla situated in a plate-like cuticular structure (**f**)

(Zhou et al. 2016). Together with their inability to fold the wings over the abdomen, adult Odonata and Ephemeroptera share other common features such as big eyes and short, reduced antennae compared with those present in their larval stage. A different situation, with young and adult stages showing well-developed antennae, is typical of Plecoptera, while Trichoptera show fairly long and threadlike antennae at the adult stage and short antennae in case-bearing species.

In reviewing the knowledge on antennal sensilla in Ephemeroptera, Odonata, Plecoptera and Trichoptera it is worth to remember that Odonata are the best-researched group in this field, while less data are available for Ephemeroptera and Plecoptera, especially at the larval stage; some data are available for Trichoptera at the adult stage while almost nothing is known for the larval stages. The data here reported are mainly based on morphological investigations under scanning and transmission electron microscope (SEM, TEM), and behavioural and electrophysiological investigations (the latter available only for Odonata and Plecoptera).

The chapter considers separately the main sensory capacities located on the antennae in the above-reported aquatic insect orders, in particular mechanoreception, chemoreception, thermo-hygroreception and their modifications from the aquatic to the adult stage.

7.2 Mechanoreception

Mechanoreception is the sense that allows insects to detect movements of objects in the environment and sounds or provides proprioceptive cues (sensory input about the position or orientation of the body and its appendages) (for reviews see Keil 1997; Tuthill and Wilson 2016). The sensory cuticle (typically a hair) is connected via an elastic “joint membrane” to a circular or oval socket in the body cuticle (Fig. 7.1). The joint membrane, due to its resilin-dominated material composition (Michels et al. 2016), is soft and flexible and allows movement and bending of the hair shaft resulting in a stimulation of the receptor. A bipolar sensory neuron is closely apposed to the base of the sensory cuticle, and its dendrite contains tightly packed microtubules constituting a distal structure called the tubular body (Fig. 7.1). The hair acts as a lever arm that exerts forces on the tip of the sensory neuron dendrites, where mechanotransduction channels open to produce electrical currents (Thurm 1965). Cuticular mechanoreceptors can be subdivided into three major groups, hairs, campaniform sensilla, or chordotonal organs. Hairs can be in the form of long, thin, or shorter hairs (trichoid sensilla) or pegs and are functionally divided into filiform hairs and bristles (Fig. 7.1). The bristle seems to be the most common type of mechanoreceptor, usually responding to direct touch, while filiform hairs or trichobothria are sensilla deflected by faint air currents and low-frequency sound, or vibrations of the surrounding environment (Keil 1997). Campaniform (dome-shaped) sensilla are frequently found on the outer surface, particularly near the joints, where they detect stress in the cuticle. Chordotonal receptors are generally found further beneath the integument and can be connected to the cuticle by attachment structures. They serve several functions, including hearing and joint movement detection.

7.2.1 Aquatic Stage

The density of water allows vibrations to be carried much farther than in atmosphere, with the consequence that sounds and movements are more readily detectable than in air. This is the reason why fishes, and many aquatic organisms such as insects, rely greatly on the ability to detect vibrations in water through mechanoreception. Moreover, mechanoreception may be the most important source of sensory information for aquatic insects in consideration that vision underwater can be very challenging in turbidity conditions. The importance of mechanoreceptors in the larval stages of aquatic insects has been highlighted in different behavioural investigations in relation to prey or predator detection (e.g. Peckarsky and Wilcox 1989; Scrimgeour et al. 1994). In Odonata larvae mechanical stimuli have a predominant role in predation (Caillère 1964, 1965, 1968; Corbet 1999; Rebora et al. 2004), as shown in the larva of *L. depressa* which relies on a non-contact mechanical sense for the detection of the prey (Rebora et al. 2004). The ability to respond to faint movements of the surrounding medium is allowed by long filiform hairs characterised by a joint membrane reduced to a very thin cuticular lamella and a complex socket septum with two projections in close connection with the tubular body (Keil 1997; Gaino and Rebora 2001) (Fig. 7.3b). These sensilla have been extensively studied in terrestrial arthropods (Tautz 1977; Shimozawa and Kanou 1984; Devarakonda et al. 1996) and Decapod Crustacea (Laverack 1962; Wiese 1976). In aquatic insects this kind of mechanoreceptors has been reported in all the

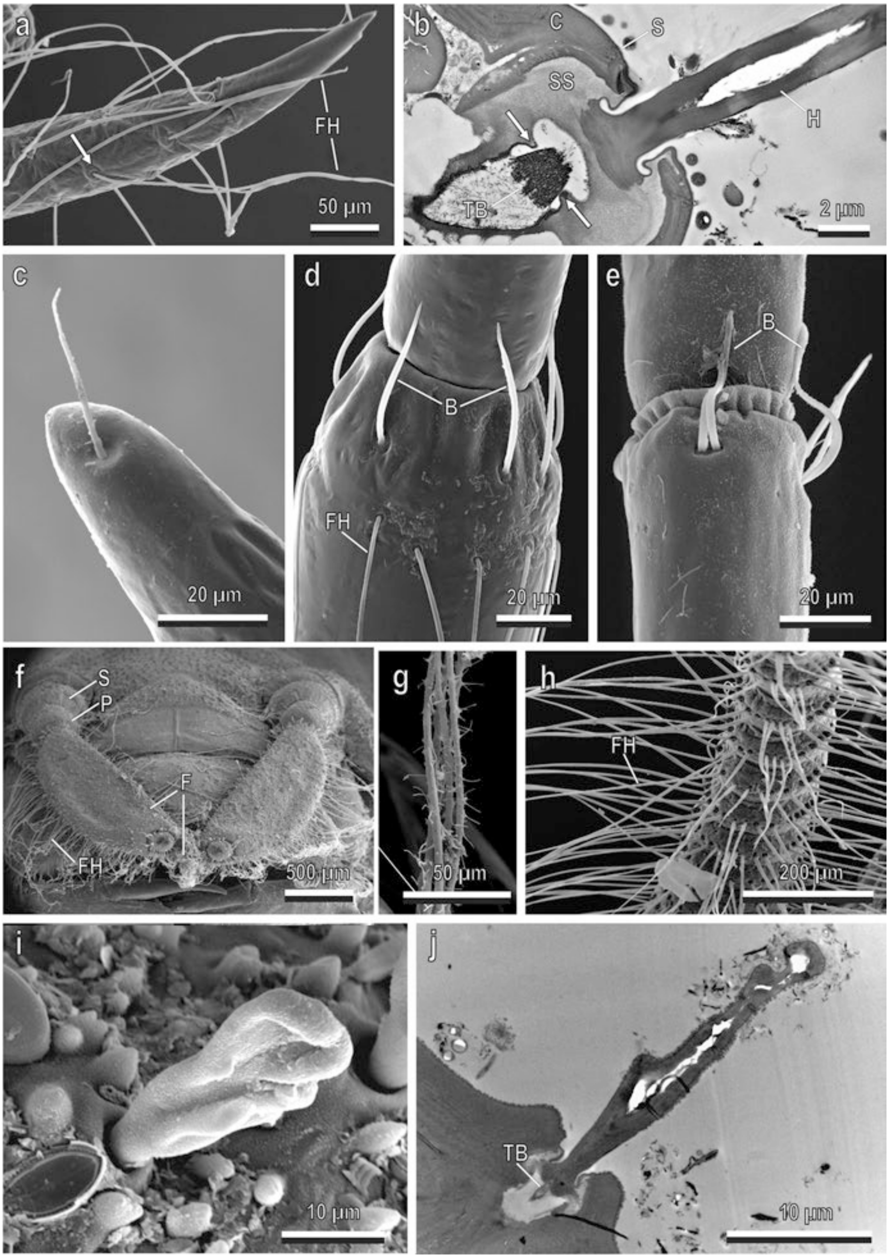

Fig. 7.3 Mechanoreceptors in the aquatic stage of different species belonging to Odonata (**a**–**d**, **f**, **g**, **i**, **j**) and Ephemeroptera (**h**) under SEM (**a**, **c**–**i**) and under TEM (**b**, **j**). (**a**) Filiform hairs (FH) on the antennal flagellum of the dragonfly *Libellula depressa*. Arrow points out the socket; (**b**) longitudinal section of a filiform hairs of *L. depressa*. Note the complex socket (S) and three-socket septum (SS) with two projections (arrows) in close connection with the tubular body (TB). C, cuticle; H, hair; (**c**) apical portion of the antennal flagellum of the dragonfly *Aeshna cyanea*

dragonflies and damselflies larval antennae observed so far (Piersanti and Rebora 2018), belonging to different families such as Libellulidae (Gaino and Rebora 2001), Gomphidae (Faucheux and Meurgey 2009; Rebora et al. 2015), Aeshnidae (Faucheux and Meurgey 2007), Petaluridae (Faucheux and Meurgey 2007), Coenagrionidae (Meurgey and Faucheux 2006a), Lestidae (Meurgey and Faucheux 2006b) and also in the relic dragonfly *E. superstes* (Faucheux 2007) belonging to the family Epiophlebiidae (suborder Anisozygoptera) (Fig. 7.3a, b, d, f, g). Filiform hairs are particularly developed in Odonata species living in lentic environments, while they seem shorter in those living in lotic water (Piersanti and Rebora 2018), probably in consideration that faint movements are easier to be detected in lentic environments. In this regard, in insect orders specialised for living in lotic waters such as Ephemeroptera and Plecoptera, filiform hairs have been described only in a mayfly burrowing species (see below) and in the stonefly *Paragnetina media* (only under SEM) (Kapoor 1985).

As far as bristles are concerned, in Odonata a well-developed mechanosensory seta is located at the apex of the flagellum in *Aeshna cyanea*, *Calopteryx haemorrhoidalis* and *Ischnura elegans* (Fig. 7.3c and 7.5a, b) (Piersanti and Rebora 2018). In different Odonata species bristles are frequently visible along the distal portion of each flagellar segment (Fig. 7.3d) suggesting a function as mechanoreceptors sensing the movements of the different flagellomeres, one in relation to the other (Piersanti and Rebora 2018). In particular, they have been observed in different species of coenagrionids (Meurgey and Faucheux 2006a; Piersanti and Rebora 2018), in *C. haemorrhoidalis* (Piersanti and Rebora 2018), in a lestid (Meurgey and Faucheux 2006b) and in *Aeshna cyanea* (Faucheux and Meurgey 2007). Mechanosensory neurons inside hairs located at the end of each flagellar segment have been observed also in the nymphs of different species belonging to Ephemeroptera (Gaino and Rebora 1997, 1998; Rebora and Gaino 2008) (Fig. 7.3e). Sensilla trichodea located along the distal portion of each flagellar segment are present also in Plecoptera nymphs (Kapoor 1985). Some of them could be mechanoreceptors.

Interesting adaptations are visible in the antennal sensilla of aquatic burrowing species living in running waters under gravel or sandy sediments to avoid the effects of current and predators (Suhling et al. 2015). In this regard, one of the most peculiar antennae in Odonata is that of gomphids, which is composed of four short and flat segments (Fig. 7.3f). The antenna of the gomphid *Onychogomphus forcipatus*

Fig. 7.3 (continued) showing an apical bristle; (**d**) bristles (B) located along the distal portion of each flagellar segment of the antenna of the damselfly *Ischnura elegans*; FH, filiform hairs; (**e**) bristles (B) located along the distal portion of each flagellar segment of the antenna of the mayfly *Ephemera danica* on the ventral side; (**f**) dorsal view of the antennae of the burrowing dragonfly *Onychogomphus forcipatus*, which is composed of four short and flat segments, scape (S), pedicel (P) and flagellum (F) with two segments. FH, filiform hairs; (**g**) detail of the thin thorny trichoid sensilla of *O. forcipatus*; (**h**) dorsal side of the antenna of the burrowing mayfly *Ephemera danica*. Note the developed filiform hairs (FH) located mainly on the lateral portion of the flagellum; (**i**) club-shaped mechanoreceptor with the typical structure of bristle on the antennal flagellum of *O. forcipatus*; (**j**) longitudinal section of the club-shaped sensillum. Note the tubular body (TB) has been observed in detail revealing a great diversity of mechanoreceptors (Rebora et al. 2015). In particular club-shaped sensilla (Fig. 7.3i, j), sensilla chaetica and treelike sensilla show the typical structure of bristles, usually responding to direct touch, while numerous long thin thorny trichoid sensilla of different length (some of them reaching 800 μm) show a morphology recalling the structure of filiform hairs (Fig. 7.3f, g). Since hair length is one of the several parameters determining a hair's mechanical sensitivity (Humphrey et al. 1993), the different length of the numerous filiform hairs of *O. forcipatus* (and the presence of thorns on some of them (Fig. 7.3g)) could serve different ranges of sensitivity, helping in the detection of variation and intensity of water flow. In this regard it is interesting to remember the ability of gomphid larvae to reach safe shelters by burrowing deeper in the sediment during flood periods (Suhling and Müller 1996). Very developed filiform hairs (reaching 800 μm) are present also on the antenna of the burrowing mayfly *Ephemera danica* (Rebora and Gaino 2008) (Fig. 7.3h). These nymphs live in "U"-shaped burrows in sandy sediments and maintain a sediment-free space beneath the head and the body through which water flows taking feeding particles. The filiform hairs located mainly on the lateral portion of the flagellum can be fundamental to inform the insect on the intensity of the water flow inside the burrow.

7.2.2 Adult Stage

The reduced antennae of Paleoptera (Odonata and Ephemeroptera) do not show particular mechanoreceptors on their flagellum except for the presence of occasional campaniform sensilla (Rebora et al. 2009a, b; Piersanti et al. 2010), proprioceptors sensing the bending of the antenna.

On the contrary, a detailed investigation on the antennal sensilla of the stonefly *Dinocras cephalotes* revealed that the most represented sensilla on the developed antenna of the adult are mechanoreceptors (shorter or longer) with a grooved surface with the typical structure of bristles (Rebora et al. 2016) (Fig. 7.6g). These mechanoreceptors could help the insect to explore the surrounding environment (e.g. to find a suitable surface to perform drumming). Indeed, both sexes continuously touch the surface with the antennae during walking on the substrate (Rebora et al. 2016). They could be important also to get information about the partner because it has been reported for some species that during the mating process the male continuously touches the female with its antennae (Tierno de Figueroa et al. 1998).

Trichoptera show a well-developed antenna only at the adult stage. A comparative analysis (based on SEM investigations) on the antennal sensilla type in representatives of various families revealed that straight trichoid sensilla are located on the lateral surface of the antenna on each flagellomere and most likely are mechanoreceptors (Melnitsky and Ivanov 2011).

7.3 Chemoreception

Chemoreception allows organisms to respond to chemical cues in their environments and depends on the senses of taste and smell. Taste is typically used for detection of aqueous chemicals, and smell, for airborne chemical cues—but the distinction is vague. Alternative terms are contact (taste, gustatory) and distant (smell, olfactory) chemoreception. In insects living in water, as in other aquatic animals, all chemicals sensed are in aqueous solution, and strictly all chemoreception should be termed "taste." However, the distinction is still used on the basis of the structure, response or particular location of the sensilla or the animal's behavioural response (Zacharuk 1980).

In insects, chemoreception is mediated by transmembrane receptors (olfactory receptors, ORs; gustatory receptors, GRs; and ionotropic receptors, IRs) located on olfactory and gustatory sensory neurons hosted inside olfactory and gustatory sensilla (see reviews in Vosshall et al. 2000; Galizia and Rössler 2010; Hansson and Stensmyr 2011).

Gustatory sensilla are typically uniporous sensilla responding to taste and tactile stimuli (touch and taste function). One neuron is mechanosensory and ends at the base of the sensillum while the remaining sensory cells reach the terminal pore, and function as contact chemoreceptors (the dendrite sheath stops at the base of the sensory hair) (Fig. 7.1). Olfactory sensilla are typically multiporous and their sensory neurons enter the sensory cuticle not enveloped by the dendrite sheath (Fig. 7.1); on the basis of their morphology they can be distinguished in single-walled sensilla and double-walled sensilla (Altner et al. 1977). Single-walled sensilla can be shaped as hairs, pegs or plates; their pore system has been described in detail by Steinbrecht (1997), and consists of cuticular canals through the hair wall, which on the inner side is connected to pore tubules (Fig. 7.4). Double-walled sensilla show typically a short hair, and are apically provided with slit-like pores that penetrate the cuticle while pore tubules are lacking (Hunger and Steinbrecht 1998) (Fig. 7.4).

7.3.1 Aquatic Stage

Chemical stimuli propagating in water, as when released in air, form a plume that can be preserved at great distances from the source (Murlis et al. 2003). Moreover, freshwater environmental conditions, such as turbidity of water and reduced light transmission, prompt aquatic insects to use chemical cues for intra- and interspecific relationships such as foraging or predator avoidance (Brönmark and Hansson 2000; Wisenden 2000). The ability to perceive chemical stimuli in water has been demonstrated in behavioural observations in larvae of many aquatic insects (see review in Crespo 2011) belonging to Odonata (Chivers et al. 1996; Wisenden et al. 1997; Stoks 2001; Crumrine 2006; Mortensen and Richardson 2008; Siepielski et al. 2016), Ephemeroptera (McIntosh and Peckarsky 1996, 2004; McIntosh et al. 1999; Alvarez et al. 2014), Plecoptera (Williams 1987) and Trichoptera (Gall and Brodie Jr 2009; Okano et al. 2017).

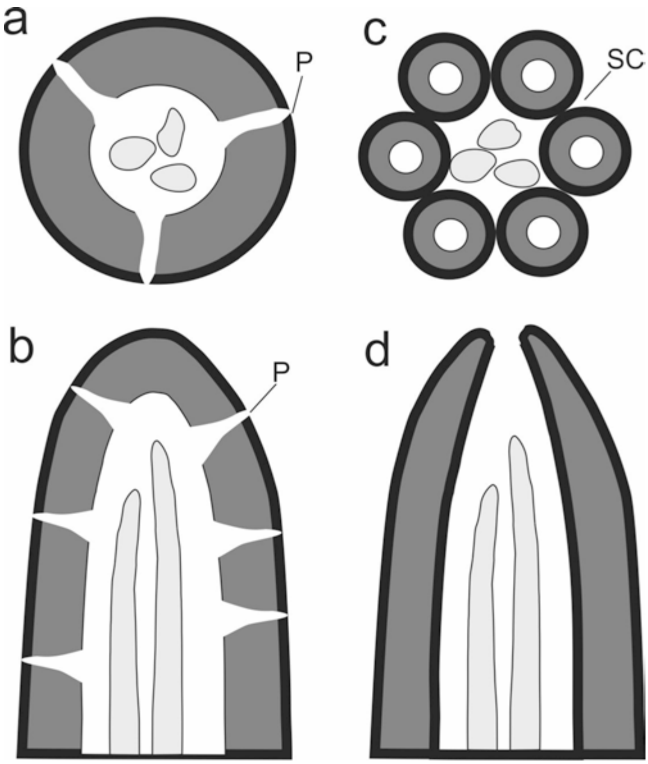

Fig. 7.4 Schematic view of single-walled sensilla (**a**, **b**) and double-walled sensilla (**c**, **d**) in transversal (**a**, **c**) and longitudinal (**b**, **d**) sections. Note in the single-walled sensilla the cuticular canals (pores, P) through the hair wall, which on the inner side is connected to pore tubules. Double-walled sensilla are apically provided with slit-like pores (spoke channels, SC) that penetrate the cuticle while pore tubules are lacking (modified from Steinbrecht 1997)

In Odonata, a composed coeloconic sensillum deriving from the fusion of two individual receptors, each innervated by a group of three neurons entering the peg without dendrite sheath, has been described in the apical portion of the antennal flagellum of all the dragonfly and damselfly species so far investigated and belonging to different families, such as *L. depressa* (Gaino and Rebora 2001), *O. forcipatus* (Rebora et al. 2015), *Epiophlebia superstes* (Anisozygoptera) (Faucheux 2007), *C. haemorrhoidalis*, *I. elegans* (Piersanti and Rebora 2018) and *A. cyanea* (Fig. 7.5a–e). In all the species observed under TEM, pores or pore tubules are not clearly visible in this sensillum but the sensory cuticle of the peg shows an irregular coat with wide channels, underlain by a more or less compact electron-dense layer surrounding the dendrites (Fig. 7.5e). Among the Odonata antennal sensilla, this apical sensillum is the best candidate to represent a chemoreceptor (Rebora et al. 2015; Piersanti and Rebora 2018). The absence of pores on the sensory cuticle could not preclude a chemosensory function; in fact, the aesthetascs, the olfactory organs in Decapod crustaceans, have a thin cuticle without any obvious pores (Tuchina et al. 2014; Derby et al. 2016). The question if and how airborne odour molecules

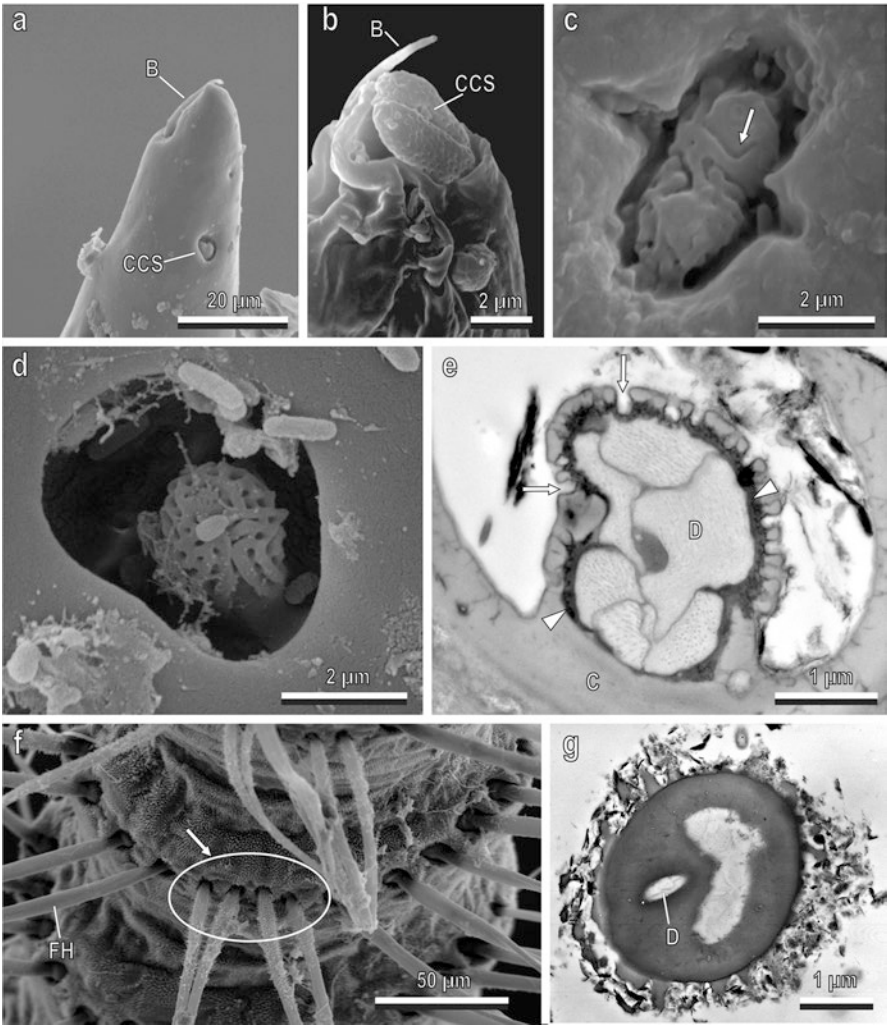

Fig. 7.5 Chemoreceptors in the aquatic stage of different species belonging to Odonata (**a–e**) and Ephemeroptera (**f**, **g**) under SEM (**a–d**, **f**) and under TEM (**e**, **g**). (**a**) Apical portion of the antennal flagellum of the dragonfly *Aeshna cyanea*. Note the subapical composed coeloconic sensillum (CCS). B, apical bristle; (**b**) apical portion of the antennal flagellum of the damselfly *Calopteryx haemorrhoidalis*. Note the apical composed coeloconic sensillum (CCS). B, apical bristle; (**c**) detail of the composed coeloconic sensillum on the flagellum of the dragonfly *Onychogomphus forcipatus*. Note the sensory cuticle of the peg showing an irregular coat with wide channels (arrow); (**d**) same sensillum in the subapical portion of the antennal flagellum of the dragonfly *Libellula depressa*; (**e**) longitudinal section of the composed coeloconic sensillum of *L. depressa*. Note the two groups of three dendrites (D) entering the peg without dendrite sheath. The sensory cuticle of the peg shows an irregular coat with wide channels (arrows), underlain by a more or less compact electron-dense layer (arrowhead) surrounding the dendrites. C, cuticle; (**f**) dorsal side of the antenna of the burrowing mayfly *Ephemera danica*. Note the group of four chemo-mechanoreceptors (arrow). FH, filiform hairs; (**g**) cross section of a chemo-mechanoreceptor of *E. danica*. Note the two dendrites extending along the shaft

penetrate the aesthetasc cuticle in crustaceans is not answered yet, even if in the past it was hypothesised that in water chemicals could simply diffuse through the cuticle (Zacharuk et al. 1971). This hypothesis on chemoreception in an aquatic environment is surely interesting and the composed coeloconic sensillum of Odonata larvae represents a good model to perform electrophysiological investigations to test it (Piersanti and Rebora 2018).

As far as Ephemeroptera are concerned, chemo-mechanoreceptors with an apical pore, a tubular body and dendrites extending along the shaft have been described on the antennae of many species belonging to different families such as Baetidae, Heptageniidae, Leptophlebiidae and Ephemeridae (Gaino and Rebora 1996, 1997, 1998, 1999) (Fig. 7.5f, g). In some families such as Heptageniidae and Baetidae they show a spatulate apical portion and they have been defined flat tipped. The interaction between chemical and tactile cues in mayfly detection of predators has been highlighted in behavioural investigations (Ode and Wissinger 2006).

As far as Plecoptera nymphs are concerned, *Paragnetina media* shows at the distal end of each flagellar segments tufts of multiporous hairs; each hair is innervated by two bipolar neurons (Kapoor 1987). In addition, uniporous basiconic and coeloconic pegs have been described on the antennal flagellum of the nymph of the same species (Kapoor 1985) but no information on their internal structure is available.

Concerning Trichoptera, there is only one paper (Akent'eva 2012) reporting the presence of a sensory area with a porous cuticle at the apex of the antenna of *Limnephilus centralis* (Limnephilidae), but further investigations are necessary to clarify the sensory function of the reduced antenna.

7.3.2 Adult Stage

As above reported, adult Paleoptera have short reduced antennae with a low number of sensilla and a very reduced role in mechanoreception (Rebora et al. 2010). Otherwise, the chemosensory role of these antennae has been supposed for the first time many years ago, because of the presence of porous coeloconic sensilla (Slifer 1977; Slifer and Sekhon 1972), and has been clearly demonstrated by our ultrastructural, electrophysiological and behavioural investigations in the last 10 years.

Damselflies and dragonflies possess multiporous coeloconic sensilla on the latero-ventral side of the antennal flagellum, whose internal structure strongly resembles that of single-walled olfactory sensilla (Rebora et al. 2008; Rebora et al. 2009a; Piersanti et al. 2010) (Fig. 7.6a–c). In detail, these sensilla are innervated by

Fig. 7.6 (continued) its surface, representing an olfactory sensillum; (**f**) longitudinal section of a sensillum coeloconicum of the mayfly *R. semicolorata*. Note the dendrites (D) inside the peg and the pores (P); (**g**) antennal flagellum of the stonefly *Dinocras cephalotes* revealing a high amount of trichoid sensilla (arrows) representing mechanoreceptors, uniporous sensilla chetica (SC) representing gustatory sensilla, digitated pegs (DP) and porous pegs (PP), both representing olfactory sensilla; (**h**) detail of **g**, showing a digitated peg; (**i**) detail of **g** showing a porous peg. P, pores

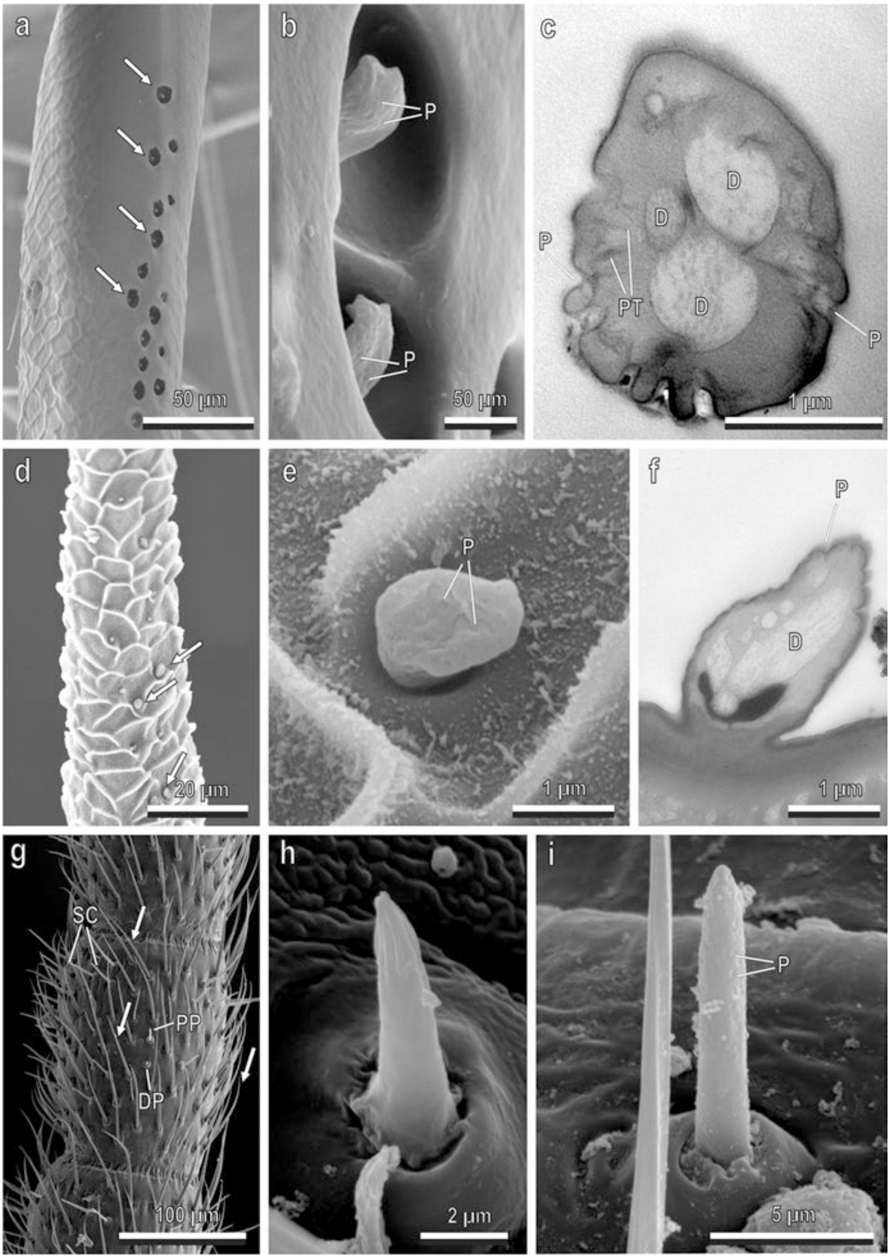

Fig. 7.6 Chemoreceptors in the adult stage of different species belonging to Odonata (**a**–**c**) and Ephemeroptera (**d**, **f**) and Plecoptera (**g**–**i**) under SEM (**a**, **b**, **d**, **e**, **g**–**i**) and under TEM (**c**, **f**). (**a**) Latero-ventral side of the antennal flagellum of the dragonfly *Libellula depressa* revealing sensilla located in pits (arrows); (**b**) detail of **a**, showing the multiporous coeloconic sensilla with pores (P) representing olfactory sensilla; (**c**) cross section of a coeloconic sensillum at the level of the peg. Note the three unbranched dendrites (D) that enter the peg, the pores (P) and the pore tubules (PT); (**d**) antennal flagellum of the mayfly *Rhithrogena semicolorata* revealing sensilla coeloconica (arrows); (**e**) detail of a sensillum coeloconicum of the mayfly *R. semicolorata* with pores (P) on

three unbranched dendrites that enter the peg in direct touch with the sensillum lymph, and contact the environment through actual pores with pore tubules in the sensory cuticle (Rebora et al. 2008, 2009a) (Fig. 7.6c). Single-walled olfactory sensilla in the form of porous pegs innervated by three neurons have been described also in the two-winged stages of mayflies, the sexually mature *imago* and the transitory immature *subimago* (Rebora et al. 2009a, 2010) (Fig. 7.6d–f).

Paleoptera (dragonflies, damselflies and mayflies) have been traditionally considered visual-dependent insects not able to perceive odours, also in consideration that their brain lacks glomerular antennal lobes and mushroom body calices, which in Neoptera are crucial neuropils involved in odour sensing (Strausfeld et al. 1998, 2009; Farris 2005). Our investigations demonstrated that dragonfly and damselfly antennae are able to perceive several odorants, encompassing mostly amines, carboxylic acids and aldehydes (Piersanti et al. 2014a; Rebora et al. 2012), and that these olfactory inputs reach the brain in an aglomerular antennal lobe provided with spherical knots that probably represent the functional connections between the afferent olfactory sensory neurons and the antennal lobe interneurons (Rebora et al. 2013). Secondary pathway of olfaction in Odonata is still unknown but we also demonstrated that olfactory cues are able to drive relevant behaviour in laboratory, such as attraction towards potential prey (Piersanti et al. 2014b) (Fig. 7.7a), recognition of suitable oviposition sites (Frati et al. 2016) and male attraction towards females (Frati et al. 2015). To investigate the role of dragonflies and damselflies olfaction in the field is much more challenging, probably also in view of the dominant role that sight plays in these insects (Corbet 1999) and of the typically noisier natural conditions. Indeed, olfactory cues from females are able to attract males in one-way olfactometer (Frati et al. 2015) but are not enough, for free-flying males, to detect and recognise potential mates along the shoreline of a natural pond (Rebora et al. 2018). The female odour acting as a cue able to elicit electrophysiological responses in male damselflies could be produced by a gland or more probably a cuticular hydrocarbon (Frati et al. 2015), but further chemical investigations are needed to clarify this aspect, totally disregarded so far. Considering the short lifespan of adult Ephemeroptera, in which the main task is reproduction, and some differences in the number and distribution of olfactory sensilla in males and females, it is plausible to hypothesise that mayfly olfaction could be involved in mating, but no behavioural assays or electrophysiological recordings have ever been performed to investigate this topic, and until now the use of chemical signals for sex attraction in Ephemeroptera is only speculative (Crespo 2011).

Despite the re-evaluation of the antennae as olfactory organs in Paleoptera, dragonfly, damselfly and mayfly smell is surely poor in comparison with the most part of Neoptera, and it is probably quite similar to what it was in the common ancestor. This is in consideration of the dominant role of sight in both orders (Corbet 1999; Kriska et al. 2007), of the simple organisation of the antennal lobe (Strausfeld et al. 1998, 2009; Farris 2005; Rebora et al. 2013), of the small number of the flagellar olfactory sensilla (Rebora et al. 2009b, 2010) and of the similarity in the response profile of damselflies and dragonflies (Piersanti et al. 2014a). In addition, Odonata antennae have been demonstrated to be sensitive to several compounds active on

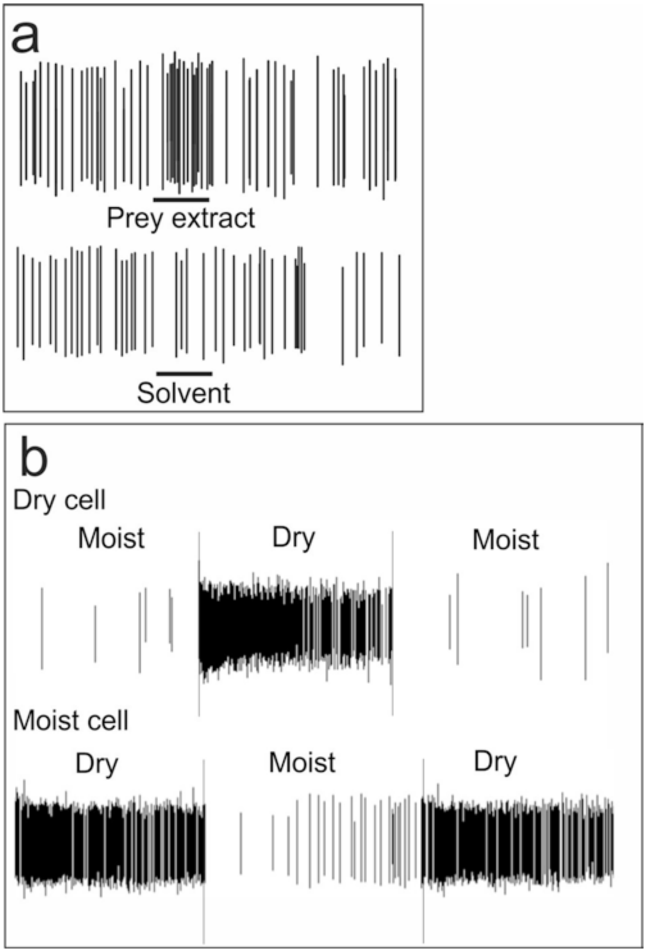

Fig. 7.7 Example of single-cell recording of sensory neurons in adult (**a**) and nymph (**b**) of *Libellula depressa*. (**a**) Response of an olfactory neuron to prey extract in an acetone and hexane blend or to the solvent blend; (**b**) response of hygro-sensory neurons to rapid changes in air relative humidity (RH)

ionotropic receptors (IRs) located in coeloconic sensilla and/or grooved peg of *Drosophila melanogaster* and other insects (Yao et al. 2005), and the odour-response properties observed in dragonflies and damselflies are very similar to those of IR-expressing neurons and very different from the OR-expressing ones (Piersanti et al. 2014a). Considering that only IRs are employed in Archaeognatha olfaction (Missbach et al. 2014) while ORs are typically present in all Neoptera investigated, it could be very interesting to perform molecular investigations also on Paleoptera.

As far as olfaction in Plecoptera is regarded, their long antennae bear porous and digitated pegs (Fig. 7.6g–i) whose internal structure is coherent with that described for single-walled and double-walled olfactory receptors, respectively (Rebora et al. 2016, 2017). In detail, the porous pegs are innervated by two neurons whose outer dendritic segments are branched and fill the lumen of the peg, the dendrite sheath stops at the base of the peg and actual pores characterise the sensory cuticle (Rebora et al. 2016; Piersanti et al. 2017). The digitated pegs can be considered olfactory sensilla in consideration that they are unsocketed and that the outer dendritic segments of the three dendrites fill the peg without dendrite sheath around; moreover, spoke channels between the fingers connect the lumen of the sensillum, containing the dendrites, with the external environment (Rebora et al. 2016; Piersanti et al. 2017). In agreement with this morpho-functional hypothesis, antennae of the stonefly *Dinocras cephalotes*, stimulated with various chemicals in an electroantennographic research, demonstrated to be able to perceive olfactory cues from some acids and ammines, and responses were very similar in males and females (Rebora et al. 2017).

In addition to olfactory receptors, the antennae of Plecoptera bear numerous sensilla chaetica with an apical pore whose internal structure reveals a typical "touch and taste" function (Rebora et al. 2016; Piersanti et al. 2017) (Fig. 7.6g). In detail, they are innervated by five or six neurons and in both cases one of them stops at the base of the shaft forming a tubular body (mechanosensory unit), while the others fill the shaft reaching the apical pore (gustatory units) (Rebora et al. 2016). Considering that the main task of adult stoneflies is reproduction and that the sexes need to encounter in stone rivers, that typically are very heterogeneous and dark habitats, it is possible to hypothesise that chemoreception is involved in this moment of their life cycle. In particular, males and females could use chemical cues to aggregate in sites where they can effectively perform their typical vibrational mating communication, called drumming, and later, after the encounter, to recognise and evaluate each other before mating (Rebora et al. 2016, 2017; Piersanti et al. 2017). At the moment no behavioural data are available on this topic and, as far as we know, no detailed neuroanatomical investigation has been performed on Plecoptera brain. These researches, together with parallel investigations in Paleoptera, could be very interesting, also considering that the adaptation to a highly derived style of life could have produced a secondary loss of the glomerular antennal lobe in terrestrial Neoptera, such as in cicadas (Strausfeld et al. 2009).

The very conspicuous antennae of adult Trichoptera vary in length according to species and sex and are involved in the major olfactory communication channel in the order, mediated by volatiles secreted by the sternal glands (Crespo 2011). The behaviour related with pheromones, the structure of the exocrine glands and the pheromone production has been extensively investigated in the last 30 years, while the antennal structure, and especially the olfactory sensilla situated on the antennal flagellum, has been disregarded so far (Crespo 2011; Melnitsky et al. 2018). Exocrine glands can be present in abdominal sternite of both males and females, and probably produce compounds that have different sexual roles in males and females (e.g. Ansteeg and Dettner 1991), together with common additional roles such as defence against predators (Duffield et al. 1977; Duffield 1981). Morphological investigations of the external structure of antennal sensilla in Limnephilidae (Slifer and Sekhon 1971), Leptoceridae (Tozer 1982), different species of Philopotamidae

(Melnitsky et al. 2018) and other families (Melnitsky and Ivanov 2011) report the presence of thick-walled chemoreceptor pegs, thin-walled chemoreceptor pegs and a special type of thin-walled chemoreceptor called plate organs. These structures are potentially involved in chemical perception, and can be uniformly or differently distributed between sexes depending on the species, but no more detailed data are available on their internal organisation and innervation. Electrophysiological experiments confirmed that identified compounds from the female exocrine glands are perceived by male's antenna (e.g. Löfstedt et al. 1994, 2008; Jewett et al. 1996; Bergmann et al. 2001), and some of these experiments also proved that active compounds produced by males can be perceived by male's antennae and similarly for females (e.g. Jewett et al. 1996; Bergmann et al. 2001). These data suggest that, notwithstanding the close phylogenetic relationship between Lepidoptera and Trichoptera (Zhou et al. 2016), the pheromone system of the latters is much less specific compared with that of the formers. On this account a recent paper (Yuvaraj et al. 2018) suggests a shift in major types of olfactory sensilla, from a high proportion of sensilla placodea or auricillica in Trichoptera and the most basal moth lineages, respectively, to sensilla trichodea in the more derived Lepidoptera, which parallels the change in the types of sex pheromones used. Although moths are typical models for insect neuroanatomy and neurophysiology, there are very few data on Trichoptera brain (Ehnbom 1948; Dacks et al. 2006), reporting that olfactory neurons from the antennae reach the brain in a glomerular antennal lobe, except the genus *Mystacides* that show long antennae and an aglomerular antennal lobe. Molecular investigations on olfaction in these aquatic Neoptera, also in comparison with other aquatic insects and model Lepidoptera, could be particularly interesting to reconstruct the evolutionary pathways of insect olfaction.

7.4 Thermo-Hygroreception

Thermoreception and hygroreception are very important for small terrestrial animals such as insects, which need to cope with a high rate of water loss, due to the large ratio of surface area to body size, have a small storage capacity for water, and depend on temperature of environment for their activity being poikilothermal. Despite its relevance, thermo- and hygro-sensitivity in insects has been poorly investigated in comparison with other sensory abilities such as olfaction (Meritt 2007). In addition to a general role in controlling water balance, to sense humidity and temperature variation can also drive specific behaviours, such as host searching for haematophagous insects (Enjin 2017). Similarly, aquatic insects that lay eggs in water or humid places must detect humidity gradient, and consequently temperature gradient, in air to search for adequate oviposition sites.

Typically, hygro- and thermoreceptors in arthropods are not numerous, located on the antennae and housing together, in a single sensillum, a physiologic triad of receptor neurons: moist receptor, dry receptor and hygrocool receptor (defined according to the input able to increase the firing rate of the neuron) (Altner and Loftus 1985; Yokohari 1999; Enjin 2017). On the other hand, different assortments of sensory neurons have been described in different insects, such as *Periplaneta americana*, which has a hygrocool receptor associated with olfactory receptors in a double-walled sensillum (Nishikawa et al. 1992); *Periplaneta, Locusta* and *Leucophaea*, which have an additional hygrocool cell (Loftus 1976, 1978; Altner et al. 1977; Schaller 1982; Nishikawa et al. 1992); or *Aedes*, which possess both warm and cold receptors in the same sensillum (Davis and Sokolove 1975).

Morphologically, the first report of modality-specific structures in a hygro- and thermoreceptive sensillum, which was unambiguously identified electrophysiologically, is the description of the sensillum capitulum on the antenna of *Periplaneta* (Yokohari et al. 1975). This is a non-perforated cone with a mushroom-shaped inner apparatus. Later, thermo-hygroreceptors have been identified with variable external morphologies in different insects, such as coeloconic in some Orthoptera or styloconic in some Lepidoptera, but some peculiar characters, both in external and internal structure (see review in Altner and Loftus 1985): they typically are protected from wind by cuticle invaginations, and they have inflexible socket, not perforated cuticle, clogged molten pore, clefts and/or cavities in the sensory cuticle and electron-dense material and or lipid-like deposits in the outer lymph cavity, and a dendritic sheath fuse with the sensory cuticle; thermoreceptive units typically differentiate lamellae and/or cylindrical branches in the outer dendritic segments (reviewed in Tichy and Loftus 1996; Steinbrecht 1998; Yokohari 1999; Enjin 2017) (Fig. 7.1).

These features are in agreement with the most accredited transduction models for thermo-hygroreceptors (Yokohari 1999), such as the mechanosensor model that hypothesises a sensory cuticle working as a hygroscopic material, but the transduction mechanism of these sense organs is still unknown (Enjin 2017; Tichy et al. 2017).

Recent molecular and neuroanatomical investigations on hygro-thermoreceptors on the antennae of *D. melanogaster* (Enjin et al. 2016; Enjin 2017) demonstrated that in fruit flies hygro- and thermoreceptor neurons express ionotropic receptors (IR) and the information is processed in a glomerular region of the antennal lobe called posterior antennal lobe. Dry, moist and hygrocool glomeruli are intermingled with hot and cool glomeruli, innervated by pure thermosensory neurons (Gallio et al. 2011), and probably information is combined in the brain to guide fly navigation through the environment. In adult Odonata, the aglomerular antennal lobe is divided in an anteroventral lobe and a larger posterodorsal lobe, probably receiving, separately, olfactory and thermo-hygroreceptor neurons (Rebora et al. 2013). This is the only neuroanatomical study on the organisation of the antennal lobe in aquatic insects and further researches are needed to test this hypothesis and investigate more deeply the topic.

7.4.1 Aquatic Stage

Larval stages of aquatic insects typically live in water, so it is quite obvious to consider as redundant hygroreception in such environment. Otherwise, many aquatic larvae, specially belonging to dragonflies, live in small shallow ponds, sometimes artificial irrigation pools, in temperate climates, and these environments can easily dry out, or reduce to a mosaic of small pools and mud, during very hot summer or because of human activities. On this account, the last larval stages of *L. depressa* (Odonata, Libellulidae) gave evidence of water deprivation tolerance and hygropositive responses out of water in experimental conditions (Rebora et al. 2007a), and in field experiments they showed a great ability to seek for residual water in response to the drying of their pond (Piersanti et al. 2007). In agreement with these behaviours, electrophysiological recordings (Rebora et al. 2007b) on the apical antennae of these larvae demonstrated the presence of moist and dry cells responding antagonistically to humidity changes (Fig. 7.7b), while thermal stimuli were not tested. These responses are related with the presence of two pegs in pits showing typical features of thermo-hygroreceptors at the antennal apex (Gaino and Rebora 2001; Rebora et al. 2007b). They have a sensory cuticle without pores but irregularly folded, a dendrite stopping at the base of the peg where it splits into several branches, and two dendrites entering the peg wrapped by an electron-dense dendrite sheath in close contact with the sensory cuticle around (Gaino and Rebora 2001; Rebora et al. 2007b). Similar coeloconic sensilla, putative hygro-thermoreceptors, have been described in other dragonfly and damselfly larvae (Rebora et al. 2015, Piersanti et al. 2018; personal observations in *Aeshna cyanea*). On this account, it could be very interesting to evaluate how much these sensory structures are widespread in Odonata, also considering the ability of some species to breed in small inconstant aquatic environments, and the need of all species to leave the water, partly or wholly and intermittently or irrevocably, during the days before the emergence (Corbet 1999). On this account it is interesting to remember that dragonfly larvae are able to breathe in air through their gills protected in the anal basket, while damselfly larvae are not, and that odonatan mesothoracic spiracles start to open at the last development stage (Gaino et al. 2007). The timing and duration of emergence also involve responses to temperature in many aquatic insects and precise temperature thresholds for ecdysis have been reported for some aquatic insects (Ward and Stanford 1982). Migration of mature larvae to shorelines where temperatures are more sensitive to terrestrial conditions has been reported for lentic and lotic species (Ward and Stanford 1982).

In Ephemeroptera, coeloconic non-porous sensilla have been reported on the antennae of Baetidae (Gaino and Rebora 1999), but their function cannot be hypothesised because the internal structure has not been described.

As far as Plecoptera is concerned ultrastructural investigations on the antennae of the stonefly nymph *Paragnetina media* describe non-porous sensilla coeloconica, located in shallow pits and innervated by a single neuron entering the peg, that strongly resembles the typical morphology of thermo-hygroreceptors (Kapoor 1991).

No references are available on thermo-hygroreceptors in the greatly reduced antennae of Trichoptera larvae.

7.4.2 Adult Stage

It is well known that many aquatic insects can "see" the presence of water, also when it is covered by bushes or is very far away, on the basis of the horizontally polarised light reflected from the water surface and perceived by the ventral region of the eye (Bernáth et al. 2002; Schwind 1991). Despite this, the ability to perceive humidity and temperature as environmental cues can obviously contribute in adult habitat selection, and can be very important for hygro-thermoregulation in "sunny insects", as dragonflies, that are very active at high temperature and spend many hours perching in sunny places. Hygro-thermoreception could also be useful in taxis behaviour with respect to water; indeed many teneral dragonflies and damselflies show a negative taxis and roost in the landscape until sexual maturation, while they come back to water to reproduce (Hardersen 2007). For fragile insects as Ephemeroptera and Trichoptera, which can dry out quickly during moulting and swarming (Kriska et al. 1998), to be able to orient in suitable hygro-thermoenvironmental conditions is fundamental.

On this account, dry, moist and cold receptor neurons have been identified on the antennal flagellum of the adult dragonfly *L. depressa* (Piersanti et al. 2011). Unfortunately, it was not possible to perform single sensillum recordings on these antennae, because the three types of sensilla present in the flagellum are hosted in pits and are not visible on the cuticular surface (Piersanti et al. 2011) (Fig. 7.8a–c). The authors suggest that the thermo- and hygroreceptive cells identified could belong to deeply sunken sensilla styloconica, described in *L. depressa* (Rebora et al. 2008) and other dragonflies (Rebora et al. 2009a) and damselflies (Piersanti et al. 2010) and "sharing common features typical of thermo-hygroreceptors" (Fig. 7.8a–d). In particular, type 2 deeply sunken sensillum is the most probable thermo-hygroreceptive unit, because it has a rugged cuticular surface with a clogged moulting pore and is innervated by three unbranched neurons, one stopping at the base of the cone and the others filling the stylus, closely adherent to each other and enveloped by a tightly adherent dendrite sheath, in close contact with the sensory cuticle characterised by internal clefts (Rebora et al. 2008, 2009a) (Fig. 7.8b–d).

In mayflies (Rebora et al. 2009b, 2010) and stoneflies (Rebora et al. 2016, 2017; Piersanti et al. 2017) antennal flagella are provided with small pegs whose structure resembles that of thermo-hygroreceptors. In Ephemeroptera they are visible on the antennal surface and innervated by two or four neurons (Fig. 7.8e), while in Plecoptera they are innervated by three neurons and protected in small domes (Fig. 7.8f). No behavioural data are available about the ability of these insects to orient in humidity and temperature gradients, but the most probable function for these sensilla is related with habitat selection and oviposition (Rebora et al. 2009b, 2010, 2016; Piersanti et al. 2017).

Antennal sensory structures in adult Trichoptera, as above reported, show a significant diversity and relevant differences in number, type and distribution between families (Ivanov and Melnitsky 2011, 2016; Melnitsky and Ivanov 2011, 2016; Melnitsky et al. 2018). Then there are no reasons to suppose that caddisfly

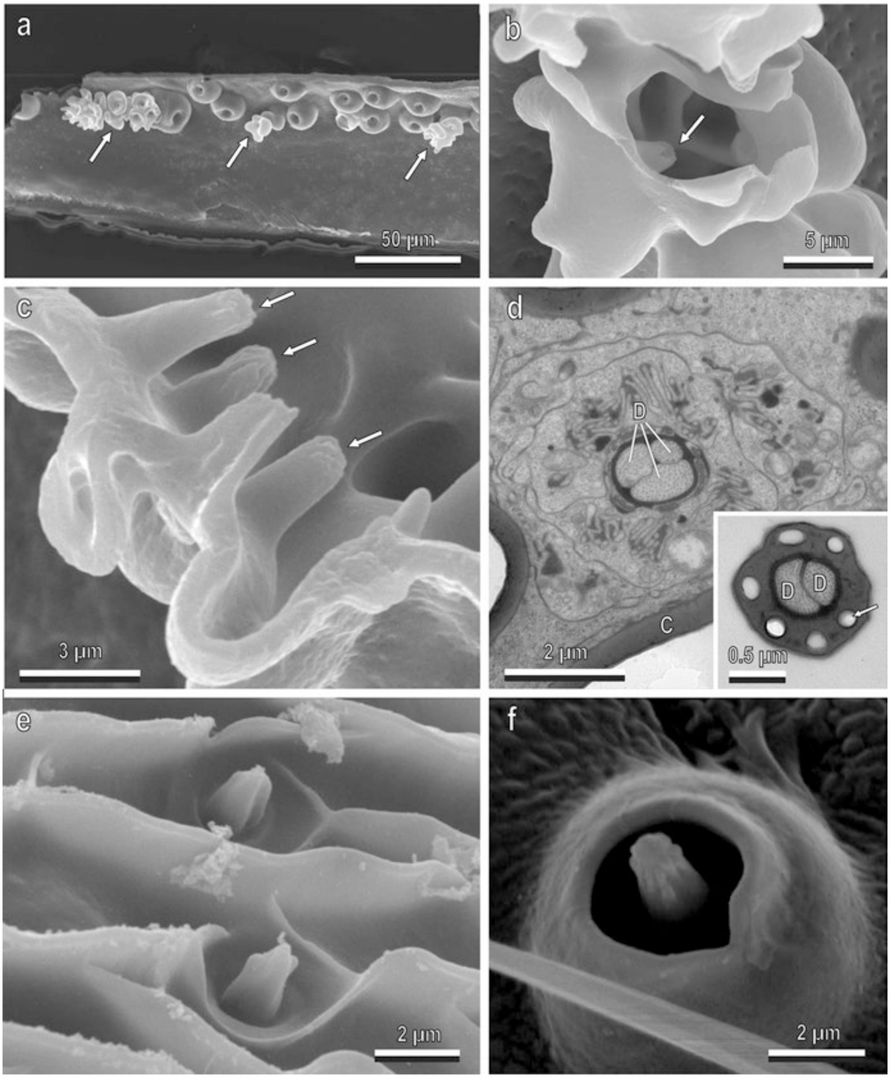

Fig. 7.8 Thermo-hygroreceptors in the adult stage of different species belonging to Odonata (**a**–**d**), Ephemeroptera (**e**) and Plecoptera (**f**) under SEM (**a**–**c**, **e**, **f**) and under TEM (**d**). (**a**) Internal cuticular surface of the antennal flagellum of the dragonfly *Libellula depressa* (treated with KOH to remove the internal tissues (for procedure, see Rebora et al. 2008). Note the convolute deep cavities (arrows) housing the deeply sunken sensilla styloconica probably representing thermo-hygroreceptors; (**b**) detail of a broken cavity showing the presence of a sensillum styloconicum (arrow) inside; (**c**) sensilla styloconica (arrows) inside the cavity. Note the rugged cuticular surface; (**d**) cross section of a sensillum styloconicum at the base of the peg. Note the three dendrites (D) innervating it. C, cuticle. Inset shows a cross section of the same sensillum at a more distal level. Note that one dendrite stops at the base of the peg while two dendrites (D) extend along the peg in close connection with the sensory cuticle characterised by internal clefts (arrow); (**e**) detail of small aporous pegs on the antennal flagellum of the mayfly *Rhithrogena semicolorata* whose internal structure resembles that of thermo-hygroreceptors; (**f**) aporous peg located in a small dome on the antennal flagellum of the stonefly *Dinocras cephalotes* whose internal structure resembles that of thermo-hygroreceptors

antennae cannot perceive relevant environmental cues such as humidity and temperature. Small sensilla of the "lower level," as defined by Melnitsky et al. (2018), probably encompass thermo-hygroreceptors, but no data are available on the internal structure of these sensilla and these sensory abilities have never been investigated in the order.

7.5 Conclusions

The knowledge on the sensory systems underlying the neuroethology of aquatic insect behaviours and the evolutionary pressures that may have shaped them is still poorly known. Further investigations in this field could be particularly relevant for many reasons. A better knowledge of aquatic insect sensilla could play a significant role in unravelling insect perception and adaptability of species to different environmental conditions. To investigate the sensory systems of hemimetabolous insects in particular could shed light on the morphological and synaptic reorganisation of the nervous systems allowing to perform new functions in the transition from the aquatic to the terrestrial environment. Particularly interesting problems such as the reduction of olfaction in adult Paleoptera would deserve attention in relation with the evolution of insect olfaction. Moreover, in consideration that insects have evolved a set of extremely effective sensory systems which are structurally simple, functionally versatile, powerful, highly distributed and noise and fault tolerant (Ma and Krings 2009), to study aquatic insect sensilla can be highly inspirational for the engineering design and biosensor development in the aquatic environment.

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Chapter 8
Territoriality in Aquatic Insects

Gregory F. Grether

Abstract Research on territoriality has barely progressed beyond the descriptive stage in most aquatic insects, but some territorial species have been studied intensively and served as model organisms for testing certain aspects of evolutionary theory. After providing a brief introduction to territoriality in general, I review the taxonomic distribution and types of territoriality reported in aquatic insects, before delving into more theoretical topics. Larval feeding territories have been described in aquatic insects of several orders (Diptera, Ephemeroptera, Odonata, Plecoptera, Trichoptera), while adult feeding and mating territories have only been reported in Odonata (damselflies and dragonflies) and Hemiptera (water striders and ripple bugs). With mostly Odonata examples, I review the following subjects more critically: (1) determinants of territorial status and the outcome of territorial contests, (2) territorial signals and cues, (3) persistence of interspecific territoriality, and (4) agonistic character displacement. Important advances have been made in each of these areas using aquatic insects, but persistent methodological issues have also impeded progress. I offer some general advice for studying territoriality and conclude by identifying areas where more research is needed.

Keywords Territorial behavior · Contests · Character displacement · Agonistic interactions

> For a large number of problems there will be some animal of choice or a few such animals on which it can be most conveniently studied—(Krogh 1929)

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8.1 Introduction

Territoriality is difficult to define in a completely satisfactory way. Simple definitions, such as "defense of space," mean different things to different people, but attempts to define it more precisely often leave out phenomena that should be included (Kaufmann 1983). Of course, biology is messy and there are bound to be cases that are difficult to categorize, but there are also important distinctions to make between territoriality and related phenomena. I will attempt to clarify what does and does not qualify as territoriality while avoiding the pitfall of being overly narrow.

Territoriality is a form of social dominance in which the resident individual (or group) has priority of access to resources (e.g., food, mates, refuges) at a particular location. Dominant-subordinate interactions that are independent of location are not considered territoriality. Not all aggressive interactions are territorial, and not all territorial interactions involve aggression. Most territorial animals have some means of advertising their presence and warding off intruders without direct confrontation (e.g., song, scent marks, visual signals). In some species, territorial aggression is seldom observed, but site fidelity alone should not be equated to territoriality.

Territories range widely in size, function, and exclusivity. Some territorial animals defend multipurpose territories that supply all their daily needs and only occasionally venture outside their territory boundaries. In other species, territories are used only for specific purposes (e.g., mating, feeding, roosting) and cover a small portion of the home range. The distinction between territory and home range is that the territory is the portion of the home range, if any, which is defended against intrusion or resource utilization by some class of individuals. The excluded class typically includes conspecifics of the same age category and sex as the resident (e.g., sexually mature males), but can be broader or narrower. In some species, residents tolerate same-sex conspecifics if they behave in particular ways (e.g., Davies and Houston 1981; Alcock 1982).

Territoriality also varies temporally, such that residents are only active in defense at certain times of day or under particular weather conditions, and it is common for territory defense to be abandoned at very low or high resource levels or population densities (e.g., Gill and Wolf 1975; Wilson et al. 1978; Davies and Houston 1981; Wilcox and Ruckdeschel 1982). The difficulty of observing territorial interactions (in some taxa), combined with spatial, temporal, and situational variation in defense, helps account for conflicting reports about whether particular species are territorial. Territoriality can also vary geographically, however, such that some populations of a species are territorial while others are not (Brown 1964).

Much has been written about the functions, and fitness costs and benefits, of territoriality (Hinde 1956; Brown 1964; Baker 1983; Kaufmann 1983; Stamps 1994). Priority of access to resources is usually at the top of the list of potential benefits, followed by spacing and site fidelity benefits. Spacing benefits can be couched in group selection or individual selection terms. The idea that territoriality reduces population density and thereby decreases the likelihood that a species will exhaust its resources is a group selection hypothesis. But there are several possible benefits of spacing at the individual level, such as avoidance of predators or parasites (Stamps 1994). Site fidelity benefits include being familiar with the location of resources and habitat features, such as efficient travel routes or refuges to escape from predators or inclement weather. While animals can be site faithful without being territorial, non-territorial animals might need to range over larger areas than territorial animals, because spacing reduces exploitative resource competition. Thus, the benefits of spacing, site fidelity, and priority of access to resources often come together as a package in territorial species.

Costs and benefits of territoriality are traditionally considered from the perspective of an undefeatable territory holder (Brown 1964; Gill and Wolf 1975; Adams 2001; Tanaka et al. 2011). This simplifies the problem to whether the benefit of having priority of access to resources in a space offsets the energetic and other costs of defending it. But in reality, territory holders are not undefeatable, and challenging intruders puts residents at risk of losing access to the space. A thorough consideration of the evolution of territoriality requires comparing the expected fitness payoff of territory defense to that of non-territorial tactics, such as scramble competition (i.e., nonaggressive resource exploitation). The payoffs are likely to be frequency dependent, meaning that the best tactic depends on what other individuals in the population are doing. This is not a trivial problem, theoretically or empirically (Grafen 1987; Kokko et al. 2006; Mesterton-Gibbons and Sherratt 2014; Sherratt and Mesterton-Gibbons 2015; Kemp 2018).

In many species, territorial behavior coexists with one or more non-territorial tactics. Much of the theoretical literature on this topic has focused on exploring scenarios in which territorial and non-territorial phenotypes represent different genotypes, and there are some well-documented examples of such genetic polymorphisms (reviewed in Taborsky and Brockmann 2010). However, in the vast majority of cases, the tactics are conditional; individuals develop into territorial or non-territorial morphs depending on their condition (e.g., body size, growth rate) at some critical stage or switch between tactics as their condition or social environment changes (Taborsky and Brockmann 2010). Usually, the territorial tactic has the highest fitness payoff for individuals with higher than average fighting ability (also known as resource holding power [RHP]) while the non-territorial tactic is the best available option for individuals with low RHP, but there are also known cases in which territoriality is the lower fitness tactic (Gross 1996).

8.2 Territoriality in Insects

In a forward-looking review, Baker (1983) asserted that every facet of territoriality in vertebrates is also exhibited by insects and that many questions about territoriality could probably be answered more easily with insects than with vertebrates. Baker (1983) did not explain the latter assertion, probably because it seemed self-evident, but at the risk of stating the obvious most insects are more abundant, shorter lived, easier to catch, easier to manipulate experimentally, and also easier to get permission to study than most vertebrates. Some insects are also extremely easy to observe in the wild without disrupting their natural behavior. Thirty-five years later, the literature on territoriality is still vertebrate biased, but insects have featured prominently in testing certain aspects of theory relating to animal contests (Suhonen et al. 2008; Vieira and Peixoto 2013; Kemp 2018) and interspecific aggression (Grether et al. 2013; Tinghitella et al. 2018).

To the best of my knowledge, the only general review of territoriality in aquatic insects is that of Hart (1987). For most groups of aquatic insects, the relevant literature consists mainly of descriptions of the behavior of particular species. Research on the ecological and evolutionary causes and consequences of territorial behavior is rare in most groups of aquatic insects, the chief exceptions being adult damselflies and dragonflies (Zygoptera and Anisoptera: Odonata; Suhonen et al. 2008) and semiaquatic bugs (Heteroptera: Hemiptera; Arnqvist 1997).

In the first section below, I review what is known about territoriality in aquatic insect larvae before turning to what is known, with greater certainty, about territoriality in aquatic insects at the adult stage.

8.3 Territoriality in Aquatic Insect Larvae

Our knowledge of territoriality in aquatic insect larvae does not appear to have advanced much since Hart's (1987) review. Hart's (1987) Table 1 lists cases of larval feeding territories in damselflies and dragonflies (Odonata), caddisflies (Trichoptera), stoneflies (Plecoptera), mayflies (Ephemeroptera), moths (Lepidoptera) and black flies (Simuliidae; Diptera). According to Hart (1987) the only orders of aquatic insects in which larval feeding territories have not been reported are dobsonflies and alderflies (Megaloptera), spongeflies (Neuroptera), and beetles (Coleoptera). Hart (1987) concluded that feeding territories are seen primarily in species with small foraging areas and high resource renewal rates, and argued that this pattern matches theoretical predictions based on economic defendability (Brown 1964).

Hart (1987) was admittedly rather liberal in classifying species as territorial, and some of the evidence for larval feeding territories has since been disputed. Behavioral studies on aquatic insect larvae are often carried out in the laboratory under conditions of questionable relevance to the natural environment, and it is often unclear whether the aggressive interactions are site dependent (territorial) or site independent (non-territorial). Testing for site dependence requires tracking individuals, and this is rarely done in studies of aquatic insect larvae. In the absence of data on individuals, it is still possible to make reasonably robust inferences about whether aggression results in spacing, however.

Corkum (1978) observed aggression in one of the two species of larval mayflies that graze on periphyton (attached algae) under still-water conditions in the laboratory. She described larvae of the aggressive species (*Paraleptophlebia mollis*) striking each other laterally with their abdomens or facing each other and touching each other with forelegs and antennae until one individual withdrew by a few millimeters. In some instances, one larva chased the other briefly. Based on these observations, Corkum (1978) suggested that aggression and drifting serve as alternative spacing mechanisms in mobile grazing mayflies. Williams (1987) also reported that aggressive interactions appeared to increase spacing among mobile grazing mayfly larvae under low-flow conditions in the laboratory.

Kohler (1992) drew a distinction between sessile grazers and mobile grazers, and questioned whether aggression among mobile grazers occurs under lotic (flowing water) conditions in the wild. Based on field and laboratory experiments, he concluded that spacing among mobile grazing mayflies (*Baetis tricaudatus*) and caddisflies (*Glossosoma nigrior*) in a stream in Michigan results from exploitative competition (i.e., periphyton depletion) alone, and that interference between mobile grazers and filter-feeding blackflies (*Simulium* spp.) and chironomids (*Rheotanytarsus* spp.) results from non-aggressive physical contact (as grazers move around, they bump into and displace filter feeders). By Kohler's (1992) account, only sessile grazers have been shown to exhibit territoriality under natural (i.e., lotic) conditions. For a particularly well-documented example of territoriality in sessile, grazing caddisflies, see Hart (1985).

Aggression appears to increase spacing among filter-feeding black fly larvae (Simuliidae: Diptera). Hart (1986) reported that *Simulium piperi* larvae were most aggressive toward upstream neighbors; filter-feeding rates increased after upstream neighbors were displaced; and aggression decreased when food availability was experimentally increased. Some filter-feeding caddisfly larvae have also been reported to be territorial. Matczak and Mackay (1990) varied food concentration and current velocity in the laboratory and found that the larvae were less aggressive and more closely spaced at higher food concentrations and flow rates. They suggested that spacing is maintained by a combination of aggression (bites and lunges) and signaling (stridulation). Some fights ended with one larva killing and partially consuming the other, but usually one larva was displaced (set adrift) (Matczak and Mackay 1990). Body-size differences and residency (possession of a retreat) both appeared to play a role in the outcome of interactions, and some larvae attempted to take over the retreats of other larvae.

Based on laboratory experiments, Sjöström (1985) concluded that predatory larval stoneflies (Plecoptera) are territorial. The experiments involved placing two or three size-matched *Dinocras cephalotes* larvae together in aquaria and observing them compete over shelters. The evidence for territoriality is that the larvae responded aggressively to each other and the first larva introduced to an aquarium usually dominated newcomers. There are other reports of aggression between larval stoneflies, but whether the behaviors observed qualify as territoriality is not clear. In a laboratory experiment with unlimited food, Lieske and Zwick (2008) inferred that intraspecific interference competition influences the growth and development of the biofilm-consuming stonefly *Nemurella pictetii* and observed aggressive interactions between the larvae, but did not specifically document territorial behavior.

Larval odonates have a well-documented repertoire of agonistic behaviors. The larvae of some species have been described as territorial (Rowe 1980; Harvey and Corbet 1986; Corbet 1999), while others have been described as non-territorial (Baker 1981, 1983; Johnson 1991; Fincke 1996). In the clearest case of territoriality that I found in the literature, Rowe (1980) observed individually color-marked *Xanthocnemis zealandica* damselfly larvae in aquaria and reported that they used the same hunting perches for several days and repelled intruders with a combination of displays (abdomen swinging) and physical attacks (labium strikes). Most such encounters ended with the original occupant keeping the perch and the intruder retreating. Fincke (1996) questioned this and other reports of territoriality in larval odonates, mostly on the grounds that the experimental designs did not allow territorial behavior to be distinguished from non-territorial dominance interactions. Fincke (1996) studied *Megaloprepus caerulatus* damselfly larvae in containers and varied the availability of food and cover. She concluded that spacing within the containers resulted from a kind of size-dependent, site-independent dominance—not territoriality. The key evidence against territoriality is that individual larvae were not site faithful (most moved at least once per day within the containers) and size differences, not prior occupancy, determined the outcome of encounters (larger larvae dominated smaller larvae). Rowe (2006) accepted Fincke's (1996) argument against territoriality in *M. caerulatus* but argued that *X. zealandica* larvae are territorial. More research is needed to establish whether territoriality is common in larval odonates.

8.4 Taxonomic Distribution of Territoriality in Adult Aquatic Insects

Most aquatic insects are not territorial at the adult stage. Adult male mating territories appear to only have been documented in damselflies (Zygoptera: Odonata), dragonflies (Anisoptera: Odonata), and semiaquatic bugs (Heteroptera: Hemiptera). In other groups of aquatic insects, aggression between adults appears to be non-territorial. For example, male-male aggression has been reported in captive Mexican dobsonflies (*Corydalus bidenticulatus*; Megaloptera), but males only responded aggressively to each other in the immediate vicinity of females (Álvarez et al. 2017). If territoriality has been documented in other aquatic insects at the adult stage, I hope this review encourages the researchers to publish their findings.

8.5 Types of Territoriality Reported in Adult Aquatic Insects

(a) Odonata (damselflies and dragonflies): The types of territories that have been reported in Odonata can be divided into feeding (hunting) territories and mating territories. While mating territories have only been documented convincingly in males, both sexes can defend feeding territories (Corbet 1999). In species that hunt from perches, aggressive defense of preferred perches, which are typically higher than surrounding perches (Gorb 1994), is common, and females often dominate males in this context (Corbet 1999).

Mating territories are usually found at water bodies where females come to oviposit, but in some species males defend territories at other sexual rendezvous sites (e.g., forest gaps), and mating pairs travel in tandem (the male clasping the female) to the aquatic habitat where oviposition occurs (e.g., Conrad and Pritchard 1988). The length of time males spend on their territory varies widely, as does the degree of site fidelity exhibited across days. In some species, a male will spend a large proportion of his reproductive life defending the same territory, while in other species males establish new territories daily (reviewed in Corbet 1999).

Territorial odonates can be divided roughly into perchers and patrollers (also known as fliers). In perching species, males adopt a sit-and-wait strategy and rarely leave their perches except to evict male intruders or pursue females. In patrolling species, males regularly fly in a circuit around their territory, searching for females and intruding males. Many species exhibit both modes of territoriality, to varying extents (Corbet 1999). Species that spend most of their time patrolling generally have larger territories than species that spend most of their time perching (Corbet 1999), perhaps because males can only defend what they see. In typical perching species, territories are only a few square meters in area, while the territories of some patrolling species are over 100 square meters (Corbet 1999).

Territorial defense by patrolling is an energetically costly behavior that can limit the length of time males spend on their territories to a small portion of the day. In *Plathemis lydia* (Libellulidae), seven males in succession have been observed patrolling the same territory (portion of a pond perimeter) on a given day (Koenig 1990). Individual males tend to arrive around the same time and defend similar sites on subsequent days, resulting in a kind of temporal partitioning or "time sharing" arrangement (Koenig 1990). By contrast, in some perching species, such as *Hetaerina americana* (Calopterygidae), individual males can reliably be found on their territories throughout the day, except when guarding an ovipositing female (Johnson 1962; Weichsel 1987; Grether 1996b).

(b) Heteroptera (water striders, ripple bugs): Feeding and male mating territories have also been documented in water striders and other semiaquatic bugs (Kaitala and Dingle 1993; Arnqvist 1997). The feeding territories consist of an area on the surface of a water body where the resident has priority of access to food (live or dead arthropods). Feeding territories are seen in both sexes, but females are generally larger and dominant over males and juveniles (nymphs). Experimental manipulations have shown that defense of feeding territories is dynamic and responsive to environmental and social conditions. For example, by manipulating food availability in the field and lab, Wilcox and Ruckdeschel (1982) showed that adult *Gerris remigis* of both sexes defend feeding territories when food availability is between two thresholds. Territoriality is abandoned when food availability is above the upper threshold or below the lower threshold. By manipulating the age and sex composition of pools, Wilson et al. (1978) showed that both sexes and age classes of *Rhagovelia scabra* will attempt to defend territories on the inflow side of the pools, where food availability is highest, but females outcompete males for these positions; at high adult female densities, juveniles and males abandon feeding and cluster together.

Male mating territories are most commonly seen in water strider species with “Type II” mating behavior (Arnqvist 1997). Typically, males anchor themselves to oviposition sites and attract females by sending out “calling” signals by rippling the water surface (Jablonski and Wilcox 1996). When females approach, males switch to “courtship” signals and the female inspects the oviposition site. The female is free to leave, but if she stays the pair copulates and the male usually guards the female from a short distance while she oviposits. Approaching males elicit aggressive “repel” signals and, if necessary, residents will fight physically to defend oviposition sites. By contrast, in species with “Type I” mating behavior, males usually exhibit non-territorial mate searching and attempt to mount and copulate with females without courtship. However, the correlation between territoriality and mating behavior is not perfect. In some territorial species, males attempt to mount females forcibly (Nummelin 1988) and in some non-territorial species males court females (Olosutean 2018). Alternative male mating tactics are found in some species, and males flexibly switch between tactics as conditions change (Arnqvist 1997).

8.6 Determinants of Territorial Status and the Outcome of Territorial Contests

A large body of research on territorial insects has been done in the service of testing animal contest theory (Suhonen et al. 2008; Vieira and Peixoto 2013; Kemp 2018). Much of this research can be characterized as attempting to identify the morphological and physiological determinants of RHP (Vieira and Peixoto 2013). This subject was recently reviewed for odonates by Suhonen et al. (2008), for insects in general by Kemp (2018), and for arthropods in general by Vieira and Peixoto (2013). One overall conclusion is that winners and losers of territorial contests usually differ from each other phenotypically, but the traits that correlate with winning are quite variable among species and cannot be predicted from the mode of fighting (Vieira and Peixoto 2013; Kemp 2018). In a meta-analysis of studies on the determinants of fight outcomes in arthropods, persistence-related traits, such as energy reserves, were not consistently better at predicting the outcome of contests than strength-related traits, such as body mass, or vice versa, regardless of whether the contests involve physical contact or instead appear to be pure endurance contests (Vieira and Peixoto 2013), which is a rather puzzling result.

Damselflies (Zygoptera) have featured prominently in this sector of the literature, but I am not convinced that we have truly learned much about how territorial contests are resolved in damselflies. I will illustrate the problem with a gem of the animal contest literature, a paper that has been cited over 300 times (Marden and Waage 1990). Taking advantage of Waage's (1988) discovery that neighboring *Calopteryx maculata* territory holders can be induced to engage in escalated fights by gradually merging their oviposition sites (clumps of bur weed, *Sparganium* spp.), Marden and Waage (1990) recorded the outcome of such fights, as well as some naturally occurring fights, and then recaptured the males, made mass and size measurements, and carried out whole-body lipid extractions. Winners usually had more remaining fat than losers but did not differ from losers in body size, wing loading, or flight muscle ratio. Since contestants mirrored each other in flight and presumably expended similar amounts of energy, winners must also have had more fat prior to fighting. Based on this, Marden and Waage (1990) inferred that "escalated damselfly territorial contests are energetic wars of attrition." Marden and Rollins (1994) subsequently replicated the study on another *C. maculata* population, with similar results. Most subsequent discussions have focused on questions such as whether male damselflies can assess each other's fat reserves and how they might do so (Marden and Rollins 1994; Mesterton-Gibbons et al. 1996; Payne 1998; Fitzstephens and Getty 2000). However, it is important to realize that while Marden et al. controlled the circumstances of staged fights, they had no control over attributes of the paired contestants. Contest outcomes might therefore have depended on factors correlated with fat reserves, instead of fat reserves per se. Young mature male *Calopteryx* usually contain more fat than older males and are also more likely to win escalated fights (Forsyth and Montgomerie 1987; Marden and Waage 1990; Marden and Rollins 1994; Plaistow and Siva-Jothy 1996). Do young males win because they have more fat, or do fat males win because they are younger? Out of 38 contests for which age estimates were available, 32 (84%) were won by the fatter male and 30 (79%) were either won by the younger male or there was no "discernable" age difference between the males (Marden and Rollins 1994). Taken at face value, these numbers suggest that fat is more important than age, but fat was measured much more precisely than age (Marden and Waage 1990; Marden and Rollins 1994). Furthermore, a male's chronological age, even if known precisely, might not correlate perfectly with age-related factors that affect endurance. In *Homo sapiens*, for example, young mature males can, on the average, outlast old males in endurance contests, but not all males senesce at the same rate (pers. obs.). Body fat reserves may well be one of the critical factors that determine the outcome of escalated contests in damselflies, but experiments disassociating fat content from other age-related factors would be required to test this rigorously.

Several other morphological and physiological variables have also been shown to correlate with territorial status and contest outcomes in damselflies (reviewed in Suhonen et al. 2008; Vieira and Peixoto 2013; Córdoba-Aguilar and González-Tokman 2014; Kemp 2018). The physiological correlates of territoriality have been particularly intensively studied in *Hetaerina* spp. damselflies (reviewed in Córdoba-Aguilar and González-Tokman 2014). Males classified as "territorial" and "non-territorial" have been shown to differ in muscle mass, energy reserves, and immune response, and in all respects territorial males appear to be in better physiological condition than non-territorial males (reviewed in Córdoba-Aguilar and González-Tokman 2014). As in *Calopteryx*, a male's ability to hold a territory first increases and then decreases with age postemergence (Guillermo-Ferreira and Del-Claro 2011; Fig. 8.1), but the relationship between physiological condition and age appears not to have been studied yet in *Hetaerina.*

I am not aware of any published studies in which morphological or physiological variables have been manipulated experimentally to evaluate their influence on the outcome of territorial contests in aquatic insects. Manipulative experiments have

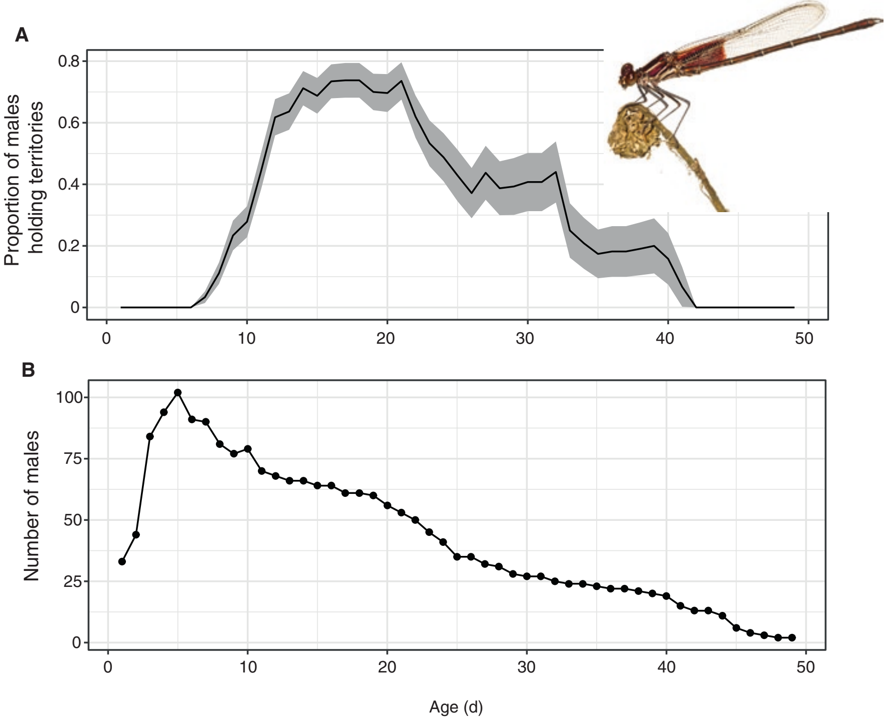

Fig. 8.1 The rise and fall in territorial fighting ability in the damselfly *Hetaerina americana.* (**a**) Variation in the probability of territory ownership with age (0 is the day of adult emergence). The shaded area shows the standard error of the proportions. Most males first acquired territories between 10 and 15 days of age. Territory-holding ability declined sharply after age 21, but some males managed to acquire a second or third territory, which probably accounts for the stepped shape of the declining function. (**b**) Sample sizes on which the proportions and standard errors in (**a**) are based. These data were collected from August 14 to October 22, 1991, on a cohort of $N = 140$ males on a stream in Northern California (for further details, see Grether 1996b, **a**). Age was either known precisely to 1 day or estimated using a multiple regression equation based on the known-age males and phenotypic traits that change with age (Grether 1996a). Sample sizes increase between ages 1 and 5 due to variation in the age at which males were marked and included in the study. Males that were sighted outside the study area, or were missing for one or more days after age 9 until their final disappearance or documented death, were excluded from the cohort. Inset photo of a male *H. americana* courtesy of Neil Losin

been carried out on other territorial insects to test for effects of specific traits on contest outcomes. For example, Kemp et al. (2006) reared butterflies (*Pararge aegeria*) under different thermal and photoperiod treatments to increase variation in morphological traits related to flight performance and staged contests between individuals with different flight morphologies. Interestingly, the only significant predictor of contest outcome was age (Kemp et al. 2006).

8.7 Territorial Signals and Cues

In the animal signaling literature, a cue is a trait that has an effect on the behavior of receivers and a signal is a trait that evolved to have a particular effect on the behavior of receivers (Laidre and Johnstone 2013). Cues and signals affect the behavior of other individuals because they convey information about the signaler, or to be more specific because they reduce uncertainty about the signaler's attributes or future actions (Maynard Smith and Harper 1995). In many if not most cases, signals are likely to have evolved from cues. For example, the disturbance of the water surface caused by a water strider's legs might have originally served merely as a cue that a conspecific is nearby, but over time become modified by selection to serve different functions, such as calling females, courting females, and repelling males (Arnqvist 1997). In this case, we can recognize that there are three distinct signals each with a different function. In other cases, the same trait might serve as a signal in multiple behavioral contexts. For example, color patches on the wings of *Hetaerina* damselflies are used for sex recognition (i.e., distinguishing between the sexes; Grether et al. 2015), male mate recognition (i.e., distinguishing between conspecific and heterospecific females; Drury et al. 2015), competitor recognition within species (i.e., distinguishing between immature and mature males; Grether et al. 2015), and competitor recognition between species (i.e., distinguishing between conspecific and heterospecific males; Anderson and Grether 2010a), and might also serve as indicators of territorial fighting ability (Grether 1996b; Contreras-Garduño et al. 2006; Contreras-Garduño et al. 2007; Guillermo-Ferreira and Del-Claro 2011; Álvarez et al. 2013; González-Santoyo et al. 2014; but see Raihani et al. 2008; González-Santoyo et al. 2010). It is not surprising that one trait (or the homologous trait in males and females) can serve multiple functions, but this is different from showing that it evolved in multiple contexts. For example, did pink wing spots evolve in immature male *Hetaerina* to reduce aggression from mature males, or is pink just a necessary transition in the development of red wing spots? The burden of proof for showing that a trait is a signal is considerably higher than that for showing that it is a cue.

Showing that a trait is a territorial cue (if not also a signal) requires showing that it affects the behavior of other individuals in a territorial context, and the most direct way to do that is to manipulate the trait experimentally. For example, after finding that male *Mnesarete pudica* (Zygoptera, Calopterygidae) with larger red wing spots are more likely to win territorial contests, Guillermo-Ferreira et al. (2015b) presented territory holders with male intruders with and without experimentally augmented red wing spots. They found that territory holders with relatively large wing spots responded more aggressively to experimental males than to control males, whereas territory holders with relatively small wing spots did not differ in their responses to the two treatment groups. Why males with larger red spots have an advantage in territorial fights remains to be determined, but this study leaves little doubt that the red spots are involved somehow. Numerous studies have provided correlational or experimental evidence that coloration affects the outcome of territorial contests in Odonata (Grether 1996b; Tsubaki et al. 1997; Hooper et al. 1999; Plaistow and Tsubaki 2000; Tynkkynen et al. 2004, 2005, 2006; Cordoba-Aguilar et al. 2007; Contreras-Garduno et al. 2008; Guillermo-Ferreira and Del-Claro 2011; Guillermo-Ferreira et al. 2014, 2015a, b; Iyengar et al. 2014; Vilela et al. 2017; Pestana et al. 2018).

There are several possible ways that territorial signals could evolve (Box 8.1). A systematic review of the evidence for, and against, the various models in aquatic insects (or more generally) would be valuable, but is beyond the scope of this chapter. However, there is good evidence that the wing coloration of male odonates directly affects their ability to hold territories (see previous paragraph), is costly for survival (Grether and Grey 1996; Grether 1997), and correlates positively with various measures of phenotypic condition (reviewed in Suhonen et al. 2008; Vieira and Peixoto 2013; Córdoba-Aguilar and González-Tokman 2014; Kemp 2018), which seems most consistent with the handicap model (Box 8.1).

Box 8.1: Classic Models for the Evolution of Territory Signals

Priority model: Territorial signals evolve from cues about the territory owner's presence and increase in conspicuousness to a level that balances the benefits of being detected by conspecifics with the costs of producing the trait and being conspicuous to predators and prey. Territory owners and receivers benefit from avoiding unnecessary interactions, but all the signal conveys to receivers is that the owner is present on the territory (Hansen and Rohwer 1986; Butcher and Rohwer 1989).

Handicap model: Traits with no effect on fighting ability evolve to become honest indicators of fighting ability because larger values of the trait are more costly and the cost of a given value of the trait is lower for individuals with higher fighting ability (Zahavi 1977; Grafen 1990).

Uncorrelated asymmetry model: The size of the trait signals aggressiveness, not fighting ability. For this type of signal to be evolutionarily stable, aggressive individuals must incur a cost independent of any particular contest, the value of the contested resource must be low relative to the costs of fighting, and individuals with deceptively large values of the trait must be punished when they encounter aggressive conspecifics (Maynard Smith and Harper 1988; Johnstone and Norris 1993).

(continued)

Box 8.1: (continued)

Arbitrary identity badge model: Territory signals evolve from cues that initially gave good fighters an advantage by making them more recognizable, but then spread through the population by mimicry; however, once such a trait is fixed in the population, it is no longer useful as a signal of fighting ability (Rohwer and Røskaft 1989).

8.8 Interspecific Territoriality

Territorial aggression between species is quite common in Odonata. In some cases, aggressive responses to other species can be explained as recognition errors (Grether 2011). For example, territorial male *Perithemis tenera* (Libellulidae) chase horseflies and butterflies that are similar in size, color, and flight height to the dragonflies (Schultz and Switzer 2001). Schultz and Switzer (2001) considered multiple alternative hypotheses and concluded that the mistaken identity hypothesis (also known as the misdirected intraspecific aggression hypothesis; Murray 1981) is the most plausible explanation. While male *P. tenera* do not seem to benefit from chasing horseflies and butterflies, the encounters are infrequent, and the costs of failing to respond to conspecific intruders might prevent improvements in discrimination ability from evolving. Similar explanations for the persistence of interspecific aggression have been offered for *Leucorrhinia* spp. dragonflies (Singer 1989, 1990) and *Calopteryx* spp. damselflies (Tynkkynen et al. 2004, 2005, 2006).

A different explanation has been proposed for interspecific territoriality in *Hetaerina* spp. damselflies. Drury et al. (2015) found that levels of territorial aggression between sympatric species in this genus are positively correlated with levels of reproductive interference (i.e., interspecific mating attempts; Fig. 8.2). Pre-clasping courtship is absent in *Hetaerina*, and males initiate mating by clasping females in flight. Females invariably reject heterospecific males, but in the time that takes the female can be transported outside the territory where she was clasped. Thus, from the standpoint of a territory holder, tolerating males of another species could be disadvantageous if they fail to discriminate between females of the two species. Evolutionary simulations based on the damselfly system showed that when males of two species compete locally for females, interspecific territoriality can evolve and be maintained indefinitely (Drury et al. 2015).

8.9 Agonistic Character Displacement

When costly territorial aggression occurs frequently between species, and there are no countervailing benefits, selection should cause the species to diverge in ways that reduce the frequency and costs of the interaction, an evolutionary process known as agonistic character displacement (ACD; Grether et al. 2009, 2013, 2017). Territorial damselflies have provided some of the best evidence for ACD.

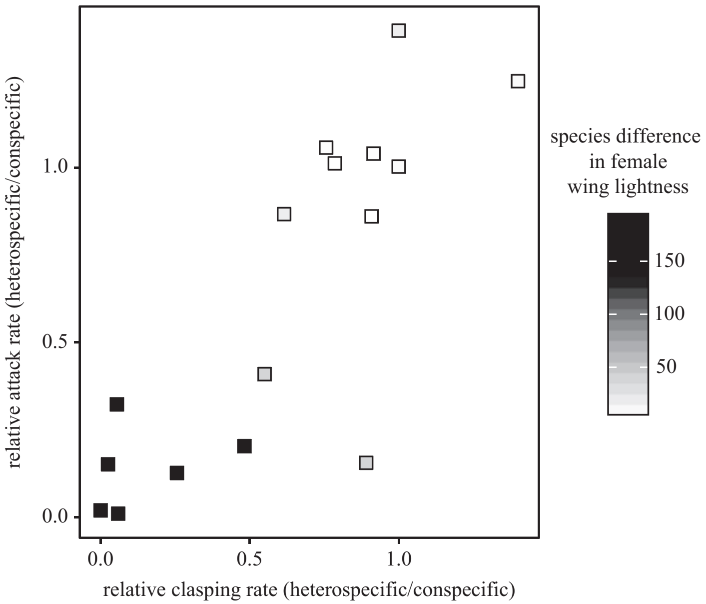

Fig. 8.2 Correlation between reproductive interference and interspecific aggression in *Hetaerina* damselflies. Relative attack rate, a measure of interspecific aggression, was obtained by presenting live, tethered males to territory holders and dividing the number of attacks elicited by heterospecific male intruders by the number of attacks elicited by conspecific male intruders. Relative clasping rate, a measure of reproductive interference, was obtained by presenting live, tethered females to territory holders and dividing the proportion of females that elicited sexual responses in trials with heterospecific males by the proportion of tethered females that elicited sexual responses in trials with conspecific males. Grayscale: Species differences in female wing lightness, as measured by reflectance spectrometry. Each point represents a population at a sympatric site. From Drury et al. (2015) (authors are allowed to reuse their own figures without permission from the publisher)

ACD has been reported in two pairs of *Calopteryx* species, one in Europe and the other in North America (Tynkkynen et al. 2004; Iyengar et al. 2014). Males of one species in each pair have fully black wings (*C. virgo* and *C. maculata*) and males of the other species have partially black wings (*C. splendens* and *C. aequabilis*). In both cases, the species with partially black wings shows a geographic pattern of character displacement in male wing coloration (Waage 1979; Tynkkynen et al. 2004; Mullen and Andres 2007; Honkavaara et al. 2011; but see Hassall 2014; Suhonen et al. 2018). Simulated territory intrusion experiments revealed that males of the species with fully black wings respond more aggressively to heterospecific males with larger amounts of black wing pigmentation (Tynkkynen et al. 2004; Iyengar et al. 2014). As further evidence that geographic wing color shifts in the European species pair were caused by ACD, Tynkkynen et al. (2005) found that survival selection on *C. splendens* wing spots switched from positive to negative as the relative abundance of *C. virgo* increased. Experiments in which *C. virgo* was removed provided further evidence that interspecific aggression is responsible for the character displacement pattern in *C. splendens* (Tynkkynen et al. 2005, 2006). Nevertheless, reproductive character displacement (RCD) is a viable alternative hypothesis for the same geographic patterns because female mate recognition is also based on male wing coloration (Honkavaara et al. 2011; Kuitunen et al. 2011), and evolutionary simulations suggest that RCD would dominate ACD in this situation (Okamoto and Grether 2013).

Two pairs of *Hetaerina* species show geographic patterns indicative of divergent ACD in both wing coloration and competitor recognition (Anderson and Grether 2010a, b). The alternative hypothesis that these patterns were caused by RCD was rejected based on evidence that female mate recognition is not based on male wing coloration (Grether 1996b; Drury and Grether 2014). The key evidence was obtained in a field experiment in which male wing coloration in one species, *H. americana,* was manipulated to resemble that of a sympatric congener, *H. titia*. Compared to controls, male *H. americana* with *H. titia* wing coloration were involved in more interspecific fights and had reduced territory tenure and survival, but experienced no reduction in any component of mating success potentially under female control (Drury and Grether 2014).

Another potential case of ACD has been reported in *Mnais* damselflies (Fig. 8.3). In allopatry, *M. costalis* and *M. pruinosa* both exhibit a male color polymorphism

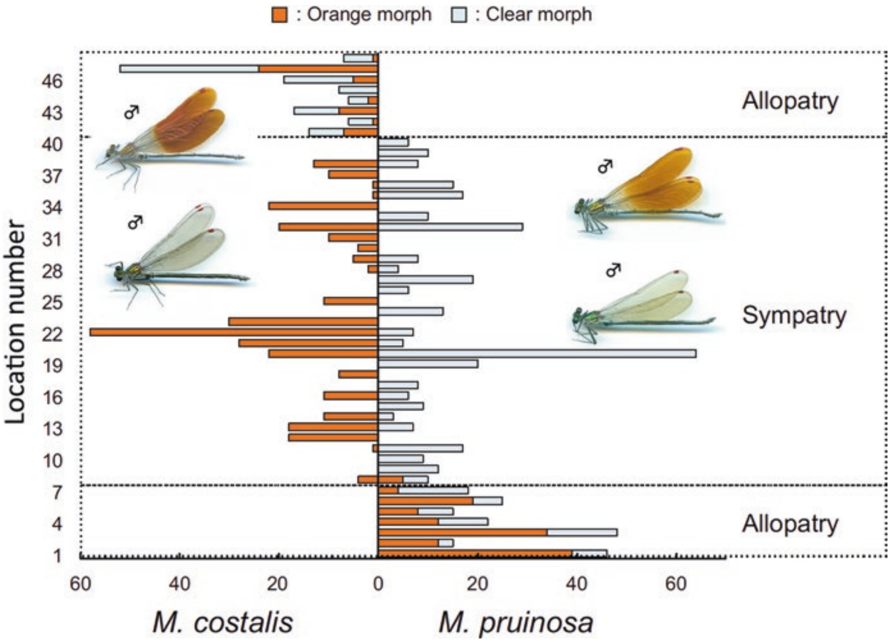

Fig. 8.3 Character displacement pattern in wing color morph ratios of *Mnais* damselflies in Japan. Bars show the number of males of the clear and orange morphs collected at each sampling location. Inset photos show orange and clear male morphs of the two species. From Tsubaki and Okuyama 2016, with permission from Springer Nature

linked to territorial behavior: males with orange wings are territorial while males with clear wings usually pursue a non-territorial sneaking tactic but can switch to territorial behavior if orange males are absent (reviewed in Tsubaki and Okuyama 2016). In sympatry, however, *M. costalis* exhibits only the orange morph and *M. pruinosa* usually exhibits only the clear morph (Fig. 8.3). Apparently, the selection trade-off that maintains the color polymorphisms in allopatry (Tsubaki et al. 1997; Plaistow and Tsubaki 2000; Tsubaki 2003) is disrupted in sympatry (Tsubaki and Okuyama 2016). Whether the character displacement pattern has resulted from aggressive or reproductive interference between the species, both kinds of interference, or some other unknown factor, remain to be determined (Tsubaki and Okuyama 2016; Tsubaki and Samejima 2016).

8.10 General Advice for Studying Territorial Behavior

Studying territorial behavior does not usually require highly specialized techniques or instruments, but it does require attention to certain details that are often overlooked, or disregarded, in studies of aquatic insects. I do not wish to criticize specific papers, but counterexamples to each of the common-sense suggestions below are easy to find in the literature. This complicates making comparisons between species, and even between studies of the same species by different researchers. While different methods might be warranted in studies with different goals, the vast majority of studies of territoriality would benefit from the following practices.

First and foremost, it is essential to have a robust method for distinguishing between individuals. Assuming that animals perching, skating, or flying in the same area at different times are the same individual is totally invalid, as demonstrated, for example, by Koenig's (1990) discovery that seven or more dragonflies can occupy the same territory in succession, on a single day. With rare exceptions, reliably distinguishing between individuals requires marking them with unique codes. It is important to choose a marking technique that allows individuals to be identified without recapturing them or otherwise affecting their behavior, and also to verify that the marks themselves do not affect territorial behavior, mating success or survival (Anderson et al. 2011; Álvarez-Covelli et al. 2015).

Second, it is important to have clearly defined, empirically based criteria for classifying individuals as territory holders and non-territory holders. Ideally, this would involve multiple observations of territory defense, but at a minimum should include establishing that an individual is site faithful on an appropriate timescale (which varies by species). Verifying territory defense does not necessarily require waiting for naturally occurring encounters; it is often possible to test for aggressive responses by simulating territory intrusion (e.g., by presenting conspecifics, models, or other stimuli that evoke territorial responses). It is also important to recognize that being a territory holder is a temporary state, not a characteristic of the individual. In some species, all individuals of a particular age and sex class are territorial in the sense that they would occupy and defend space if they had the opportunity and ability to do so.

Third, while it might be convenient to assume that individuals that have disappeared from the study area have died, this is a very tenuous assumption for flying insects, unless the study area encompasses the dispersal range of the species. Equating disappearance to death is particularly problematic in studies correlating territorial behavior and associated phenotypic traits with components of fitness, such as survival and mating success (i.e., selection studies), because individuals that fail to secure a territory in the study area might succeed elsewhere. Survival analysis is a statistical method that allows "censored" observations to be included without bias, and is often a good choice for analyzing these kinds of data.

Finally, as is always the case in science, it is important not to confuse a statistical correlation between two variables with evidence that one variable has a causal influence on the other. In a true experiment, the researcher has control over one or more independent variables. Just because a manipulation of some sort has been carried out does not necessarily mean that the hypothesis of interest has been subjected to an experimental test. This issue has surfaced repeatedly in studies attempting to identify the determinants of territorial status or the outcome of territorial contests. Unless the predictor variable has been manipulated experimentally, it might be confounded with other variables that also affect territorial contests (Grether 1996a; Suhonen et al. 2008).

Overcoming the methodological issues described above is relatively easy with damselflies and water striders, and some species of dragonflies are highly tractable too. In addition to being easy to catch and mark individually, these insects habituate to humans and consequently can be observed directly at very close range. If more behavioral ecologists followed Krogh's (1929) principle, I think territorial aquatic insects would be even more popular for ecological and evolutionary studies than they already are.

8.11 Future Directions

Most behavioral ecologists would probably rank territoriality among the best understood and least controversial subjects in their field. But it is rather easy to identify important questions about territoriality that have received very little rigorous scientific attention. Why are some species territorial while others are not? Why do some species defend multipurpose territories while others only defend mating or feeding territories? What effects does territoriality have on dispersal and population connectivity? Does territoriality regulate population size? What role does territoriality play in speciation? Under what circumstances is interspecific territoriality adaptive? How do territorial interactions between species affect their coexistence and evolution? How does interspecific territoriality affect the structure of ecological communities? Does territoriality affect whether introduced species become invasive? Should territoriality be taken into account when projecting effects of climate change on species ranges? None of these questions is specific to aquatic insects, but as Baker (1983) suggested they could probably be answered more easily with insects than vertebrates.

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Chapter 9
Defenses of Water Insects

Konrad Dettner

Abstract This chapter compiles active and passive defensive mechanisms of aquatic and semiaquatic developmental stages of all insect orders against various predators. Mainly escape reactions, mechanical defense, defensive stridulation, and especially chemical defenses are described, illustrated, and tabulated. Apart from the large aquatic groups of ephemeropteran, Odonata or Trichoptera larvae especially aquatic bugs and water beetles are considered by even including small groups from Collembola up to Mecoptera.

Differences between defensive mechanisms and strategies in aquatic and terrestrial insects are described. Aquatic insects especially rely on escape, mechanical defenses, defensive stridulation, and chemical defenses. Exocrine glands are mainly restricted to large taxa with both terrestrial and aquatic representatives (adephagan beetles, Heteroptera) and not invented in aquatic groups. Chemically aquatic insects especially evolved biosynthesis of aromatic and few aliphatic compounds against microorganisms. In contrast mainly steroids are targeted against cold-blooded vertebrates such as fishes and amphibians. As compared with terrestrial insects, aquatic representatives lack many mechanisms of defense such as reflex bleeding, incorporation of toxic compounds from plants, freshwater animals, or microorganisms. Exocrine secretions of water insects are usually externalized by secretion grooming in order to receive a clean body surface, to achieve an optimal breathing, and to modify the wettability of the body surface. Generally there exists a considerable lack of knowledge concerning bionomy and especially defenses of aquatic insects.

Keywords Mechanical · Chemical defense · Compilation aquatic insect orders

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9.1 Introduction

Adults and developmental stages of aquatic insects are eaten by many predators (e.g., carnivorous fishes, predatory insects, various invertebrates), suffer from parasitoids, and have problems with insect pathogenic microorganisms (Protozoa, Bacteria) and fungi. In extreme cases water insects may suffer from snake attacks (Peddle and Larson 1999) and reversally prey on vertebrates (McCormick and Polis 1982). Therefore water insects which are found in various sometimes unique habitats (Heckman 2018) have to defend against these natural enemies and evolved various strategies of defense, sometimes even multiple defenses against these target organisms.

There exist many important general books dealing with defense mechanisms of animals or insects: Curio (1976), Edmunds (1974), Evans and Schmidt (1990), and Ruxton et al. (2004). In 1990 Witz studied antipredator mechanisms of hundreds of arthropods from terrestrial and aquatic habitats and showed that active or secondary defenses are most important. These defenses are energetically expensive mechanisms, which increase the probability of surviving attacks of predators. They include for example chemical defenses (46%), fighting (11%), escape reactions (8%), postural defenses (4%), armors (3%), or defensive stridulation (2%). In contrast Witz (1990) showed that passive or primary defenses such as cryptic appearance (9%) or group size (4%) are of minor importance. These defenses seem relatively inexpensive and reduce the probability of an encounter between predator and prey.

The main aim of this review is to compile such active and passive defenses in all aquatic insect orders and aquatic or semiaquatic developmental stages (especially larvae) of water insects. Also aquatic representatives of usually terrestrial orders are considered, because now many data from these and other taxa are available due to publications on biodiversity and many valuable books, for example "Thorp and Covich's Freshwater Invertebrates" (Thorp and Rogers 2015, 2016; Hamada et al. 2018). With regard to insect species numbers in different biogeographical regions (Stork 2018) especially the incredible species diversity in the neotropics (1,620,000 insect species) as compared with the Palaearctic (524,165 insect species; albeit terrestrial taxa) were helpful for this compilation, because the various strategies of defense increase towards tropical areas.

Since theoretical data on predator-prey interactions are abundant (e.g., Resh and Rosenberg 1984; Kerfoot and Sih 1987; Williams and Feltmate 1992; Lampert and Sommer 2007; Lancaster and Downes 2013) these interesting aspects were not considered. The same applies to chemical signals such as pheromones or kairomones which were compiled by Chivers and Smith (1998), Burks and Lodge (2002), Sotka et al. (2009), Ferrari et al. (2010), and Brönmark and Hansson (2012), although our knowledge on chemistry of these interesting signal molecules is very poor. For this review it is highly interesting to consider and to compare with valuable papers dealing with defense of water insects such as from Peckarsky (1984), Scrimshaw and Kerfoot (1987), Crespo (2011), or Kicklighter (2012). Also chemical defenses of lower freshwater animals (apart from insects) may be of interest (Dettner 2010) because these animals might be fed by aquatic insects (Bay 1974).

Unfortunately data on bionomy of eggs, egg deposition (Hinton 1981; Hilker and Meiners 2002), and especially pupation in most holometabolous taxa are scarce or unknown especially with respect to aquatic and semiaquatic taxa. Therefore these data are nearly unavailable for this compilation. Moreover it seems interesting for forthcoming evaluations to consider the significance of attachment devices (Gorb 2007) and the role of adhesives (Betz and Kölsch 2004; Betz 2010) as defense mechanisms of aquatic insects. Apart from the dytiscid beetles (Dettner 2014) the same lack of knowledge concerns interactions between symbiontic and parasitic internal but also external microorganisms (bacteria, fungi), protozoa (peritrichic Ciliata, Laboulbeniales), and in/external parasites (mites, trematodes) and their water insect hosts.

Depending on the number of aquatic taxa within each insect order, the data on defenses of aquatic insects are presented on the level of the order or alternatively on the family level. The percentual value of aquatic or semiaquatic species as compared with the total species number per taxon is indicated after each insect order. Bold numbers in the text and legends indicate numbers of compounds (see Tables 9.1, 9.2, and 9.3).

I hope that further studies of biology and bionomy of water insects may help to complete our fragmentary knowledge concerning defense mechanisms of these interesting animals, especially if tropical taxa are additionally taken into consideration.

A lot of phylogenetic trees indicate that the elder arrangement of entognathous taxa as insects (e.g., Dettner and Peters 2010) has to be corrected. Rather now ectognathous taxa represent Insecta whereas Entognatha + Ectognatha are named Hexapoda (e.g., Beutel et al. 2014). Nevertheless semiaquatic Collembola as representatives of Entognatha are treated in this chapter.

COLLEMBOLA (springtails; about 45% hydrophilous): With worldwide approximately 9000 species (Stork 2018: 8140; according to Cipola et al. 2018 probably 50,000 species) this is the largest group of apterygote and endognathous insects or hexapods. Due to their jumping ability with furca and retinaculum (springtails) and detachable hairs and scales this is a well-defended taxon. Unusually for insects springtails continue to molt (up to 52 stages) after reaching sexual maturity. However there is a gap of knowledge with respect to collembolan biology which might be correlated to their small body size and the difficulty to determine all species. With respect to their habitats about 45% of all Collembola species are hydrophilous, represent riparian species, are associated with wet habitats as shores of ponds and lakes, or are frequent in marine littoral zones (Thorp and O'Neill 2015). Cipola et al. (2018) divided Collembola into primary or water-dependent and secondary (epigean hydrophilous) aquatic-associated species. However no species has developed a permanent underwater lifestyle, wherefore no special adaptations for swimming or diving have evolved. Instead most species have hydrophobic hairs, a type of wax and/or a specific surface geometry like microtubercles. Even under high pressure, with the addition of surfactants or other organic fluids Collembola are not

Table 9.1 Constituents **1–23** of pygidial glands in genera (number of species) of predacious diving beetles (Dytiscidae; for species data see Dettner 2014)

Dytiscidae, Hydroporinae	
Hyphydrus (2 sp.).	(2), (3), 11, 12, 13, 16
Hydrovatus (1 sp.)	(3), (11), 12, 13, 16, 17, (18), 21, 22
Hydroglyphus (1 sp.)	11, 13, 16
Geodessus (1 sp.)	11
Hygrotus (2 sp.)	(6), 7, 11, 12, 13, (16), 17, 22
Deronectes (4 sp.)	(1), (3), (5), 7, 11, 16
Graptodytes (1 sp.)	(3), 11, 12, 13, 16
Suphrodytes (1 sp.)	(3), 11, 12, (16)
Hydroporus (13 sp.)	(2), (3), (5), (6), 11, 12, 13, 16, 19
Oreodytes (1 sp.)	(3), (6), 11, 13
Nebrioporus (2 sp.)	(2), (3), 11, 12, (13), 16
Scarodytes (1 sp.)	(3), (5), 11, 12, 13, 16
Stictonectes (1 sp.)	(5), (6), 11, (16)
Stictotarsus (1 sp.)	11, 12, 13, 16
Dytiscidae: Colymbetinae	
Liopterus (2 sp.)	(1), 2, 3, 5, 6, 11, 13
Agabus (18 sp.)	1, 2, 3, 5, 6, 7, (11), (13), 15
Ilybiosoma (1 sp.)	5, 6
Platambus (1 sp.)	(1), 2, 3, 5, 6, (7), (11), 18, 19
Colymbetes (2 sp.)	(1), 2, 3, 5, 6, 7, (11)
Ilybius (10 sp.)	1, 2, 3, 4, 5, 6, 7, (10), (11), 23
Meladema (2 sp.)	1, 2, 3, 4, 5, 6, (7), (11), (13)
Rhantus (4 sp.)	1, 2, 3, 4, 5, 6, 7, (11), (13)
Dytiscidae, Dytiscinae	
Eretes (1 sp.)	(2), 3, 5, 6, (7), (11)
Hydaticus (2 sp.)	2, 3, 5, 6, 10, (11)
Acilius (5 sp.)	1, 2, 3, 5, 6
Graphoderus (2 sp.)	1, (2), 3, 5, 6, 7
Dytiscus (4 sp.)	1, 2, 3, 5, 6, 7, (11), (13), 15
Cybister (3 sp.)	3, 5, 6, 7, 8, 10, 11
Dytiscidae, Laccophilinae	
Laccophilus (2 sp.)	(2), (3), (5), (6), 14, 17, 19, 20, 22

1: 4-Hydroxybenzoic acid, **2:** hydroquinone, **3:** benzoic acid, **4:** benzoic acid ethyl ester, **5:** 4-hydroxybenzaldehyde, **6:** 4-hydroxybenzoic acid methyl ester, **7:** 3,4-dihydroxybenzoic acid methyl ester, **8:** 3,4-dihydroxybenzoic acid ethyl ester, **9:** 2,5-dihydroxyphenylacetic acid methyl ester, **10:** phenylpropionic acid, **11:** phenylacetic acid, **12:** 4-hydroxyphenylacetic acid, **13:** phenylpyruvic acid, **14:** 3,4-dihydroxyphenylacetic acid methyl ester, **15:** marginalin (= 4′5-dihydroxy-benzalisocumaranone), **16:** 3-indoleacetic acid, **17:** 3-hydroxyoctanoic acid, **18:** octanoic acid, **19:** *Z*-3-octenoic acid, **20:** 3-hydroxynonanoic acid, **21:** nonanoic acid, **22:** 3-hydroxydecanoic acid, **23:** tiglic acid

(): minor component; without brackets: major component (see Dettner 2014)

Table 9.2 Constituents **24–108** of prothoracic glands in genera (number of species) of predacious diving beetles (Dytiscidae; for species data see Dettner 2014)

Dytiscidae, Colymbetinae	
Ilybiosoma (1 sp.)	43
Agabus (11 sp.)	25, 29, 34, 38, 41, 42, 43, 44, 45, 46, 47, 48, 50, 52, 55, 59, 61, 62, 64, 66, 68, 70, 73, 74, 76, 77, 78, 80, 81, 82, 83, 84, 85, 86, 102, 103, 104, 105
Platambus (1 sp.)	54, 80, 101
Colymbetes (1 sp.)	Colymbetin
Ilybius (6 sp.)	24,25,29,26,27,28,29,30,31,32,33,35,44,50,51,53,54,57,63,65,69,71,72,87,88,89,90,91,92,93,94,95,96,97,98,99
Dytiscidae, Dytiscinae	
Acilius (4 sp.)	43, 44, 49, 50, 51, 56, 57, 63, unknown steroid
Graphoderus (2 sp.)	43, 67, 75, 78
Dytiscus (2 sp.)	36, 37, 43, 50, 52, 53, 56, 57, 68
Cybister (6 sp.)	3, 39, 40, 43, 50, 51, 57, 58, 63, 64, pentadecanoic acid, octadecanoic acid
Thermonectes (1 sp.)	57, 60
Dytiscidae, Laccophilinae	
Laccophilus (1 sp.)	73, 77
Dytiscidae, Hydroporinae	
Hyphydrus (1sp.)	106, 107, 108

24: 3-Hydroxyestra-1,3,5(10)-trien-17-one; estrone, **25:** 3,17ß-dihydroxyestra-1,3,5(10)-triene; 17ß-estradiol, **26:** 17ß-hydroandrost-1,4-dien-3-one; boldenon, **27:** 2α,17ß-dihydroxy-androst-4-ene-3-one; 2α-hydroxytestosterone, **28:** 2ß,17ß-dihydroxyandrost-4-ene-3-one; 2ß-hydroxytestosterone **29:** 17ß-hydroxyandrost-4-ene-3-one; testosterone, **30:** 17ß,19-di-hydroxyandrost-4-ene-3-one; 19-hydroxytestosterone, **31:** 3ß,17ß, dihydroxyandrost-5-ene, **32:** 3α,17ß, dihydroxyandrost-5-ene, **33:** 3ß,17α, dihydroxyandrost-5-ene, **34:** androst-4-ene-3,17-dione, **35:** 3ß,16ß,18-trihydroxyandrost-5-ene-17-one, **36:** pregn-4-ene-3-one, **37:** pregn-4-ene-3,20-dione; progesterone, **38:** 6ß-hydroxy-pregn-4-ene-3,20-dione; 6ß-hydroxy-progesterone, **39:** 12ß-hydroxypregne-4-ene-3,20-dione; 12ß-hydroxyprogesterone, **40:** 12ß-(3′pentenoyl-)pregn-4-ene-3,20-dione, **41:** 17α-hydroxypregn-4-ene-3,20-dione; 17α-hydroxyprogesterone, **42:** 11,15-dihydroxypregn-4-ene-3,20-dione; 11,15-di-hydroxy-progesterone, **43:** 21-hydroxypregn-4-ene-3,20-dione; 21-hydroxyprogesterone; cortexone; deoxycorticosterone, **44:** 11α,21-dihydroxypregn-4-ene-3,20-dione; 11α,21-dihydroxy-progesterone; **45:** 11ß,21-dihydroxypregn-4-ene-3,20-dione; 11ß,21-dihydroxyprogesterone; corticosterone, **46:** 18,21-dihydroxypregn-4-ene-3,20-dione; 18,21-dihydroxyprogesterone, **47:** 15α-hydroxy-

(continued)

Table 9.2 (continued)

progesterone-7α-isobutyrate, **48:** 15α-hydroxyprogesterone-7α-hydroxy-isobutyrate, **49:** pregn-4-ene-3,19,20-trione; 19-oxoprogesterone, **50:** 20α-hydroxypregn-4-ene-3-one, **51:** 20ß-hydroxy-pregn-4-ene-3-one, **52:** 20 α,21-dihydroxypregn-4-ene-3-one, **53:** 20ß,21-dihydroxypregn-4-ene-3-one, **54:** 15α,20ß-dihydroxypregn-4-ene-3-one, **55:** 16ß, 20ß-dihydroxypregn-4-ene-3-one, **56:** pregna-4,6-diene-3,20-dione;6-dehydro-progesterone, **57:** 20α-hydroxypregna-4,6-diene-3-one; cybisterone, **58:** 12ß-hydroxypregna-4,6-diene-3,20-dione; cybisterol, **59:** 15α-hydroxypregna-4,6-diene-3,20-one, **60:** 18-hydroxypregna-4,6-diene-3-one-18,20-hemiketal; mirasorvone, **61:** pregna-4,6-diene-3,20-dione-15α-isobutyrate, **62:** 15α-hydroxypregna-4,6-diene-3-on-20-isobutyrate, **63:** 21-hydroxypregna-4,6-diene-3,20-dione; 6,7-dehydrocortexone, **64:** 12ß,20α-dihydroxypregna-4,6-diene-3-one, **65:** 20ß,21-dihydroxypregna-4,6-diene-3-one, **66:** 15a,20ß-dihydroxypregna-4,6-diene-3-one-20-isobutyrate, **67:** 3ß-hydroxypregn-5-ene-20-one; pregnenolone, **68:** 3ß,20α-dihydroxypregn-5-ene, **69:** 3ß,20α, 21-trihydroxypregn-5-ene, **70:** 3ß,21-dihydroxypregn-5-ene-20-one; 21-hydroxypregnenolone, **71:** 3ß,16α,21-trihydroxypregn-5-ene-20-one; 16α,21-dihydroxypregnenolone, **72**: 3ß-hydroxypregn-5-ene-7,20-dione; 7-oxopregnenolone, **73:** 3α-hydroxy-5ß-pregnane-20-one, **74:** 3α,20α -dihydroxy-5α-pregnane, **75:** 11α-hydroxy-5ß-pregnane-3,20-dione, **76:**21-hydroxy-5ß-pregnane-3,20-dione, **77:** 3α,12 α -dihydroxy-5ß-pregnane-20-one, **78:** 3α,11α-dihydroxy-5ß-pregnane-20-one, **79:** 3α,11ß-dihydroxy-5ß-pregnane-20-one, **80:** 3α,21-dihydroxy-5α-pregnane-20-one, **81:** 3α,21 -dihydroxy-5ß-pregnane-20-one, **82:** 3ß,11ß,15α-trihydroxy-5α-pregnane-20-one, **83**: 3α,11ß,15α-tri-hydroxy-5α-pregnane-20-one, **84:** 3α,11ß,15ß,20ß-tetrahydroxy-5α-pregnane, **85:** 3ß-hydroxy-5α-cholestane, **86:** 3ß-hydroxy-5ß-cholestane, **87**: methylisobutanoate, **88:** α-copaene, **89:** α-muurolene, **90:** γ-muurolene, **91:** ε-muurolene, **92:** γ-cadinene, **93:** δ-cadinene, **94:** α-cubebene, **95:** β-cubebene, **96:** torreyol, **97:** trans-β-farnesene, **98:** γ-gurjunene, **99:** α-cedrene, **100:** methyl-8-hydroxy-quinolinecarboxylate, **101:** 7α,5ß,10α-endesin-4(14)-ene-12,6α-diol; platambin, **102:** 2-(*cis*-5,8,11,14-eicosatetraenoyl)glycerol (2-ara-gl), **103:** 2-(*cis*-5,8,11,14,17-eicosapentaenoyl)glycerol (2-epa-gl), **104:** 1-(*cis*-5,8,11,14-eicosatetraenoyl)glycerol (1-ara-gl), **105:** 1-(*cis*-5,8,11,14,17-eicosapentaenoyl)glycerol (1-epa-gl), **106:** 1-hexadecanoate-glycerol, **107:** 2-octadecanoate-glycerol, **108:** 1-octa-decanoate-glycerol

A selection of gland constituents is presented in Fig. 9.8

Table 9.3 Pygidial gland constituents of whirligig beetles (Gyrinidae) and crawling water beetles (Haliplidae)

Gyrinidae, Gyrinini	
Gyrinus frosti	110, 111 (Newhart and Mumma 1979)
Gyrinus minutus	109, 110, 111, 114, 115, 118, 120 (Dettner and Luthardt unpubl.)
Gyrinus natator	110, 114, 115 (Blum 1981)
Gyrinus substriatus	109–118, 120 (Dettner and Luthardt unpubl.; Ivarsson et al. 1996)
Gyrinus ventralis	110 (Dettner 1985)
Gyrinus aeratus	114, 115 (Ivarsson et al. 1996)
Gyrinus marinus	109–111, 114, 115, 118, 120 (Dettner and Luthardt unpubl.)
Gyrinus paykulli	109–111, 114, 115 (Dettner and Luthardt unpubl.)
Gyrinus urinator	109–111, 114, 115, 118, 120 (Dettner and Luthardt unpubl.)
Gyrinidae, Enhydrini	
Dineutus assimilis	110–113 (Miller et al. 1975; Newhart and Mumma 1979)
Dineutus discolor	113, 119 (Wheeler et al. 1972; Blum 1981)
Dineutus hornii	110 (Eisner and Aneshansley 2000)
Dineutus nigrior	11, 12, 110–113 (Miller et al. 1975)
Dineutus serrulatus	110
Macrogyrus oblongus	Various unknown terpenes, not 110–113 (Dettner and Luthardt unpubl.)
Gyrinidae, Orectochilini	
Orectochilus villosus	Odor like *Viola,* no known products apart from octadecan, heptadecan, n-heneicosan, n-docosan (Dettner and Luthardt unpubl.)
Haliplidae	
Peltodytes caesus	11, 12, 17, 22 (Dettner and Böhner 2009)
Peltodytes rotundatus	11, 12, 22, 122 (Dettner and Böhner 2009)
Brychius elevates	3, 11, 17, 22 (Dettner and Böhner 2009)
Haliplus (Neohaliplus) lineatocollis	11, 12, 17, 22 (Dettner and Böhner 2009)
Haliplus (Haliplus) ruficollis	11, 12, 17, 22, 121 (122) (Dettner and Böhner 2009)
Haliplus (Liaphlus) laminatus	11, 17, 22, 121 (Dettner and Böhner 2009)
Haliplus (Liaphlus) flavicollis	11, 17, 22, 121 (Dettner and Böhner 2009)
Haliplus (Liaphlus) fulvus	11, 17, 22 (Dettner and Böhner 2009)
Haliplus (Haliplus) heydeni	3, 11, 17, 22, 121 (?) (Dettner and Böhner 2009)

109: phenylacetaldehyde, **110:** gyrinidal, **111:** isogyrinidal, **112:** gyrinidione, **113:** gyrinidone **114:** 3-methyl-1-butanal, **115:** 3-methyl-1-butanol, **116:** 2-methyl-1-propanol, **117:** 6-methyl-5-hept-2-on, **118:** 3-methyl-2-butanol, **119:** octanal, **120:** 3-methylbutyric acid, **121:** phenyl- lactid acid, **122:** 3-hydroxy phenylacetic acid
For numbers below **109** see Table 9.1
For numbers of compounds see Table 9.1 (**1–23**), Table 9.2 (**24–108**), and Table 9.3 (**109–122**)

immersed due to their unwettable cuticle. Only representatives of genera *Spinactaletes*, *Arlesminthurus*, and *Pseudobourletiella* are capable of being submerged (Cipola et al. 2018). Interestingly young springtails after molting lose their nonwetting properties for a short time. If they stand on the water surface this is due to their nonwetting claws. If forced to submerge larvae will sink, have cutaneous respiration, and can also be invaded by microorganisms (Chang 1966; Thorp and O'Neill 2015). These underwater larvae will not molt. If gravid females are disturbed expelled eggs float on the water surface and later sink down. The underwater development continued and most eggs hatched (Chang 1966). An interesting movement in order to escape predators was observed in *Anurida maritima* (Fig. 9.1/4) on coastal pools and *Podura aquatica* (Fig. 9.1/3) at the surface of ponds. They lay on the water surface and pull up with a central wetting tube or ventral tube (collophore) at the same time as nonwetting head and abdominal tip are pushed down. When they release the wetting tube from the surface film, the animal is propelled into the air (Fig. 9.1/4, Bush et al. 2008). This posture by forming a meniscus also enables them to attract neighbors over a small distance.

Some semiaquatic species live and feed on water surfaces. Especially *Podura aquatica* (Fig. 9.1/3, Poduridae), *Isotomurus palustris* (Isotomidae), *Sminthurides aquaticus* (Sminthuridae) and *S. malmgreni* live on open water surfaces. Other more specialized species such as representatives of *Arrhopalites* (Sminthuridae) live on surface films of cave waters or other species prefer surfaces of aquatic plants such as *Lemna* or *Nasturtium*). Interestingly Collembola which are mainly found on water surfaces are characterized by distinctly paddle-like broadened mucrones, the claws of the abdominal springing organ (*Podura aquatica*; *Proisotoma crassicauda*, *P. borealis* Isotomidae; *Archisotoma* Isotomidae; *Sminthurides*; Schulze 1924). These mucrones prevent the breakthrough of the surface tension during a jump (Hopkin 1997).

Chemical defense is obvious in very different Collembola taxa and not only significant for those species which are eyeless or have lost their jumping ability (Dettner 2015). Defensive compounds were especially found in representatives of Onychiuridae (Fig. 9.1/1 *Onychiurus* spec. depletes secretion from a pseudocellus), Hypogastruridae, Neanuridae, or Tullbergiidae. These allomones are usually externalized by integumental pores, so-called pseudocells, (Fig. 9.1/2 pseudocellus from *Tetrodontophora* spec.), but there exist also springtails exhibiting warning colorations or exposing club-like defensive glands. Among the semiaquatic families there exist chemical data from Poduridae and Isotomidae. From *Podura aquatica* body surfaces a new hydrocarbon named poduran, with an unusual tricyclo(6.2.0.0) decane system was identified (Fig. 9.1/5; Schulz et al. 1997). Finally representatives of Isotomidae such as *Folsomia fimetaria* contain unknown hemolymph toxins which negatively influence the reproduction of the main predatory species, the spider *Erigone atra* (Marcussen et al. 1999).

EPHEMEROPTERA (mayflies; 100% aquatic): Mayflies represent the oldest order of winged insects. About 3500 species worldwide (Salles et al. 2018; Stork 2018: 3240) are characterized by aquatic eggs, phytophagous larvae (nymphs), and 2 terrestrial winged stages (subimago, imago) (Sartori and Brittain 2015a, b). The

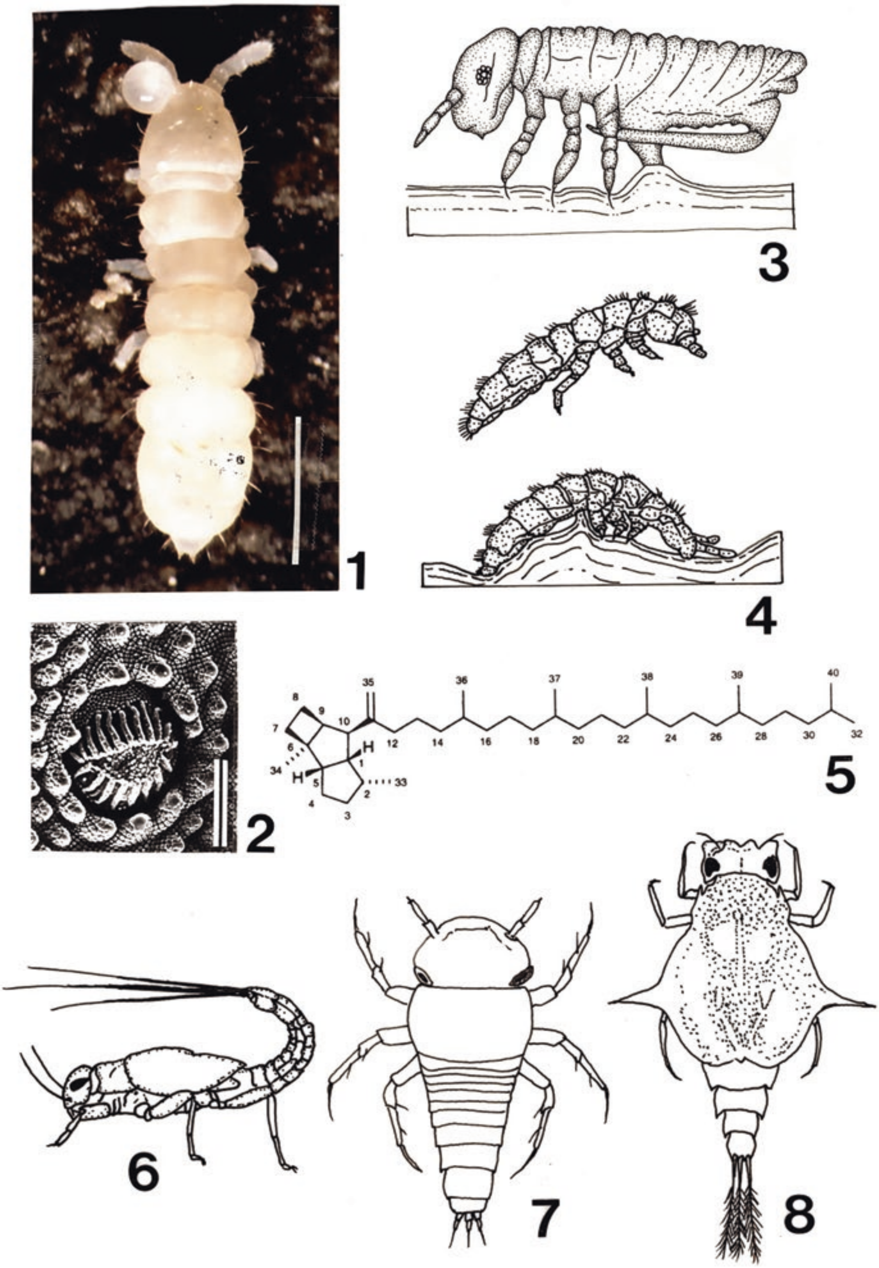

Fig. 9.1 Defenses of Collembola (1–5), Ephemeroptera (6–8). 1. *Onychiurus* spec. depletes defensive droplet from pseudocell (scale: 0.5 mm). 2. Pseudocell of *Tetrodontophora bielanensis* (scale: 10 um). 3. *Podura aquatica* on water surface. 4. Springtail *Anurida maritima* escapes predators by using its ventral tube. 5. Unusual hydrophobous hydrocarbon poduran from *P. aquatica*. 6. High-intensity scorpion posture of *Ephemerella subvaria*. 7. First larval instar of *Baetisca rogersi*. 8. Last larval instar of *Baetisca* spec. Sources: 1, 2, 3: Dettner and Peters 2010. 4. Modified after Lancaster and Downes 2013. 5. After Schulz et al. 1997. 6. Modified after Peckarsky 1987. 7. Modified after Pescador and Peters (1974). 8. Modified after Pescador et al. (2009)

unique subimago is covered by hydrofugous hairs which allows this stage to escape the water surface tension (Sartori and Brittain 2015a, b). There are 9–45 larval stages which live 3 weeks to 2 years, whereas adults live from 1 h to few days (Morse 2017). Mayfly larvae and subimagines which may be very diverse with respect to morphology represent a major part of the macroinvertebrate biomass and are therefore eaten by a wide range of aquatic invertebrates (Plecoptera, Trichoptera, Sialidae, Odonata, aquatic bugs and water beetles, leeches, triclads, crayfish) and vertebrates (fishes, specialized birds; Grant 2001). 42 fish families analyzed fed on aquatic insects and in Nearctic plecopteran genera 50% of the gut contents consisted of mayfly larvae (Bauernfeind and Soldan 2012). As compared with larvae of stoneflies which often show a greater degree of chitinization, larvae of Ephemeroptera are more soft and often have large lamellar gills (Brittain 1990). It is astonishing that there exist no chemical or acoustical defense mechanisms of mayfly developmental stages (neither stridulation, Aiken 1985, nor chemical defense, Dettner 2015) against predators, parasitoids, or pathogenic organisms. Instead depending on the presence of predators mayflies have evolved behavioral defensive mechanisms such as drifting, swimming, crawling away, hiding, scorpion posturings, or timing of activities (mass emergence, mating swarms) in order to reduce the chance of predation (Peckarsky 1996). As shown by Crespo (2011) for mayfly larvae chemical signals are highly important. Synchronous emergence could saturate potential predators whereas dispersed emergence eventually lowers the possibility of predator-prey encounters (Sartori and Brittain 2015a, b). After contact with predacious stonefly larvae *Ephemerella infrequens* (Ephemerellidae) exhibited a scorpion posture (Fig. 9.1/6). This reaction was usually evoked by touch of body parts; sometimes the reaction was shown when predators approached from upstream (Peckarsky 1987). In contrast *Baetis bicaudatus* (Baetidae) showed a “tail curl” posture in flexing cerci (which represent sensory structures, Crespo 2011) and posterior abdominal segments against predators. Peckarsky (1980, 1987) reports that *Ephemerella* deflects stoneflies because the posture may increase the apparent size of the mayflies which are then rejected by tactile predators. On the other hand *Baetis* detects predator’s wave disturbances and enables the prey to avoid predator encounters. In other species defence reactions such as crawling evasions and tactile (chemotactile) stimuli were observed as being responsible for these behaviors (Peckarsky 1980). Moreover chemical interactions between predator and mayfly-larvae-prey were supposed, because larvae of *Baetis* actively left the vicinity of stonefly larvae (see Bauernfeind and Soldan 2012). Elder larvae of Baetiscidae (Fig. 9.1/8) as compared with freshly hatched stages (Fig. 9.1/7) have a unique and bizarre appearance due to the thoracic notum and the presence of large spines (two lateral, two dorsal projections) and various lobes and humps (“armored mayflies”; Pescador et al. 2009). In addition these larvae exhibit cuticles which are harder than most mayfly larvae. The thoracic notum of Baetiscidae is fused, covers various abdominal segments (5), and encloses the gills underneath. According to Pescador and Peters (1974) the mesonotal shield helps to protect the gills and the lateral spines act as balancers and maintain the dorsoventral position of the larvae. Here I interpret the spines and the hardened cuticle as a typical mechanical defense against larger predators. Moreover it is noteworthy that *Baetisca* larvae exhibited thanatosis after mechanical molestation and show a coloration closely resembling their habitat (Pescador and Peters 1974). Both cryptic colorations (other larval genera such as *Baetis* and *Rhithrogena*) and aposematic color patterns (*Ecdyonurus, Heptagenia, Ephemerella*) are observed (Bauernfeind and Soldan 2012). However the presence of toxic natural compounds in mayflies has not been observed at all. Apart from thanatosis or scorpion postures common other defensive reactions observed in mayfly larvae are escape into the substrate (Bauernfeind and Soldan 2012). There are no data available on how mayflies defend against parasitic or commensalic organisms. However mayflies parasitized by mermithid nematodes showed increased defensive activities against predaceous stoneflies (Benton & Pritchard 1990).

9.2 ODONATA (damselflies, dragonflies; 99–100% aquatic)

Worldwide there exist about 6000 species (Stork 2018: 5899; another 1000 to 1500 species are expected to exist per Pessaq et al. 2018) of Odonata which comprise the three suborders Zygoptera (damselflies), Anisoptera (dragonflies), and Anisozygoptera (damsel dragons) (Suhling et al. 2015; Morse 2017; St. Quentin and Beier 1968). Eggs and larvae are aquatic and are found in various types of freshwater habitats including water-filled bromeliads. Few species are semiaquatic, whereas adults are terrestrial flying near water. Depending on species larvae need few weeks to 5 years to complete their development comprising 10–15 instars. Aquatic larvae and aerial adults of Odonata are predators with extrudable mouthparts of larvae and developed sight and flight in adults. Odonata represent one of the best known insect orders concerning taxonomy, zoogeography, or studies on sexual selection and conflicts by sperm displacement (Cordoba-Aguilar 2008; Dijkstra et al. 2014).

In addition predators of Odonata larvae, their prey, and their various defense mechanisms against opponents are well known in spite of the fact that there was not realized any chemical defense mechanism in larvae or adults of this insect order (Corbet 1999; Suhling et al. 2015). The risk of fish predation is reduced by various behavioral and morphological features of the odonate larvae. As was demonstrated by Wohlfahrt et al. (2005) these traits may be fixed and occur both in the presence and absence of predators. On the other hand on response to predators these traits may be flexible. Main predators of Odonata larvae are fishes which are significant in shaping odonate community structures as was demonstrated in North American *Enallagma* species (Johnson 1991). Larvae of certain species reduce their movements and their foraging activity when fishes are present, whereas other species escape predators by swimming away (Johnson 1991). As was shown by Crespo (2011), larvae of Odonata can sense infochemicals from various predators and even learn to associate them with predator presence. Invertebrate predators include other Odonata larvae including conspecifics (cannibalism), dytiscid beetles (larvae and adults), crayfish, belostomatid bugs, and several water birds (see Suhling et al.

2015). Other larvae exhibit nocturnal circadian rhythms in order to reduce predation pressure (Pierce 1988). It was also reported from zygopteran larvae that avoidance responses after contacts with predators may change during ontogeny (Corbet 1999). Many Odonata larvae show cryptic colorations which correspond to the microhabitat background, being greenish, yellowish, darkened, or with dark spots on pale ground (mixture or mixtures of sediments). In young instars of *Anax* transverse dark bands are observed followed by pale stripes. As in adults also in larvae there are abilities to change coloration. Larvae of other species may bear many setae on their body surface; adhering to fine detritus may result in an excellent camouflage. Many Odonata larvae hide in dense vegetation (Thompson 1987) or burrow in suitable substrates (Suhling and Müller 1996) in order to reduce predation pressure.

Larvae of *Epiophlebia* (Anisozygoptera) which represent living fossils are unusual in producing sound and sometimes exhibiting thanatosis when molested. The production of sounds after molestation was also reported in *Uropetala carvei* (Petaluridae; see Corbet 1999). Larvae with 14 instars need maximally 8 years (longest record for Odonata) for their development. Elder larvae are terrestrial for several months and breathe via thoracic stigma. In laboratory experiments it could be shown that larval stridulation was produced in response to mechanical disturbance (Aiken 1985; Asahina 1950). In order to stridulate lateral stridulatory files on abdominal segments 3–7 (Fig. 9.2/1) are pressed against metafemur serrations. Sounds are produced when the abdomen is twisted and telescoped. Stridulatory files are first evident in the sixth instar before eclosion (Aiken 1985). *Epiophlebia* larvae which appear like larvae from the Anisoptera are unable to use the anisopteran jet propulsion mode of escape but walk. In elder anisopteran larvae a kind of jet propulsion as a rapid escape mechanism was described (Corbet 1999) which is elicited by stimulation of paraproct nerves. These larvae may suddenly deplete their water-filled hindgut. In elder larvae this is the only way of locomotion, because leg muscles degenerate before larvae leave the water. When zygopteran larvae are irritated they may lose their caudal appendages (Stoks 1999), which possess breaking joints (Corbet 1999). Thus influx of water or loss of hemolymph is prevented. Autotomized body parts regenerate during succeeding moltings. These abdominal appendages are sometimes broadened in order to increase swimming speed (McPeek 2000). In other genera such as *Aeshna*, *Enallagma*, or *Ischnura* also whole legs are autotomized (Corbet 1999). In many cases larvae of Odonata are immobilized and show thanatosis (Fig. 9.2/6, 7) when they are molested (Wildermuth 2000). In *Somatochlora* larvae either extended their legs laterally, held them obliquely upwards (Fig. 9.2/6), or folded them close to their bodies. Among 18 investigated anisopteran species larvae of *Brachytron pratense* and three *Somatochlora* species revealed an obligatory reaction to tactile stimulation (Wildermuth 2000). Corbet (1999) reports reflex immobilization from 11 families of Odonata (Aeshnidae, Coenagrionidae, Cordulegastridae, Corduliidae, Epiophlebiidae, Gomphidae, Hemiphlebiidae, Libellulidae, Neopetaliidae, Petaluridae, and Pseudolestidae). Within ten species duration of immobilization ranged from more than 20 s to about 889 s; the maximum recorded time was more than 30 min. Many zygopteran larvae show distinct "unnatural" postures mainly of their caudal appendages (*Xanthocnemis*, Corbet 1999). Various anisoptera larvae have extremely flexible abdomina. Due to

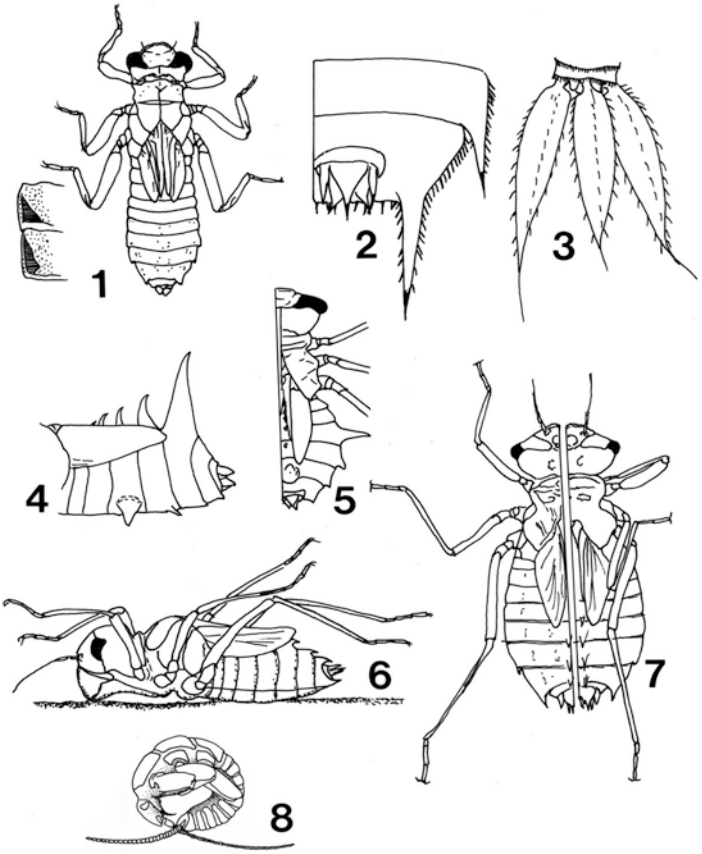

Fig. 9.2 Defenses of Odonata (1–7), Plecoptera (8). 1. Last-stage larva of *Epiophlebia superstes* and stridulatory files on tergites of abdominal segments 5/6 (left). 2. Apex half of abdomen larva of *Aeschnosoma* sp. (dorsal view). 3. Apex of abdomen with caudal appendages of female larva of *Heteragrion consors* (Megapodagrionidae, dorsal view). 4. Left lateral view of abdomen of last-stage larva of *Orionothemis felixorioni*. 5. Half last-stage larva (dorsal view) of *Orionothemis felixorioni*. 6. Thanatosis of *Somatochlora flavomaculata* after molestation (side view). 7. *Somatochlora flavomaculata* last instar larva (dorsal view), normal sitting position (left), thanatosis after molestation (right). 8. Plecopteran larva of family Taeniopterygidae after molestation in curling defence position. Sources: 1. Modified after Aiken 1985. 2. Modified after Neiss et al. 2018. 3. Modified after Anjos-Santos et al. 2018. 4, 5. Modified after Fleck et al. 2009. 6, 7. Modified after Wildermuth 2000. 8. Modified after Zwick 1980

spines which are arranged laterally and dorsally various predators and especially fishes are warded off (Johansson and Mikolajewski 2008). Spines of anisopteran larvae occur especially on the last third of the abdomina and form a spiky pyramid in order to "sting" potential predators. Remarkable examples for abdominal "weapons" are known from representatives of the anisopteran genera *Aeshnosoma* (Fig. 9.2/2), *Melanocacus*, *Orionothemis* (Fig. 9.2/4, 5), or *Paracordulia* and even from zygopteran species such as *Heteragrion consors* (Fig. 9.2/3; Pessacq et al.

2018). Sometimes large anisopteran larvae as *Tanypteryx pryeri* or *Anax junius* use their mandibles in order to bite aggressors (Corbet 1999).

Recently there were published several results in order to test hypotheses about parasite (water mites, gregarines) mediated selection with odonate hosts (Forbes and Robb 2008; Honkavaara et al. 2009). Probably mite infections may compromise a male's resistance against further infections by parasites which is achieved by hemolymph encapsulation in *Coenagrion armatum*. In addition the pseudopeptide antibiotic amicoumacin was isolated from *Bacillus* species which were isolated from *Coenagrion* guts. However it is not known if the bacteria produce this compounds in the Zygoptera larva (see Dettner 2015).

PLECOPTERA (stoneflies; 100% aquatic): As basal order of the Neoptera stoneflies have worldwide about 4000 species (Stork 2018: 3743) and are characterized by terrestrial adults and aquatic eggs and larvae (Avelino-Capistrano et al. 2018). Plecoptera are usually associated with cool and cold waters and possess 10–22 larval instars (Morse 2017). Stoneflies and especially their larvae have a lot of enemies and parasites ranging from salmonid fishes, birds, and predatory arthropods to gregarines, insect-pathogenic fungi, and water mites (Zwick 1980). Communication between males and females is often achieved by tapping on substrate ("drumming"; DeWalt et al. 2015). Crespo (2011) demonstrated in stonefly larvae both mechanosensory and chemical cues, which means nonvisual modalities were involved in detection of prey. In various especially young adult species (*Pteronarcys proteus*, *Peltoperla maria*, Benfield 1974; *Perla burmeisteriana*, *Acroneuria arenosa*, Zwick 1980) and one larval species (*P. dorsata*; Moore and Williams 1990) reflex bleeding behavior was recorded after molestations. Beaty (2015) reported that preserved larvae of Pteronarcyidae showed white exudates originating from thoracic nota and coxae. Also in various Plecoptera adults reflex bleeding was observed; however no active compound could be isolated (Stocks 2004). Zwick (1980) suggested that plecopteran hemolymph acts as an adhesive. Zwick (1980) reported that hemolymph of *Pteronarcys* can be sprayed away up to 25 cm by reflex bleeding, a behavior which is accompanied by an audible popping sound. Apparently hemolymph of stoneflies is not malodorous and represents no deterrent (Zwick 1980). The basis for this autohemorrhage was presumed to be increased hemolymph pressure (Stocks 2004). Moore and Williams (1990) were the first who demonstrated that the larvae of *Pteronarcys dorsata* show different responses which depends on the predators. Reflex bleeding and retreat were observed after contact with benthic crayfish predators. In contrast freezing and thanatosis were observed after contacts with benthic and pelagic fish predators. Beaty (2015) reported that *Pteronarcys* larvae exhibit thanatosis and turn into a ball. Further predator-prey studies were performed by Peckarsky (1980). Finally it is well known that larvae of Taeniopterygidae (e.g., *Brachyptera*) exhibit a characteristic of curled thanatosis position (Fig. 9.2/8; Zwick 1980). In various plecopteran taxa coiling movements were observed in order to escape from carnivorous insect larvae such as Odonata or Dytiscidae (Zwick 1980). Few larvae are also characterized by spines which might be located on thorax (*Kempnyia*, *Gripopteryx*) or abdomen

(*Neopentura*) and one species may be covered by detritus (*Pelurgoperla personata*) (Avelino-Capistrano et al. 2018).

ORTHOPTERA (bush crickets, crickets, grasshoppers, locusts; 0.3% aquatic): Among the over 28,000 orthopteran species (Stork 2018: 23,855) about 80 species with adaptations to aquatic life are aquatic whereas additional 110 species are water dependant (associated with aquatic habitats; Cover and Bogan 2015; Heckman 2018). Adaptations of aquatic Orthoptera are paddle-shaped hind tibiae (adapted for swimming), use of a plastron when submerged (Acrididae: Leptysminae), and diving in order to feed on submerged plants and to escape predators (Gutjahr and Braga 2018). Following families include Nearctic aquatic species: grasshoppers (Acrididae), pygmy grasshoppers (Tetrigidae), pygmy mole grasshoppers (Tridactylidae), katydids (Tettigoniidae), crickets (Gryllidae), and mole crickets (Gryllotalpidae). Also from Asia aquatic representatives are registered from the subfamilies Oxyinae (Acrididae), Tropidopolinae, and Hemiacridinae. Interestingly one aquatic and South American acridid species *Cornops aquaticum* feeds on water hyacinths and is being bred for possible release as a way to control this weed (Cover and Bogan 2015). Other South American species from the genera *Paulinia* and *Marellia* exclusively consume aquatic plants and are used in biocontrol of aquatic weeds in Africa and Australia (Cover and Bogan 2015). Unfortunately biology and ecology of these aquatic species are mainly unknown. However the semi-aquatic grasshopper *Paulinia acuminata* and its food plant *Salvinia auricularia* exhibit mimicry and ultrastructural analogy in order to achieve water-repellent surfaces (Barthlott et al. 1994). Generally among Orthoptera a lot of primary and secondary defensive mechanisms such as crypsis, aposematism, jumping, biting, flight, stridulation, or autotomy are realized (Dettner 2015). Employed chemical defenses are regurgitation, defecation, glandular defensive secretions, and internal toxins (Dettner 2015).

Within Tetrigoidea (about 1000 species), members of Scelimini are fully aquatic and can swim effectively (Rentz and Su 2003). Usually Tetrigidae are common near water, to which they readily take to escape from predators. They swim below the surface, and cling to plants until the danger has passed. Honma et al. (2006) studied the death-feigning posture in *Criotettix japonicus* against the frog *Rana nigromaculata*, which represents a sit-and-wait, gape-limited predator. The characteristic posture of this pygmy grasshopper enlarges its body size because pronotum, hind legs, and lateral spines project in different directions. Therefore the predator is unable to swallow the prey. Therefore it was shown that thanatosis does not generally means to mimic the posture of dead animals.

Concerning aquatic Orthoptera only few defensive mechanisms have been described. Members of Tridactylidae prefer damp habitats, where they construct nests out of mud and debris. Many species are active swimmers. Larvae and both sexes of adult Tridactylidae possess paired sternal glands with openings and opening muscles associated with the second abdominal sternum. When disturbed *Tridactylus japonicus* discharges a characteristic scent. Chemically the defensive secretions are unknown but they effectively repel *Tetramorium* ants and *Pardosa* spiders (Moriya and Ichinose 1988; Moriya 1989). In addition within mesotibiae of

Tridactylus variegatus further exocrine glands were identified (Messner 1969). Probably the mucus secretion serves to strengthen the wall of the nest tunnels of the pygmy mole grasshopper. Stridulation in which the tegmina are pulled against the hind wings occurs in some species. Members of Pauliniidae (Acridoidea) represent small- to medium-sized aquatic grasshoppers from South America. They can skate on water surface, they dive, and they can swim. Egg deposition takes place below water on water plants. Another species *Paulinia acuminata* was introduced into Africa for control of *Salvinia* (Rentz and Su 2003). There were reported further defensive mechanisms of selected orthopterans (Heckman 2018). When attacked by insectivorous fishes various *Cornops* species (Acrididae) fly away. Other species such as Southamerican cricket *Argizala* spec. (Gryllidae) or *Marilia* spec. dive beneath water surface and conceal among roots of water plants. Few species such as *Paraneonotus* spec. (Stenopelmatidae) dive as long as 12 m and remain motionless until the danger has departed.

BLATTODEA (roaches, termites; 0.8% aquatic): Among the more than 6400 described cockroach species (Stork 2018: 7314) including termites, most representatives of the aquatic and amphibious Blattodea belong to subfamily Epilamprinae (Blaberidae; Cover and Bogan 2015). Many species inhabit small ecosystems as phytotelmata in neotropics and Indomalaya and about 60 cockroach species were reported from leaf bases of bromeliads. Especially representatives of the genera *Epilampra, Phlebonotus*, *Poeciloderrhis, Opisthoplatia*, *Rhabdoblatta*, and *Rhicnoda* have been reported as aquatic/amphibious in spite of the fact that little is known on both the biology of these phytotelmata species and those taxa which are found along streams and rivers. When disturbed the rapidly swimming species *Epilampra maya* from Central America enters the aquatic habitat and remain submerged up to 15 min (Crowell 1946). Females of *Phlebonotus pallens* from India protect their larvae when they are crawling along the stream bottom (Bell et al. 2007). Larvae and apterous females of the Indian species *Rhicnoda natatrix* are active swimmers and hide under submerged stones (Nesemann et al. 2010).

Reports on defensive mechanisms especially in aquatic and amphibious cockroaches are not available. Generally Blattodea show a diverse array of defensive mechanisms. Sometimes they are camouflaged and resemble dead or green leafs; otherwise they mimic toxic insects (Dettner 2015). In addition they show evasive behavior; they stridulate; they fight, fly, or run away; and they dive into and quickly swim in water. Finally they cause allergic symptoms in humans and many species have exocrine glands where a lot of allomones are produced (Brossut 1993; Schal et al. 1982; Dettner 2015).

HETEROPTERA (true bugs; 13% aquatic): Heteroptera represent an insect order (about 40,500 sp.; Stork (2018): Hemiptera: 103,590) within Hemiptera. Numbers of special heteropteran taxa were from Lytle (2015) and Moreira et al. (2018); careful morphological characterizations of complex exocrine glands are compiled by Slater (1982); chemical data concerning complex glands were given by Aldrich (1988), Blum (1981), Dazzini-Valcurone and Pavan (1978), Weatherston and Percy (1978), and Millar (2005). Data on maxillary glands are based on Puchkova (1965). Moreira et al. (2018) report that representatives of Gerromorpha, Nepomorpha, and Leptopodomorpha (the three infraorders have more than 4800 species) are primarily associated with freshwater and sometimes with saltwater. Biological data on Heteroptera are especially based on Wesenberg-Lund (1943), Andersen and Weir (2004), Scholtz and Holm (1986), Schuh and Slater (1995), and Scholtz and Holm (1986).

Gerromorpha (semiaquatic bugs): According to this compilation there exist 2846 Gerromorpha species (Moreira et al. (2018): 2100 sp.). Members of this specialized group use the surface water film and glide on it rapidly in search for prey. Several data on Gerromorpha were compiled by Andersen (1982). In accordance with Moreira et al. (2018) only eight families (not superfamilies, and Madeoveliidae) are considered. Antipredator adaptations in Gerromorpha include cryptic coloration, countershading, and defensive behavior (Andersen 1996). The metasternal secretions of Gerromorpha are chemically unknown but may have repellent functions against predators (Andersen 1996). Nearly nothing is known on the composition of salivary glands (Walker et al. 2016). Schmidt (1982) reports that representatives of Gerromorpha (e.g., Veliidae, Gerridae) possess lethal and painful venoms. Aldrich (1988) speculates that the widespread occurrence of communication via waves may explain the frequent loss of exocrine glands especially in these semiaquatic bugs.

Mesoveliidae (water treaders; 49 sp.): Metasternal scent glands are present as a single median reservoir which is at least partially lined with glandular cells. Larvae have a somewhat reduced dorsal scent gland opening between terga III and IV.

Hydrometridae (water measurers; 129 sp.): Representatives of *Hydrometra* exhibit thanatosis and have an extreme slender body. Combined with rhythmical, vertical movements probably this may have the function of obscuring the outline of the insect (Andersen 1996). Hydrometridae possess a rapidly lethal venom within their salivary glands (Schmidt 1982). The metasternal scent glands have glandular cells opening into the collecting ducts and there is a reservoir with a dorsal accessory gland. Larvae lack dorsal abdominal scent glands.

Hebridae (velvet shore bugs; 233 sp.): The metasternal scent gland is a single simple median pouch with a narrow slit opening and without differentiated evaporative area. Larvae have a somewhat reduced dorsal scent gland opening between abdominal terga III and IV.

Paraphrynoveliidae (two sp.): The abdominal scent gland is situated between terga III and IV. No data are available with respect to the metasternal glands.

Macroveliidae (Macroveliid shore bugs; 3 sp.): The metasternal scent glands open into collecting ducts and contain a reservoir with a dorsal accessory gland and an opening of the median elevation on the posterior part. There are no fully developed lateral scent gland channels. There is a dorsal abdominal scent gland opening on the tubercle on tergum IV.

Veliidae (riffle bugs; 903 sp.): Representatives of this family can hop or jump or remain motionless (Scrimshaw and Kerfoot 1987). The escape movements called expansion skating might be the most elaborate defense mechanism of Heteroptera at all. It is observed in the genera *Velia* and *Microvelia* (Andersen 1996) and is comparable to the staphylinid beetles of Steninae (Betz et al. 2018). The detergent saliva which is ejected through the rostrum lowers the surface tension of the water. The metasternal scent glands on the sternum open into collecting ducts and have a dorsal accessory gland. The ostiolar channels on the metapleuron are usually elongated and prolonged on metapleura, ending in elongated evaporative areas with hair tufts in front of the hind coxae. Henrikson and Stenson (1993) concluded that aggregations of the dark, highly contrasting neustonic *Velia caprai* in exposed areas advertise their bad taste, which represents a case of aposematism. Species of *Velia caprai* were rejected by *Salmo trutta* and *Lepomis macrochirus* (Scrimshaw and Kerfoot 1987).

Madeoveliidae (one sp.): These predacious bugs live among wet rocks. Lateral metathoracic scent gland channels are present.

Gerridae (water striders; 713 sp.): Within genus *Gerris* death feigning and thanatosis are observed (Andersen 1996). Water striders can also hop and jump and often have countershading to reduce shadows (Scrimshaw and Kerfoot 1987). In order to defend optimally against bottom-striking predators it was found that long midlegs were especially important. The genetic basis of this interaction between a Hox protein Ubx and a new target gene (*gilt*) was studied by Armisen et al. (2015). The metasternal scent gland apparatus consists of two lateral glands and a median reservoir discharging through the median ventral aperture. Obviously the secretions evaporate due to many setae (Scrimshaw and Kerfoot 1987). Lateral secretory channels are "retained" in *Brachymetra* and *Cylindrostethus*. Usually there are no dorsal abdominal scent glands present in adults or larvae. Bioassays showed that some adult gerrids were rejected by bluegills (*Lepomis macrochirus*; Scrimshaw and Kerfoot 1987). Interestingly diapausing representatives of *Gerris* develop a diapause secretion that means there is a coat of densely packed microparticles on their body surfaces (Fig. 9.3/8) before leaving the water surface (Hauser 1985). It was speculated that these particles either represent fungicides or prevent freezing.

Hermatobatidae (coral treaters, 12 sp.): In this family the abdomen is extremely short and has a single scent gland opening on the fourth mediotergite.

Leptopodomorpha (shore bugs): There exist 382 sp. worldwide. Chemical data from metathoracic glands are not available. Maxillary glands are present in representatives of Leptopodomorpha (Puchkova 1965). According to Moreira et al. (2018) Saldidae and Aepophilidae represent sister groups to Omaniidae and Leptopodidae.

Fig. 9.3 (continued) emission of secretion is indicated by arrow. 5. Secretion grooming of *Sigara arguta* on the water surface prior to flying away. 6. Glands of *Ranatra linearis*: Paired maxillary glands (max) and bipartite paired labial glands (only one gland system figured) consisting of an accessory gland (ag) and a main gland (mg). Reservoirs of maxillary glands open at the base of proboscis (paired arrows); emission of secretion of labial glands occurs at the apex of proboscis (arrow). 7. Foreleg of male *Anisops stali* with stridulation organ (arrow). 8. Diapause secretion (stippled) according to REM figure of *Gerris costae* 5 weeks after imaginal molt. 9. Adult larva of *Nevrorthus fallax*; side view (left), after molestation, side view (right). Gland constituents: **1.** (E)-4-oxo-hex-2-enal; **2.** (E)2-hexenal, **3.** (E)-2-octenal, **4**. hydrogen peroxide, **5**. deoxycorticosterone, **6**. 4-hydroxy benzaldehyde. Sources: 1–3. Modified according to Staddon and Thorne (1973). 4. Modified according to Kovac et al. 1991. 5. Modified according to Kovac and Maschwitz (1991). 6. Modified according to Pawlowsky (Pawlowsky 1927) and A. Böttcher (Böttcher and Dettner unpubl.). 7–9. Modified according to Andersen and Weir (7. Andersen and Weir 2004, 8. Hauser 1985, and 9. Zwick 1967).

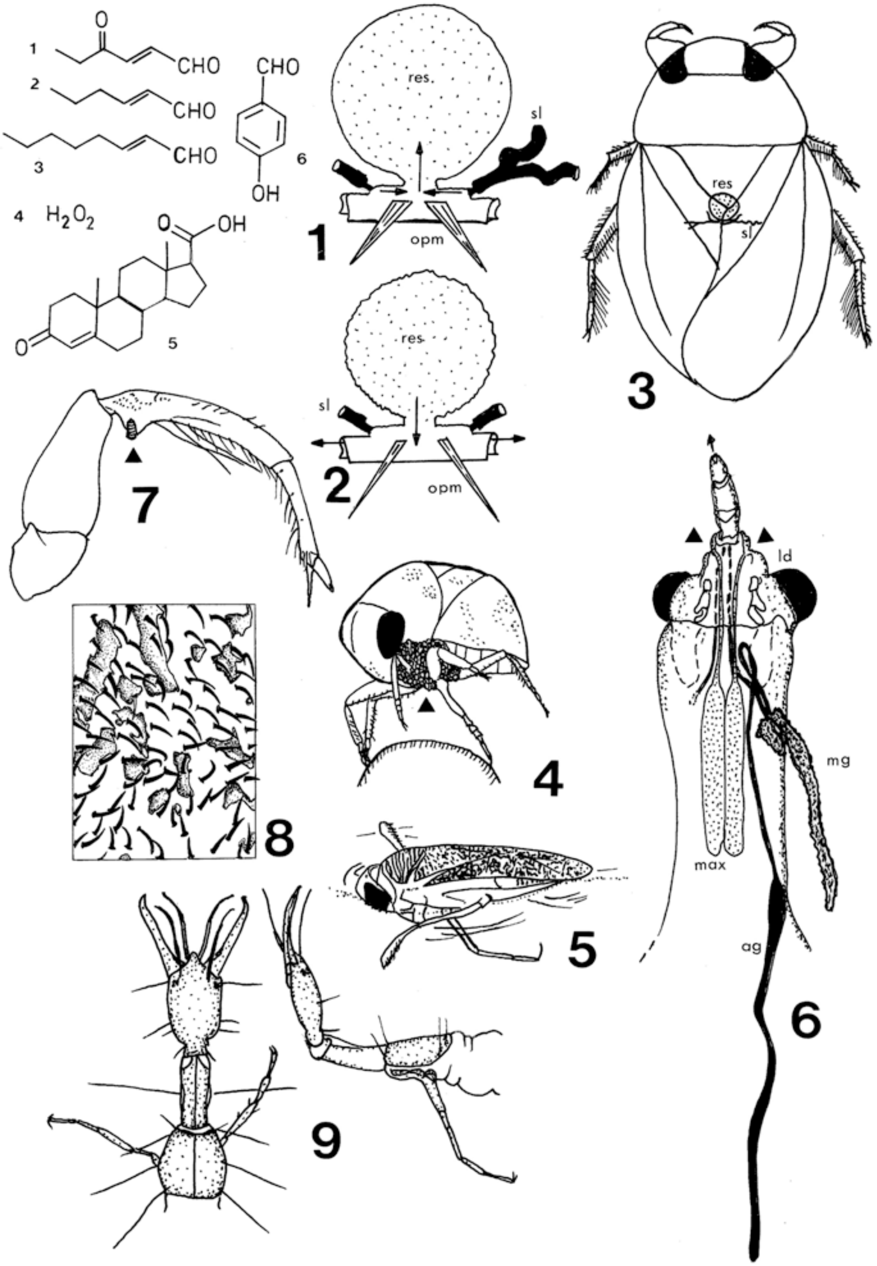

Fig. 9.3 Defenses of Heteroptera (1–8), Neuroptera (9). 1 and 2: Probable operating of opening and closing mechanism of defensive glands in *Ilyocoris cimicoides*. 1. Opening muscles (opm) are relaxed and secretion flows from the secretory lobes (sl) into the reservoir (res). 2. Opening muscles are contracted and secretion flows from the reservoir into the vestibule and through efferent channels to the ostioles (arrows). 3. Dorsal view of adult *I. cimicoides* showing the position of metathoracic gland reservoir (res) and secretory lobes (sl). 4. Secretion grooming of *Plea minutissima*;

Saldidae (shore bugs; 382 sp.) and **Aepophilidae** (marine bugs; 1 sp.): When disturbed saldids run fast, leap into the air, and land some distance away after which they scurry into shelter. The metathoracic scent gland has one median reservoir and one ostiole located on the sternum of the metathorax. Pregenital eversible glands are present at the posterolateral corners of the seventh sternum (not in Aepophilidae). Schmidt (1982) reports that Saldidae probably produce venomous saliva.

Omaniidae (intertidal dwarf bugs; five sp.): Omaniidae are predacious and intertidal bugs. They are able to jump readily. The metathoracic scent gland has four reservoirs of a paired gland system with a single median ostiole. Chemical data are not available.

Leptopodidae (spiny-legged bugs; 32 sp.): Leptopodidae fly swiftly from rock to rock when disturbed. The metathoracic scent gland has two reservoirs and two ostioles. Other exocrine glands (including pregenital glands) are missing.

Nepomorpha (aquatic bugs): According to Slater (1982) the group has 2404 sp. worlwide. Both aquatic and terrestrial nepomorphs inject venom to immobilize and liquefy their prey. Apart from Nepidae, Aphelocheiridae, and few Belostomatidae, Gelastocoridae, and Notonectidae within all remaining species there exists a metasternal gland (see Staddon and Thorne 1979). Absence of this type of gland is interpreted as a secondary condition. Several representatives of Nepomorpha are able to spread secretion from the metathoracic gland actively over their bodies (Andersen and Weir 2004). Therefore these species crawl out of the water (Naucoridae, Notonectidae, Pleidae) or lie on the water surface (Corixidae) in order to show secretion grooming. Usually these antimicrobic secretions serve to clean the hair pile which holds the air store (Andersen and Weir 2004). Therefore secretion grooming is primarily found in species with a physical gill. In addition also cephalic glands are present. The classification of Nepomorpha was based on Moreira et al. (2018).

Nepoidea: According to Moreira et al. (2018) Nepoidea (Belostomatidae + Nepidae) represent a basal sister group to other Nepomorpha. The Nepoidea species are ambush predators, which are hidden in submerged vegetation to wait on prey. They possess no abdominal scent glands.

Nepidae (water scorpions) 268 sp.: *Nepa rubra* and also the Australian genus *Laccotrephes* are well camouflaged due to their brown color and their mud body cover (Andersen and Weir 2004). Its dorsoventral compression is similar to dead leaf. On molestations *Nepa* and other genera show thanatosis; in some cases with its raptatorial forelegs water scorpions cling 1 h motionless to vegetation. Bites of both *Nepa* and *Ranatra* are painful for humans (Pawlowsky 1927). The poisonous secretion is produced by paired salivary or labial glands, which consist of a main gland and an accessory gland (Fig. 9.3/6). The accessory gland duct transports secretion from the accessory gland into the bipartid main gland. From there the lateral duct leads to the salivary pump and proboscis (Pawlowsky 1927). By transcriptomic studies the salivary glands of *Ranatra chinensis* revealed many transcripts encoding proteins with homology to proteases, acid phosphatases, apyrases, dipeptidylpeptidases IV, hyaluronidases, and prophenoloxidases. No metathoracic scent glands are present within Nepidae; however it is of interest that Nepidae preen only the eyes and the respiratory siphon (Andersen and Weir 2004). This indicates that they might use other secretions as from dermal or salivary glands or anal fluids (see Weiss 2006). Larvae lack dorsal abdominal scent glands. The secretion of the cephalic or maxillary glands (Fig. 9.3/6) is insecticidal and produces a burning sensation on human skin (Walker et al. 2016). Stridulations and vibrations were reported for the forelegs of *Ranatra* with a femoral plectrum and a coxal pars stridens (Aiken 1985).

Belostomatidae (giant water bugs) 169 sp.: They are general predators and feed on aquatic invertebrates and vertebrates (amphibians, fishes, turtles, birds), which are captured with their raptorial forelegs and quickly immobilized with the poisonous secretion from the salivary glands (de Carlo et al. 1973). The bites which are very painful for humans also represent effective defense mechanisms (Haddad et al. 2010). The belostomatid saliva reveals proteins from 5 to 55 kDa (Walker et al. 2016). Enzymic assays revealed activities of phospholipase A2, hyaluronidase, protease, amylase, esterase, a-glucosidase, glucosaminidase, invertase, lipase, nuclease, phosphatase, and phosphohydrolase (Walker et al. 2016). The saliva of the larger *Lethocerus uhleri* (Lethocerinae) which only feed on small vertebrates contains three proteolytic enzymes and no amylase, while the smaller *Belostoma lutarium* (Belostomatidae), which feeds on small invertebrates and snails, produces two proteolytic enzymes and amylase (Swart et al. 2006). The authors suggest that the presence of amylase allows to exploit the plant material already ingested by their prey. There are also reports of rich lipidic contents from the venom of *Belostoma anurum* (Walker et al. 2016). Walker et al. (2018) presented a transcriptomic and proteomic study on *Lethocerus distinctifemur* and found 132 venom proteins including putative enzymes, cytolytic toxins, and antimicrobial peptides. 73% of proteins were homologous to assassin bugs (Reduviidae), and 21% are not known from other sources (Walker et al. 2018). Metasternal scent glands of Lethocerinae and Horvathiniinae contain a median undivided lip valve, dorsoventral valve-opener muscles, and accessory glands (glands absent in Belostomatinae; Aldrich 1988). Especially in males these glands are well developed and may be detected due to their odor. (*E*)-2-hexenyl acetate was identified as main constituent in *Lethocerus indicus* males, with the corresponding butyrate as minor compound (Aldrich 1988). The functions of these esters remain unknown and might fulfill a secondary, probably sexual role (Scrimshaw and Kerfoot (1987). In Asia where especially *Lethocerus* is eaten by humans the scent gland odor and taste can be perceived (Schuh and Slater 1995). Belostomatidae larvae lack dorsal abdominal scent glands (Aldrich 1988). As defense reaction most Belostomatidae are additionally capable of ejecting a foul-smelling inky black anal liquid. Finally many families have paired so-called cephalic or maxillary glands (Fig. 9.3/6) which are saclike and open at the base of the beak (de Carlo 1961). The gland reservoirs are lined by a cuticle and bear ventrally glandular cells. In *Abedus herberti* the reservoirs are depleted after a molestation (Eisner et al. 2005). The viscous white fluid contains the four pregnanes desoxycorticosterone (Fig. 9.3/**5**), pregnenolone, progesterone, and 3a-hydroxy-pregn-5-en-20-one (Lokensgard et al. 1993). The first three pregnanes were also identified from prothoracic defensive glands of dytiscid beetles. It was evaluated that one *A. herberti* specimen contained about 0.1 mg desoxycorticosterone (in dytiscid beetles 0.03–0.4 mg/beetle). In the genus *Abedus* a soft chirping was described, which is produced by expulsion of air through the ventral spiracles (Aiken 1985).

Corixoidea: **Corixidae** (water boatmen; 662 sp.): Corixids are unable to use their rostrum and salivary secretion for defense. The opening of the large metathoracic scent glands is located laterally of the mesocoxae and contains a median, an undivided flap valve, and a ventral valve opener muscles. Obviously the pale yellow oil-like secretion with an aldehyde odor is depleted due to the elasticity of the gland reservoir. Larvae have dorsal abdominal scent gland openings between terga III–IV, IV–V, and V–VI. Corixids have defensive secretions composed of (*E*)-4-oxo-hex-2-enal (95% of adult secretion; Fig. 9.3/**1**) and of (*E*)-4-oxo-oct-2-enal (92% in larval secretions; Staddon et al. 1979). When attacked both adult corixids and larvae may eject secretions under water. It was found that fish guts only contain low numbers of corixids (Scrimshaw and Kerfoot 1987). The majority of corixids (Diaprepocorinae, Cymatiainae, Corixinae) rub their metathoracic gland secretions over their body parts covered with hydrofuge hairs. Within 2–3 s secretion grooming was observed while floating on the water surface (Fig. 9.3/5; Kovac and Maschwitz 1991). Secretion grooming of *Diaprepocoris* takes place on land. The behavior is released when light intensity and water temperature are raised. Due to the antibacterial properties of the aldehyde secretion, the contamination of hydrofuge hairs by microorganisms is minimized and thus loss of air store is reduced. It is peculiar that in all instars of *Micronecta* and earliest corixid instars secretion grooming is lacking: They have no hydrofuge hairs and obtain oxygen by cutaneous diffusion. Probably their strongly smelling secretions are directed against aquatic or terrestrial predators (Kovac and Maschwitz 1991).

Stridulation in Corixidae was found to be a component of the reproductive behavior and was observed in Micronectinae and Corixinae and probably occurs in Diaprepocorinae and Cymatiinae (Aiken 1985). The position and function of stridulatory organs vary considerably within Corixidae (Aiken 1985). In few cases (e.g., *Cenocorixa*) stridulation was shown to maintain individual distances between males. Corixids are able to leap out of the water into the air and take flight. Maxillary glands are present (Puchkova 1965).

Ochteroidea: **Ochteridae** + **Gelastocoridae**: Schmidt (1982) reports that Ochteridae and Gelastocoridae produce saliva which is probably venomous (Ochteridae) or paralytic and painful (Gelastocoridae).

Gelastocoridae (toad bugs; 116 sp.): Many representatives of toad bugs are cryptic and take on the color of the substrate; moreover they are characterized by their jumping ability. They usually occur near water in wet mud and vegetable debris where they usually blend well with their background. The metathoracic scent glands of Gelastocorinae contain a pair of stop valves and a dorsoventral valve with a polygonal cuticular microsculpture (scent glands are absent in Nerthrinae). The glands contain 4-oxo-2-hexenal (63%), octenal (25%; Fig. 9.3/**3**), 4-oxo-octenal (9%), and hexanal (3%; see Scrimshaw and Kerfoot 1987). Larvae lack dorsal abdominal scent glands. Maxillary glands are present (Puchkova 1965).

Ochteridae (velvety shore bugs; 75 sp.): Some Ochteridae species have larvae that scoop sand over the head and then push it over the dorsal surface with their front legs, thus making them closely resemble sand grains. Metathoracic scent glands are present. Adults and larvae lack dorsal abdominal scent glands. Maxillary glands are present (Puchkova 1965).

Naucoroidea: **Naucoridae** (creeping water bugs; 398 sp.): Naucorid bugs such as *Pelocoris* and *Ilyocoris (= Naucoris) cimicoides* should be handled with care as they can inflict a painful bite (Pawlowsky 1927) due to the venom of their salivary glands (Schmidt 1982). Their bite is characterized by Wesenberg-Lund (1943) as "worse than a bee sting." The metathoracic scent gland system *of Ilyocoris cimicoides* consists of a pair of glands, a reservoir, a closing apparatus, and an efferent apparatus (Fig. 9.3/1–3; Staddon and Thorne 1973). The complex gland system possesses a medium undivided lip valve and dorsoventral valve opener muscles (Fig. 9.3/1, 2); accessory glands are missing. In *Ilyocoris cimicoides* the aromatic compounds 4-hydroxy-benzaldehyde (Fig. 9.3/**6**) and 4-hydroxy benzoic acid methylester were identified (see Scrimshaw and Kerfoot 1987) along with minor constituents. From time to time *Ilyocoris cimicoides* leave the water in order to distribute metathoracic gland secretion over the ventral hairs (Kovac and Maschwitz 1990a). This grooming behavior prevents the contamination of these hairs with microorganisms, which would result in wetting of this region and loss of the air bubble. There is one pair of larval scent glands (gland divided) present between abdominal terga III and IV. Maxillary glands are present (Puchkova 1965). A sound production was reported from *Ilyocoris cimicoides* males; however both stridulatory structures and significance of sound production are discussed controversially (Aiken 1985). Horta et al. (2010) described a possible case of mimicry involving the naucorid Limnocoris porphyrus and an anuran tadpole of the hylid frog Scinax machadoi. Because both can sting or might be toxic it is not clear whether it is Mullerian mimicry or Bates mimicry.

9.3 Aphelocheiroidea: Potamocoridae + Aphelocheiridae

Potamocoridae (eight sp.): Tropical species which are related to Aphelocheiridae (Lytle 2015).

Aphelocheiridae (benthic water bugs; 78 sp.): There are reports that *Aphelocheirus* may occasionally sting or bite, which can be painful to man (Andersen and Weir 2004). No metathoracic scent glands are present in this family (Staddon and Thorne 1979) and it is of interest that *Aphelocheirus* does not show grooming behavior (Andersen and Weir 2004). Larvae possess divided dorsal abdominal scent gland openings between terga III and IV. Maxillary glands are present (Puchkova 1965).

Notonectoidea: **Notonectidae** (backswimmers; 422 sp.): Backswimmers swim on their backs, and often have reverse countershading. When disturbed they swim rapidly down. They are also able to leap into the air from the water and take flight.

When handled they can inject painful venomous saliva (German name "Wasserbiene," water bee; Pawlowsky 1927; Schmidt 1982). In Notonectinae the metasternal scent glands have paired stop valves, dorsoventral valve opener muscles, and a polygonal cuticular microsculpture. The glands are absent in representatives of Anisopinae, e.g., *Anisops* and *Buenoa*. Interestingly *Anisops* does not show any grooming behavior (Andersen and Weir 2004). Apart from Anisopinae in other notonectids paired accessory glands are associated with the reservoir which has a midventral opening. The odorless, brownish secretion consists of 4-hydroxybenzaldehyde (Fig. 9.3/**6**) and methyl-4-hydroxy benzoate, compounds which were also identified from pygidial glands of water beetles. It is remarkable that these antimicrobics also are deterrents (at 6×10^{-7} moles) against cichlids as *Tilapia* (Scrimshaw and Kerfoot 1987). Larvae lack dorsal abdominal scent gland openings. Maxillary glands are present (Puchkova 1965). It is remarkable that only members of genera *Buenoa*, *Anisops,* and *Walambianisops* can stridulate, which definitely lack thoracic defensive glands. In contrast other genera of Notonectinae possess no stridulatory apparatus (Aiken 1985; Andersen and Weir 2004). The stridulatory repertoire of *Buenoa* is very complex (tibial comb/rostral prong; femur/coxal peg; femoral setae/rostral flange) but obviously and exclusively used in courtship and mating. The same type of chirping behavior as in *Buenoa* is also typical for males of *Anisops* stridulating with their forelegs (Fig. 9.3/7). It seems important to denote that *Notonecta maculata* as predators release hydrocarbons such as n-heneicosane and n-tricosane which repel oviposition by mosquitoes such as *Culiseta longiareolata* (Silberbush et al. 2010). It would be interesting to know if these hydrocarbons, which might be valuable in eliminating mosquitoes, are produced in complex glands.

9.4 Pleoidea: Helotrephidae + Pleidae

Pleidae (pygmy backswimmers; 44 sp.): Like Notonectidae, representatives of Pleidae swim in the inverted position. The predacious pygmy backswimmers have a saclike metathoracic scent gland with a single midventral opening (Aldrich 1988). Paired accessory glands are associated with the scent gland. The colorless secretion of *Plea leachi* was reported to contain a 10–15% solution of hydrogen peroxide (Fig. 9.3/**4**) together with traces of an unknown carbonyl compound (Maschwitz 1971). From time to time *Plea minutissima* leaves the water in order to distribute this secretion by its legs (secretion grooming) over its hydrofuge ventral pubescence (Fig. 9.3/4; Kovac 1993). This efficient disinfectant probably destroys epzoic microorganisms and guarantees respiration via an intact air sheath when submerged. Increase of light intensity and higher water temperatures promote secretion grooming and probably flight behavior (Kovac 1993). If adults of *Plea* are dissected very often foams are apparent, which is obviously due to a catalytical decomposition of hydrogen peroxide into water and oxygen. Scrimshaw and Kerfoot (1987) also report that the *Plea* secretion is an effective deterrent against small fishes as *Gambusia*. Pleidae larvae have dorsal abdominal scent gland openings between terga III and IV. Stridulation is known to occur in both sexes of *Plea minutissima* by contacts of a mesothoracic file with a prothoracic projection (Aiken 1985). Maxillary glands are present (Puchkova 1965). According to Schmidt (1982) the saliva of Pleidae is probably venomous.

Helotrephidae (164 sp.): As Notonectidae they swim with the venter up. Larvae of the tropical Helotrephidae have a single median unpaired dorsal scent gland opening located between terga II and IV. In Helotrephinae stridulatory structures were identified. Especially a serrated lateral margin of hemielytron contacts a ridge dorsally on hind femur (Schuh and Slater 1995). Finally it must be noted that the first aquatic plant-sucking insects are two **homopteran** larvae of spittlebugs of genus *Mahanarva* from Costa Rica. They live submerged in water filled flowers of various *Heliconia* species (Thompson 1997).

MEGALOPTERA (alderflies, dobsonflies, fish flies; 100% aquatic): Worldwide there exist around 380 megalopteran species (Stork 2018: 354; Dijkstra et al. 2014; Ardila-Camacho and Contreras-Ramos 2018) which contain the families Sialidae (alderflies) and Corydalidae (dobsonflies and fish flies). All representatives have long-living aquatic larvae (up to 5 years; 10–12 stages) and short-lived terrestrial pupae and adults (Cover and Bogan 2015). The larvae feed on small invertebrates and vertebrates (e.g., mayfly and caddisfly larvae; small tadpoles) and also cannibalize smaller conspecifics. Few publications dealing with larval bionomy show that there exist defensive mechanisms. In the genus *Neohermes* (Corydalidae) an avoidance reaction was observed, when conspecific larvae had contacts (Smith 1970). When disturbed last-stage *Neohermes californicus* larvae (and prepupae) vomit an extremely foul-smelling, dark, greenish liquid (Smith 1970). Also adults of *Corydalus* can bite when they are disturbed (Parfin 1952). Recently defensive reactions were described for *Neoneuromus ignobilis* (Corydalidae; Cao et al. 2012). When disturbed due to the high flexibility of their bodies the larvae curl up into a ball or immediately open the palates. Cao et al. (2012) also observed the depletion of milky and water-insoluble substances from the end of the larval abdomen, a behavior which was compared with depletion of defensive secretions by whirligig beetles (Gyrinidae) or secretion grooming in aquatic *Plea* bugs. *Corydalus* females protect their egg masses with a hardening substance which appears like bird feces (Ardila-Camacho and Contreras-Ramos 2018).

NEUROPTERA (net-winged insects; 4% aquatic): There exist more than 6000 neuropteran species worldwide (Stork 2018: 5868; probably 10,000). Among the 17 known familes only 2 are aquatic (Sisyridae: 60 sp.; Nevrorthidae: 19 sp.) and 1 semiaquatic (Osmylidae: 160 sp.). Neuropteran larvae are characterized by specialized sucking jaws which are formed by mandibles and distal parts of maxillae (Beutel et al. 2014). This food uptake apparatus exhibits a sucking channel and a poison channel; the paired poison and salivary glands are associated with this specialized food apparatus (Beutel et al. 2010; Beutel et al. 2014). Aquatic larvae of Sisyridae (spongillaflies) have piercing mouthparts and are specialized predators or commensales of freshwater sponges (with symbiontic Zoochlorellae) and limnic bryozoans (Heckman 2018). Their stylets curve outwards distally. For constructing their pupal cocoons by using their spinning glands, full-grown third-stage larvae (lengths 2.7–8.5 mm) leave the water (Cover and Bogan 2015). Because other larval Neuroptera such as lacewings (Chrysopidae) use their pointed jaws in piercing and sucking prey and even are capable of piercing human skins where they may cause injuries (Southcott 1991), the same situation is suggested for Sisyridae. Larvae of Nevrothidae and even their pupal stages are aquatic and larvae represent predators of benthic invertebrates. Nevrorthidae represent the sister group of all other Neuroptera, suggesting an aquatic ancestor for all Neuroptera (Cover and Bogan 2015). The slender and agile predatory larvae are usually found in mountain brooks. As described by Zwick (1967) larvae of *Nevrothus fallax* showed an unusual behavior after molestation. The larvae rapidly moved foreward and backward and then suddenly lifted the head by an extremely quick tossing movement in order to form a right angle between head with prominent sucking jaws and rest of the body (Fig. 9.3/9). This peculiar behavior is interpreted as defensive behavior. Several representatives of the Osmylidae larvae are associated with freshwater habitats and occur in riparian areas. Many species consume trichopteran eggs, and hunt on Tipulidae and Chironomidae larvae (Cover and Bogan 2015). Because chironomid prey larvae die immediately after encountering osmylid larva, it can be suggested that the larval saliva is toxic (Wesenberg-Lund 1943; Schmidt 1982). Adults of Osmylidae are characterized by defensive glands and disagreable odors are perceivable after molestation (Dettner 2015).

COLEOPTERA (beetles; 3% aquatic): Most data are from Short (2018), Jäch and Balke (2008), Arnett and Thomas (2001), Beutel and Leschen (2016), and Leschen et al. (2010). According to Jäch and Balke (2008) about 3% of the known Coleoptera species described are regarded "aquatic." In considering undescribed species it can be assumed that 18,000 water beetle species might exist among 386,500 species worldwide (Stork 2018). The following beetle families are not arranged phylogenetically but according to Jäch and Balke (2008).

9.5 Predominantly Aquatic Families (Jäch and Balke 2008)

Myxophaga: Defensive mechanisms of the four families are only known from Lepiceridae (Navarrete-Heredia 2005). **Hydroscaphidae** (skiff beetles and their larvae are hygropetric; 13 sp.). Skiff beetles live on algae covered by a thin water film.

Lepiceridae (two sp.): Adults are found at the edge of rivers and prefer moist environments; larvae are probably aquatic. Recently collecterd Lepicerus adults were capable to retract body appendages and show thanatosis. In addition they cover their body surface with subtrate particles, are strongly sclerotized and colored similar to substrate where they are living (Navarrete-Heredia et al. 2005). **Sphaeriusidae** (minute bog beetles; 19 sp.): Adults of many species are found along banks of streams, in stagnant waters, or in *Sphagnum* mosses. Ecological data are scarce. **Torridincolidae** (torrent beetles; Short 2018: 60 sp.): All torrent beetles have aquatic developmental stages and prefer hygropetric habitats. Even pupae are aquatic with plastron-bearing gills (Lawrence 1991).

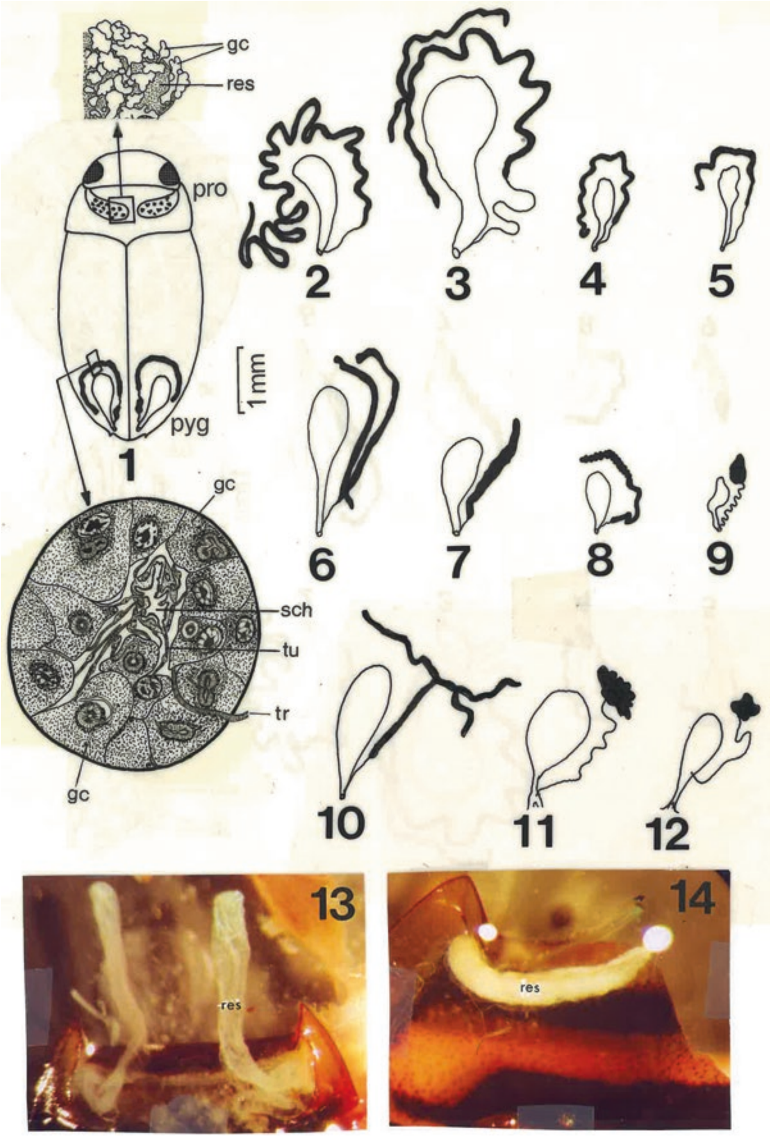

Fig. 9.4 Site of defensive glands (prothoracic glands and pygidial glands) of Hydradephaga (1–10; according to Dettner 1985) and Geadephaga (11–12) in *Nebrioporus depressus* (1). 2. *Acilius sulcatus,* 3. *Colymbetes fuscus*, 4. *Liopterus haemorrhoidalis*, 5. *Laccophilus minutus*, 6. *Hygrobia hermanni*, 7. *Gyrinus substriatus*, 8. *Noterus clavicornis*, 9. *Haliplus heydeni*, 10. *Amphizoa lecontei*, 11. *Trachypachus gibbsi*, 12. *Omophron dentatum*. 13–14: Prothoracic gland reservoirs of *Ilybius fenestratus* (13) and *Acilius canaliculatus* (14). Abbreviation: *Pro* prothoracic glands; *Pyg* pygidial glands; *res* reservoir; *gc* glandular cells; *sch* secretory channel; *tu* tubule; *tr* trachea. 1–10: Modified according to Dettner 1985. 11–12: Modified according to Forsyth (1972). 13–14: Originals in Dettner 2014

Adephaga: All aquatic Adephaga (= Hydradephaga) possess paired abdominal pygidial glands (Fig. 9.4). Secretions of all Hydradephaga hitherto tested topically on the cuticles of each representative show an increase in wettability for water of treated cuticles (Fig. 9.6).

Amphizoidae (trout stream beetles): Larvae and adults (five species worldwide; Dettner 2016b) prefer fast-flowing rivers but are poorly adapted to aquatic environment. They share plesiomorphic features with Carabidae. Eggs are deposited submers, and mature larvae leave the water for pupation. Freshly emerged adults are often covered with mud. Larvae live gregariously, show thanatosis, and roll their bodies into balls when disturbed (Yu et al. 1993). Adults possess pygidial glands with a tripartite secretory lobe (Fig. 9.4/10; prothoracic glands absent) which are filled with a yellow fluid, which is depleted over the hind body (as in Carabidae) upon disturbance (Edwards 1953). The gland reservoir is covered by muscles; as in *Hygrobia* (Fig. 9.4/6) the gland tissue is lengthened (Fig. 9.4/10; Forsyth 1970). The secretion contains the strongly smelling dimethyl disulfide (Fig. 9.9/Formula 3), and antimicrobics and fungicides like methyl-3-indole carboxylate (Fig. 9.9/Formula 1) and methyl-4-hydroxycarboxylate (Fig. 9.5/Formula 6; Dettner 1990).

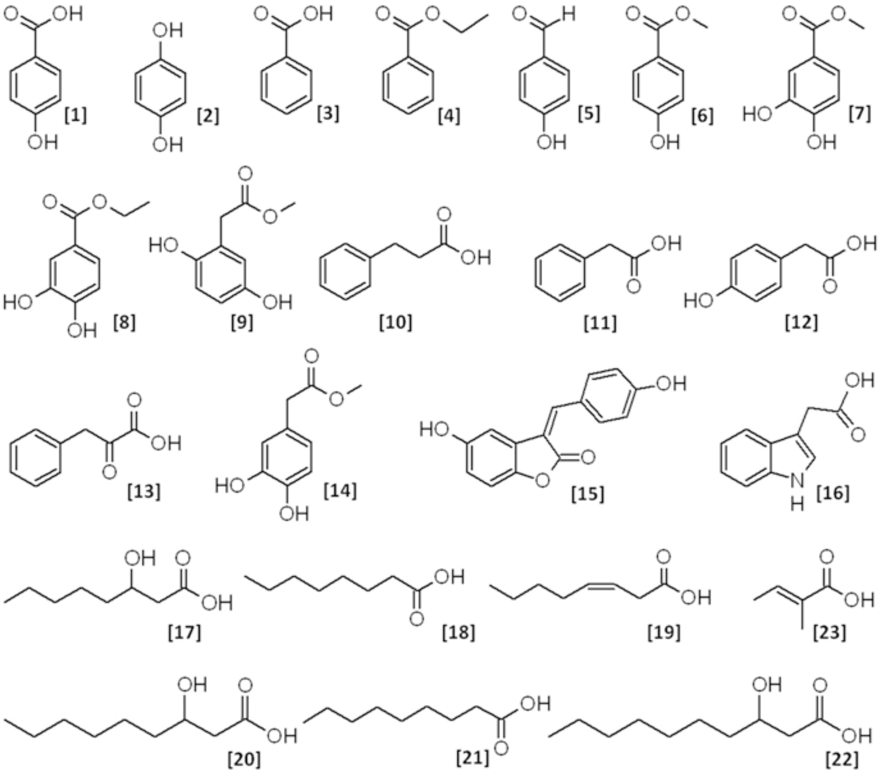

Fig. 9.5 Pygidial gland constituents (**1–23**) of predacious diving beetles (Dytiscidae)(according to Dettner 2014). For abbreviations see Table 9.1

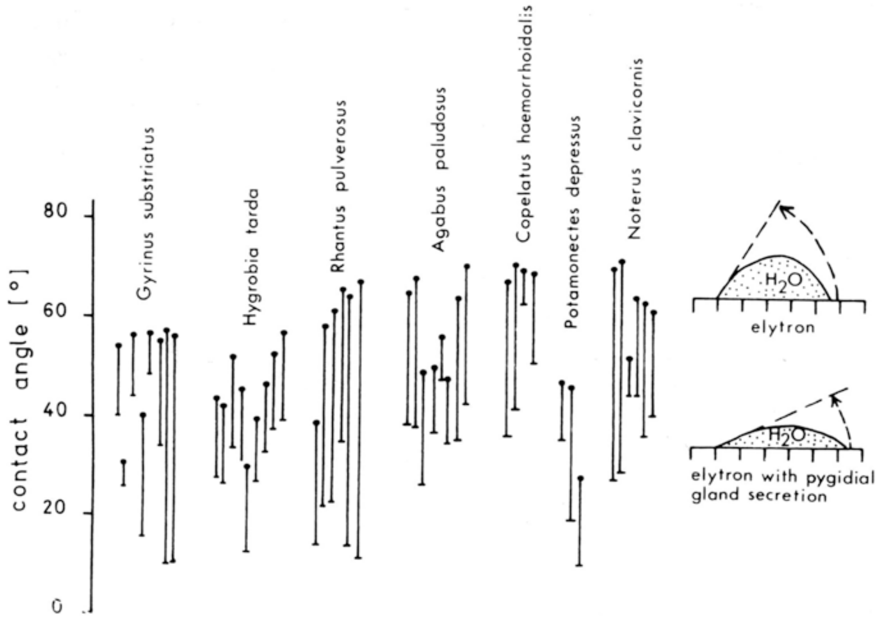

Fig. 9.6 Contact angles of water droplets, placed on elytral surfaces of different Hydradephaga species. Vertical bars: measurements per specimen: above value = untreated control elytra; below = elytra treated with pygidial gland secretion (according to Dettner 1985)

The yellow coloration of the secretion, which according to Darlington (1929) leaves a cigarette-like stain on the fingers, is due to 4′,5-dihydroxybenzalisocumaranone (= marginalin; Fig. 9.5/Formula 15) which was first discovered from pygidial glands of *Dytiscus marginalis* (Dettner 2014).

Aspidytidae (cliff water beetles; two sp.): Larvae and adults of this monophyletic family (Vasilikopoulos et al. 2019) prefer hygropetric habitats and are probably predacious (Beutel et al. 2016). When disturbed adults walk rapidly. Pygidial glands must be present; until now however they are not recorded from this family , which is also true for the prothoracic glands.

Dytiscidae (predacious diving beetles; according to Yee 2014: 4303 sp.): Jäch and Balke (2008) estimated up to 4800 sp. of diving beetles and predacious diving beetles, which means that this water beetle family which occurs on all continents where it is found in all aquatic habitats has the first position with respect to global water beetle diversity (Balke and Hendrich 2016; Yee 2014; Miller and Bergsten 2016). Larvae and adults of nearly all species are carnivorous and aquatic. Habitats range from ponds and bogs to rivers, phytotelmata, hygropetric areas, and even subterranean waters (Yee 2014; Miller and Bergsten 2016). A lot of predacious diving beetles leave the water for secretion grooming or before flight, another fraction of species stay on land during winter or summer, and few species of the genera *Geodessus* and *Typhlodessus* are reported to be terrestrial. Thus they have reduced swimming hairs and are unable to swim (Brancucci 1985).

Dytiscidae have a lot of predators ranging from vertebrates such as fishes or amphibians to invertebrates as Odonata, Heteroptera, or other predacious water beetles. Therefore we find a lot of defensive mechanisms (Dettner 2014; Miller and Bergsten 2016). Various mechanical defenses can be observed. Larger species such as Cybistrinae or Dytiscinae can kick with their hind legs which are supplied with large spurs. In addition both larvae and adults of these larger dytiscids bite with their mandibles which is painful for humans and may result in bleeding. In addition various Laccophilinae show a characteristic jumping behavior. In contrast many dytiscid beetles may quickly escape or in contrast can hide, whereas certain larvae of Cybistrinae exhibit thanatosis when molested (Miller and Bergsten 2016). As in other water insects coloration in Dytiscidae can be variable ranging from crypsis to aposematism and resulting from structural, secretion, and pigmentary colors (Dettner 2014). Colorful taxa which are attractively marked often are found in clear water with mineral substrates (Larson 1996; Young 1960) whereas dark melanistically or green-colored species (*Laccophilus* with yellow carotenoids and blue bile pigments; Dettner 2014) often prefer habitats with dark substrates or dense vegetation (Balke et al. 1997).

Several species of Dytiscidae can produce sounds and have organs of possible stridulatory function (Larson and Pritchard 1974; Franciscolo 1979). Although detailed bioacoustical studies are missing, the significance of most stridulations seems to be courtship behavior or intraspecific communication. It is suggested that stridulations also represent alarm and stress signals and might represent defense signals (Smith 1973).

Chemical defense through allomones is widespread in Dytiscidae (Dettner 2014). Both adults and larvae possess huge rectal ampullae that means diverticuli of hindgut. These ampullae primarily represent hydrostatic organs which are normally filled with feces and water. If adults of larger Dytiscidae (e.g., Dytiscinae) are handled at first they deplete an unpleasant smelling fluid from their rectal ampulla containing also hydrogen sulfide and ammonia. During severe molestations the two complex gland secretions from pygidial and prothoracic glands are suddenly or gradually depleted. Pygidial glands are present in all Dytiscidae and contain an ovoid reservoir, covered by muscles (Fig. 9.4). The lengthened, sometimes branched, secretory lobes (Fig. 9.4/1–5) are connected to the reservoir by a shorter or longer central collecting canal (Forsyth 1968). There exist various types of glandular cells with tubules. In several hydroporine species (*Hyphydrus, Stictotarsus*) an accessory gland and an integumental gland were described (see Dettner 2014).

Pygidial gland secretion very often is like a paste and dytiscid beetles distribute the material (about 10–15% of one gland reservoir) on body surface by using their legs. This behavior was described by Dettner (1985) and Kovac and Maschwitz (1990b). The secretion represents one of the richest sources for aromatic compounds within arthropods (Figs. 9.5 and 9.11). 14 aromatic compounds were identified (Table 9.1), 7 aliphatic gland constituents, the unusual yellow pigment marginalin, the tryptophane metabolite 3-indoleacetic acid, and tiglic acid which is probably also derived from amino acids (Schildknecht et al. 1962; Dettner 2014). Now chemical data are known from 91 dytiscid species comprising 29 genera. Several aromatics can be used as chemotaxonomic markers (phenylacetic acid for Hydroporinae and Copelatinae and responsible for the strong sweetish odor of *Hydrodessus fragrans* or *Hydrotarsus*; 4-hydroxybenzaldehyde for Colymbetinae/Dytiscinae) (Dettner 2014). It is remarkable that 4-hydroxybenzaldehyde and 4-hydoxybenzoic acid methylester from pygidial glands of Dytiscidae are also present in metathoracic glands of water bugs *Notonecta glauca* and *Ilyocoris cimicoides* (see Naucoridae, Notonectidae).

Concerning the functions of pygidial glands (Fig. 9.5) both aromatics (e.g., **3**, **6**, **11**) and aliphatics (e.g.,**17**, **19**, **20**, **22**) represent excellent preservatives which maintain a clean body surface that means protection from contamination of body surface by bacteria, protozoa, or fungi. Even in the terrestrial water beetle *Geodessus besucheti* phenylacetic acid represents the main constituent of the pygidial glands as compared with its aquatic bidessine relatives (Dettner 2014; Brancucci 1985). In addition it was suggested that each of the following pygidial gland constituents, the yellow pigment marginalin (Fig. 9.5/Formula 15) acts as fixative), the glycoproteins (form coherent films), and 3-hydroxy acids (**17**, **20**, **22**; polyesters) fix and entangle epizoic microorganisms which are subsequently stripped off (Schildknecht and Bühner 1968; Barbier 1990). The significance of the plant auxin 3-indoleacetic acid (Fig. 9.5/**16**) in Hydroporinae is unknown. The pygidial gland secretion of *Acilius sulcatus* especially with compounds **5** and **6** was shown to act against ciliates. This seems important because many aquatic arthropods and especially dytiscid beetles are contaminated with many epitrichic ciliates. The effect of pygidial gland secretion on the wettability of dytiscid integument by water is highly significant. As compared with the untreated elytral control, contact angles of standard water droplets on elytra previously treated with pygidial gland secretion of various Dytiscidae species were significantly lowered (Fig. 9.6). This increase of wettability was also observed with solutions of single pygidial gland constituents (Dettner 2014). When water beetles leave the water their integument becomes hydrophobic and they have enormous difficulties to break through the water surface and reenter into the water (Brancucci 1975). In addition especially after flights the weight of the beetles is reduced due to the filled tracheal system and the empty rectal ampulla. Therefore especially small Dytiscidae such as Hydroporinae are overcompensated and are pressed out of the water (Fig. 9.7/Hydroporinae 1). In this situation the beetles start rubbing and show secretion grooming in distributing pygidial gland secretion over their bodies (Fig. 9.7/Hydroporinae 9–11). After few minutes on or below the water surface the beetles fill their rectal ampulla with water and become more and more hydrophilous and as a consequence receive a stable position within the water (Fig. 9.7/Hydroporinae 12, 13; Dettner 1985). These findings amply demonstrate that exocrine glands and their secretions have usually a multifunctional significance.

Seasonal fluctuations of pygidial gland titers in *Acilius* (Newhart and Mumma 1979) and *Agabus* (Classen and Dettner 1983) do not reflect different degrees of utilization of the secretion but are due to the different age structures of population titers. Young specimens namely after pupation have low amounts of aromatics and other compositions as compared with elder specimens (Dettner 1985).

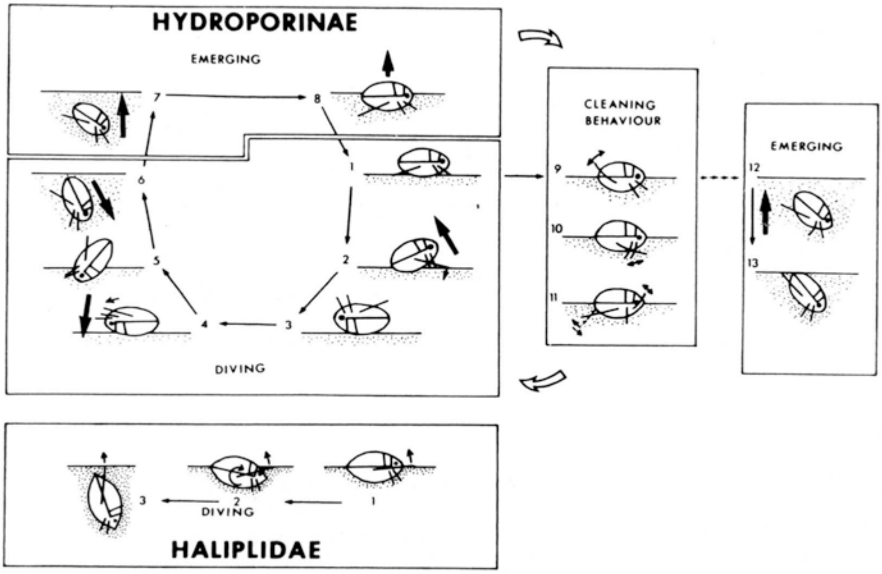

Fig. 9.7 Diving behavior (left), subsequent cleaning behavior (center), and sloping position (right side) of Hydroporinae (Dytiscidae). Diving behavior of Haliplidae (below). According to Dettner (1985)

Prothoracic exocrine glands are present in all dytiscid beetles (Fig. 9.4/1, 13, 14). The homology of the prothoracic gland of Hygrobiidae (Fig. 9.9/10) with the gland of Dytiscidae is questionable. Prothoracic exocrine glands represent paired saclike reservoirs which open anterolaterally of prothorax. As exocrine glands they are not homologues with endocrine prothoracic glands which are present in all insects. Forsyth (1968) describes that tubule-carrying gland cells cover these paired reservoirs which have no muscles. The usually odorous prothoracic secretion often is fluid and can be exuded as a milk after a strong molestation. Several Dytiscidae such as *Ilybius fenestratus* (Fig. 9.4/13), *Hyphydrus ovatus*, or *Laccophilus minutus* possess large prothoracic gland reservoirs extending from prothorax into the abdomen (Dettner 2014).

The chemistry of the prothoracic glands was especially investigated by Schildknecht (1970). An impressive array of vertebrate steroidal hormones was identified and a lot of new beetle steroids with C_{18}, C_{19}, and C_{21} skeletons (Fig. 9.8). Together with Chrysomelidae, Silphidae, Lampyridae, and Belostomatidae, Dytiscidae represent those insects, with an extraordinary biosynthetical capacity to produce these essential compounds from cholesterol precursors from their food. It was shown that labeled steroid precursors are incorporated into defensive steroids of *Acilius sulcatus* (Chapman et al. 1977). Obviously microorganisms from the crop of these beetles play an important role in transforming these steroids into prothoracic gland compounds (for details see Dettner 2014). Altogether 63 steroids are recorded (e.g., Compounds **25**, **28**, **37**, **57**, **67**, **73**, Fig. 9.8, Table 9.2). Among the

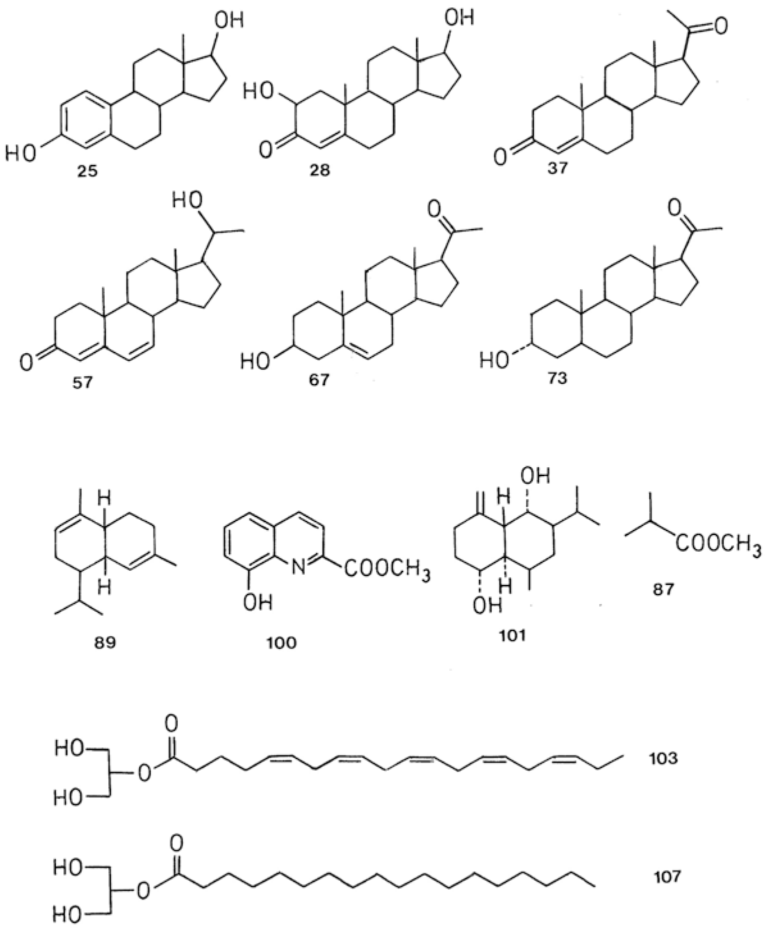

Fig. 9.8 Prothoracic gland constituents **24–108** (for names see Table 9.2) from predacious diving beetles (Dytiscidae) (according to Dettner 2014). **25**: C_{18} steroid of estratriene structure; **28**: C_{19} steroid of androstene structure; **37**: C_{21} steroid of pregn-4-ene structure; **57**: C_{21} steroid of pregna-4,6-diene structure; **67**: C_{21} steroid of pregn-5-ene structure; **73**: C_{21} steroid of pregnane structure; **89** and **101**: sesquiterpenes alpha-muurolene (**89**) and platambin (**101**). Alkaloid (**100**), ester (**87**), and monoglycerides (**103**, **107**)

nonsteroidal constituents of the prothoracic glands there is methylisobutanoate (Fig. 9.8/**87**), benzoic acid (Fig. 9.5/**3**), pentadecanoic and octadecanoic acids, and monoglycerides with saturated and unsaturated side chains (Fig. 9.8/**103**, **107**; Table 9.2). In addition the yellow alkaloid methyl-8-hydroxquinoline carboxylate was found (Fig. 9.8/**100**) in *Ilybius fenestratus*, which is derived from tryptophane, and the same species together with *Dytiscus marginalis* also contains methyl esters of leucine, valine, and isoleucine. In *Ilybius fenestratus* and *Platambus maculatus* Schildknecht and his group (Schildknecht 1977) identified 13 sesquiterpenes (including for example platambin, Fig. 9.8/**101**, and alpha muurolene, Fig. 9.8/**89**)

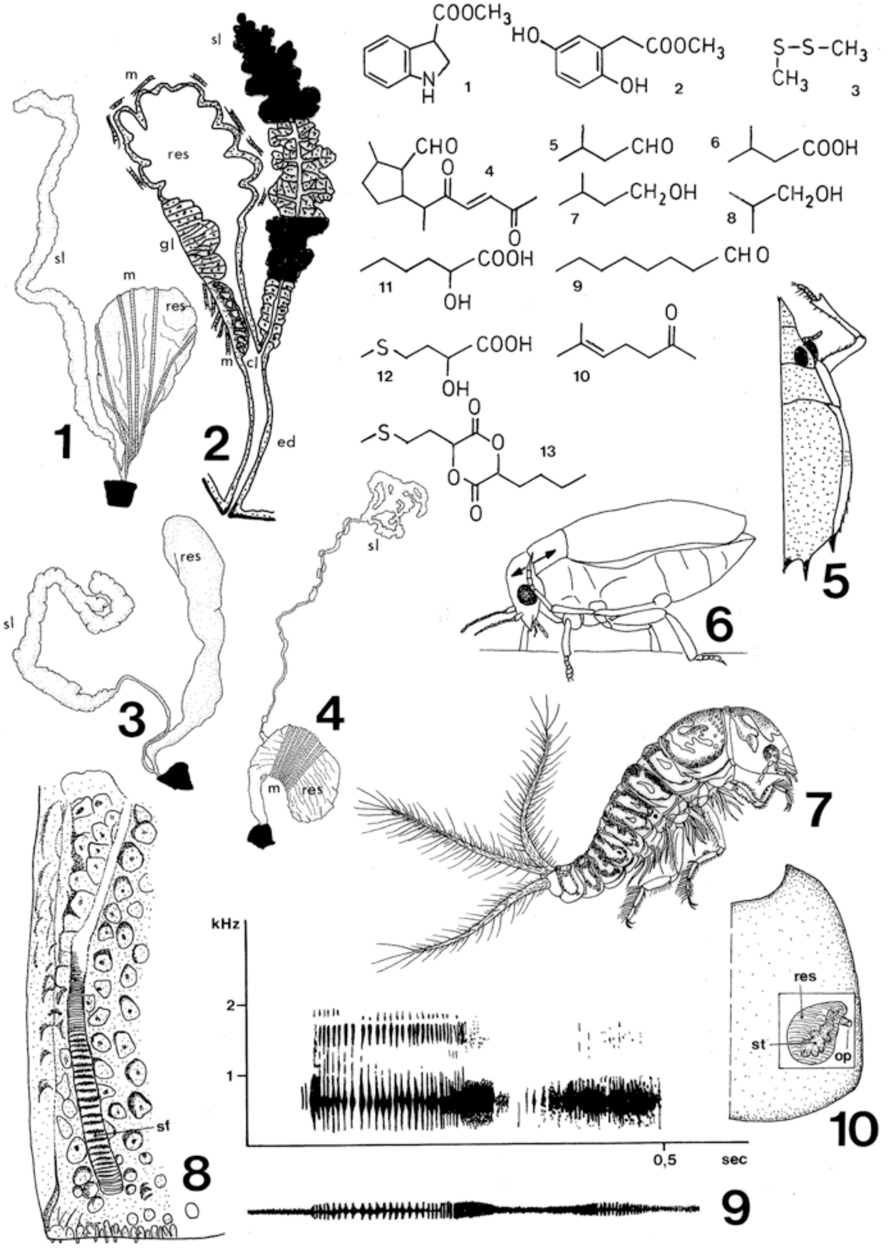

Fig. 9.9 Morphological defenses (5), stridulation (8, 9), coloration (7), pygidial glands (1–4), prothoracic gland (10) of Gyrinidae (2, 5), Hygrobiidae (6–10), Haliplidae (1,3,4). Pygidial glands of 1. *Haliplus* (*Neohaliplus) lineatocollis* (Haliplidae). 2. *Enhydrus sulcatus* (Gyrinidae). 3. *Brychius elevatus* (Gyrinidae). 4. *Peltodytes caesus* (Haliplidae). 5. Morphological defence *Porrorhynchus marginatus* (Gyrinidae). 6. Secretion grooming of *Hygrobia hermanni*. 7. Coloration of last instar larva of *H. hermanni*. 8. Stridulatory file on interior elytral apex of *H. hermanni*. 9. Oscillogram (above) and

which are defensive compounds and additionally responsible for the characteristic odor of the prothoracic secretion of these two and other species. *Colymbetes fuscus* does not produce steroids but instead contains the nucleoproteid colymbetin (Table 9.2), which can lower blood pressure in small mammals.

Biological activities of prothoracic steroids which are often present in huge amounts in the secretion are primarily directed against fishes and amphibians (newts and frogs). If the beetles are ingested, the secretion and especially the steroids are absorbed via the gill membranes, partly via skin. Many of these compounds from prothoracic glands of dytiscid beetles but also constituents from pygidial glands of whirligig beetles (Gyrinidae, which lack prothoracic glands) are toxic and exhibit especially anesthetic activities, which was investigated by Miller and Mumma (1976a, b) with minnows (Fig. 9.10; *Pimephales promelas*) or by Gerhart et al. (1991) with bluegill sunfishes (*Lepomis macrochirus*). In many experiments they evaluated survival time of test fishes which was correlated with the steroid concentration and the type of steroids used in the experiments (Fig. 9.10). The activity of steroids was highly related to the degree of oxygenation (see Dettner 2014). It was suggested that the aforementioned alkaloid (Fig. 9.8/**100**) and the sesquiterpene platambin (Fig. 9.8/**101**) are directed against small mammals, because *Ilybius fenestratus* often stays on land (Schildknecht 1970, 1977). The amino acids and their methyl esters exhibit various effects on fishes and they can be both feeding stimulants and deterrents (Dettner 2014). According to Kasumyan and Doving (2003) this applies especially to the found valine, isoleucine, and leucine. In bioassays with minnows *(Phoxinus phoxinus*) it was found that two polyunsaturated monoglycerides showed a deterrent effect and may act as emulsifiers for prothoracic steroids (Schaaf and Dettner 2000).

As with pygidial gland secretion also prothoracic defensive fluid is not exclusively directed against predatory vertebrates. When peritrichic ciliates isolated from the water beetle *Agabus sturmii* were treated with prothoracic gland secretion there was a drastic negative effect that means stop of cilia movement after a short time (Dettner 2014).

When last-stage dytiscid larvae leave the water in order to construct a firmly closed pupal chamber it was noticed that within the opened chamber an aromatic lactonic odor was perceivable (Blunck 1923). It is suggested that peristigmatic glands of pupae produce these antisepticals; the same phenomenon was described in Carabidae pupal chambers (Giglio et al. 2009).

Fig. 9.9 (continued) spectrogram (below) of stridulation noise of *H. hermanni*, 10. Half of prothorax of *H. hermanni* with prothoracic gland, covered by muscles. Abbreviation: *cl* closure; *ed* efferent duct; *op* opening of reservoir; *ogl* gland; *m* muscles; *res* reservoir; *sf* stridulatory file; *sl* secretory lobe; *st* secretory tissue. Pygidial gland constituents: *Amphizoa*: **1**. Methylindol-3-carboxylate, **2.** methyl homogentisate, **3.** dimethyl disulfide; Gyrinidae, **4**. gyrinidione, **5**. 3-methyl-1-butanal, **6**. 3-methyl-1-butanoic acid, **7**. 3-methyl-1-butanol, **8**. 2-methyl-1-propanol, **9.** octanal, **10.** 6-methyl-5-hepten-2-on, *Hygrobia*: **11**. 2-hydroxyhexanoic acid, **12**. S-methyl-2-mercaptobutanoi acid, **13**. lactide between **11** and **12**. 1, 3, 4: Dettner and Böhner 2009, 8–10: Dettner 1997, modified according to Barth 1960 (2), Miller and Bergsten 2012 (5), Kovac and Maschwitz 1990a, b (6), Klausnitzer 1996 (7)

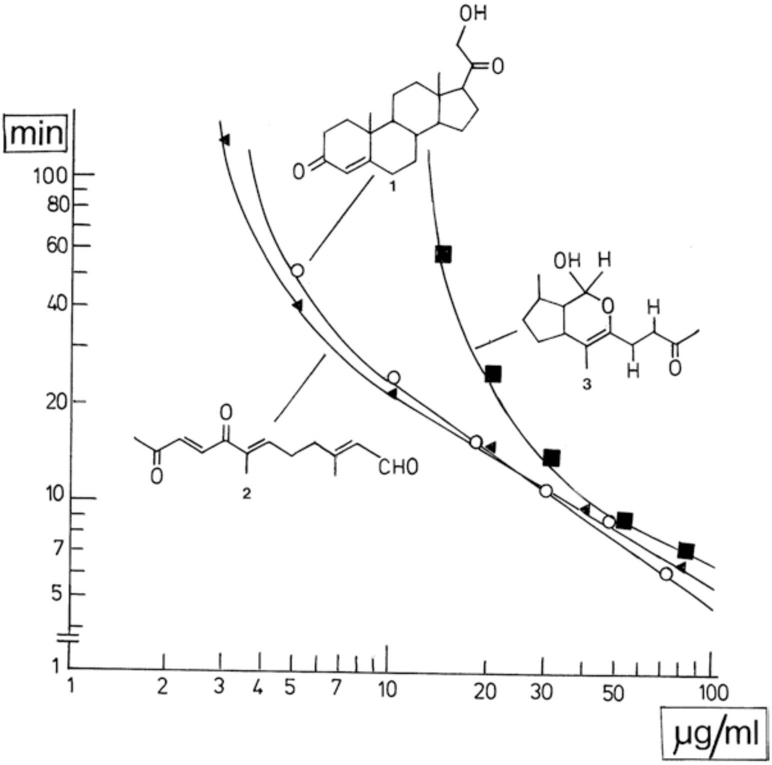

Fig. 9.10 Structure-activity of steroid deoxycorticosterone (1), gyrinidal (2) and gyrinidone (3) from pygidial rsp. prothoracic glands of whirligig beetles (2, 3) and predacious water beetles (1). Log x log plots of the survival time of fathead minnows (*Pimephales promelas*) in 50 mL solutions of norsesquiterpenes and steroid (ug/ml). Modified according to Miller et al. (1975)

Within Dytiscidae larvae (e.g., Hydroporinae, Laccophilinae, Colymbetinae, Dytiscinae) there exist glandular organs of epipharynx. From outside many spines are found which are confined to those areas where the tips of mandibles touch the ventral surface of head (De Marzo and Nilsson 1986). Glandular cells without tubules either form a single epithelium behind spinulose areas or represent a large gland with secretory ducts (*Cybister*). The role of these secretions is discussed controversially as detergents for cleaning mandibular tips ("Organes de toilette," Bertrand 1928), poisonous secretions, or attractants for prey.

Gyrinidae (whirligig beetles; 850 sp.; Beutel and Roughley 2016; Jäch and Balke 2008 estimated 1000 sp.; with respect to global diversity among water beetles this family has position 6); Phylogenetically there exist three subfamilies (Spanglerogyrinae, Heterogyrinae, Gyrininae) with Orectochilini, Gyrinini, and Enhydrini based on molecular and morphological data from both adults (Miller and Bergsten 2012) and larvae (Beutel and Roughley 1993). Adults by active movements whirl on the water surface (loops, zigzags), but they can also dive and fly after leaving the water. Gyrinids are often found in aggregations with sometimes 50,000 individuals, which is interpreted as a kind of defense strategy (Yee and Kehl 2015; Vulinec and Miller 1989). Vulinec and Miller (1989) showed that adult whirligig beetles are adapted to aquatic and terrestrial life by divided compound eyes and by hind leg strokes of about 50 to 60 s with speeds of 53–144 cm/s (Yee and Kehl 2015). Larvae are strictly aquatic, need a lot of oxygen, and possess tracheal gills. Preys are digested extraintestinally. All developmental stages are carnivorous, and pupation takes place on land. If there is a danger, the heavily sclerotized adults drastically increase their movements, can immediately dive, and may move under the water surface. There they swim and must quickly sting on solid objects. Apart from these unusual neustonic adaptations whirligig beetles possess paired abdominal pygidial glands (Fig. 9.4/7; Fig. 9.9/2) with odoriferous, volatile, and fluid secretions. The paired glands of *Gyrinus caspius* were described by Forsyth (1968), and the glands of *Enhydrus sulcatus* were figured by Barth (Fig. 9.9/2; 1960). The gland reservoirs are covered by muscles, and the secretory tissue evacuates secretion into efferent ducts of reservoirs close to or far away from the reservoir opening. *Enhydrus* is unusual as its gland reservoir hosts a second type of secretory tissue, apart from the secretory lobe (Fig. 9.9/2), an analogue situation resembling the anal glands of primitive Steninae staphylinid beetles (Fig. 9.13; Betz et al. 2018). It would be interesting to know if phylogenetic data from pygidial gland morphology and chemistry are in accordance with the abovementioned phylogenies of whirligig beetles. There exist various investigations with respect to the defensive secretions which contain the norsesquiterpenes gyrinidal, isogyrinidal, gyrinidon, and gyrinidion (Fig. 9.9/Formula 4) exhibiting strong repellencies against fishes (Fig. 9.10), newts (*Notophthalmus*), birds, and small mammals (Schildknecht et al. 1972; Miller et al. 1975; Scrimshaw and Kerfoot 1987).

In all cases when the beetles were attacked all whirligig beetles were rejected and the individuals survived without damage. Eisner and Aneshansley (2000) demonstrated that the oral tolerance of the bass *Micropterus salmoides* varied, dependent on gyrinidal dosage and satiation of the fish. Most of these experiments were performed by offering topically treated mealworms to the bass in an aquarium. Moreover the bass showed an intensive oral flushing behavior during which beetle sesquiterpenes were absorbed (about 80%) by the gills of the bass. Depending on gyrinid species there are also stinking volatiles in the pygidial gland secretions (Ivarsson et al. 1996) such as 3-methyl-1-butanal (Fig. 9.9/Formula 5), 3-methyl-1-butanol (Fig. 9.9/Formula 7), 2-methyl-1-propanol (Fig. 9.9/Formula 8), 3-methyl butyric acid (Fig. 9.9/Formula 6), and octanal (Fig. 9.9/Formula 9). In few *Gyrinus* species traces of 6-methyl-5-hepten-2-one (Fig. 9.9/Formula 10) and phenylacetaldehyde were recorded (Table 9.3; Fig. 9.11). Remarkably *Macrogyrus oblongus* did not contain the aforementioned four norsesquiterpenes, but instead other unidentified terpenes. Finally pygidial glands of *Orectochilus villosus* contained C_{17}, C_{18}, C_{21}, and C_{22} alkanes; however the chemistry of the strong violet odor as described by Lucht (1974) remains unknown (Table 9.3). In addition the pygidial gland secretions are applied to the body surface by using their legs in order to keep it free from contaminating bacteria, protozoa, or fungi. In gyrinid beetles this secretion groom-

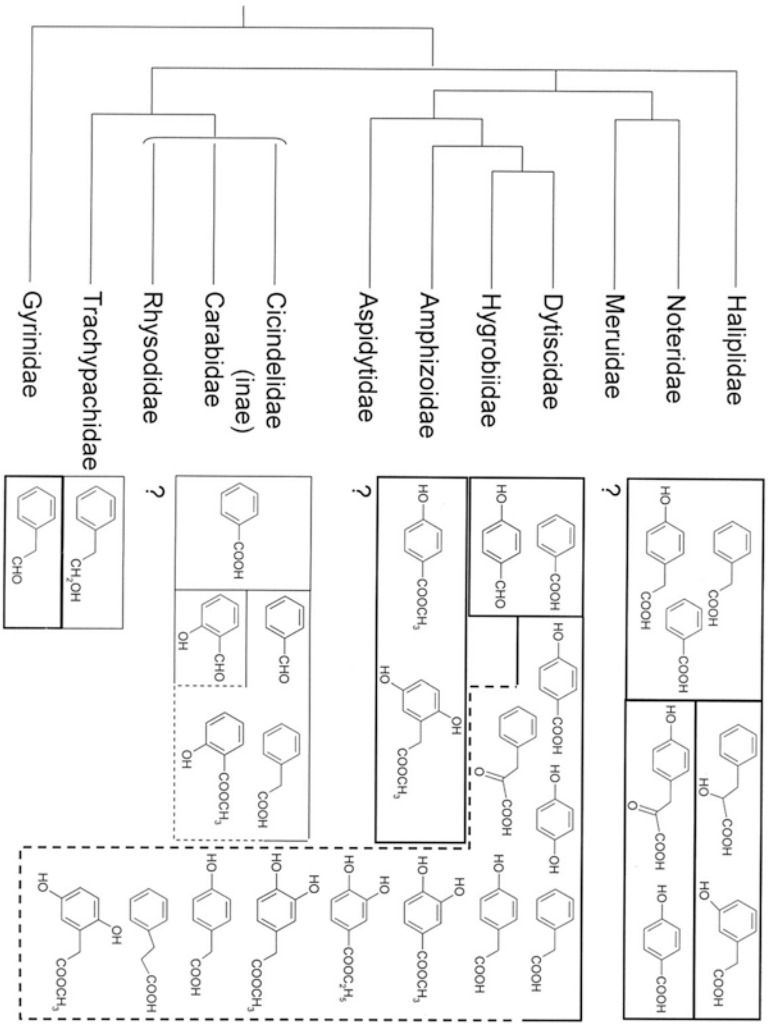

Fig. 9.11 Aromatic pygidial gland constituents in aquatic and terrestrial adephagan beetles (Dettner and Böhner 2009). Fat boxes: Aromatics are present in nearly all members of appropriate families. Interrupted boxes: Compounds only present in these taxa, especially large rectangular box of Dytiscidae. Thin boxes: Compounds only in minor amounts in single species per taxon. Phylogeny according to Beutel et al. 2006. Terrestrial families: Cicindelidae, Carabidae, Rhysodidae, Trachypachidae

ing was described by Kovac and Maschwitz (1990b). In addition pygidial gland secretion of *Gyrinus substriatus* increased wettability of the beetle integument (Fig. 9.6). As compared with the untreated elytral control, contact angles of standard water droplets on elytra previously treated with pygidial gland secretion were significantly lowered.

As demonstrated by fossil Permian Gyrinidae this family became adapted to swimming on the water surface long before the mesozoic invasion of the aquatic environment by Dytiscoidea took place (Yan et al. 2018). In the primitive Spanglerogyrinae the dorsal and ventral eyes are only narrowly separated as compared with the more derived Gyrininae. Molested *Spanglerogyrus albiventris* shows a peculiar jumping behavior (Steiner and Anderson 1981) which is also typical for some other gyrinid beetles. It is remarkable that *Gyrinus* larvae have a nonwettable integument and therefore are captured at the water surface (Bott 1928). *Gyrinus* larvae also gather debris which is mixed with mucopolysaccharides from midgut cells (Rupprecht 1971) in order to construct a pupal chamber on the top of emergent plants.

Various studies demonstrated the role of the aggregations of gyrinid beetles. It was found that they aggregate in the daytime into single- and multispecies groups (rafting of 100 to 1000 individuals). With increasing temperature the beetles dispersed from these rafts to shallow edges of the waters (Fitzgerald 1987; Heinrich and Vogt 1980). Naive fishes ate single beetles; however they learned to avoid these beetles, indicating that rafting places represent safe places for gyrinids (Heinrich and Vogt 1980). Henrikson and Stenson (1993) finally demonstrated that water prepared with gyrinid elicited evasive behavior in the beetles. They concluded that aggregations of the dark, highly contrasting beetles in exposed areas advertise their bad taste, which represents a case of aposematism. Probably, the spreading activity of the Gyrinidae secretion on the water surface has no relevance for living beetles (Vulinec 1987), since this activity is typically found in defensive secretions of many arthropods. It is important to denote that most adult Gyrinidae have a hard integument. Very often the upper body sideboard is brightly colored and elytra exhibit large and small spines at elytral apices as found in *Porrorhynchus marginatus* (Fig. 9.9/5; Gustafson and Miller 2016), which might be interpreted as defense against fishes.

Haliplidae (crawling water beetles; 240 sp.): Haliplidae hold the 11th position with respect to global water beetle diversity according to Jäch and Balke (2008). Larvae and adults are strictly aquatic and prefer stagnant or slow-running waters often with filamentous algae and characeans (van Vondel 2016). Adults are characterized by metacoxal plates and move their hind legs alternately. The three herbivorous larval stages have tracheal gills, move very slowly, and are often hidden within water plants. Haliplid larvae have a slender body shape and show a hard integument. Elder larvae are often camouflaged and covered by diatoms rendering a black body coloration; however they are fed by fishes, frogs, or carnivorous insect larvae (Hickman 1931). According to Falkenström (1926) pupae of *Haliplus* and in contrast to Dytiscidae pupae exhibit thanatosis. Mousseau and Roughley (2007) discuss that characteristic elytral maculations in Haliplidae and especially in *Brychius* can have deceptive character or may represent a warning coloration. Adult haliplids are consumed by fishes, frogs, ducks, or carnivorous insects (larvae of Dytiscidae and Odonata, adult dytiscid beetles, Hickman 1931).

The paired pygidial glands of adults of *Haliplus ruficollis* were described by Forsyth (1968), and the glands of other species from the genera *Peltodytes*, *Brychius*, and *Haliplus* were figured by Dettner and Böhner (2009). The gland reservoirs are covered by muscles, which either are confined to the reservoir in the primitive genus *Peltodytes* (Fig. 9.9/4) or extend to the reservoir opening in other genera (Fig. 9.9/1). The more primitive *Peltodytes* representatives exhibit compact glandular tissues (Fig. 9.9/4) as in Carabidae (Fig. 9.4/12) and show longer collecting channels which unite with the gland reservoir far away from the gland opening. In *Brychius* and *Haliplus* the glandular tissue is lengthened; however *Brychius* and *Haliplus* (subgenus *Neohaliplus*) exhibit short collecting channels and have reservoirs which gradually narrow towards opening (Fig. 9.9/1, 3, 4). Phylogenetic data from pygidial gland morphology are in accordance with phylogenies based on adult characters (Beutel and Ruhnau 1990). Phenylacetic acid (Fig. 9.5/**11**) which is also found in hydroporine Dytiscidae (and *Copelatus*) and Noteridae was recorded in all haliplid species investigated (Table 9.3). In all genera also further antimicrobials from selected Dytiscidae (*Hydrovatus, Hygrotus, Laccophilus*) such as 3-hydroxy octanoic, 3-hydroxy decanoic acid (Fig. 9.5/**17**, **22**), benzoic acid (Fig. 9.5/**3**; Dytiscidae: Colymbetinae, Dytiscinae), or 4-hydroxyphenylacetic acid (Fig. 9.5/**12**; Dytiscidae: Hydroporinae; Noteridae) were recorded (Dettner and Böhner 2009). Exclusively few Haliplidae species secrete 3-hydroxyphenylacetic acid and phenyllactic acid (Fig. 9.11). All aliphatic and aromatic recorded gland constituents from Haliplidae are bactericidals, fungicidals, and disinfectants and are distributed on the beetle surfaces by secretion grooming (Dettner 1985; Kovac and Maschwitz 1990b). On land and on water surface the beetles distributed secretions with their legs on their body surface in order to dive in a characteristic way typical for Haliplidae (Fig. 9.7/Haliplidae 1–3). In addition phenylacetic acid and other components increase wettability of the haliplid body surface when the beetles hang on the water surface and show their characteristic cleaning behavior in order to dive (Fig. 9.6/Haliplidae; Dettner 1985). Whether the 3-hydroxyesters are transformed to polyesters on the body surface in order to enclose, kill, and eliminate epizoic microorganisms has to be investigated (Dettner and Böhner 2009). Stridulation was reported from three *Haliplus* species (Beier 1929; Seeger 1971; Aiken 1985). Sclerotized teeth at the underside of the elytra represent the pars stridens, whereas the plectrum is found in the pleural fold of abdominal segments 2–4. Stridulation behavior which is achieved by stretching of abdomen was described before and during mating and probably is not a defense mechanism.

Hygrobiidae (squeak beetles; six sp.): It is a relict family (also named Paelobiidae) with species in China, Australia, and Europe. Larvae and adults live in mud, silt, and detritus of ponds (Dettner 1997b; Dettner 2016c). Eggs are deposited on submerged plants. There exist three larval instars with tubular gills and characteristic strong but variable brownish pigmentation (Fig. 9.9/7). They pupate in a pupal chamber on land. Adults possess pygidial glands consisting of a gland reservoir (covered by muscles) with efferent duct and bifurcated secretory lobe (Fig. 9.4/6; Forsyth 1970) filled with colorless to white fluid which is depleted on land and distributed on the body surface of adult beetles (Kovac and Maschwitz 1990b). *Hygrobia* produces a series of unusual 2-hydroxyacids such as 2-hydroxyhexanoic acid (Fig. 9.9/Formula 11) and S-methyl-2-hydroxy mercaptobutanoic acid (Fig. 9.9/Formula 12), which may form diverse lactides (Fig. 9.9/Formula 13). Traces of benzoic acid and 4-hydroxybenzaldehyde, which also represent main gland constituents in Dytiscidae, were also recorded (Fig. 9.11; see Dettner 1985, 1987). *Hygrobia hermanni* also showed a typical behavior which was described as secretion grooming (Fig. 9.9/6, Kovac and Maschwitz 1990b). In addition pygidial gland secretion of *H. hermanni* increased wettability of the beetle integument (Fig. 9.6). As compared with the untreated elytral control, contact angles of standard water droplets on elytra previously treated with pygidial gland secretion were significantly lowered (Fig. 9.6). As in Dytiscidae the sister group of Hygrobiidae (Fig. 9.11) *Hygrobia hermanni* is characterized by paired prothoracic glands which are covered by secretory cells and a muscle cover (Fig. 9.9/10; Forsyth 1970). In contrast to Dytiscidae the prothoracic glands of *Hygrobia* are situated posterolaterally within the prothorax wherefore homology seems questionable. Recent molecular data indicate that there is a sistergroup relationship of Hygrobiidae to a clade comprising Amphizoidae, Aspidytidae and Dytiscidae (Vasilikopoulos et al. 2019). The separate evolution of a prothoracic gland in Hygrobiidae therefore seems possible. Since there are no chemical data available, significance of the secretion remains unknown. When molested both sexes of the beetles (“squeak beetles”) produce audible stridulations (Fig. 9.9/9) by rubbing abdominal apex on a file at the underside of an elytron (Fig. 9.9/8; Beutel 1986; Aiken 1985; Wichard et al. 1995). Probably *Hygrobia* also stridulates during contacts with conspecifics and in courtship.

Meruidae (comb-clawed cascade beetles; one sp.): The single small-sized species (adult body length 0.9 mm) was described from Venezuela and lives in the margins of cascades and mountain streams (Balke et al. 2018). Its larva has several characteristics of *Noterus* larvae. In order to submerge, adults turnover with the head directed downward and kick with their alternating leg motion until finding an underwater foothold. Similar behaviors are known from Haliplidae or small Dytiscidae. Pygidial glands were identified morphologically, and prothoracic glands are absent (Beutel et al. 2006).

Noteridae (burrowing water beetles; 280 sp., according to Jäch and Balke (2008)): Noteridae hold the 9th position with respect to global water beetle diversity. Noteridae are especially found burrowing in muddy substrate and in root mats in ponds and marshes, there exist few subterranean species. Adults and larvae are mainly carnivorous, and larvae (only few species have been described) have a siphon at abdominal tip in order to expire oxygen from aquatic plant aerenchyma. Air-filled pupae of some species are attached to the aerenchyma of water plants. Prothoracic glands are absent, and typical paired pygidial glands are present. They consist of a reservoir covered with muscles and a bipartite secretory lobe with two types of glandular cells (Fig. 9.4/**8**; Forsyth 1968). As in Dytiscidae main gland constituents are antimicrobics as phenylacetic (sweet odor; Fig. 9.5/**11**; Fig. 9.11), 4-hydroxybenzoic (Fig. 9.5/**5**), benzoic (Fig. 9.5/**3**), and 4-hydroxyphenylacetic acids (Fig. 9.5/**12**). Also 3-indole-acetic acid (Fig. 9.5/**16**) of unknown function is present. Noteridae also show secretion grooming behavior outside the water in order to distribute pygidial gland secretions on their bodies (Kovac and Maschwitz

1990b). In addition pygidial gland secretion of *Noterus clavicornis* increased wettability of the beetle integument (Fig. 9.6; Dettner 1985, 1997a, 2016a). As compared with the untreated elytral control, contact angles of standard water droplets on elytra previously treated with pygidial gland secretion were significantly lowered.

9.5.1 Polyphaga: Hydrophiloidea

Hydrophilidae (water scavenger beetles or silver water beetles; 2932 sp.; Short: 2950 sp.; according to Jäch and Balke 2008: 3rd position with respect to global water beetle diversity): Hydrophilids and their larvae are mainly found in stagnant and also running waters and hygropetric habitats; however their ecologic habits are extremely broad. Adults prefer plants and decaying organic matters as food whereas larvae are usually predacious. There are no complex glands present. Nevertheless Kovac and Maschwitz (2000) observed terrestrial and submerged grooming in various Hydrophilidae (*Hydrophilus, Laccobius, Berosus, Enochrus, Spercheus*: Spercheidae) apart from the terrestrial *Helophorus nubilus* (see Helophoridae). It is remarkable that *Hydrochus*, *Hydrobius*, and *Berosus* use anal droplets for grooming behavior.

Stridulation is widely distributed in adult Hydrophilidae and was obviously evolved several times (Aiken 1985). In many cases hydrophilid beetles stridulate when they are irritated, and sometimes sonograms indicate that sounds are important during courtship (Scheloske 1975). In several cases stridulatory structures in hydrophilid beetles are controversially discussed (Hansen 1991; Scheloske 1975).

Within Berosini (*Berosus*) and Oocyclini (*Laccobius*; Scheloske 1975; Fig. 9.12/2) both sexes stridulate. In both genera laterosternite 3, which is concealed under the elytra, exhibits a ribbed area representing a stridulatory organ together with protuberances on the underside of elytra (Hansen 1991). Within Hydrophilini stridulatory organs are present in genera *Hydrophilus*, *Hydrobius, Limnoxenus*, and *Tropisternus* (Wilson et al. 2015) and seem to be reduced in *Helochares* and *Enochrus* (Hansen 1991). In *Tropisternus* this behavior was named disturbance stridulation and acoustic aposematism which deters predators such as wolf spiders (Masters 1979). In Chaetarthriini, Sperchopsini, and Sphaeridiinae stridulatory structures are missing (Hansen 1991).

→

Fig. 9.12 (continued) and metatibia and metatarsus (d). 4. Ventral aspect of head and prothorax of *Ochthebius quadricollis* (Hydraenidae) with part of exocrine secretion delivery system (e: end apparatus of gland cells, su: sulcus for collecting secretion, ssd: setae for secretion delivery). 5. Venter of left side of prothorax of *Hydraena riparia* with part of secretion delivery system (*e*: end apparatus of gland cells; *hh* hydrofuge hypomeron; *su* sulcus; *wh* wet hypomeron). 6 and 7. Macerated larvae of *Luciola leii* (Lampyridae) with everted, fork-like reservoirs of defensive glands (arrows in enlarged right figure). 8. *Georyssus* spec. (Georyssidae) with camouflage (covered by sand/mud; left), clean surface (right). 9. Aposematically colored *Ancyronyx* spec. (Elmidae). Gland constituents of lampyrid larva *L. leii*: **1.** Terpinolene, **2**. gamma-terpinene. Originals (1, 6, 7). Modified according to Scheloske (2), Perkins 1997 (3–5), Merritt and Cummins 1984 (8), 1996 (9).

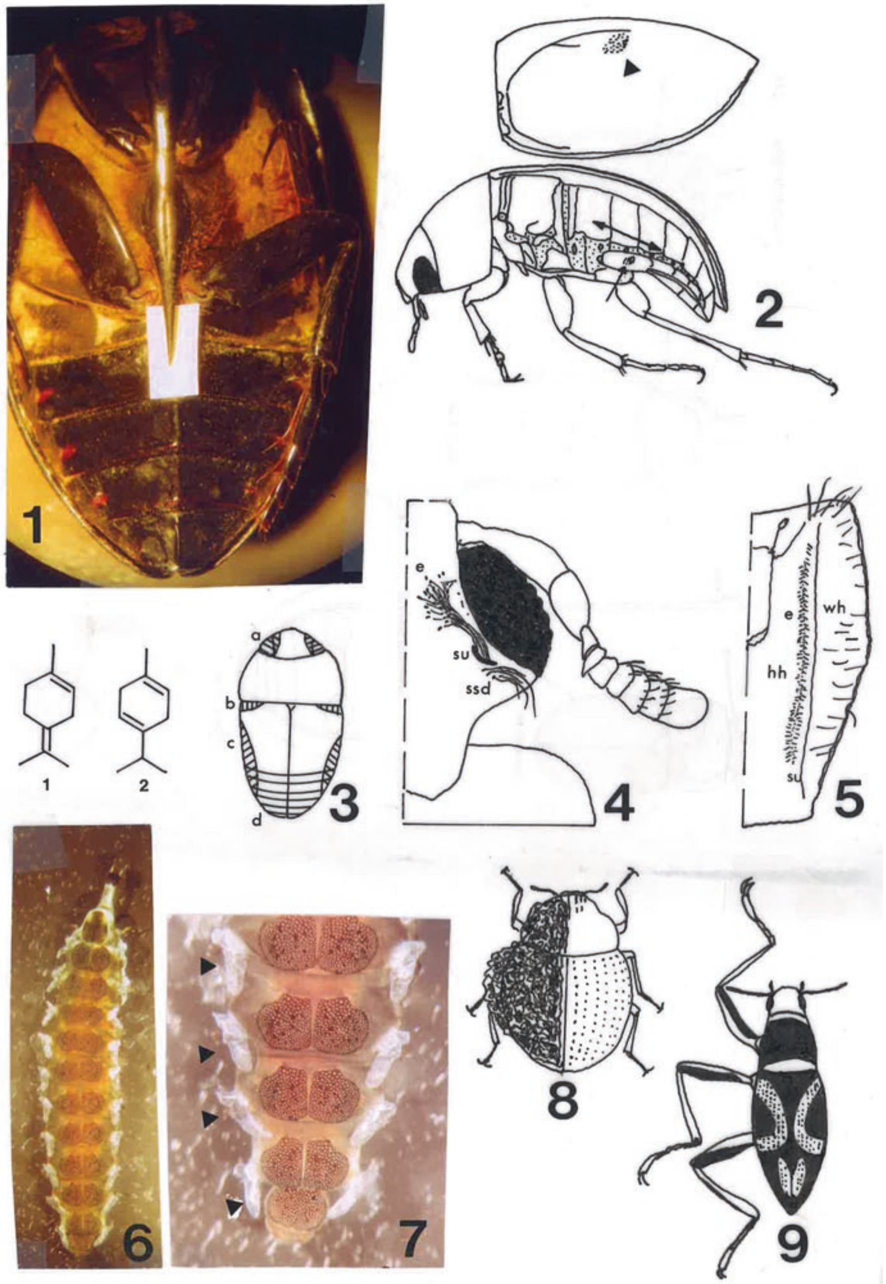

Fig. 9.12 Defensive structures of Hydrophilidae, Hydraenidae, and Lampyridae and defensive components. 1. Posterior metasternal process of *Hydrophilus aterrimus* (Hydrophilidae). 2. Stridulation organs of *Laccobius minutus* (Hydrophilidae) with protuberances on underside of elytron and pleural area (pars stridens) of third abdominal segment. 3. Dorsal side of *Limnebius piceus* (Hydraenidae) with areas groomed by protibia and protarsus (a), protibia (b), mesotibia (c),

The posterior metasternal process of *Hydrophilus*-species (Fig. 9.12/1) probably represents a defensive structure. In addition this process serves for keeping the ventral air bubble. Predator avoidance in Hydrophilidae also may include crypsis. For example *Derallus* larvae bear setiferous projections with a lot of algae and detritus. When molested larvae of *Hydrophilus* may immediately defecate like an explosion and suddenly lift their head backwards (Pavlovsky 1922).

Helophoridae (192 sp.): Helophoridae hold the 12th position with respect to global water beetle diversity according to Jäch and Balke (2008). Due to sticky dermal glands, adults are often dirty or covered by sand and must be cleaned before determination of these brownish, metallic, or black specimens. Adult Helophoridae are found especially in shallow water, and their larvae are found among vegetation an in soil near water (Angus 1992). The laterosternite 3 of adult *Helophorus* has no ribbed area (which would represent a stridulatory organ; Hansen 1991) and no stridulation has been recorded (Oliva 1992).

Epimetopidae (56 sp.; Short 2018: 66 sp.): The beetles seem to be riparian and live within sand substrates. Adults may be covered by soil particles, and they possess no abdominal stridulatory organ (Hansen 1991).

Hydrochidae (181 sp.): Hydrochidae hold the 11th position with respect to global water beetle diversity according to Jäch and Balke (2008). Hydrochid beetles are found in stagnant to slowly flowing water. The dark or metallic adults are often covered by a secretion and crust of vegetable matter (Oliva 1992). Adults feign death when disturbed and possess no abdominal stridulatory organ (Hansen 1991).

Spercheidae (filter-feeding water scavenger beetles; 20 sp., Yee and Kehl 2015): Representatives of these filter-feeding beetle family are found in stagnant waters and in mud. When molested on land or within water *Spercheus* adults of both sexes are able to stridulate in a different manner. Obviously stridulation is primarily a defensive reaction but can also be important in sexual communication (Von Frankenberg 1937). Laterosternites 3, which are concealed under the elytra, exhibit transversely ribbed areas which are moved against the ridges under each elytra in order to stridulate. Remarkably *Spercheus* adults also exhibit thanatosis (longer lasting) together with the defensive stridulation (Von Frankenberg 1937).

9.5.2 Polyphaga; Staphylinoidea

Hydraenidae (minute moss beetles; about 1300 sp.; Short 2018: 1600 described species; according to Jäch and Balke 2008 there was an estimation of 2500 sp. which means that Hydraenidae occupy the second position among water beetles with respect to global water beetle diversity): Many species of these true water beetles (few of them are terrestrial) possess a microplastron that means a ventrally situated thin layer of air, which is held by hydrofuge setae (Jäch et al. 2016). An exocrine secretion delivery system with various glands especially located at head and prothorax, e.g., in *Ochthebius* or *Hydraena* species and various cuticular structures such as grooves, ridges, and setae (Fig. 9.12/4, 5), plays an enormous role in secretion grooming (Jäch et al. 2016; Kovac and Maschwitz 2000; Perkins 1997). Perkins (1997) presented a detailed morphological investigation on these secretion delivery systems, the wetted and hydrofuge integumental body areas, and studied grooming behavior of selected species such as *Limnebius* (Fig. 9.12/3); however due to the small body size of these hydraenid beetles no chemical data are available. Integument of terrestrial and coastal species is covered with encrustations. Adult hydraenids cannot swim but walk on underside of surface film. Stridulation is quite common and two main stridulatory areas are known: (a) abdomen/elytra (all species) and (b) head/pronotum (only few species). Since stridulatory organs are sexually dimorphic, a role in courtship and mating was suggested (Aiken 1985). The similar grooming patterns of Hydraenidae within water and on land were described by Kovac and Maschwitz (2000).

Scirtidae (marsh beetles; Yee and Kehl 2015: 1000 sp.; over 1800 sp.): Scirtidae hold the 11th position with respect to global water beetle diversity according to Jäch and Balke (2008). They prefer various habitats such as streams, pools, phytotelmata, and groundwater. Marsh beetle larvae are usually aquatic, and ecology and bionomy of the family are poorly studied. If molested larvae are very sensitive and immediately stop feeding and may even escape (Klausnitzer 1996).

Elmidae (riffle beetles; 1500 sp.; Yee and Kehl: 1300 sp.): Elmidae hold the 11th position with respect to global water beetle diversity according to Jäch and Balke (2008). Aquatic Elmidae are herbivores or detrivores and are usually found in running water with high oxygen content, and seldom lakes and ponds. Adults possess an efficient plastron that means a thin air film coats the body surface. Interestingly secretion grooming by brushing legs over the ventral air layer is important but can be only observed under water (Kovac and Maschwitz 2000). White (1989) offered elmid specimens to a turtle and predatory fishes and showed that aposematically colored (red to yellow markings on elytra and thorax) beetles were almost always rejected (Fig. 9.12/9). Larvae do not have aposematic colorations and were never rejected or ignored by fishes. It was further proven that elmid adults have a chemical defense restricted to the elytra; until now active principles have not been elucidated. Elliott (2008) showed that lanceolate larvae of *Elmis*, *Esolus*, or *Oulimnius* rolled up like an armadillo when disturbed. Both larvae and adults usually have hard integuments.

Dryopidae (long-toed water beetles; 280 sp.; according to Jäch and Balke 2008/ Yee and Kehl 2015: 300 sp.): Dryopidae hold the 8th position with respect to global water beetle diversity according to Jäch and Balke (2008). Adults are found in aquatic or other habitats, and larvae are terrestrial or under water surface. Beetles and larvae are slowly moving and generally lethargic insects. Adults are purely aquatic and are characterized by a plastron. For *Dryops* secretion grooming by using their legs was reported (Kovac and Maschwitz 2000). Ecology of Dryopidae is only purely known. Adults and larvae do not have aposematic colorations and are accepted by predators (Scrimshaw and Kerfoot 1987). According to Lawrence (1991) Dryopidae pupae have unpaired gin traps, which means sclerotized and often armed portions of two adjacent sclerites (Lawrence 1991).

Psephenidae (water pennies; 287 sp.; Jäch and Balke 2008: 272 sp.): Psephenidae hold the 11th position with respect to global water beetle diversity according to Jäch and Balke (2008): The flattened larvae with their powerful claws are usually in running waters. They can hug the rocks as tenaciously as limpets, so they are safe from predators. Their coloration varies and often they match with their background substrate (Lawrence 1991). Aquatic psephenid pupae are characterized by plastron-bearing gills; in addition they have gin traps (Lawrence 1991), and adults are terrestrial. The nocturnal feeding behavoir of the larvae was reported to be a defense mechanism against predators. In addition the larvae can form a ball when being swept away (Beutel and Leschen 2016).

Cneoglossidae (eight sp.; Yee and Kehl 2015: ten sp.): Beetles are found in submerged bushwood in small streams. Larvae are aquatic, and adults are terrestrial. The life history of this small family is unknown.

Eulichadidae (forest stream beetles; 42 sp.): Larvae are aquatic; the beetles are in sand or litter under rocks in streams.

Lutrochidae (travertine beetles; Jäch and Balke 2008/Yee and Kehl 2015: 15 sp.): Travertine beetles occur submerged in decaying wood. Their life history is unknown and their taxonomy has to be revised. Adults which inhabit calcareous water streams may be encrusted with this material (Yee and Kehl 2015).

9.6 Not Predominantly Aquatic Families According to Jäch and Balke (2008)

Nitidulidae (sap beetles; according to Jäch and Balke 2008 about 3000 sp.): One species *Amphicrossus japonicus* is aquatic and can be found in in water-filled stems of bamboo.

Carabidae (ground beetles; 37,600 sp.; Beutel and Leschen 2016): Among these Geadephaga there are a lot of species which are riparian, found near freshwater habitats, or even stay underwater for feeding or concealing (*Carabus clathratus, Oodes, Nebria, Bembidion, Chlaenius, Brachygnathus*). Representatives of the genus *Omophron* are found within wet sand and even resemble dytiscid water beetles. However phylogenetically there is no relation between *Omophron* and Hydradephaga. All Geadephaga share the same pygidial glands with Hydradephaga. However the gland morphology of *Carabus* or *Omophron* (Fig. 9.4/12) is not similar with Hydradephaga, because secretory tissues are compact and not lengthened. In addition they produce other pygidial gland constituents (e.g., *Omophron*: 2-methylpropanoic acid, 3-methylbutyric acid; *Carabus*: 2-methylpropenoic acid, (E)-2-methyl-but-2-enoic acid; also in water beetle *Ilybius*; Dazzini Valcurone and Pavan 1980). In *Omophron* stridulation was investigated and was named disturbance stridulation and acoustic aposematism which deters predators such as wolf spiders (Masters 1979).

Staphylinidae (rove beetles; 55,244 sp. Beutel and Leschen 2016): Rove beetles from many subfamilies (e.g., *Aleochara, Omalium, Paederus, Philonthus, Thinobius*) are semiaquatic and can be found on beaches, along rivers, ponds, bogs, and nearly every kind of freshwater. Due to their short elytra and their unprotected abdomina most staphylinid species have defensive glands or toxic hemolymph in order to defend against predators (Dettner 1993). Especially two taxa have special relationships with water. Many species of *Bledius* (Oxytelinae) live subsocially within wet sand of shores (freshwater; sea) where they feed on algae. Females feed and defend their larvae and use their quinoid abdominal gland secretions against aggressors (Dettner 1993; Thayer 2016). In many cases the formulation of these mixtures of defensive secretions is optimized against special target organisms (Steidle and Dettner 1993, 1995). Another rove beetle group, representatives of Steninae (worldwide with 3300 sp.), is typical for the water surface of all kind of freshwaters (Betz et al. 2018). The beetles are predators of aquatic springtails and other small arthropods and are found in every wet place. Many species walk on the water surface and depending on species show a unique skimming behavior after a molestation. They secrete terpenes and alkaloids such as stenusin or cicindeloin from their anal glands (Fig. 9.13; Dettner 1987, 1993; Betz et al. 2018). Comparable to *Enhydrus* glands

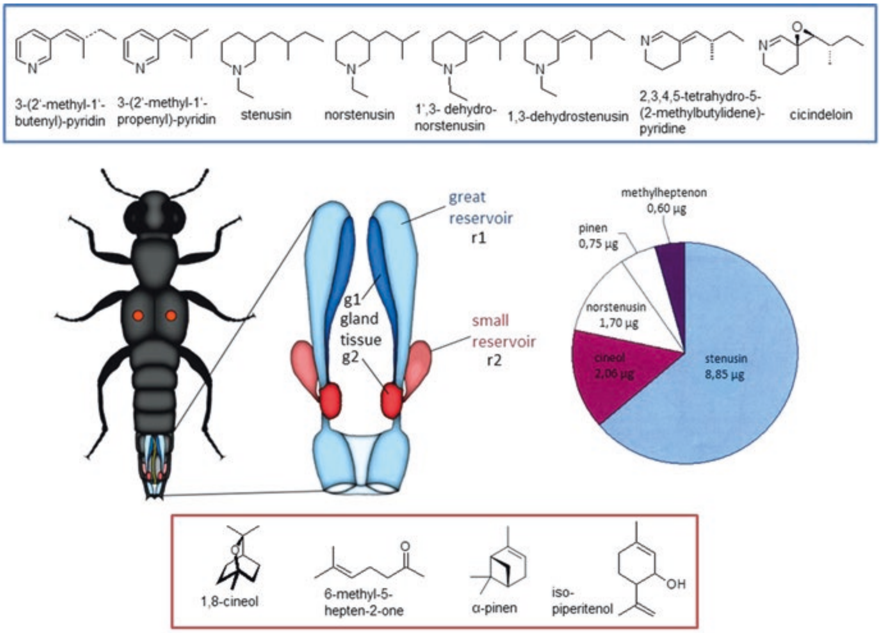

Fig. 9.13 Anal glands and secretions of *Stenus* rove beetles (Staphylinidae). Paired anal glands with large reservoirs (gland tissue g1 and gland reservoir r1; blue) and small gland reservoirs (r2) and gland tissue (g2; red). Alkaloids from the large gland are figured above (blue box), terpenes from the small gland are figured below (red box). Circle demonstrates quantitative amounts of alkaloids stenusin and norstenusine from large gland as compared with remaining terpenes from smaller glands of *Stenus comma* (according to Betz et al. 2018)

(Gyrinidae), *Stenus* abdominal glands have two types of secretory tissues (gland 1 and gland 2) which are morphologically separated and synthesize different compounds. The large gland 1 delivers alkaloids; in contrast the small gland produces terpenes. All alkaloids are biosynthetically derived from amino acids from food (e.g., springtails, aphids). Together with molecular data, the Steninae alkaloids are excellent chemotaxonomic markers (Betz et al. 2018).

Both special alkaloids (formerly named "spreading alkaloids") and selected terpenes may have considerable spreading activity. However the spreading ability and velocity of a *Stenus* species on the water surface vary. These differences are due to gland composition and the ability of the beetle species to deplete their outer gland reservoir on the water surface (Fig. 9.13; Lang et al. 2012). These compounds have multiple functions as antimicrobics, fungicides, and deterrents against predatory arthropods and fishes (Schierling et al. 2013). In addition the rove beetles exhibit grooming behavior or deplete parts of their anal glands, when molested. Spreading abilities are unusual phenomena in nature; however it is also observed in semi-aquatic Veliidae (Heteroptera) which in contrast spray saliva on the water surface. As mentioned by Bush et al. (2008) even pine needles floating on the water surface are propelled across the surface since the resin at its base decreases the surface tension.

Leiodidae (round fungus beetles): *Platypsyllus castoris* lives on beavers, and *Silphopsyllus desmanae* lives on water moles. These two species represent parasitic water beetles (Jäch and Balke 2008).

Scarabaeidae (scarab beetles; 27,000 sp.): Among this large cosmopolitan family there exists the aquatic rice beetle *Dyscinetus morator*. This species is often found underwater, especially while escaping disturbances (Jäch and Balke 2008).

Ptilodactylidae (toe-winged beetles; Yee and Kehl 2015: approximately 500 sp.): They are found in aquatic, especially riparian, habitats. Larvae feed on submerged decaying wood. As defense ptilodactylid pupae have abdominal gin traps (Beutel and Leschen 2016). Not all species are aquatic. Ecological information is mostly lacking.

Lampyridae (lightning bugs/fireflies; approx. 2000 sp. according to Jäch and Balke (2008) and Yee and Kehl (2015)): Larvae of few species (*Luciola, Pyractomena, Pristolycus*) are secondarily aquatic (sometimes with tracheal gills) and are found in running water (lotic systems) or ditches (lentic systems). As terrestrial larvae which feed on land snails, the aquatic larvae feed on aquatic molluscs such as mussels and snails. Elder larvae may be good swimmers in order to catch prey. Since the snail preys in Japan sometimes represent hosts for human parasites these larvae are important for biocontrol (Yee and Kehl 2015). Aquatic and semi-aquatic lampyrid larvae leave the water before pupation in order to construct terrestrial mud cells (Branham 2010). All lampyrid larvae aposematically produce light via paired photic organs which are located ventrally at the eighth abdominal segment (Branham 2010). Fu et al. (2007, 2009) reported that the glow intensity of three aquatic *Luciola* species is weak. Okada (1928) and Fu et al. (2007, 2009) described defensive glands in larvae of the genus *Luciola*. After molestation from meso- and metathorax and every abdominal segment (8) paired forked organs are everted from slit-like crevices which are situated above the gills (Fig. 9.12/6, 7). The anterior branch of these glandular sacs is longer than the posterior one. Fu et al. (2007) described the odor of *Luciola leii* secretion (present in all six instars) as pine oil-like, whereas Okada (1928) reported an odor in a Japanese *Luciola*-species resembling resin and peppermint. Until now terpinolene (Fig. 9.12/Formula 1) and gamma-terpinene (Fig. 9.12/Formula 2) could be identified in the defensive secretion of *L. leii* (Fu et al. 2007). When aquatic larvae are under attack they may run away, and exhibit thanatosis, glowing and with release of defensive secretion. Preliminary bioassays showed that *L. leii* larvae were refused by various predatory fishes or dragonfly larvae (Fu et al. 2007). However one has to take into consideration that most lampyrid beetles and their larvae synthesize toxic cardiac glycosides, the lucibufagins (Eisner et al. 2005).

Chrysomelidae (leaf beetles; about 46,000 species in many subfamilies are known): From several subfamilies such as Alticinae, Chrysomelinae, Galerucinae, or Hispinae there are known members living on emergent aquatic plants or even within phytotelmata. Adults of several species can live underwater or at the water surface (Jäch and Balke 2008). Representatives of subfamily Donaciinae with genera such as *Donacia, Macroplea*, or *Plateumaris* are especially adapted to freshwater. Their larvae and pupae are generally submerged, but also adults, which may carry an extensive plastron, are often found underwater. Larvae have caudal spines in order to penetrate tissues of aquatic plants to take up air. Cocoons which are spun from larval silk glands are fixed underwater and are water- and airtight. Donaciinae usually feed on monocotyledonous host plants or Nymphaeaceae; adults also prefer pollen. Defense mechanisms in Donaciinae are not known; however the abovementioned subfamilies of Chrysomelidae with semiaquatic species represent interesting taxa to investigate, since they exhibit various mechanisms of mechanical (Hispinae) and chemical defenses including sequestration of plant toxins (e.g., Burse and Boland 2015; Dettner 1987, 2015; Hilker and Meiners 2002; Opitz and Müller 2009; Pasteels et al. 1984, 1990).

Nanophyidae (about 300 species Jäch and Balke 2008): Several species of *Nanophyes* represent phytophilous water beetles feeding on *Alternanthera* and *Ludwigia.*

Erirhinidae (about 300 species, Jäch and Balke 2008) with some phytophilous water beetles.

Curculionidae (weevils; largest family of animals; more than 60,000 species, Jäch and Balke 2008): Few species from various subfamilies have invaded aquatic environments. Most species belong to Bagoinae but also those from Cleoninae, Notarinae, Stenopelminae, Tanysphyrinae, or Ceutorhynchinae aquatic representatives are known. Many species (larvae and adults) are mono- and oligophageous (e.g., *Alisma, Azolla*, *Equisetum, Butomus*, *Eichhornia, Glyceria, Lemna, Myriophyllum, Pistia, Potamogeton, Ranunculus, Ricciocarpus, Salvalina, Stratiotes*) and few species are used as biological control agents of introduced nuisance water plants (Merritt and Cummings 1996).

Most aquatic weevils swim and dive underwater and use plastron respiration. Larvae are mining but usually slowly crawl on host plants and pupate within air-filled cocoons located on roots of plants (Klausnitzer 1996). Adults of most species are mechanically defended by hard integuments; sometimes as in *Dicranthus elegans* they have additionally long and hard elytral spines. In several genera such as *Helodytes, Eubrychius*, or *Hydronomus* terrestrial and aquatic grooming pattern was described (Kovac and Maschwitz 2000). For grooming dark and later clear fecal droplets were repeatedly released from the abdominal tips.

Trachypachidae (false ground beetles; six sp.): The enigmatic Trachypachidae (Adephaga) have many morphological similarities with Dytiscoidea (e.g., Arndt and Beutel 1995); however they are not found in wet habitats and therefore not covered by Jäch and Balke (2008). In contrast they are xerophilous (Beutel and Arndt 2016) and molecular data place them phylogenetically within Geadephaga (Maddison et al. 2008). Although biology of this family is nearly unknown, the pygidial glands resemble those of carabids (Fig. 9.4/11, 12). The defensive chemicals of two *Trachypachus* species (Attygalle et al. 2004) with methacrylic acid and tiglic acid also resemble those secretions of terrestrial carabids. In contrast, trachypachids secrete octanoic acid, unknown sulfur compounds, or an aromatic (Fig. 9.11) which is typical for Hydradephaga (Dettner 1985; Dettner and Böhner 2009). Therefore further research is necessary in order to evaluate the chemotaxonomic value of these micrometabolites.

9.7 Shore Beetles According to Jäch and Balke (2009)

Georissidae (minute mud-loving beetles; 80 sp.): These beetles are usually riparian. By using buccal secretions adults are often covered by sand or mud (Fig. 9.12/8) and it is difficult to observe the melanized or metallic surfaces. Bameul (1989) described the camouflage of *G. crenulatus* which even prevents flight (Shepard 2003). In spring when georissid beetles are very active they exhibit a short thanatosis before moving away. Adults have no stridulatory organs (Hansen 1991).

Limnichidae (minute mars-loving beetles; 387 sp., Beutel and Leschen 2016; according to Yee and Kehl 2015: 335 sp.): These beetles feed on algae, are semiaquatic, and can be found on sandy beaches or coralline formations. Adults of Thaumastodinae (jumping shore beetles) can jump. Beetles of this family are accepted by fishes (Scrimshaw and Kerfoot 1987).

Heteroceridae (variegated mud-loving beetles; 300 sp.; Yee and Kehl: over 250 sp.): Adults and larvae live in tunnels in wet sand at water edges, in riparian areas. Adult heterocerid larvae can use secretion from dermal or salivary glands in order to stabilize their pupal chamber. After molestations beetles break through the mud and fly away (Klausnitzer 1996).

HYMENOPTERA (sawflies, wood wasps, bees, wasps, ants; 0.1% aquatic): Among worldwide 132,000 hymenoptera species (Stork 2018: 116,861) only about 150 from 11 families represent mostly internal parasitoids of aquatic stages (eggs, larvae) of various water insects and hygrophilic spiders (Cover and Bogan 2015; Morse 2017; Wesenberg-Lund 1943). In contrast selected Agriotypinae and Pompilidae (e.g., *Anoplius*) represent external parasitoids of Trichoptera pupae (*Goera, Silo*) of, respectively, *Dolomedes* or *Pardosa* spiders (Morse 2017).

Interestingly by abdominal silk glands *Agriotypus* larvae produce a helical outgrowth from the trichopteran pupa which serves as a breathing device (Wesenberg-Lund 1943). Wesenberg-Lund (1943) and Heckman (2018) summarized typical aquatic hymenopterans from Chalcididae (e.g., *Pleurotropis, Trichogramma, Prestwichia*; hosts: cocoons and eggs of Gyrinidae, Dytiscidae, *Sialis*, Odonata, water bugs), Proctotrupidae (*Limnodytes, Litus, Anteris, Anagrus, Anaphes* = *Polynema*; hosts: eggs of water beetles, and water bugs, Odonata), Ichneumonidae (*Hemiteles, Apsilops, Atractodes*, *Trichocryptus*; hosts: cocoons of Gyrinidae, larvae, and pupae of various Diptera, Trichoptera, Lepidoptera), Braconidae (e.g., *Dacnusa, Chaenusa, Liposcia, Gyrocampa Hydroplitis*; hosts: larvae of *Hydrellia*, *Hydrocampa*), and Agriotypinae (see above). Several biological aspects of aquatic parasitoid species were discussed by Heckman (2018).

As in other insects, parasitic wasps are attacked by various predators ranging from vertebrates to invertebrates such as spiders and other insects. Because natural histories of aquatic hymenopteran species are mainly unknown, here only selected defensive mechanisms within those families are presented where aquatic representatives were reported. As known from various hymenopteran parasitoids they may be brightly colored, which indicates their unpalatability (Quicke 1997). Other larger species such as ichneumonids and braconids defend against vertebrates and invertebrates by stinging (Quicke 1997), which sometimes might be really painful. Certainly only females are effective, since males lack ovipositors for venom injection. Certain parasitoids in addition produce distinct, sometimes unpleasant, odors which originate from exocrine glands. In female *Alloxysta* species mandibular glands produce deterrents such as 6-methyl-5-hepten-2-one, actinidin, and various iridoids (Völkl et al. 1994) which are directed against predators. Other species produce also perillene-isomers or iridoids such as nepetalactone and iridomyrmecin (Hübner et al. 2002). Many ichneumonids but also braconids and certain Oppiinae are odoriferous which may also originate from mandibular glands (own observations, Quicke 1997) and are probably directed against wasps. Unfortunately only few data exist on exocrinology of hymenopteran parasitoid wasps; however some pheromones, kairomones, and venom proteins are compiled by Keeling et al. (2004), Dettner (2015), and Asgari and Rivers (2010). Other parasitic Hymenoptera show thanatosis (death feigning). Interestingly some braconids are polymorphic for this behavior and in *Habrobracon* the gene controlling thanatotic behavior is inherited as a single dominant allele (Grosch 1988; Quicke 1997). Parasitic wasps may act as models in mimicry systems or may be mimics themselves (for theory see Dettner and Liepert 1994). In addition especially ichneumonids also might construct cryptic or mimetic cocoons (Quicke 1997). Finally larger braconids may be protected from predators by heavily sclerotized thoracic spines (Quicke 1997). In larger ichneumonids there occur even poison claws and urticating hairs (Hanson and Gauld 1995).

DIPTERA (true flies; about 50% aquatic): Worldwide there exist about 154,000 species of Diptera (Stork 2018: 155,477), most of which have aquatic or semiaquatic eggs and larvae. There exist various reviews where aquatic and semiaquatic dipteran larvae are compiled (e.g., Italian and European species: Rivosecchi 1984; Faasch 2015; neotropical species: Fusari et al. 2018; world: Hennig 1968, Morse 2017). Especially the following aquatic and subaquatic families should be denoted: Ceratopogonidae, Chironomidae, Deuterophlebiidae, Simuliidae, Thaumaleidae, Canacidae, Culicidae, Dixidae, Corethrellidae, Chaoboridae, Blephariceridae, Nymphomyiidae, Psychodidae, Stratiomyidae, Dryomyzidae, Syrphidae, Periscelididae, and Ephydridae. In addition further families may also be of importance: Cylindrotomidae, Tipulidae, Limoniidae, Tanyderidae, Ptychopteridae, Scatopsidae, Athericidae, Rhagionidae, Tabanidae, Pelecorhynchidae, Empididae, Dolichopodidae, Lonchopteridae, Phoridae, Muscidae, Scathophagidae, Sarcophagidae, and Sciomyzidae. Since bionomics of many Diptera are unknown (Oosterbroek 2006), especially at the larval stage (Hennig 1968), the knowledge on defenses of dipteran larvae is deficient. As demonstrated by Crespo (2011) *Chaoborus* larvae (Chaoboridae) can sense fish kairomones which affect their vertical migration. Also chironomids can assess different concentrations of infochemicals. For the predatory *Toxorhynchites* larvae it was shown that not chemical cues but vibrations (detected by thoracic and abdominal setae) were necessary to detect prey organisms (Crespo 2011). As a whole Crespo (2011) stressed that studies on predator avoidance have not received the same attention in Diptera as in other aquatic insects.

One fascinating aspect of mosquito perceiving of kairomones of larval predators was presented by Crespo (2011). Recent molecular data on olfactory binding proteins in larvae and adult mosquitoes showed that several of them are present in both immature and mature stages. Therefore it seems conceivable that adult mosquitoes may utilize information which is relevant during their larval stages. That female *Culiseta* mosquitoes only oviposit in those waters where no *Notonecta* kairomones (such as n-heneicosane), the predators of the *Culiseta*-larvae, are present was discussed in chapter Notonectidae.

Apart from flight reactions (often achieved by peristaltic movements) which might be abundant in dipteran larvae, secondary defenses such as chemical defense or thanatosis obviously are rare (Dettner 2015). However primary defense mechanisms such as larval shelters (Chironomidae, Simuliidae), crypsis, translucence, or stable and elastic cuticles may be more abundant in spite of the fact that larval body colors are not abundant (Dettner 2015). Tergites and sternites of fly larvae usually are reduced in order to obtain optimal mobility.

Larval integuments of Diptera may sometimes possess micro- and macrotrichia, spines, and dermal glands but no complex glands. Often larvae show fleshy projections, papillae, pseudopods, or suctorial discs. Even pupae of aquatic Diptera often have abdominal spines. That the abovementioned structural characters such as hairs and/or body sizes of the larvae can protect chironomid larvae from different kind of predators is amply illustrated by the study of Hershey and Dodson (1987). Large larvae of *Cricotopus bicinctus* were less susceptible to predation by *Hydra* and small *Ischnura* larvae. In contrast long hairs protected *Cricotopus sylvestris* from *Hydra* but not from *Ischnura.*

In the following examples of defense in aquatic or semiaquatic dipteran larvae are given.

Ceratopogonidae (biting midges): According to Ronderos et al. (2018) there exist worldwide 6268 sp. In Ceratopogonidae it was proved that female canthariphilous species such as *Atrichopogon trifasciatus* are able to transfer toxic cantharidin into their eggs and larvae (Dettner 1997). Larvae of *Forcipomyia* possess secretory setae dorsally on their bodies (Fig. 9.14/2), where various antibacterial and hygroscopic

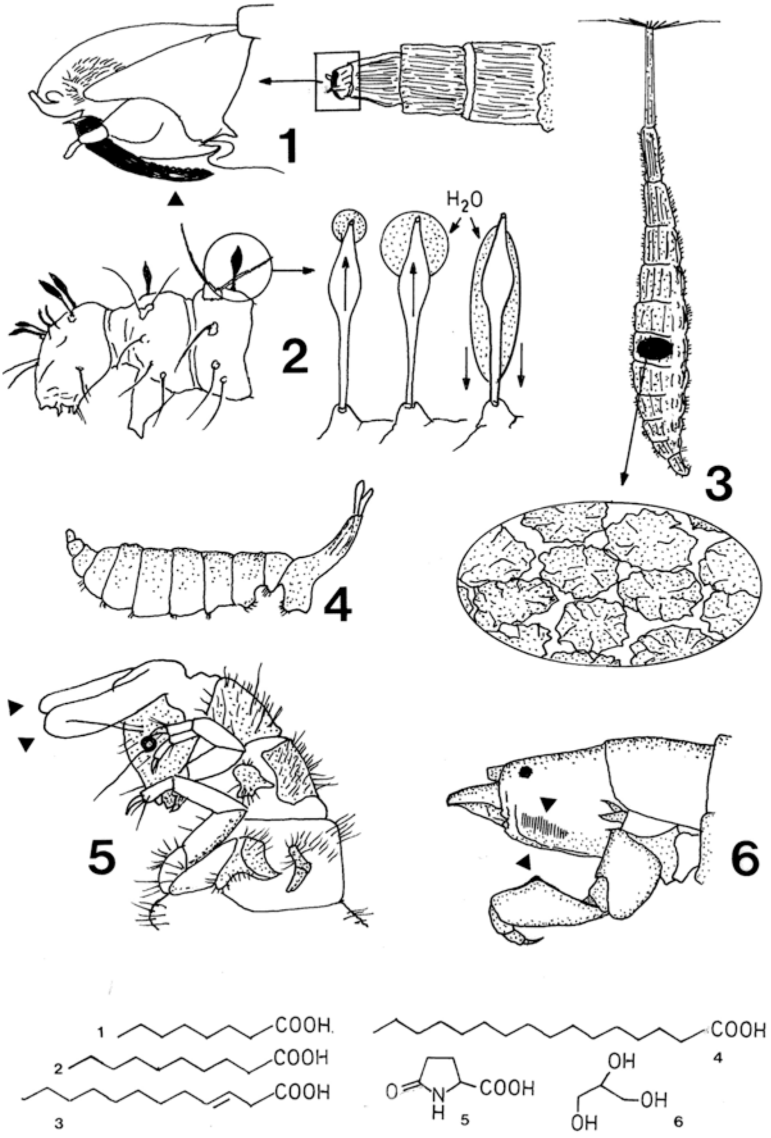

Fig. 9.14 Morphological defense, defensive glands, and stridulatory organ of dipteran (1–4) and trichopteran larvae (5, 6). 1. *Tabanus* spec. larva (Tabanidae; right) and head capsule with pierced mandible (left). 2. Fore-end of *Forcipomyia* larva (Ceratopogonidae) with secretory setae (black; left side). Enlargement of secretory setae (right) showing depletion of secretion and its hydroscopic effects. 3. Larva of *Stratiomys* spec. (Stratiomyidae) with hard integument by calcareous crystals (enlargement). 4. Pupa of *Ephydra bivittata* (Ephydridae) with gin trap between segments 6 and 8. 5. Head and thorax of *Apataniana hellenica* (Limnephilidae) with everted prothoracic glands (arrows). 6. Stridulatory organ of *Hydropsyche pellucidula* (Hydropsychidae) with file on head underside and scraper on profemur (arrows). Defensive secretions: **1.** Caprylic acid (*Apatania, Forcipomyia*), **2**. capric acid (*Apatania, Forcipomyia*), **3**. 3-dodecenoic acid (*Apatania*), **4**. palmitic acid (*Forcipomyia*), **5**. pyroglutamic acid (*Forcipomyia*), **6.** glycerol (*Forcipomyia*).
Modified according to Jacobs and Renner 1974 (1, 3), Urbanek et al. 2011 (2), Rivosecchi 1984 (4), Wichard et al. 1995 (5), Aiken (1985)

compounds such as fatty acids (Fig. 9.14/**1**, **2**, **4**), glycerol (Fig. 9.14/**6**), and pyroglutamic acid (Fig. 9.14/**5**) are produced (Urbanek et al. 2012). *Atrichopogon* larvae and pupae of various genera bear abdominal spines which may represent a kind of mechanical defense (Ronderos et al. 2018).

Lonchopteridae (spur-winged flies): 58 species worldwide (Fusari et al. 2018): Lonchopterid larvae live on shores of water. They are often dark colored and have broad dorsal and smaller lateral sclerotized plates which may have a protective value.

Tabanidae (horse and deer flies): According to Fusari et al. (2018) there exist worldwide about 4500 species. Larvae are predators and often have a thick integument (Fig. 9.14/1). From each segment 4–10 of the often colored larvae there exists a thick ring, each supplied with various parapodia and sometimes with additional spines. Larvae have a retractile head capsule with pierced mandibles, where toxins from the salivary gland are applied (Fig. 9.14/1). Bites of some *Tabanus* larvae are known to be as painful as bee stings. Injections of tabanid venoms into insects produce moveless animals after one or two spasms (Schmidt 1982). In the field even tadpoles are killed immediately.

Stratiomyidae (soldier flies): According to Pitaluga de Godoi and Pujol-Luz (2018) there exist worlwide 2800 species (928 species are aquatic, Morse 2017). The integument of armored, dorsoventrally flattened larvae is leatherlike, with a lot of calcareous crystals which are produced within malpighian tubules (Fig. 9.14/3). The hard and flexible integument protects the larvae from predators but also represents a protective device against hymenopteroid parasitoids (Wesenberg-Lund 1943).

Syrphidae (syrphid flies; worldwide about 6000 sp.; 1341 aquatic species according to Morse 2017): Certain larvae of usually saprophagous aquatic Eristalinae possess a long anal segment (“rat-tailed larvae”) which acts as a protecting sheath for the breathing tube. Since *Eristalis tenax* and various other syrphid species are able to survive in extremely polluted aquatic habitats various antibacterial peptides could be identified within the hemolymph of these larvae (Altincicek and Vilcincskas 2007). In contrast cuticles of syrphid larvae with both short and long breathing tubes have impervious cuticles which prevent entering of many toxic substances from the water (Heckman 2018). Similar microbiological results and unusual products were achieved by analysis of *Helaeomyia petrolei* larvae (**Ephydridae**, shore flies; 1251 species Morse 2017) from extreme habitats (Kadavy et al. 2000). Pupal representatives of this family such as *Ephydra bivittata* also possess gin traps as defense against parasitoids (Fig. 9.14/4). Predatory syrphid larvae of *Ocyptamus* live in tanks of bromeliads and subdue their prey with venoms (Miranda and Rotheray 2018).

TRICHOPTERA (caddisflies; more than 99% aquatic): Few defensive mechanisms are known from Trichoptera, the sister group of Lepidoptera. They have worldwide about 15,000 species (Stork 2018: 14,391) and are found in nearly all freshwater habitats (Heckman 2018; Pes et al. 2018). Nearly all species have long-living aquatic larvae with about five larval stages. In 1984 Otto showed that trout in daylight preferably attacked caddis-larvae which possessed head capsules with contrasting color patterns compared to uniformly colored specimens. However this preference was reversed under reduced illuminations (Otto 1984). Many Trichoptera larvae produce transportable case buildings from silk glands as primary defensive behavior against both vertebrate and invertebrate predators (Morse 2003). A wide range of plant and mineral materials are used and are orientated longitudinally or horizontally. Such caddisfly cases may be classified as tube cases (most Integripalpia: Limnephilidae, Goeridae, Phryganeidae, Brachycentridae, Lepidostomatidae, Beraeidae, Sericostomatidae, Odontoceridae, Molannidae, Leptoceridae), saddle or tortoise cases (Glossosomatidae), or purse cases (Hydroptilidae). Some cases are only made from silk, and may contain shells of freshwater molluscs, freshwater sponges, or pieces of corals (marine species). In contrast about half the caddisfly species do not build cases, but spin silken retreats which are fixed on the substrates and serve for capturing food (e.g., Philopotamidae, Psychomyiidae, Ecnomidae, Polycentropodidae, Hydropsychidae, Arctopsychidae). There are also free-living larvae moving on substrates (e.g., Rhyacophilidae, Hydrobiosidae). Efficiency of different trichopteran larvae with various types of cases was tested against predatory *Anax* dragonfly larvae (Ferry et al. 2013). It was astonishing that the presence of any case, regardless of the material used, offers survival benefits against dragonfly larvae. In contrast caddisflies removed from their case were attacked and captured. Larval cases of *Limnephilus* larvae surviving exposure to dragonfly larvae and predacious minnows were significantly stronger (greater mineral fraction), longer, and wider than cases of victims (Nislow and Molles Jr 1993). Finally Boyero et al. (2006) showed that *Potamophylax* larvae can discriminate predators such as dragonfly larvae, salamander larvae, and trouts by chemical cues and alter their choice of case type according to risks of predation. As mentioned by Crespo (2011) long-range identification of food was not dependent on intact antennae of trichopteran larvae but may be achieved by sensilla in maxillary and galeal palps. He also stressed that predator avoidance responses had not been studied so far in trichopteran larvae.

However one exceptional example is described below. When disturbed aquatic larvae of the genera *Apatania* and *Apataniana* (Limnephilidae) release a defensive fluid (1–2 μg secretion per specimen) from an eversible prothoracic gland (Fig. 9.14/5; Wichard et al. 1995), which shows paralyzing effects against small invertebrates (other trichopteran larvae such as *Rhyacophila*). When *Rhyacophila* penetrates the *Apatania* case, at first the larvae withdraw, and then release droplets of the secretion. In contrast the secretion is ineffective against larger targets such as plecopteran larvae or fishes (Wagner et al. 1990). The secretion contains about 40 C_7- to C_{14}-carboxylic acids (Fig. 9.14/**1–3**) with the main constituents 5-octenoic-, octanoic-, decanoic-, 3-dodecenoic- (Fig. 9.14/**3**), 3,5-dodecadienoic-, and 3,5,7,11-tetradecatetrenoic acids (Wagner et al. 1990). These eversible larval limnephilid defensive glands resemble the osmeteria which are found in various caterpillars such as Notodontidae or Papilionidae. It is noteworthy that a single irritation does not result in a complete loss of defensive secretion. Another defensive behavior was observed in larvae of Hydropsychidae. In order to defend their retreats against intruders they communicate and produce stridulatory signals in rubbing the scraper of the forefemur against a file on the underside of the head (Fig. 9.14/6; Aiken

1985). Also *Plectrocnemia* larvae will defend their retreats and fight with open mandibles against intruders (Solem and Gullefors 1996).

LEPIDOPTERA (moths, butterflies; 0.5% aquatic): According to Graca and Solis (2018) there exist 157,000 lepidopteran species worldwide (Stork 2018: 157,338). Most of the species are terrestrial; however several families contain few or various semiaquatic or aquatic species at least caterpillars. Females of aquatic species usually deposit eggs in underwater vegetation. In few species females cover their egg masses with thick secretion. In *Acentria ephemerella* there exist even females which have no wings and are living completely underwater (Reichholf 1970; Vallenduuk and Cuppen 2004; Wesenberg-Lund 1943). Newly hatched larvae may attach silken threads to the leaf as anchor. As a kind of protection from enemies especially early larval instars of several species feed as miners or boreres within stems or leaves of aquatic or semiaquatic plants. By using their salivary glands later instars or larvae from other species may construct cases from their food plants like trichopteran larvae and therefore to some extent might be protected. Oxygen intake by larvae may be achieved through tracheal gills, plastron-like devices, and use of bubbles in interstitial places or in cases made with the host plant. Depending on species and larval stages hydrophobicity and wettability of larval integuments may vary considerably. Pupation of aquatic lepidopteran larvae takes place in or out of water inside silken cocoons.

Examples of aquatic lepidopteran families, some genera involved, and food plant families are given below: **Cosmopterigidae** (1792 sp.): *Cosmopterix atte* (Cyperaceae); **Momphidae** (114 sp.): *Monpha* (Onagraceae); **Tortricidae** (10,387 sp.): *Bactra* (Cyperaceae); *Clepsis* more than 60 species associated with (Cyperaceae) *Choristoneura* and *Archips* (Typhaceae); **Pyralidae** (5921 sp.): *Acola* (Amaranthaceae); and **Crambidae** (9655 sp.) within subfamily Acentropinae according to Cover and Bogan (2015) most of the 730 species worldwide are aquatic: *Acentria*, *Argyractis, Cataclysta, Donacaula*, *Elophila, Hygraula, Neargyractis, Niphograpta, Nomophila, Nymphula*, *Ostrinia*, *Oxyelophia, Parapoynx*, *Petrophila, Samea, Sameodes, Schoenobius, Thalia*, *Usingeriessa,* and *Xubida*. Their food plant families are Alismataceae, Amaranthaceae, Araceae, Callitrichaceae, Cannaceae, Ceratophyllaceae, Characeae, Cyperaceae, Gramineae, Haloragaceae, Hydrocharitaceae, Lemnaceae, Marantaceae, Nelumbonaceae, Nymphaeaceae, Poaceae, Polygonaceae, Pontederiaceae, Potamogetonaceae, Salviniaceae, Sparganiaceae, Typhaceae, and Zosteraceae.

Sphingidae (1463 sp.): *Eumorpha* (Onagraceae), **Erebidae** (24,600 sp. including Arctiidae and Lymantriidae): *Paracles*, and **Noctuidae**: *Bellura* (Cambombaceae, Gramineae, Hydrocharitaceae, Lentibulariaceae, Nymphaceae, Pontederiaceae, Typhaceae).

As a whole there are not known defensive mechanisms of aquatic Lepidoptera. Generally Pyralidae larvae are known to regurgitate as a response to disturbance (Dettner 2015). A lot of terrestrial caterpillars feed on toxic plants and are able to tolerate and to enrich these toxins as defense mechanisms (Nishida 2002; Opitz and Müller 2009). In comparing the abovementioned aquatic lepidopteran families and their food plants (plant family level) with defensive mechanisms and toxin sequestration in terrestrial Lepidoptera there was no correspondence at all.

MECOPTERA (scorpionflies, hangingflies; 1% aquatic): There is one relict family (with 8 species) in Australia and South America among 9 families worldwide (600 species; Stork 2018: 757) which is characterized by long, slender aquatic larvae, which resemble Corydalidae or Trichoptera larvae. These representatives of Nannochoristidae have four instars and live in stream benthos and prey upon larvae of Chironomidae and other dipterans (Machado 2018; Cover and Bogan 2015; Pilgrim 1972). Adults of many Mecoptera fall to the ground and show thanatosis when disturbed (Dettner 2015). Very often they emit a malodorous digestive fluid from the mouth when they are irritated. Until now larval defense in Mecoptera is unknown.

9.8 Conclusions

After surveying defense mechanisms of aquatic and semiaquatic water insects and after comparing the results with antipredatory data of Witz (1990) there are some interesting results. Generally there is a high significance of thanatosis, escape, withdrawal, and especially stabile elastic or hard exoskeleton. Comparable to all arthropods (Witz 1990) defensive stridulation is more abundant in water insects and especially distributed in adults of different water beetles or Heteroptera, but also uniquely in larvae of Odonata and Trichoptera. Following result is astonishing: Exclusively notonectid bugs which have secondarily lost their complex thoracic defensive gland exhibit stridulatory organs. Such stridulatory organs are not found in those notonectids with intact thoracic glands. Generally stridulation in water insects seems primarily defensive stridulation, before it is used intraspecifically for alarm or communication.

The presence of hard exoskeletons and spines as observed in larvae of Odonata or Ephemeroptera should not only represent defenses against fishes but also might be due to kairomonal effects which seem to be abundant in freshwater ecosystems (Brönmark and Hansson 2012). Many phenomena concerning such mechanisms of defense have to be investigated in the future and especially in tropical water insects (especially Indo-Malayan or Afrotropical regions, see Stork 2018). Moreover behavior and bionomy of aquatic dipteran larvae are mostly unknown.

Exocrine glands and chemical defense in aquatic insects are not so widespread and abundant as in terrestrial arthropods (Witz 1990) or in marine systems. The only widespread complex gland in adephagan beetles is present within all Adephaga. In addition the thoracic gland of water bugs is primarily present in all Heteroptera. The same applies to the diversity and biosynthetic variations of the constituents. It is remarkable that the ubiquitous defensive system in terrestrial habitats, the quinones, is absolutely absent in water insects (Blum 1981; Dettner and Peters 2010). The extensive use of aromatic compounds and antimicrobics in freshwater in contrast to terrestrial systems is amply demonstrated by comparing adephagan land and water beetles. Since insects do not possess the metabolic capacity to generate the steroid skeleton de novo, steroids are seldom, because precursors must be taken from outside. Therefore it is remarkable that steroids are abundant in prothoracic glands of larger Dytiscidae and the maxillary glands of belostomatid bugs. Three of four steroids from the maxillary gland of belostomatids are also present in prothoracic beetle glands and this convergent evolution might indicate that these qualitatively identical compounds in extremely high concentrations are targeted against larger predators such as fishes or amphibians. Typical defensive mechanisms of terrestrial taxa such as reflex bleeding of toxic hemolymph or sequestration of toxic plant compounds and use for own defense are absolutely missing in water insects. The only case of reflex bleeding in Ephemeroptera seems to be a mechanical defense and has nothing to do with toxic hemolymph. Moreover there are no toxic spines or urticating hairs in aquatic insects. Apart from tabanid larvae and several predatory bugs also venoms and stings in freshwater insects evolved only few times as compared with terrestrial arthropods.

Highly astonishing is the scarcity of defensive mechanisms in aquatic larval stages. Chemical defense by exocrine glands in larval stages is only present in aquatic lampyrids and one trichopteran group. In contrast larvae of Odonata, Plecoptera, Ephemeroptera, and most of Trichoptera lack any defensive chemicals. Also defensive stridulation is rare within larvae; however larval mechanical defense seems widespread. Many larvae of Heteroptera possess abdominal defensive glands; however there exist no chemical or behavioral data. In contrast to Heteroptera larvae the larval dytiscid cephalic gland seems not to be defensive. What are the reasons for missing larval defenses in aquatic freshwater habitats? Larvae are often short-lived (not in Odonata, etc.); therefore biosynthesis of allomones or development of stridulation structures might be too expensive.

As compared with marine or terrestrial systems, in freshwater arthropods we cannot observe any uptake of toxic compounds from plants in order to generate and optimize own chemical defense and increase of fitness. Obviously there exist no trichopteran or aquatic lepidopteran larvae, which would incorporate toxic plant structures in their case or alternatively would incorporate these compounds into their body. In terrestrial systems incorporation of toxic plant constituents is widely distributed and overwhelming at least in lepidopteran larvae (Nishida 2002; Opitz and Müller 2009). In addition there was no record that toxic invertebrates from freshwater such as aposematically colored and toxic water mites or flatworms (Dettner 2010) were fed by carnivorous water insects in order to incorporate toxic chemicals. Finally urticating hairs or allergic reactions which are widespread in terrestrial arthropods are not known in aquatic insects apart from allergic reactions to haemoglobin of certain Chironomidae.

There is another chapter with only few data in aquatic entomology. The significance of microorganisms as producers of behavioral modifying compounds such as allomones or their role as symbionts or parasites of their insect hosts is mainly unknown. In Dytiscidae a rich aerobic, heterotrophic bacterial flora was identified inside the foregut which shows elements of an autochthonous bacterial flora in the foregut (Schaaf and Dettner 1997). Later it was shown that actinomycete species within the crops of beetles play an important role in transformation of food steroid precursors into prothoracic defensive steroids (Dettner 2014). Furthermore the role and significance of intracellular microorganisms in water insects have to be investigated. However their phylogenetic relationships seem interesting: *Rickettsia* species from Dytiscidae were shown to be related to rickettsial isolates from aquatic Limoniidae (Diptera), *Lutzomyia apache* (Diptera: Psychodidae), or *Hemiclepsis* or *Torix* leeches (Küchler et al. 2009).

As was demonstrated by various publications of Kovac and Maschwitz (1990b, 1991, 2000) secretion grooming is an abundant behavior especially in adult freshwater insects. This behavior prevents contamination of the hydrofuge respiratory regions by bacteria or peritrichic ciliates, which would otherwise lead to loss of the air bubble, wetting of these areas, and finally drowning of the insect. Usually the antimicrobial secretions of complex glands such as pygidial glands of water beetles or thoracic glands of aquatic bugs increase wettability of the hydrophobous integuments of aquatic insects (Dettner 1985). In order to decrease this wettability there must be certain dermal glands which can rapidly produce (maybe through oil-secreting) waterproofing surface areas (Holdgate 1955; Beament 1976). There is considerable knowledge on physicochemical properties of integuments of water-walking arthropods (Bush et al. 2008) in contrast to true water insects which may also show amphibious habits. Certainly the qualitative and quantitative distribution, chemistry and functional role of these dermal glands must be investigated in selected water insects especially with respect to the passage from terrestrial into aquatic environment and vice versa (a), a stable and balanced position within the water (b), and an optimal function of breathing (c). In order to fulfill these various demands as change of terrestrial/aquatic habitats, breathing, care of body, and predator defenses it is conceivable that most exocrine secretions of water insects have a multifunctional significance.

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Chapter 10
Reproductive Behavior and Sexual Selection

Diogo Silva Vilela and Iago Sanmartín-Villar

Abstract Aquatic insects present diverse reproductive strategies, tactics, and complex life cycles which require distinct amounts of space and different food sources. And to achieve the reproductive goals they make use of many other strategies. Such reproductive repertoire allowed these insects to evolve the most intricate and fantastic mating systems, often involving conspicuous ornaments. This chapter treats some of these subjects, providing examples from studies carried out worldwide with aquatic insect orders, approaching differences among males and females, sex ratio, sex maturation, reproductive strategies, and all aspects that are involved in success or failure of the competitors. In the first part of this chapter, we treat all insect orders that are aquatic (complete cycle under the water) and semiaquatic (larval stage under the water), mentioning the life cycles and some reproductive tactics. In the second part, we discuss about the theoretical approach concerning insect reproduction such as sexual selection, trade-offs, and roles of polymorphism.

Keywords Behavior · Evolution · Mating systems · Territoriality · Sexual ornaments

10.1 Introduction

Among aquatic insects, a great array of reproductive strategies, tactics, and behaviors are known to exist, as well as complex life cycles which require distinct space and food sources. For instance, there are the territorial strategies, where males (in most of the cases) defend a small portion of the habitat from other males (i.e., competitors). In counterpoint, there are also the sneakers, males that are incapable to hold a territory and sneak behind the “landlord” to gain access to females. There are

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many other ways in which insects reach its final goal: to reproduce. This reproductive repertoire allowed these insects to evolve the most intricate and fantastic mating systems, often involving conspicuous ornaments such as morphological structures and colorful patterns, which were, in 1871, called by Charles Darwin as secondary sexual characters, closely related to the reproductive success, but not part of the sex per se. Finally, when put together variation in morphological and colorful ornaments, different strategies from what to make use of those ornaments, and a limited resource (often females), a war is started.

In this chapter we treat some of these issues providing some interesting examples from studies carried out worldwide with aquatic insect orders, differences among males and females, sex ratio, sex maturation, reproductive strategies, and all aspects that are involved in success or failure of the competitors, which can lead to an arms race between them. In the first part of this chapter, we treat all insect orders that have aquatic (complete cycle under the water) and semiaquatic (larval stage under the water) developments separately, approaching the life cycles and reproductive tactics. In the second part, we treat the theoretical approach concerning insect reproduction such as sexual selection, trade-offs, and roles of polymorphism.

10.2 Aquatic Insects with Terrestrial Adult Life

In this part is treated orders in which immatures are developed inside water or closely related to water environments, and the adults have a terrestrial life. Most of the insect orders that spend some of their time in aquatic habitats (11 out of 13) have only the immature stage completely water dependent. Despite remaining close to water as adults (e.g., for oviposition, territorial defense), they all emerge to a terrestrial life.

10.2.1 Blattodea

Blattodea is a well-distributed and successful group, inhabiting several terrestrial environments such as forests, urban areas, deserts, and also aquatic habitats (Roth 1970; Bell et al. 2007; Nessimian 2014). Freshwater representatives of the order are proven to be found in the suborder Blaberidae and range from semiaquatic (e.g., Blaberidae: Epilamprinae) to aquatic (e.g., Blaberidae: *Rhicnoda*) habitats of development (Bell et al. 2007; Nesemann et al. 2010; Lopes 2018).

The aquatic habitats inhabited by cockroaches vary from the hitherto little studied species from phytotelmata like bromeliads to streams, ponds, and other small aquatic environments (Nessimian 2014). Cockroaches are great organic matter decomposers in terrestrial environments (Bell et al. 2007). This is also true for the aquatic species, being among the main agents responsible for disintegrated organic debris in streams and pools inside forests (Irmler and Furch 1979; Nessimian 2014).

Although spending most of the time in the water, aquatic cockroaches did not have any specialized modifications to swim like modified legs (Bell et al. 2007; Nessimian 2014). Despite that, they can easily swim (including terrestrial species such as *Periplaneta americana* L., Bell et al. 2007) below water surface to either feed or flee from potential predators and also under rocks (Shelford 1909; Bell et al. 2007; Nesemann et al. 2010; Lopes 2018).

The reproductive system of aquatic cockroaches (Blaberidae) frequently involves ovoviviparity and mating is poorly reported, mainly due to its crepuscular and nocturnal habits (Roth 1970; Bell et al. 2007). Therefore, the females are more often observed and hence have greater behavioral repertoire recorded (Roth 1970). After mating, females extrude its fertilized eggs into a structure called brood sac or uterus. There the eggs will remain until mature and the female finally makes the posture of the ootheca (Roth 1970). After hatching from the ootheca, nymphs remain sheltered by its mother, in a space between her abdomen and forewings (Pruthi 1933; Roth 1970, 1981; Bell et al. 2007; Fig. 10.1), until ready to obtain food and shelter by themselves, which may not happen until they reach second instar (Roth 1981).

Fig. 10.1 Blaberid female with many newly hatched nymphs on her back. Photography of Natasha Mhatre

10.2.2 Diptera

The order Diptera is one of the megadiverse holometabolous groups of hexapoda, containing over 150,000 described species of flies, of which about 50% are aquatic (Carvalho et al. 2012; Fusari et al. 2018). Among aquatic flies are species with an important financial and public health appeal, vectors of tropical diseases like dengue and yellow fever by the genus *Aedes* and malaria by *Anopheles* species. Aquatic immature dipterans are also important from the ecological point of view, being part of the regular diet of fishes and other insects that controls their numerous populations (Fusari et al. 2018). Dipterans are found in all continents including Antarctica and the immature stages of aquatic species occupy all freshwater habitats and even marine zones, except for the open sea (Pinho 2008).

The reproductive rendezvous for most of the aquatic flies consists of a swarm composed by males who try to get the best spots of the swarm to grab a passing female, similarly to other ancient lineages such as Ephemeroptera (Marchand 1984; Gullan and Cranston 2014). Yuval et al. (1993) found that the numerous fly aggregations of the culicid *Anopheles freeborni* Aitken may favor some males to the detriment of other, due to physical characteristics. In early evening (5–10 min after sunset), they observed and sampled over 6000 mosquito swarms (97% composed of males), in which males showed significant body and wing size differences. Resting mosquitoes were, on average, 0.2 mm smaller than swarming mosquitoes and its mating success was related to wing size (Fig. 10.2), thus indicating that size played a role in reproduction in this species.

After mating, females remain to the task of ovipositing, a delicate time for mosquitoes that may influence the chances for the larvae to thrive until emergence to adult phase and even determine the timing of disease transmission to humans (Reiskind and Wilson 2004). To mitigate the risks of mortality, at the time of oviposition females may choose to lay the eggs in sites according to the amount of competition with other larvae. Reiskind and Wilson (2004) found that in the culicid *Culex restuans* Theobald females maintained under artificial conditions laid more eggs in sites with increased amount of nutrients, and fewer egg clutches from conspecifics, and the number of eggs deposited per day increased with the availability of oviposition sites, or plots (Fig. 10.3a–b). These results indicate that in natural conditions, females of *Cx. restuans* may be attracted to oviposit in sites with greater amount of nutrients and less competition to ensure larvae development and mitigate predation. Furthermore, the oviposition behavior and habitat preferences of this culicid seem to be common for mosquitoes and its understanding may also help control programs in cases of disease transmission risk (Reiskind and Wilson 2004).

10.2.3 Ephemeroptera

The mayflies, insects of the order Ephemeroptera (Fig. 10.4), compose a small group of about 3500 species which occupies freshwater habitats worldwide, except Antarctica (Sartori and Brittain 2015). An interesting feature about mayflies is

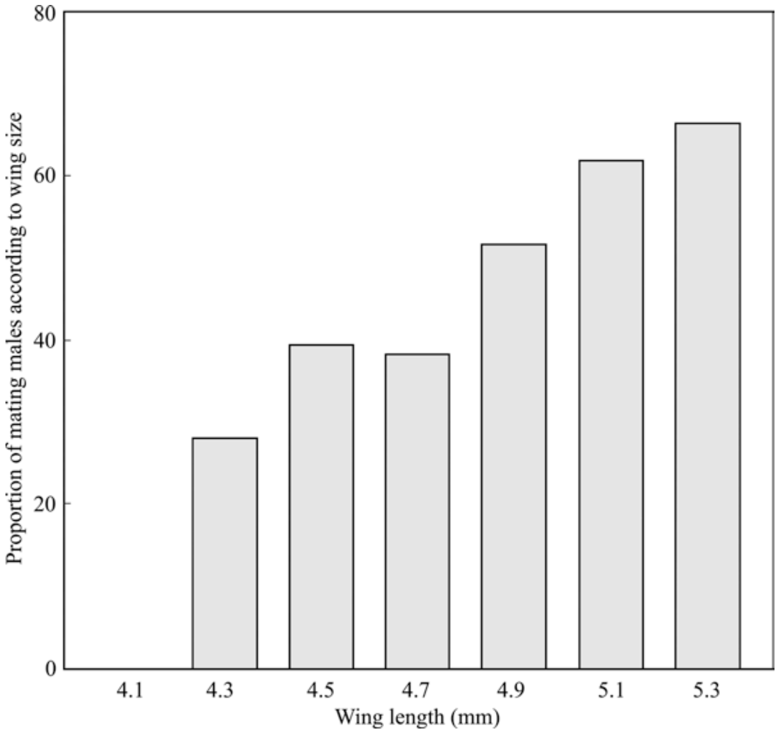

Fig. 10.2 Correlations between wing size and proportion of matings by the culicid *Anopheles freeborni* Aitken. Adapted from Yuval et al. 1993

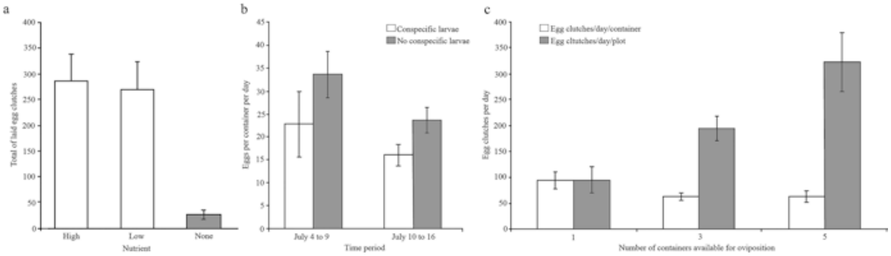

Fig. 10.3 Graphics showing: **a**—the total eggs laid in proportion to the amount of provided nutrients, **b**—eggs laid in the presence or absence of conspecific larvae, and **c**—number of eggs laid according to the number of available containers. Adapted from Reiskind and Wilson 2004

present as soon as the aquatic nymph emerges to adult stage: Ephemeroptera is the only insect order in which a winged form passes through a molting phase (Burks 1975; Brittain 1982). When the nymph emerges, it remains for some hours (or even days, depending on the species) in a stage known as subimago. Recently emerged insect adults are known as imagos and, thus, the subimago stands for a stage before

Fig. 10.4 Adult male mayfly (Ephemeroptera: Leptophlebiidae: *Miroculis yulieae* Raimundi and Salles) on the substrate. Photography of Frederico F. Salles

the winged molt takes part. The subimago has the aspect of an immature adult with the wings yet opaque and this form is not generally capable to mate, as its sexual structures are in final maturation stage (Brittain 1982; Da-Silva and Salles 2012).

After molting to the imago stage, which now has functional wings and fully developed reproductive organs, it begins its ephemeral journey to find a sexual partner. Mayfly lives are short; they usually live no more than few hours (Clifford 1982) and therefore its adult life is totally devoted to sex (Brittain 1982). In fact, most of the Ephemeroptera groups have stunted mouthparts and some species even present vestigial legs (Da-Silva and Salles 2012).

In order to reproduce, males have to be able to recognize the females within a "cloud" (i.e., swarm) of mayflies that are mostly formed by males at the emergence place. To do so, males make use of their large compound eyes that gives them greater possibilities in recognizing the females even in low-light conditions, while females fly towards the "male cloud" to mate, in the air (Brodskiy 1973; Allan and Flecker 1989). It is important to point out that those swarms have complex behavioral patterns, serving as a specific mechanism to isolate the species, such as the drumming behavior of stoneflies (Brittain 1990). In fact, the whole wing apparatus of mayflies is specialized to perform the most important behavior of their lives (Brodskiy 1973). The nuptial dance precedes the mating and consists of an intricate pattern of display by males, which can assume the right position to mate, only achieved during flight (Brodskiy 1973; Allan and Flecker 1989). It consists of low horizontal flights, mostly according to wind direction.

During mating, males grasp the females with the aid of its forelegs and then the mating takes place, for just a few seconds to some minutes. After mating ends, the work of the males is done. To the females, the last task is to lay the eggs (often thousands of them) dipping the abdomen in the water, preferably away from predators, to ensure that they will hatch (Brittain 1982). In some species, this dipping behavior causes female abdomen to break as it touches the water, releasing the eggs (Da-Silva and Salles 2012).

As exceptions to the regular egg development, reproductive system, and swarming behaviors of Ephemeroptera, some species of mayflies (Baetidae) can be ovoviviparous (Gibbs 1979; Brittain 1990; Gaino and Rebora 2005) and even parthenogenetic (Degrange 1960; Bergman and Hilsenhoff 1978; Kazuki and Tojo 2010). Ovoviviparous species are only found in baetids and has been reported in many species of that family (Gibbs 1979; Gaino and Rebora 2005). Gibbs (1979) first reported ovoviviparity in two species of *Callibaetis*, in which imagos presented longevity up to 14 days, which is very rare among mayflies, associating this longevity with the ovoviviparity. An interesting feature about ovoviviparous species is shown by Gaino and Rebora (2005), where the authors demonstrated that the egg structure of oviparous species *Baetis rhodani* Pictet is far more complex and thicker than in the ovoviviparous *Cloeon dipterum* L. This is due to the fact that the ovoviviparous egg hatches almost simultaneously to the contact with the water, and the oviparous egg has to provide a certain security for the embryo to complete its development.

Regarding the parthenogenetic species of mayflies, some are obligatory, as in *Baetis hageni* Eaton, and others are facultative, as in *B. spinosus* McDunnough and some *Cloeon* species (Bergman and Hilsenhoff 1978; Harker 1997). In fact, Harker (1997) demonstrated that in the European species *Cloeon dipterum*, if mature nymphs and recently emerged subimagos are somehow injured (e.g., by predators), it should release eggs which thrive and develop to adults. Further evidence to this facultative parthenogenesis is that oviposition was recorded for both virgin and swarming imagos (Harker 1997).

10.2.4 Hymenoptera

With near 150,000 described species, Hymenoptera is one of the most diverse and cosmopolitan insect orders, inhabiting both terrestrial and aquatic environments (Melo et al. 2012; Fernandes et al. 2018). Most of the success can be attributed to the diversity if niches that hymenopterans occupy, ranging from plant dependents such as pollinators and seed dispersers to predators and parasitoids (Fernandes et al. 2018). Although being very speciose, the amount of aquatic Hymenoptera represents less than 0.2% (150 taxa of 11 families) of all species of the order, and all of them are parasitoids (Bennett 2007).

Being strictly parasitoids, aquatic wasps often depend on aquatic hosts to complete the life cycle. For example, in the species *Caraphractus cinctus* Walker (Mymaridae), females oviposit submerged and place its eggs inside the eggs of other insects, preferably of Dytiscidae beetles. However, when lacking aquatic hosts, females may leave the water to search for potential organisms and lay the eggs flying towards the marginal vegetation (Jackson 1958, 1966). Jackson (1961, 1963, 1966) made a thorough description on the biology of this mymarid. He demonstrated that mating (lasts about 10 s) occurs under water in the majority of times; males (which emerge first) wait for females to hatch from the eggs of the host, then raise the wings vibrating it, and then mount the female remaining on the top, curving its abdomen to reach female genitalia. Males may wait for several females to emerge and then mate with them subsequently. Females can also be parthenogenetic, laying eggs almost immediately after emergence (Jackson 1966). After mating, females actively search for the eggs of potential hosts under water, often placed under leaves (Jackson 1963, 1966).

Other species may paralyze their hosts and take them away from the water to lay the eggs (Guarisco 2010). This is the case of the pompilid *Anoplius depressipes* Banks, which are specialized to lay eggs on spiders, often from the genus *Dolomedes*. Roble (1985) documented the oviposition behavior of the pompilid on the spider, remarking that this is the only aquatic wasp with parasitoid habits, unlike other species that are parasites. These pompilids choose only female spiders standing at the water surface and place just one egg per spider. The wasp followed the fleeing spider, which submerged in an attempt to escape from the parasitoid, and stung its ovipositor on its abdomen, paralyzing the spider in a few seconds. Then, the wasp took the spider to a burrow, a safe place for the larvae to feed on its paralyzed host (Roble 1985).

10.2.5 Lepidoptera

Another megadiverse insect order, Lepidoptera have almost 160,000 described species, occurring in all continents and occupying nearly all habitats, in both land and freshwater. There are no aquatic butterflies, though. All freshwater lepidopterans are moths, which are represented in eight families, with Crambidae being the family with most aquatic representatives (Duarte et al. 2012; Graça and Solis 2018). Aquatic moths are also part of the trophic chain of freshwater environments by acting as leaf miners and root eaters and also acting as predators of small insects and being predated by small vertebrates (Gorayeb and Pinger 1978; Adis 1983; Solis 2008). For instance, the larvae of the erebid *Palustra laboulbeni* Bar were found in lentic and slow waters of French Guiana and North Brazil feeding on the leaves and roots of water plants and also algae, and being predated by frogs (Adis 1983).

The biology of aquatic moths is poorly reported and consequently their reproductive habits. Odor plume seems to be an important agent in helping adult moths to find potential mates; however, this subject is unexplored for aquatic species (Vickers 2005). Nevertheless, there are studies on species with biological control importance (Bennett 1970; Denoth et al. 2002), such as the pyralid *Sameodes albiguttalis* Warren, that damage leaves of invasive aquatic plants. Females take advantage of small cuts and other deformities that the leaves may have to lay the eggs inside plant cells. Then, the larvae will develop eating the plant tissues, eventually leading to its decay (DeLoach and Cordo 1978). Another reported issue concerning aquatic moth larvae is the accidental introduction of species, which may lead to the decreasing of native aquatic plants (Buckingham and Bennett 1989). Finally, one of the greatest challenges of studying aquatic moths, leading to a poor knowledge of its natural history, seems to be the aquatic habitat per se, often located in areas hard to access which makes it difficult to find the small larvae (Graça and Solis 2018).

10.2.6 Neuroptera

With more than 4000 described species, Neuroptera (i.e., antlions and lacewings) has a great arrange of morphological variation and also habitat preferences Freitas and Penny 2012). Being predominantly terrestrial, neuropterans are represented by only 3 of the 17 families in aquatic environments. Of these three aquatic families, Sisyridae and Osmylidae have worldwide distribution and Nevrorthidae are restricted to Asia and Oceania (Martins and Ardila-Camacho 2018). Sisyrids are commonly known as parasites of freshwater sponges (e.g., *Spongilla* genus) and they rely on these hosts as food source and substrate until they leave to pupate and emerge as adults (Poirrier 1969). On the other hand, the sisyrids *Climacia areolaris* Hagen and *Sisyra vicaria* Walker were reported to feed on a wider range of food, such as aphid nymphs and adults, alderfly eggs, and even pollen grains (Pupedis 1987).

Most of the freshwater-related species of Neuroptera have nocturnal habits; thus, mating, oviposition, and larvae migration are present in the hours between dusk and dawn (Pupedis 1987). Although remaining in land, after emergence adults forage and rest near the aquatic environments in vegetal substrate like shrubs and small plants. Searching for food, adult sisyrids would check actively on the borders of the leaves on the shrubs, touching it with their antennae, until anything edible is found (Pupedis 1987). Aquatic neuropterans are also predated, and have specialized taxa to be careful with: *Sisyridivora* (i.e., eater of sisyrids) females are parasitoids that construct a “feeding tube” on the sisyrid’s cocoon with its ovipositor (Fig. 10.5). The tube is filled with fluids of the host, and once the female finds the tip of the tube, it starts to feed moving its mouthparts, in a movement similar to licking (Pupedis 1978).

Reproductive behavior on aquatic neuropterans often involves the use of pheromones in a courtship. In the genus *Osmylus*, during the courtship males would signalize with their wings and evert structures similar to glands located at the end of the abdomen, and the female touches it with antennae and palpi. This occurs before mating takes part and can last for over an hour, before the male grabs the female with his front legs and also with the aid of his mouthparts (Withycombe 2009; Henry 1997). After mating, males transfer a spermatophore to the female, which they often feed upon. To avoid that energetic loss, males may rest with the females for several hours after mating, to ensure egg fertilization. In a couple days, females lay the eggs side by side, where the larvae will hatch few weeks later (Withycombe 2009).

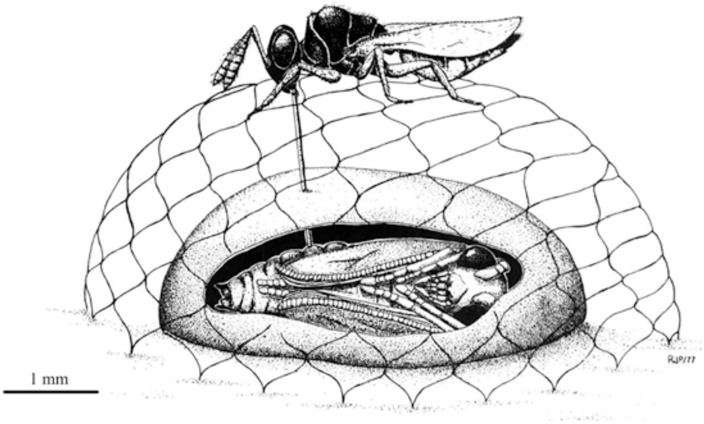

Fig. 10.5 The parasitoid wasp *Sisyridivora cavigena* Gahan feeding on the pupa of the sisyrid *Climacia areolaris* Hagen. Adapted from Pupedis 1978

10.2.7 Odonata

The order Odonata comprises the group of dragonflies and damselflies (Fig. 10.6a–d). Odonata is, today, composed by over 6000 species described, which occurs in all continents except Antarctica (Dijkstra et al. 2013). Nearly 1800 of those species are from the neotropical region (Neiss and Hamada 2014). The individuals of this order inhabit ponds, lakes, streams, and rivers, being one of the most important organisms to the freshwater ecosystems which they occur due to its highly predatory behavior, which controls the population of other invertebrates in the larval stages (Corbet 1999; Mandal et al. 2008; Saha et al. 2012), and also bioindicators of pristine environments (Monteiro-Júnior et al. 2013; Nasirian and Irvine 2017). The larval stage is aquatic for almost all species. In few species larvae seem to be semiaquatic.

The reproductive system in Odonata often involves courtship, elaborated behavioral contest between males, and sperm competition; the latter is treated further in this chapter (Cordero-Rivera et al. 2004; Córdoba-Aguilar and Cordero-Rivera 2005; Guillermo-Ferreira and Bispo 2012). Recently, Guillermo-Ferreira and collaborators have been investigating the case of the neotropical calopterygid *Mnesarete pudica* Hagen in Selys (Guillermo-Ferreira and Bispo 2012; Guillermo-Ferreira et al. 2014, 2015), in which males exhibit elaborated courtship displays and territorial disputes prior to mating. They found that, unlike other calopterygids, males also perform a cross-display with their red-colored wings perched in front of females, while other calopterygid species often perform circular hovering flights only (Guillermo-Ferreira and Bispo 2012; Fig. 10.7). Furthermore, they found that the red coloration of the wings can trigger an aggressive response in other males, which are territorial and fight over patches near oviposition sites (Guillermo-Ferreira et al. 2014). Those fights are usually settled when *M. pudica* males assess rival quality by the opaqueness and size of wing red spots: the larger, the better (Guillermo-Ferreira

Fig. 10.6 Dragonflies (**a**—larvae and **b**—adult) and damselflies (**d**—larvae and **c**—adult). Photographies by Frederico Falcão Salles (**a**, **d**), Adolfo Cordero Rivera (**c**), and Diogo Vilela (**b**)

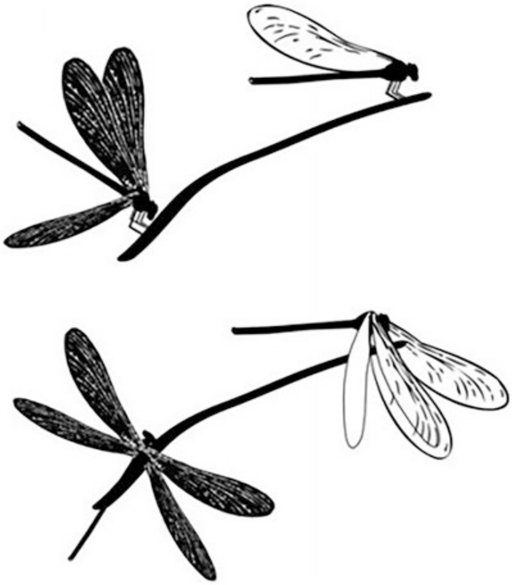

Fig. 10.7 The wing display by *Mnesarete pudica* Hagen in Selys male. Adapted from Guillermo-Ferreira and Bispo 2012

et al. 2015). On the other hand, the same visual signal incites a sexual response by females: spreading the wings as a signal of refusal to mate, leaves flying to a distant perch, or the wing-flapping behavior, which allows the male to carry on with the courtship display (Guillermo-Ferreira and Bispo 2012).

Another interesting feature about the group, which increases its behavioral peculiarities, is that males have two different organs responsible for reproduction. One effectively produces gametes (i.e., primary gonopore) and is located on the ventral portion of the ninth segment and the other, the genital ligula or penis, is responsible to place the sperm on the females and often to remove sperm from other males, located on the ventral side of second abdominal segment (Waage 1979; Siva-Jothy 1987; Corbet 1999). This condition leads the males to an important behavioral task: prior to mating, they have to ensure that its penis is "loaded" in order to fertilize the eggs; to do so, they curve the abdomen so that its ninth segment (which contains the primary gonopore) is placed facing the second segment (which contains the penis) and then make the sperm transfer. The sperm transfer can occur in distinct moments: after grabbing the female, in tandem or alone, immediately after one mating event.

Mating in odonates can be as fast as 10 s long (as observed in *Orthetrum coerulescens* Fabricius, Rehfeldt 1991) or last for some hours (as in *Ceriagrion tenellum* de Villers, Andres and Cordero-Rivera 2000, and *Ischnura graellsii* Rambur, Cordero 1992). Despite the time spent on mating, it is important to complete successfully the sperm displacement and sperm transfer to female. After this transfer is ended, males can remain in tandem position to guard females as they oviposit, as observed in *Acanthagrion truncatum* Selys; guard females with no contact, as observed in *Diastatops obscura* Fabricius; or even leave the female to oviposit alone as in the coenagrionids *Cyanallagma nigrinuchale* Selys and *Argia reclusa* Selys (Vilela et al. 2016).

10.2.8 Orthoptera

Only 0.16% of all valid species of Orthoptera are semiaquatic. This order has over 28,000 described species in all continents, with Amazon being the most diverse region (Gutjahr and Braga 2018). Semiaquatic orthopterans are only found in the family of the true locusts, Acrididae, which complete its development associated and feeding to aquatic plants such as *Eichhornia* and *Paspalum* (Nunes 1989; Vieira and Santos 2003; Braga et al. 2011). In this sense, species such as *Paulinia acuminata* De Geer are even used as biological control to mitigate populations of the macrophyte *Salvinia molesta* Mitchell, a weed that disperses faster in areas altered by deposition of organic waste, causing a hydric disbalance (De Olivera 2014).

Together with their ecological importance, the life cycles of some semiaquatic orthopterans were also well studied in the Brazilian Amazon (Nunes 1989; Nunes et al. 1992; Nunes and Adis 1994; Nunes-Gutjahr and Braga 2012; Vieira and Santos 2003; Braga et al. 2011; De Olivera 2014). The species *Cornops aquaticum* Bruner, one of the most studied, is a biological controller of the *Eichhornia* macrophytes, where they feed. Matings occur on the plant and may last from 40 to 120 min, with the females ovipositing on the petiole of the leaves. Eggs are protected with a cement-like substance and will hatch within 30–40 days where the nymphs will consume the host and adjacent plants (Vieira and Santos 2003).

10.2.9 Megaloptera

The small order Megaloptera (alderflies, dobsonflies, and fish flies) is comprised by almost 400 species present in all continents except Antarctica. Larval stage of all species is aquatic, which may inhabit lakes, streams, and turbulent waters of rivers (Hamada and Azevêdo 2012; Ardila-Camacho and Contreras-Ramos 2018).

Mating occurs near water, on the adjacent vegetation. Males of Sialidae may use acoustic signals in a courtship behavior. Similarly to stoneflies, some Megaloptera species may use abdominal vibrations to find potential mates and, as the females approach, males may tap wings and abdomen on the ground (Rupprecht 1975; Theischinger 2000). After mating, females aggregate with others to place the eggs on rocks, vegetation, bridges, and some other substrate near the water. After hatching, larvae have to immediately search for water, to prevent dehydration from heat and sunlight exposure (Theischinger 2000; Hamada and Azevêdo 2012). Megalopteran larvae are commonly found under rocks of rapid streams, where they feed on other small invertebrates. After completing the development, larvae leave the water and build small chambers on the soil adjacent to the water body to pupate for few weeks until they emerge as an adult (Theischinger 2000). Adult lives are short (10 days) and almost entirely devoted to find a partner to mate. They feed only on liquids, as their intestines are atrophied (Hamada and Azevêdo 2012).

10.2.10 Plecoptera

Insects of the order Plecoptera (Fig. 10.8), also commonly named stoneflies, are hemimetabolous insects whose nymphs inhabit pristine and well-oxygenated habitats, occurring in the freshwaters of all continents except Antarctica (Hynes 1976; Fochetti et al. 2009). These insects are closely related to freshwater habitats even though its adults are terrestrial, due to the poor ability of the adults to disperse for long distances. This limited flight ability combined with the strict preferences of the

Fig. 10.8 Adult Plecoptera (stonefly, *Anacroneuria debilis* Pictet) in vegetation near a water body. Photography of Frederico F. Salles

nymphs is probably the main reason that makes this group highly endemic (Fochetti and Figueroa 2008). In its turn, nymphs are aquatic and depend on a combination of ecological traits to develop to the adult stage, which are mainly well-oxygenated and preserved running water bodies (Hynes 1976). After emerging to adults, stoneflies pass through a maturation period, which can last from 3 to 5 days (Harper 1973). Males are, in general, smaller than females (Froelich 2012), and its sexing can be difficult to determine without examining through a microscope, although some females can be spotted with visible eggs on the abdomen.

An interesting feature about mature male stoneflies is their drumming behavior. The drumming behavior of stoneflies consists of a complex communication system in which males use his abdominal hammer to produce substrate-borne vibrations, to communicate with females (Stewart 1997; Sandberg and Stewart 2003). Males and females, then, engage in a duet-like communication mode (Abbott and Stewart 1993; Fig. 10.9), which can help individuals to find potential mates, help in species recognition, and even help females assess male fitness (Stewart 1997).

After finding its sexual partner, at the copulation the males stay on top of females, curving its abdomen to reach female reproductive organs. Copulations can occur several times a day and after insemination females can lay batches of dozens to hundreds of eggs (Harper 1973). After the egg development, which varies between species and usually takes from 30 to 60 days to hatch, the nymphs begin to rapidly grow, passing through several molts until they emerge to the adult form.

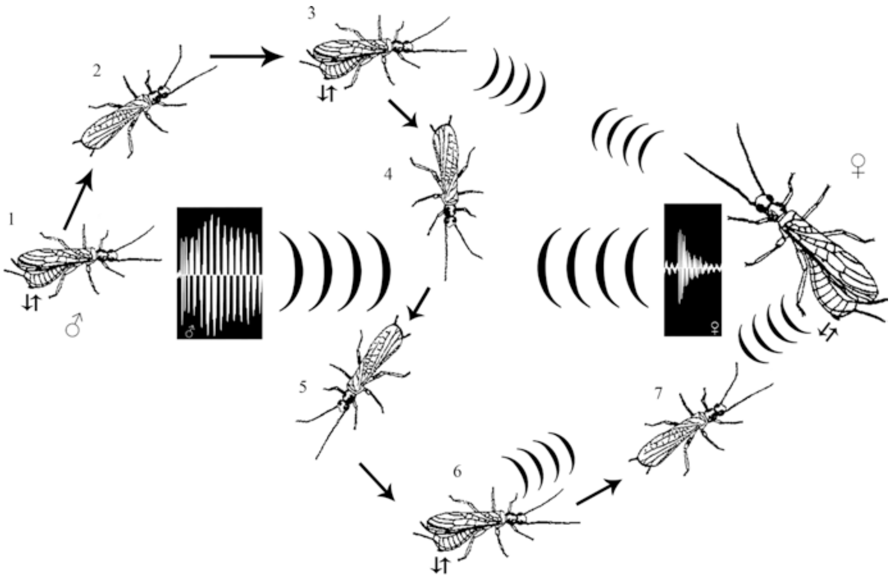

Fig. 10.9 Scheme representing the duet-like drumming behavior of male and female stoneflies. Adapted from Abbott and Stewart 1993

10.2.11 *Trichoptera*

The Trichoptera, or caddisflies (Fig. 10.10), are cosmopolitan, present in freshwater habitats of every continent, except Antarctica. With over 15,000 described species, Trichoptera is one of the most successful aquatic orders in terms of diversity (Paprocki 2012; Pes et al. 2018). Larval and pupal stages are all aquatic, depending, in its large majority, on running waters (Paprocki 2012), except for two genera of Limnephilinae (Mackay and Wiggins 1979).

As in its sister group, Lepidoptera, trichopterans also rely on pheromones to perform its sex activities of searching and locating potential mates (Resh et al. 1987). First thought as being of defensive use, sex pheromones were evidenced first by Wood and Resh (1984). They found in a field experiment that, in cages with females *Gumaga griseola* McLachlan the number of approaching males was significantly higher than in control cages without females. Furthermore, in cages with the pheromone extract only, males were less abundant, indicating that the visual clues are also important to find a mate (Wood and Resh 1984). After pheromones reach their targets and many individuals are gathered, they would swarm near the water face forming a column, where mating takes part (Paprocki 2012).

After mating, females may lay the eggs on top of rocks, leaves, directly on water surface, and diving or even evolve in association with other organisms such as the starfish *Patiriella regularis* Verrill (Winterbourn and Anderson 1980; Reich et al. 2011; Paprocki 2012). Caddisfly larvae can explore a great deal of food resources, as different groups may present different adaptations to scrap, predate other organisms, and feed on plant fluids (Paprocki 2012). An important ecological and taxonomic feature of trichopteran larvae is their capacity to build portable cases (Fig. 10.11). Using silk, they put together tiny grains of sand, twigs, and leaves which shelters the larvae until the moment of pupate (Paprocki 2012; Pes et al. 2018).

Fig. 10.10 An adult male Trichoptera (Odontoceridae: *Marilia sp.*). Photography of Frederico F. Salles

Fig. 10.11 A larvae of Odontoceridae (*Marilia sp.*) carrying its case. Photography of Frederico F. Salles

10.3 Aquatic Insects with Aquatic Adult Life

The two following orders have totally aquatic representatives, that is, both immature and mature stages remain on freshwater environments. Living so close to the water has pressured these organisms to develop into structures, mechanisms which have allowed them to explore different niches and habitats that, therefore, have demanded different life strategies and behavioral traits.

10.3.1 Coleoptera

By far the most speciose insect order, with over 400,000 described species, Coleoptera (i.e., beetles) is present throughout all regions of the planet except Antarctica. Beetles are extremely diverse in terms of morphology, habitats, and niche occupancy and it may be the main reason for its radiation success (Grimaldi et al. 2005; Jäch and Balke 2007; Casari and Ide 2012; Benetti et al. 2018). In this sense, the aquatic Coleoptera is expected to be numerous. They indeed are with almost 20,000 species distributed in 37 families; Coleoptera has also the largest number of aquatic representatives among insects, and more speciose than many entire orders (Benetti et al. 2018). With regard to so many differences within the order, there are also different types of aquatic beetles. Some are true water beetles—submerges for most of its life in adult stage, leaving water just for dispersal (e.g., Dytiscidae, Gyrinidae, and Elmidae)—or false water beetles—terrestrial adult life (Scirtidae, Psephenidae). There are other four categories of water-related beetles: phytophilous, parasitic, facultative, and shore beetles (Jäch 1998). Here, we treat the true water beetles.

One of the most diverse true water beetle families, Dytiscidae or diving beetles have its bodies shaped perfectly for the aquatic life (Fig. 10.12). Their middle and hind legs are flattened to help in the swimming, in which they are very skillful. Another modified trait is the dilated tarsomeres on the forelegs, which helps to grab females during mating (Casari and Ide 2012). Mating behavior was reported

Fig. 10.12 A water beetle (Coleoptera: Dytiscidae). Photography of Frederico F. Salles

for the Japanese water beetle *Dytiscus alaskanus* Balfour-Browne (Aiken 1992). At the rendezvous, while females are swimming around, the male mounts on top of female without apparent courtship behavior, grasping her with his modified foreleg tarsomeres (see Kolmes 1983 for similar precopulatory behavior in Gyrinidae). If the mounting is successful, that is, the male was able to be in the right position so that female does not escape, the mating is completed (Aiken 1992). To fit in the optimal position, after mounting males make lateral shakes to prevent the escaping attempts from females, which have drawn their legs, and the mating takes place. When the males succeed to transfer its spermatophores, the males build a plug on female's gonopore, preventing them from extruding his gametes. After mating, females would oviposit mainly in aquatic plants, such as *Oenanthe javanica* Blume (Inoda 2010).

10.3.2 Hemiptera

Hemiptera (true bugs) is the largest and most diverse order among hemimetabolous insects with almost 90,000 species described worldwide. Members of the family Heteroptera (Fig. 10.13) are the only actual aquatic, although in some other families as Gerridae the species are found close to freshwater environments, skating on the water surface (Grazia et al. 2012; Gullan and Cranston 2014; Moreira et al. 2018). Among the most remarkable water bugs are the representatives of Belostomatidae family. Their large size is intimidating; they are predators of invertebrates and even small vertebrates of ponds, lakes, and streams (Aldrich 1988). Also, if attacked, these bugs may squirt a black secretion and flee to avoid predation (Leston 1979).

Still in belostomatidae, parental care is essential to ensure that the eggs will hatch safely. Males are the ones who take care of the eggs, either by watching them on the sites of oviposition (often marginal vegetation) or by caring for the eggs placed on its back, preventing them from desiccation and drowning. Females of the subfamily Lethocerinae place the eggs on marginal vegetation and those of Belostomatinae oviposit directly on males' backs (Tallamy 2001). In the lethocerin

Fig. 10.13 A water bug on the substrate (Hemiptera: Naucoridae: *Ambrysus lamprus* Nieser, Pelli, and Melo). Photography of Frederico F. Salles

Lethocerus deyrollei Vuillefroy, females mate repeatedly (over 20 times) with the same male which, in its turn, is convinced of the paternity (see Smith 1979) and perform the postcopulatory paternal care (Ichikawa 1989). The repeated mating also occurs in belostomatines. Females can store sperm from previous males and fertilize the eggs. So, to ensure that the majority (if not all) of the eggs placed on its back belong to them, males repeatedly mate with females, because the last male to copulate ensures the paternity of the majority of fertilized eggs (Smith 1979).

10.4 Sexual Selection in Aquatic Insects

10.4.1 Sexual Selection as Evolutionary Pressure

By walking across a stream or taking a look in a pond we are able to perceive in a fast look the diversity of shapes, colors, and behaviors that present the aquatic (complete cycle under the water) and semiaquatic (larval stage under the water) insects. Under the Darwinian interpretation (Darwin 1859), this variability is produced by the effect of natural selection. This concept explains the evolutionary pressure that promotes the reproductive success of individuals better adapted to their contemporary environmental conditions. Individuals that possess advantageous characters are able to better survive until maturity, compete with their conspecifics, being selected by their mates, and produce better adapted offspring. In the case of insects, this specialization was produced by at least more than 400 millions of years (around 10,000 times more than the apparition of the human species).

Back to our excursion along the water mass and after discriminating individuals by species with the help of a book guide or a taxonomic key, we still observe variability among individuals of the same species. Males and females show different morphological and behavioral traits. In general, females are larger and males present more complex structures. The existence of this sexual dimorphism (two forms/phenotypes among sexes) was interpreted as the product of another different evolutionary pressure: the sexual selection (Darwin 1871). This concept explains how traits are maintained across generations due to the mate preferences of selection more than the adaptation of the rest of environmental factors. It is assumed that the individual preference for a trait is genetically determined because it is correlated with the expression of the trait (Fisher 1958) or because of the inheritance of genes from parents that already possessed the preference (Dawkins 1996). The selected traits can be morphological characteristics as ornaments or armaments or behavioral displays or abilities. For instance, color-winged males that perform costly courtships in territorial damselflies are preferred by females (e.g., Orr and Hämäläinen 2007; Watanabe and Taguchi 1990); thicopteran females are selected among males according to the pheromones produced (e.g., Jackson and Resh 1991); in the stonefly *Pteronarcella badia* Hagen (Plecoptera: Pteronarcyidae), males that perform drum duets (timing vibrations) find females faster than those that do not drum or perform anomalous drums (Abbott and Stewart 1993). Traits try to stimulate the perception of possible future partners according to their sensorial system. For instance, dragonflies use colors and movements because they possess complex eyes, thicopterans use pheromones due to the chemical receptors of the adult antennae, and stoneflies use drums because of their developed mechanoreceptors. According to the runaway hypothesis (Fisher 1958), attractive traits are those that allow to win competitions and/or are related with the male fitness. For instance, bold-aggressive behaviors are selected in several species (even in humans) because they allow to obtain more resources as food and territories (see Schuett et al. 2010). *Ephemera danica* Müller (Ephemeroptera: Ephemeridae) females prefer courtships performed by long-winged males, who are better jostle competitors and obtain more reproductive success in at least four other ephemeropteran species (see Harker 1992). In the water boatman *Sigara falleni* Fieber (Heteroptera: Corixidae), females select males according to the size of their body and foreleg, a trait developed during the juvenile stage that allows the competition against other males.

The selection of traits across generations produces by positive feedback the exaggeration of characters, a fact increased in species in which females can determine the phenotype of their offspring (see Mousseau and Fox 1998). However, the investment of resources in attractive traits possesses consequences when natural and sexual selections follow opposed directions. The boundaries of the trait exaggeration appear when they decrease the probabilities to survive or reproduce. Instead small individuals achieve more matings due to their aerobatic behavior in the midge *Chironomus plumosus* L. (Diptera: Chironomidae), and very small individuals are not able to perform longer flights (Neems et al. 1990). Based on this phenomenon, the handicap selection hypothesis (Zahavi 1975) explains that traits are selected by the cost that they represent in production, maintenance, and ability to survive with a trait that disrupts with the efficiency to survive. For instance, colorful, noisy, or bolder individuals increase the encounter with predators, so individuals must be healthy and competitive if they are able to survive under these handicapped conditions.

After identifying the sexual variability in different species in our excursion we perceive that in general females are larger than males while males show more exaggerated traits (morphology and behavior) than females. Due to the conflict arisen by the different conditions and costs of each sex (Chapter *Sexual Conflict*), the probability to mate is commonly ensured for females but it is more variable for males (Bateman 1948). This produces an ecological scenario in which (a) the ratio of male:female searching for copulas is frequently biased towards the formers (e.g., in ephemeropteran, thicopteran, and dipteran swarms; Sullivan 1981; Svensson and Petersson 1987; also see Janicke and Morrow 2018); (b) males possess higher variability (Fairbairn and Preziosi 1994); and (c) wrong matings produce higher costs in females due to the investment in reproduction (Thornhill 1983). Therefore, the selection of mates is generally performed by females. As this reduces the probabilities to mate by males, the latter employ different strategies to compete between them for the access of copula. The firefly *Luciola lei* males compete against other males with the emission of flash lights but stop to produce them at the end of the copula to reduce the conspicuousness of the female (Fu et al. 2006). The increase of competition and the variability produces intrasexual selection and enrichment of the species genome (Janicke et al. 2018). Therefore, females suffer the harassment of territorial and sneaker males. The competition among males increases the differences towards females, emphasizing sexual dimorphism and producing intersexual selection. However, females can also be subject of selection. In the case of the long-tailed dance fly *Rhamphomyia longicauda* Loew (Diptera: Empididae), males select and give nuptial gifts to females concentrated in the same location (lek) according to the size of their abdomen, which represents a signal of fertility (Funk and Tallamy 2000).

10.4.2 Reproductive Trade-Off

The copula formation constitutes a costly and risky phenomenon for both sexes: it is time and resource consuming (e.g., Martens and Rehfeldt 1989), produces injuries performed by the genitalia interactions (Chapman et al. 1995), increases the exposure to diseases and parasites (Daly 1978; Hamilton and Zuk 1982) and the conspicuousness towards predators (e.g., Yuval and Bouskila 1993), and decreases individual locomotion and general life span (in mosquitoes, South et al. 2009; in stoneflies, Taylor and Peckarsky 1998). However, it is considered that copulation process is more costly for females. In several species, females can fertilize all their eggs with a single ejaculation of a male (compare Cordero et al. 1995, 1998). Therefore, female fitness is based on the quality of the mate. However, the advantages of the polyandry should be taken into account (see Fincke 1984; Zeh and Zeh 2003), especially if the first copula was performed by a poor-quality male. For instance, damselfly females of *Mnais costalis* Selys (Odonata: Calopterygidae) mate with a dominant male after a copula with a subordinate (Watanabe and Taguchi 1990). On the other side, the sperm of males can be extracted from the sperm chamber of the female by other males that mate after or can be removed by the female (see sperm competition and female cryptic selection in Chapter *Sexual Conflict*). To ensure their mating success, male reproductive strategy is focused on the quantity of matings. Under this scenario, the previous selection of mates described turns into an intersexual arms race based on the female harassment and the male avoidance (by both sexes). For example, in the water strider *Aquarius remigis* Say (Heteroptera: Gerridae), males are able to increase the length, mobility, strength, and rigidity of the phallus to fix the female during copula, while females increase the length of their abdominal spines to avoid the male assemblage (Adriaenssens and Johnsson 2010; Arnqvist and Rowe 1995; Fairbairn et al. 2003). It was proposed that in the damselfly *Platycypha caligata* Selys, females perform a collective defense mechanism against male reproductive attempts by grasping their wings in groups (Martens and Rehfeldt 1989). As male and female reproductive structures and strategies were coevolved under millions of years to reach opposed goals (see Rice 1998) complex interactions aroused during all stages of the reproductive events to promote the selection of mates. As we saw, the selection starts before copula by the presentation of morphological traits (ornaments/armaments) or resources (e.g., nuptial gifts, territories). However, the strength of the male harassment can suppose drastic consequences for females, especially in non-territorial species and/or those that do not possess mechanisms or signals to be selected. Therefore, female reduces the cost of the male attempts by the acceptance of the copula, especially if they are able to modify the outcome of the mate. The morphological assemblage of the genitalia and the secondary sexual structures were proposed as mechanisms of interspecific recognition and sexual selection by fertilization success (Simmons 2014). Due to the species-specific evolution of the genital structures, these traits constitute nowadays the best key to identify insect species. Even if a male was accepted, the lock-and-key compatibility between individuals will determine the success of the copula and the selection of the best partner. The selection of males is also dependent on their behavioral tactics during copula, meaning by their copulatory courtship (Eberhard 1991). This behavior is based on the capability of males to stimulate females with the intromission and movement of their genitalia and secondary sexual characters. The last selection is produced after copulation. Females judge the male behavior and determine the use of their sperm or the inversion in the eggs fertilized with this sperm. For instance, long guarding events could be interpreted as a postmating courtship to condition the female investment in the next oviposition (Eberhard 1996). Damselflies of the genus Coenagrionidae (Odonata: Zygoptera) perform pre- and postcopulatory tandems for hours, even until the end of the day (e.g., Andrés and Cordero-Rivera 2000; Cordero 1989). In the case of the water strider *Gerris lateralis* (Hemiptera: Gerridae) the sperm recovery increases with the time of the copula, a factor positively related with the fertilization success (Arnqvist and Danielsson 1999). In this case, the multiplicity of mates reduces the amount of sperm transfer in mates performed closer in time. *Mystacides azurea* L. (Trichoptera: Leptoceridae) old males prolong the duration of mating due to their reduced possibilities to reach a mate (Petersson 1990). After all the processes, females of several species possess the last word by the use or the rejection of the sperm (e.g., Córdoba-Aguilar and Cordero-Rivera 2008). In some cases, females that expulsed the sperm of the last male exploit the male guarding to profit the protection towards new male attempts (personal observation in *Polythore derivata* McLachlan and *Archineura incarnata* Karsch).

10.4.3 Established Variability: Polymorphism

As we saw, sexual selection could increase the intrasexual variability until creation of different phenotypes (polymorphism). The maintenance of polymorphism is assumed by the dependence of mating success on environmental factors (e.g., see Cordero 1992). The female color di/polymorphism of damselflies (reviewed in Sanmartín-Villar 2017) is currently interpreted by a mechanism of male harassment avoidance dependent on the frequency of phenotypes in the population (Van Gossum et al. 2008). At lower population frequencies of color male-like females (those that mimic males in color and behavior; Robertson 1985), males identify them as other males and do not try to develop sexual interactions (Cordero and Andrés 1996; Sanmartín-Villar and Cordero-Rivera 2016). In the case of the territorial damselflies of the genus *Mnais* (Zygoptera: Calopterygidae), dominant color winged males are preferred by females. However, color female-like male phenotypes can infiltrate the territories of the dominant phenotype and sneak their protected females when the territorial males fight with intruders (e.g., Watanabe and Taguchi 1997). In at least five *Dytiscus* species (Coleoptera: Dytiscidae), female dimorphism prevents male grasping. In these species, the number and position of the male tarsal discs (setae) varied according to each female phenotype (smooth or structured dorsum) (Bergsten et al. 2001; Bilton et al. 2008; Inoda et al. 2012). One of the most extreme dimorphisms is represented by the aquatic moth *Acentria ephemerella* Denis and Schiffermüller (Lepidoptera: Crambidae). If the preference or the mating success is not balanced between phenotypes (e.g., phenotypes of one sex prefer different phenotypes of the other sex or only phenotype is always selected and the other does not reach enough fitness), the outcome of sexual selection could be the radiation of species by divergent evolution or the loss of variability by the extinction of phenotypes.

10.4.4 Plasticity: Counteracting Sexual Selection

To finish, the fact that the outcome of sexual selection is not only a question of genes should be taken into account. The evolutionary pressure can punctually be modified by plasticity and/or learning processes. For instance, territorial males become sneakers with the age or when the population frequency of territorial males is elevated in damselflies of the genus *Mnais* (Odonata: Calopterygidae), even when they still present the territorial wing coloration (Tsubaki et al. 1997; Watanabe and Taguchi 1990). The perception and posterior selection of females are also conditioned by factors as the female status. Water strider females of the species *Gerris buenoi* Kirkaldy (Heteroptera: Gerridae) prefer large males only when they are hungry (Ortigosa and Rowe 2002). Under lower frequencies of heteromorphic females (different color than males) and after trying to mate with all kind of conspecific phenotypes (even with other males), damselfly males of the genus *Enallagma* (Zygoptera: Coenagrionidae) identify the mimesis of color male-like females as individuals of the opposed sex (Miller and Fincke 1999). Instead the capability of inflating the abdomen is commonly related with the maturity of the eggs in female long-tailed dance flies *Rhamphomyia longicauda* Loew (Diptera: Empididae); females not ready to mate can cheat increasing their abdomen to obtain nuptial gifts from males (Funk and Tallamy 2000).

Despite their apparent simplicity, the insect world hides sophisticated structures and strategies shaped by long-term evolutionary processes. Their protection and study will continue to give us a source of knowledge and will teach us about the complexity of life and how to modify our technology in order to solve problems as they do. Performing this chapter we evidenced the elevated lack of information referent to the reproductive behavior and the evolutionary pressures that they concern in many aquatic insect orders, so we would like to encourage teams and students to continue discovering the incredible mysterious mechanisms that underlie the biology, ethology, and ecology of the aquatic insects.

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Chapter 11
Sexual Conflict in Water Striders, Dragonflies and Diving Beetles

Adolfo Cordero-Rivera and Anais Rivas-Torres

Abstract The field of sexual selection has been historically dominated by a stereotyped view of the sexual roles, with competing males and selective females, but in recent decades there has been a paradigm switch, with the emergence and dominance of the concept of sexual conflict. Put simply, there is sexual conflict when the optimum value for a trait (or a group of traits) is different for females and males. Although the recent literature mainly considers sexual conflict as a process separate from the other well-known processes in the field of postcopulatory sexual selection (sperm competition and cryptic female choice), our approach is that sexual conflict is the consequence of several pressures related to natural and sexual selection, and not a process by itself. Therefore, here we consider sexual conflict as a part of a continuum of sexual selection mechanisms. We concentrate on the effects of sexual conflict on reproductive behaviour of three groups of aquatic insects, whose habitats differ markedly, water striders, odonates and diving beetles, but also include some examples of studies addressing sexual conflict in other groups of aquatic insects. Our hypothesis is that the dimensional structure of the habitat will affect the intensity of sexual conflict over mating rate, copulation duration and postcopulatory guarding. There is abundant evidence and comprehensive reviews of the conflict over mating rates in water striders, odonates and, to a lesser degree, diving beetles. The bi-dimensionality of the water surface allows an easy monopolisation of females by males in this microhabitat, and water striders conform to this rule, so that the commonest mating system is characterised by strong conflicts and struggles before and after copulation. For animals like odonates, which are fast fliers and can use diverse terrestrial microhabitats, the opportunities for males to force females to copulate are certainly limited. In the case of diving beetles, the situation seems more favourable for the females, as they could control male approaches by hiding easily in the vegetation, or even in the case of extreme male density they could fly away and move to a different water body. The sexual conflict over mating duration is also intense in water striders, and also relevant in the other reviewed groups. In the field of postcopulatory conflicts, odonates have offered the best examples of male

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adaptations and female counter-adaptations, which are even more elaborated when studying the evolution of genitalia. We end by summarising our main conclusions and propose some ideas for future work. We stress that a comprehensive understanding of sexual conflicts in animals requires the study of both male and female anatomies, as well as their behaviours, avoiding assumptions or gender stereotypes, which have historically biased research to a male-view approach.

Keywords Behaviour · Equity · Cryptic female choice · Sperm competition

11.1 What Is Sexual Conflict

Observing a pair of animals contributing to the rearing of the next generation may seem at first sight a beautiful example of cooperation for a common goal. However, as many other widespread layman misconceptions about animal behaviour, the two members of a pair cooperate but are at the same time in permanent conflict (Arnqvist and Rowe 2005). This is especially strong in species with high parental investment, where both partners will have more to gain than to lose if "convincing" the other progenitor to invest more in the offspring. Sexual selection will therefore favour cheating the partner. This "sexual conflict" is only one of the many evolutionary conflicts of interests that can be found in all levels of biological complexity (Queller and Strassmann 2018).

George C. Williams was the first to use the term "sexual conflict" in his book "Adaptation and Natural Selection" (Williams 1966, p. 184), and although it received some attention the dominant view at that time was cooperation between males and females. After some years of silent, the concept of sexual conflict was brought to life again thanks to the chapter on "Parental Investment and Sexual Selection" by Trivers (1972).

In 1983, as a second-year biology student, the first author was "gently obliged" by his genetics professor to read a recent book (at that moment) with the curious title "The Selfish Gene" (Dawkins 1976). This book, that has sold more than a million copies, clearly proposed the idea of conflicts between genes as one of the main forces in evolution. There is a chapter entitled "The Battle of the Sexes", where the idea of sexual conflict is introduced, using these terms:

> "As a convenient approximation, we can once again assume that each individual body is a selfish machine, trying to do the best for all its genes. The best policy for such a selfish machine will often be one thing if it is male, and quite a different thing if it is female."

However, the credit for popularising the concept of sexual conflict among evolutionary biologists is for Geoff Parker, who in 1970 published a review of mating behaviour in insects, and defined the term "sperm competition". He introduced the idea that intrasexual selection between ejaculates continues after mating, inside the female (Parker 1970), and a few years after studied the evolutionary consequences of the conflict between the sexes (Parker 1979). Parker (2006) defined the term as

> "[…] a conflict between the evolutionary interests of individuals of the two sexes".

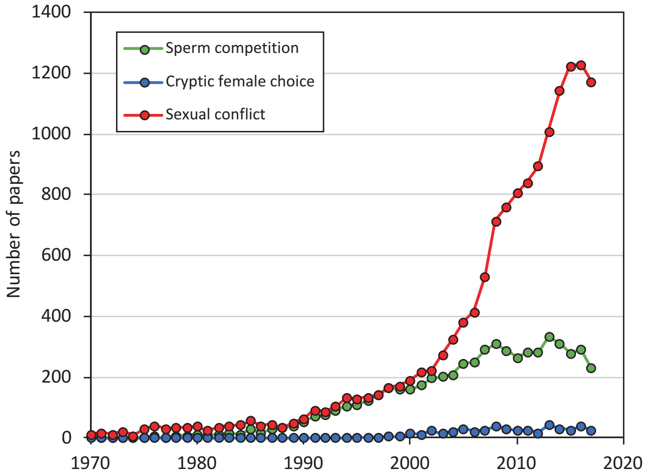


Fig. 11.1 The diffusion of the idea of sexual conflict is an example of a paradigm switch in evolutionary ecology. The figure shows the trends in the number of papers that cite each concept in their title or abstract since 1970 to 2017. Note that "cryptic female choice" does not appear in the titles of papers until 1995. Source: Web of Sciences, accessed October 2018

The picture was completed when the female perspective was also explicitly considered in models of sexual selection, and was denominated "cryptic female choice", because it was not apparent to an observer (Thornhill 1983; Eberhard 1996). Put it simply, there is sexual conflict when the optimum value for a trait (or a group of traits) is different for females and males. The "trait" can also be different for both sexes. The recent literature tends to use the term "sexual conflict" (Fig. 11.1), as a process separate from the other well-known processes in the field of postcopulatory sexual selection (sperm competition and cryptic female choice), but sexual conflict is in fact the consequence of several pressures related to natural and sexual selection (Cordero Rivera and Córdoba-Aguilar 2016), and not a process by itself (Shuker 2014). Therefore we here consider sexual conflict as a part of a continuum of sexual selection mechanisms (Simmons 2014). Some have argued that sexual conflict is so intrinsically linked to sexual selection, that both terms can be synonymous or that sexual selection is better described by the term "sex-dependent selection" (Carranza 2009). The important question for us is that sexual conflict can occur before, during and/or after mating, and therefore it can affect almost all the behavioural repertories of males and females related to reproduction. Sexual conflict can even occur in monogamous species (for instance for mating rate), while sexual selection will be weak.

Although sexual conflict can be obvious in animals with parental care, particularly vertebrates, the first conceptual and experimental studies were mainly inspired by insects, where parental care is extremely rare (Machado and Trumbo 2018). If parents die before the offspring hatches, as it occurs in many insects, parental care cannot evolve. Insects are therefore good models to study conflicts over mating rate and postcopulatory conflicts over fertilisation. For a general review of what is known about sexual conflict in animals see Arnqvist and Rowe (2005).

11.2 The Ecology of Sexual Conflict in Aquatic Insects

We here concentrate on the effects of sexual conflict on reproductive behaviour of three groups of aquatic insects, whose habitats differ markedly, water striders, odonates and diving beetles, but also include some examples of studies addressing sexual conflict in other groups of aquatic insects. Our hypothesis is that the dimensional structure of the habitat will affect the intensity of sexual conflict over mating rate, copulation duration and postcopulatory guarding. There is ample evidence for the relevance of local ecological settings in the evolution of sexual conflict (Perry and Rowe 2018).

Water striders have been at the core of sexual conflict studies over mating rate, due to the prolific studies of Locke Rowe and Göran Arnqvist, who pioneered the field (e.g. Rowe et al. 1994). Water striders live in a world essentially bi-dimensional, on the surface of rivers, ponds, lakes and even the sea (Fig. 11.2). This fact conditions the ability of females to avoid unwanted male mating attempts, and likely is a factor contributing to the extreme adaptations exhibited by some species. For a review of their ecology and behaviour see Spence and Anderson (1994).

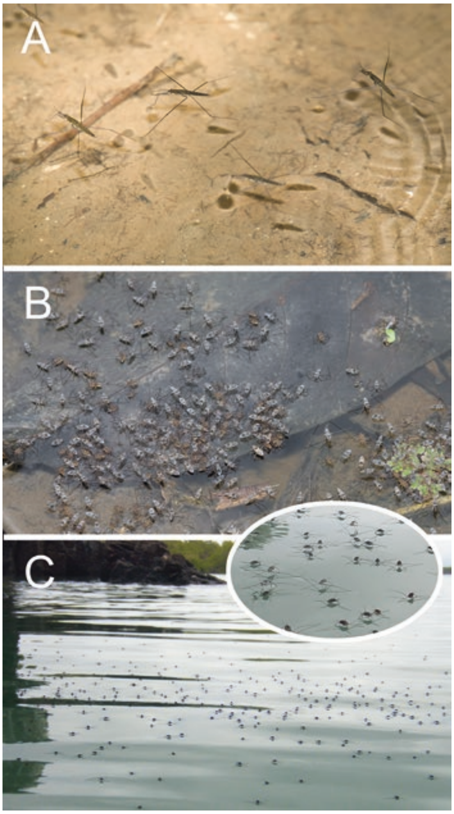


Fig. 11.2 The bi-dimensionality of the water surface, and the high densities of many populations of water striders around the world, conditions the ability of females to avoid unwanted matings, and therefore sexual conflict over mating rate is usually very high. (**a**) A group of *Aquarius najas* in an Italian stream; (**b**) an aggregation of water striders and veliids (likely *Microvelia*) in a pond in the National Park Pacaya-Samiria in Peru; (**c**) an aggregation ("flotilla") of *Halobates robustus* in the coast of Santa Cruz island (Galapagos), consisting of males, with a detail in the insert. Pictures by ACR

The second group that we will review is totally different, in the sense that the adults live in a complex tri-dimensional world, are highly mobile and are fast flyers: the odonates. Since the early studies of postcopulatory sexual selection, damselflies and dragonflies have been a textbook example for sperm competition, particularly after the clever experiments of Jonathan Waage (1979) showing that the male intromittent organ can be used to remove sperm from rival males before insemination (Cordero-Rivera and Córdoba-Aguilar 2010). This fact conditioned for long time our view of odonate mating behaviour, but recent evidence has shown the relevance of other mechanisms apart from sperm competition (Córdoba-Aguilar and Cordero-Rivera 2008).

Finally, we review the literature on reproductive behaviour and sexual conflict in a group of aquatic insects whose adults live in the water, but also have the ability to fly, the diving beetles (the family Dytiscidae), and therefore have a multidimensional world available: the aquatic and the aerial habitats. We predict that this multidimensional space will increase the ability of females to escape from males and therefore this fact will diminish the intensity of sexual selection and particularly of sexual conflict.

11.2.1 Sexual Conflict Over Mating Rate

There is ample evidence that the optimum number of matings is different for males and females. The common pattern is the so-called Bateman's principle that states that male reproductive success increases in a direct way with the number of matings achieved (i.e. males are limited by the number of females they mate with), whereas in females the limitation is the amount of energy and time available for egg production and maturation (i.e. females are limited by resources and less by the number of mates) (Bateman 1948). This asymmetry predicts that males will be more indiscriminate and try to maximise the number of matings, whereas females are predicted to be more selective and maximise mate quality and resources. Some studies have shown that increasing the number of matings over the optimum can be negative for females (Arnqvist and Nilsson 2000). Therefore, there is sexual conflict over the number of matings.

If the optimum number of matings is different for males and females, then another prediction of sexual conflict theory is that selection would favour the evolution of adaptations in males that allow them to hold females and even force copulation (a diverse array of grasping appendages—see Fig. 11.6—but also behavioural adaptations) (Clutton and Parker 1995). The same hypothesis predicts the evolution of mechanisms in females to avoid being grasped by males or to make this extremely difficult or even dangerous. For instance, females can evolve anti-grasping mechanisms (like in *Gerris*; Arnqvist and Rowe 2002). Sexual cannibalism (Fig. 11.3b) could also be a way for females to solve the conflict, and at the same time get extra resources for future reproduction (Schneider 2014).

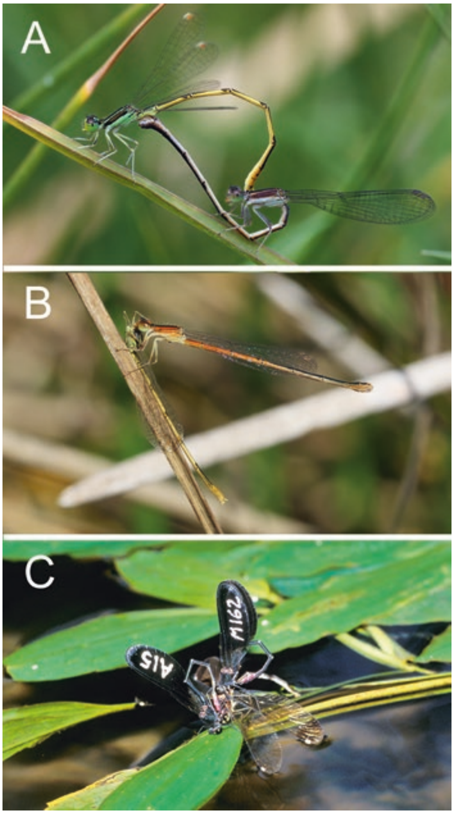


Fig. 11.3 Odonates are fast fliers and live in a complex tri-dimensional habitat. Female odonates have to collaborate to mate (like in **a**, *Ischnura hastata* at the Galapagos). Sexual conflict over mating rate and mating duration can be very intense, and sometimes females show sexual cannibalism (**b**, a female *I. hastata* cannibalising a mature male; Zarabanda, Cuba). Males cannot force copulations under normal densities, but can harass females until a convenience polyandry is the best of a bad job for them (**c**, an ovipositing female of *Calopteryx haemorrhoidalis* being taken forcibly in tandem by two males; Pontecorvo, Italy). Pictures by ACR

The bi-dimensionality of the water surface allows an easy monopolisation of females by males in this microhabitat, and water striders conform to this rule, so that the commonest mating system is characterised by strong conflicts and struggles before and after copulation (type I sensu Arnqvist 1997). For example, in *Gerris buenoi* females are frequently harassed by males in search of mating, and the only way to escape for females is to fight with the male (pre-mating struggles; Fig. 11.4a), which has the negative effect of increasing predation rate by backswimmers (Notonectidae) (Rowe 1994). In fact, the mating frequency of females in *Aquarius remigis* is positively related to male density (Lauer et al. 1996). Mating is specially costly for females, because they have to carry the males on their back for long periods of time (Fig. 11.4b, c), decreasing their skating efficiency (Rowe et al. 1994), and likely increasing predation. A review of 15 species of the genus *Gerris* indicates that conflict over mating rate is widespread in the group, with species where males apparently have gained control over mating rate, and others where females retain a relative advantage (Rowe and Arnqvist 2002). When harassment rate is experimentally increased, females reduce their resistance and therefore mating rates increase (Fig. 11.5), a fact that suggests that this mating system can be characterised as "convenience polyandry" (Rowe 1992). However, water striders can exhibit also

Fig. 11.4 Sexual conflict over mating rate in water striders is evident by pre- and postcopulatory mating struggles. (**a**) Struggle between two *Gerris* individuals; (**b**) copulation (*Gerris* sp., Pontecorvo, Italy) can be brief or very long, and in many species males remain in the back of females for hours, days or even weeks, increasing predation risk, like this couple of *Aquarius najas*, heavily parasitised by water mites (**c**; Tarragona, Spain). Pictures by ACR

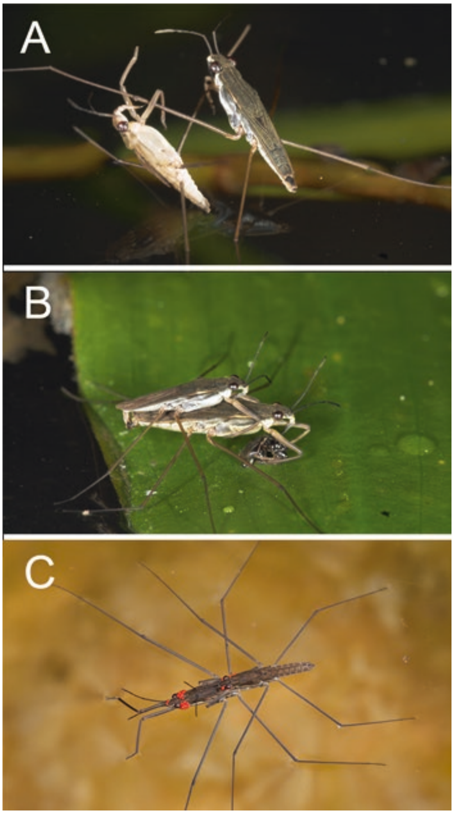
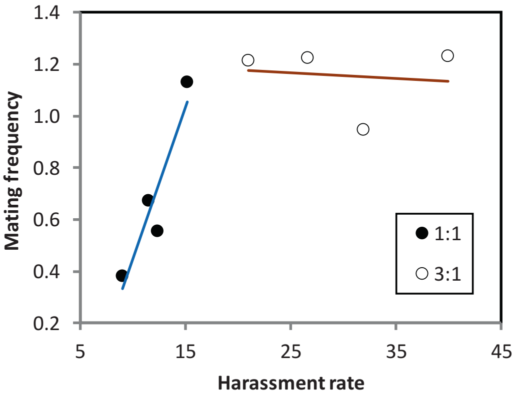


Fig. 11.5 The effect of harassment rate of male *Gerris buenoi* over female mating frequency, at two different sex ratios. Harassment was measured as the number of male attempts to copulate with females per single female hour. Lines represent regressions. Source: modified from Rowe (1992)



a second mating system, with little apparent conflict (type II sensu Arnqvist 1997). In the commonest case, males have apparently "won" the battle for controlling mating rate, but in the type II mating system males have become territorial and court females, so that females have higher control over mating rates (Arnqvist 1997).

The above discussion can be extended to other groups of aquatic insects that live on the water surface, like Mesoveliidae, Veliidae and Hydrometridae (Heteroptera). However, very little research has been done using these other families as models. Searching for sexual conflict and the family name in the Web of Sciences gives no papers for Mesoveliidae and Hydrometridae and only two papers for Veliidae. One of such studies for the subfamily Microveliinae found several examples of putative grasping and anti-grasping adaptations, suggesting that they have evolved due to sexual conflict over mating rate (Cassis et al. 2018). Some Veliidae show males that remain for long periods over their females (Polhemus 1974), a situation paralleling a common behaviour in water striders, which is known to generate costs on females (see above). There is even one case where females have evolved a gland on their dorsal surface that produces a secretion used by males to feed, a clear example of a counter-adaptation of females to reduce kleptoparasitism by their mates, which remain on the back of females for long periods of time (Arnqvist et al. 2006).

For animals like odonates, which are fast fliers and can use diverse terrestrial microhabitats, the opportunities for males to force females to copulate are certainly limited. Female odonates have to blend up their abdomen and cooperate with the male for a successful copulation (Figs. 11.3a and 11.8a). This has led some authors to assume that female odonates cannot be forced to mate (e.g. Fincke 1997). This view is probably true in most ecological settings. However, males have evolved the ability to concentrate in places that females have to visit to lay their eggs, monopolising the area; that is, they behave as territorial (Baker 1983). Under these circumstances, males can be so insistent as to force copulation (Fig. 11.3c), again in a case of "convenience polyandry" (Cordero 1999; Cordero and Andrés 2002).

The odonates are also particular because males have a secondary genitalia, and therefore both individuals contact in two body regions to mate. The typical pattern is for males to search for females either actively or waiting at the shore of the water bodies. When a female is found, the male tries to grasp her in tandem, using his anal appendages (Cordero-Rivera 2002), and at this moment conflict over mating rate can be intense. Females can avoid being grasped by escape flights, by refusal displays (Utzeri 1988) or by visiting the water bodies when males are absent (Cordero-Rivera et al. 1999). Once grasped, they can also refuse to bring the abdomen in contact with male genitalia, even if males can be insistent (Cordero et al. 1992). In *Phylolestes ethelae*, and endemic species of the mountains of the island of Hispaniola, males commonly grasp females in tandem during the morning, and remain in this position until the night, when they mate and release the female (ACR unpubl. obs.). This is probably the longest precopulatory tandem in the order. In general, however, the tri-dimensional habitat of adult odonates allows females to have greater control over their mating rate. In an extreme case, females of some species have been observed practising sexual cannibalism (Cordero 1992), which is the most dramatic (for the male) way of solving the conflict (Fig. 11.3b). On the other hand, the existence of conflict over mating rate seems to explain the widespread occurrence of female colour polymorphism in odonates (Cordero et al. 1998; Fincke 2004), a topic out of the scope of this chapter (for a review see Van Gossum et al. 2008).

Males of odonates are selected to be efficient in grasping females in tandem, and the structure, size and orientation of their anal appendages seem the result of conflict over mating rate, particularly among the Gomphidae, a family whose males have conspicuous forceps as anal appendages (Fig. 11.6). However, the only experimental study that has addressed this question did not find any pattern of hyperallometry in the grasping apparatus of five species, a prediction from the sexual conflict hypothesis (Córdoba-Aguilar et al. 2015). This topic needs to be studied in a large number of species, and in a phylogenetic context. Other possible ways for males to control mating frequency derive from ethological adaptations. For example, males could search for newly emerged females and force mating, because these females cannot refuse or escape with efficiency. This has been observed in *Ischnura aurora*, whose New Zealand populations consist of males that mate with teneral females (Rowe 1978).

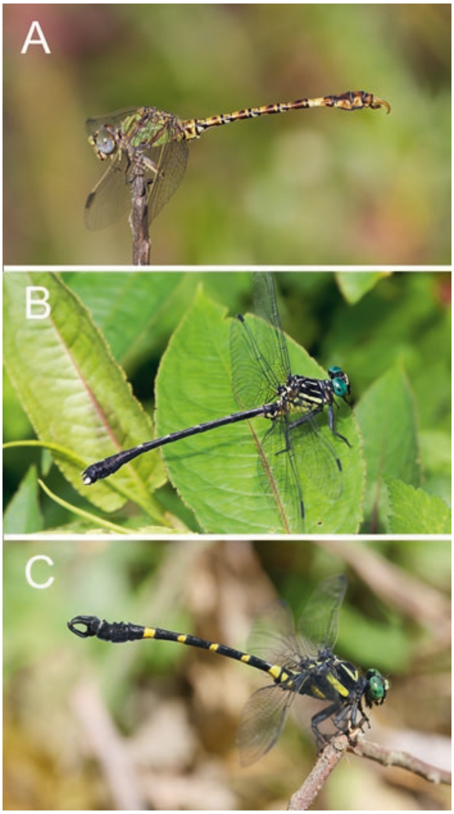


Fig. 11.6 Sexual conflict over mating rates may select for complex and strong "grasping devices" in males, and for "anti-grasping devices" in females. Among the odonates, the family Gomphidae shows the most elaborated anal appendages, whose function as potential sexual conflict adaptations merits further study. (**a**) Male of *Paragomphus genei* (Cáceres, Spain); (**b**) male of *Leptogomphus intermedius* (Nankunshan, China); and (**c**) male of *Lamelligomphus annakarlorum* (Yunnan, China). Pictures by ACR

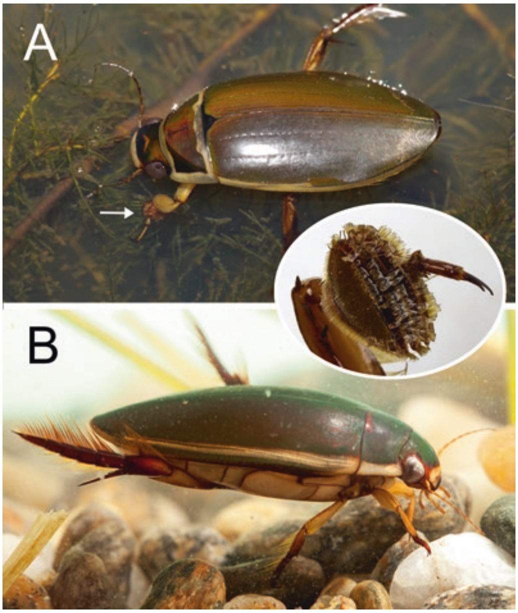


Fig. 11.7 Sexual conflict is evident in the sexually dimorphic forelegs of dytiscid beetles. (**a**) Male of *Dytiscus* in a pond. The arrow indicates the enlarged foreleg, used as a grasping device during mating, and a detail of the adhesive setae of a male *Cybister* (ventral view; the size of the sucker is 2.4 × 3.3 mm). (**b**) Lateral view of a female *Cybister*. Note the absence of modifications in the forelegs. Pictures by ACR

In the case of diving beetles, the situation seems more favourable for the females, as they could control male approaches by hiding easily in the vegetation, or even in the case of extreme male density they could fly away and move to a different water body. Apparently, in some species, there is intense conflict for mating rates, because grasping and anti-grasping mechanisms have been found (Miller 2003). Although little or no courtship behaviour is known, it seems that males could perform acoustic and chemical signals to attract and detect females. Diving beetles produce chemicals for defence and it could be that males also use their chemical senses to detect or attract females (Dettner and Schwinger 1980). In some species, males use stridulatory devices to produce acoustic signals to attract receptive females (Miller and Bergsten 2014).

From the scarce evidence available, we can say that the Dytiscidae show three phases during their reproduction, some divided into subphases. The first phase would be divided into attachment and female resistance, the second in copulation and postcopulatory guarding (see below in the next sections), and finally the release phase, end of copula (Cleavall 2009). In this section, we are concerned with the first phase, attachment and female resistance. These two subphases are the result of the arms war derived from sexual conflict. The males develop sucker-shaped adhesive setae on the pro-tarsomeres, principally (Fig. 11.7). These setae vary in density, number or size, and this fact is not random; the complexity of these sucker setae will go hand in hand with the mechanisms of resistance that the females possess, and these go from modifications of the cuticular surface of the pronotum and the elytra, by dense punctuations, striations or furrows (Miller 2003). In fact, it is possible to establish a parallel classification joining the adaptations of the setae in the males and the surface of the elytra in the females. Sucker setae with three large and smaller cups are related to dense and large punctures on the surface of females' elytra, and furrows on females' elytra co-evolved with setae that have three medium and minute cups or one large and two medium cups (Miller and Bergsten 2014).

11.2.2 Sexual Conflict Over Mating Duration

During copulation, the ability of the pair to move, fly and escape from predators is evidently reduced, and these are only part of the costs of mating (see Daly 1978). Therefore, if there is sexual conflict for copulation duration, the prediction is that both sexes will be continuously under antagonistic coevolution.

Natural selection should favour brief copulations, enough to complete insemination, but sexual selection often favours the opposite. From a natural selection perspective, copulation should be efficient in sperm transfer, and should be completed as soon as possible. However, when copulatory processes are studied in detail, often we discover that insemination occurs at the end of copulation, after several minutes (Cordero-Rivera and Zhang 2018), or even hours (Andrés and Cordero-Rivera 2000). Prolonged copulations can be the result of sperm competition, cryptic female choice or both (Andrés and Cordero-Rivera 2000). In the case of water striders, copulation duration can be highly variable among species. In most cases, copulations are brief, between 5 and 20 min (Arnqvist 1997). In the American water strider *Aquarius remigis*, it lasts for 2–3 h in the laboratory, and insemination occurs at the end (Campbell and Fairbairn 2001). In *A. remigis*, copulations lasting less than 15 min did not produce any viable egg, suggesting that no sperm was transferred during that period of time, whereas "once sperm transfer began, however, virtually the entire sperm load was delivered instantaneously to the female" (Rubenstein 1989). Surprisingly, the European *Aquarius najas* (see Fig. 11.4c) mates for only 1–4 min, but males remain over their mates for weeks (Sattler 1957). It is clear that insemination can be completed in a brief copulation, and the experimental evidence in water striders indicates that copulation duration has high relevance for paternity (Arnqvist and Danielsson 1999).

Some odonates are known for their long copulations (even 7 h; Fig. 11.8) which may be a way for males to guard their mates while still in copula, acting as a living mating plug (Cordero 1990). However, long copulations can be costly for both partners, and conflict is expected. Copulatory processes in odonates are well studied. Copulation starts with a stage I, very variable in duration, which is employed by the male to remove rivals' sperm from the sperm storage organs of the female, and only the last phase is employed for insemination (stage II) (Cordero-Rivera and Córdoba-Aguilar 2010). The damselfly *Ischnura graellsii* mates during the afternoon, and males of this species have apparently evolved the ability to retain their females in copula until the end of reproductive activity (Fig. 11.8), so that females are forced to lay their eggs the day after, at noon (Cordero 1989). Interestingly, its sister species, *Ischnura elegans*, usually mates early in the morning, also for several hours,

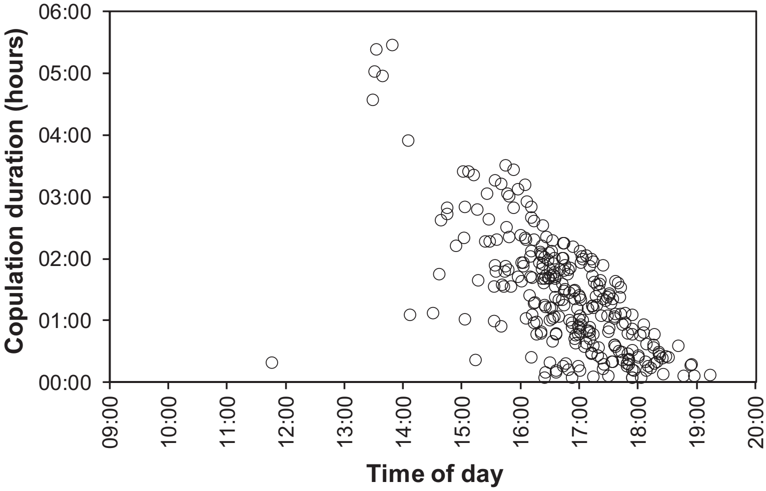


Fig. 11.8 The relationship between time of day and copulation duration in a high-density population of the damselfly *Ischnura graellsii* at Cangas (Spain). Copulation duration (N = 282) was estimated as the time between the first and the last observation of marked mating pairs, and in most cases is therefore an underestimation of the whole copulation duration. Note that there is a limit to copulation duration, which in this case coincides with the end of reproductive activity. In this species males control copulation duration, and females are released too late, and therefore are forced to lay eggs the day after. The maximum density of ovipositing females occurs between 12 and 14 h. Source: unpublished data from Cordero-Rivera and Egido Pérez (1998)

and ends copulations by noon, seemingly the best moment for females to lay eggs (Miller 1987a). These two species exemplify contrasting solutions to the same problem by closely related species, by means of interspecific ethodiversity (Cordero-Rivera 2017a). As a by-result, this time separation between the activity of both species contributes also to minimise hybridisation when they are sympatric (Sánchez-Guillén et al. 2014).

Copulation duration has been investigated in detail in many species of odonates, and has been classified as short (less than 1 min), medium (1–5 min) and long (more than 5 min to several hours) (Corbet 1962). The fact that very brief copulations are as effective as copulations that last for hours clearly indicates that copulation duration in many species is not optimised by natural selection. Postcopulatory sexual selection affects copulation duration in odonates, by means of sperm competition and cryptic female choice mechanisms, which usually determine sexual conflict (reviewed by Córdoba-Aguilar and Cordero-Rivera 2008). Sexual selection also affects copulation duration by its interaction with territorial behaviour, and as a consequence territorial species of odonates copulate on average for shorter times than non-territorial ones (Córdoba-Aguilar et al. 2009).

Experimental manipulations in damselflies have shown that copulation duration is under male control (Miller 1987a). Males have sensilla in their genital ligula and are able to detect female mating status, prolonging copulation with mated females compared to virgin females (Andrés and Cordero-Rivera 2000; Uhía and

Cordero-Rivera 2005). Only the pre-insemination phase of copulation is prolonged, suggesting that this is the result of postcopulatory sexual selection (cryptic female choice) rather than natural selection (Andrés and Cordero-Rivera 2000). Previous studies have concluded that the source of conflict is the sperm stored in the spermatheca (Cordero-Rivera et al. 2004), the organ used by females for long-term storage of sperm (see below).

In diving beetles, as we mentioned above, their mating behaviour includes three phases, and in this section we are interested in the second phase, copulation and the transfer of the spermatophore. Copula durations range from 1 to 10 min in species such as *Thermonectus nigrofasciatus* and *Rhantus binotatus* (Cleavall 2009). In contrast, in *Dytiscus alaskanus* copulation varies between 5.4 and 8.3 h (Aiken 1992). In other species, the only information available includes the complete duration of the mating, which includes the three phases discussed above. In this case, a mating event duration would last between 4 and 45 min in species of the genera *Agabus*, *Colymbetes*, *Acilius* and *Rhantus* (Cleavall 2009). Due to the large duration of the mating event, especially in the Dysticinae subfamily, it could be that the females have evolved to a smaller size and thus avoid the risk to be drowned by the male, since these would be able to breathe directly from the water (Madsen 2012) and discard asphyxiation by the male as a coercive strategy.

11.2.3 Postcopulatory Sexual Conflicts

There is a large variation in the association between males and females after copulation. In a classic paper, Parker (1970) showed that the competition between males continues after copulation, by battles between the ejaculates inside the female, a process he named "sperm competition". He also showed that many postcopulatory behaviours of males could be interpreted as adaptations to reduce sperm competition. In fact, postcopulatory associations between the male and the female are widespread in the insects (Alcock 1994).

Again, if costs and benefits are taken into account, the fact that males remain in close contact with the females, grasping them or in the females' back, is likely to be costly for females (Figs. 11.3a, 11.4b, c), who probably would benefit by ending the association immediately after copulation. However, in some circumstances, the presence of the male could be beneficial for the female, if the male helps in finding suitable oviposition sites (Byers and Eason 2009), defends the female from the interference of other males (e.g. type II mating of Gerridae, sensu Arnqvist 1997) or helps to detect predators. The duration of postcopulatory associations can be therefore a matter of sexual conflict, and it has been shown to be highly variable among and inside species (Alcock 1994).

As occurred with mating rate, the dimensionality of the habitat can theoretically affect the outcome of this conflict. Many water striders (Gerridae), but also other insects of the water surface, are typical examples of males kleptoparasiting their females, by remaining over their backs for weeks, feeding on the prey that the female has secured. To dislodge their mates, females of water striders use vigorous struggles (Fig. 11.4a), which in some species invariably dislodge the male, but in others do not (Arnqvist 1997). These struggles are clear indicators of conflict over (post)mating duration, but are a risky behaviour: predators are five times more successful capturing struggling pairs compared to single individuals (Rowe 1994). On the other hand, the costs related to carrying the males are likely to be density dependent, because, at high density, other males will try to mount the females if they are successful in dislodging the first male. In fact, in *A. remigis* it has been found that paired females can be more efficient in foraging (85% of efficiency) compared to lone females (32%) precisely because they receive less disturbance by mate-searching males (Wilcox 1984).

In the case of odonates, there is a large variation in the extent of male-female associations after copulation. In a classical paper, Waage (1984) argued that most postcopulatory behaviours could easily be interpreted in the context of sperm competition theory, but also included a cautionary note about other possible functions of postcopulatory mate associations. For instance, males in tandem sometimes adopt a vertical position, which could allow them a better vision over the oviposition substrates and help in detecting potential predators. In this case, both individuals would benefit from the behaviour. The possible behavioural alternatives were recently reviewed as an example of the concept of ethodiversity (Cordero-Rivera 2017a), and are here presented in Table 11.1.

One example of a female behaviour which could be related to cryptic female choice due to sexual conflict is the ejection of sperm after some copulations, provided that the sperm ejected belongs to the last male to copulate with her (Fig. 11.9). This has not been demonstrated with genetic markers, and is a priority for future research. However, the fact that in the laboratory, where female mating history is controlled, females sometimes eject sperm after their first mating agrees with a sexual conflict interpretation via cryptic female choice. The presence and duration of postcopulatory tandem have been associated to male density and disturbance (e.g. Utzeri and Ercoli 2004), and understood as an example of male adaptation to reduce sperm competition. In agreement with this, in some species, males show plasticity in this behaviour, remaining in tandem after copula when rivals' density is high but switching to non-contact guarding at low density (Latty 2006).

The mode of oviposition, including site selection and duration, can also be a source of sexual conflict (Table 11.1). There is apparently a trend from females that are never guarded by males, to others that always lay their eggs in tandem, and this trend seems related to the intensity of male disturbance. In the Libellulidae, the level of male harassment affects female oviposition behaviour, but inconsistently among species (Koch 2006), and there is no evidence for a special female strategy to cope with male disturbance. Perhaps the most extreme case of female behaviour apparently evolved to avoid the negative effects of male disturbance in underwater oviposition (Fig. 11.10), a behaviour which is the rule in some *Enallagma* species (Fincke 1986). If this behaviour has the function to reduce sexual conflict, the expectation is that females would submerge more often at higher male densities. To our knowledge this topic has not been experimentally addressed. However, females

Table 11.1 Alternative behaviours after copulation in the Odonata, with representative examples

Behaviour	Alternative	Example	Reference
Postcopulatory sperm ejection	Never	*Hemiphlebia mirabilis*	Cordero-Rivera (2016)
	Occasional	*Ischnura graellsii*	Pers. obs.
	Common, almost immediately after copulation	*Enallagma praevarum*	Córdoba-Aguilar (2006)
Postcopulatory tandem duration	Absent	*Pseudolestes mirabilis*	Cordero-Rivera and Zhang (2018)
	Short (<1 min)	*Ischnura graellsii*	Cordero (1989)
	Medium (1–10 min)	*Sympetrum internum*	Latty (2006)
	Long (>10 min)	*Lestes virens*	Utzeri and Ercoli (2004)
Postcopulatory courtship	Absent	*Ischnura graellsii*	Cordero (1989)
	Depending on male strategy	*Diastatops obscura*	Bañuelos Irusta and Araújo (2007)
	Common, almost always after copulation	*Calopteryx haemorrhoidalis*	Córdoba-Aguilar (2000)
Oviposition mode	Female alone, not guarded	*Anax imperator*	Corbet (1957)
	Female alone, non-contact guarding	*Calopteryx maculata*	Alcock (1979)
	In tandem	*Lestes sponsa*	Stoks et al. (1997)
	Male and female submerge	*Pseudagrion pilidorsum*	Matsubara and Hironaka (2005)
	Submerged, male guarding out of water	*Hetaerina vulnerata*	Alcock (1982)

Some alternatives are clearly more favourable for males' interests (e.g. prolonged postcopulatory tandem), and others for females (e.g. sperm ejection), suggesting that postcopulatory sexual conflict is common in the order

of some species do submerge to oviposit, even at very low male density, or in the complete absence of males, like parthenogenetic females of *Ischnura hastata* at the Azores (Fig. 11.10b, c; Lorenzo-Carballa et al. 2009). Furthermore, in some species both the male and the female submerge to oviposit (e.g. Matsubara and Hironaka 2005). It seems therefore premature to interpret that underwater oviposition is a result of postcopulatory sexual conflicts. Alternative explanations are to avoid the risk of eggs drying due to changing water levels, or even to escape from egg parasitoids (Santolamazza et al. 2011).

In diving beetles, there is a high complexity in the female reproductive tract and a diverse array of sperm morphology (Miller and Bergsten 2014). As expected by sexual conflict theories, both the modifications of the reproductive tract and the great variety of morphology in the sperm seem to have evolved due to an arms race. Therefore, for the female these modifications of the tract would allow long-term sperm storage and then make a selection of sperm, and consequently a high control over paternity (i.e. cryptic female choice). The common disposition of the

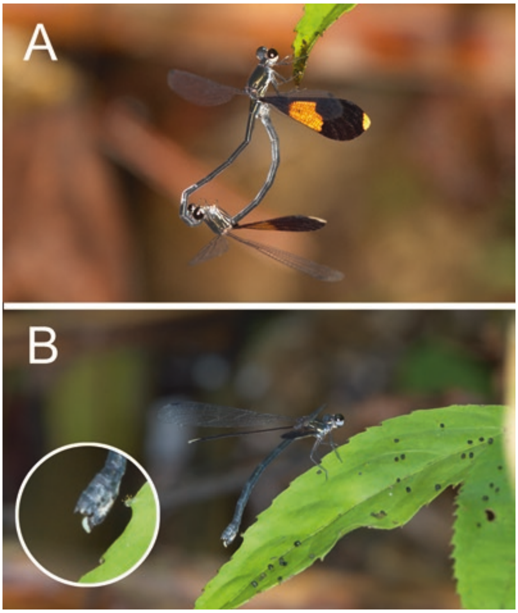


Fig. 11.9 Postcopulatory sexual conflicts can be subtle, like the ejection of sperm after copulation. In odonates this behaviour is known in several species and can be labelled as "cryptic female choice" (Córdoba-Aguilar 2006). (**a**) The figure shows a mating pair of *Pseudolestes mirabilis* (Hainan, China), and (**b**) the female perched after copulation, ejecting sperm (see detail in the insert). Source: Cordero-Rivera and Zhang (2018). Pictures by ACR

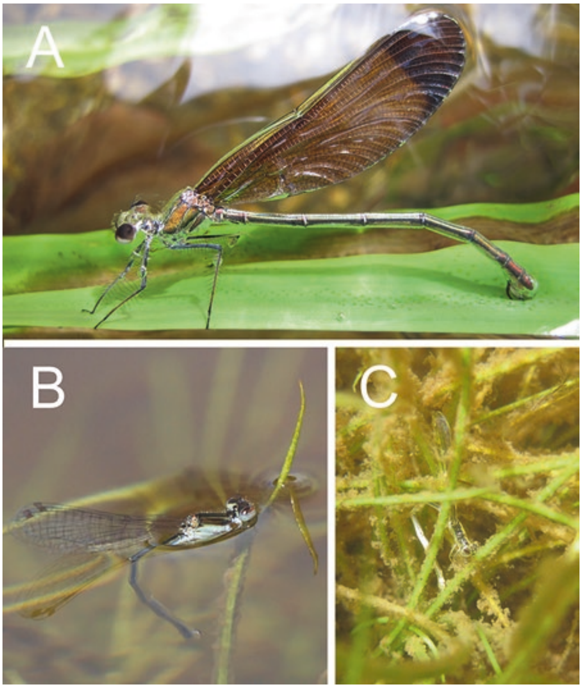


Fig. 11.10 Male disturbance is a source of conflict after copulation, if females are accessible to mate-searching males during oviposition. Underwater oviposition (**a**; *Calopteryx haemorrhoidalis* from Pontevedra, Spain) could be a female adaptation to cope with unwanted male mating attempts, but other explanations, not related to sexual conflict, are also possible. For instance, parthenogenetic females of *Ischnura hastata* from the Azores islands frequently oviposit underwater, in the absence of males (**b** and **c**), although sometimes are harassed by males of *Ischnura pumilio*

reproductive tract is in loop with two genital openings (Heberdey 1931). One of the openings receives the spermatophore and is named *bursa copulatrix*. From this bursa, a spermathecal duct leads to the spermatheca and from this a fertilisation duct to the vagina near the oviduct (see Miller and Bergsten 2014). Therefore, we are facing a decoupling between the site of fertilisation and oviposition, allowing the female this cryptic choice. Miller (2001) was the first to establish a Dytiscidae female internal genital morphology classification, based principally on the number of genital openings, “Amphizoid type” and “Hydroporine type” with two genital openings, and “Dytiscinae type” with a single genital opening. Therefore, the main differences between Dytiscidae subfamilies, Hydroporinae and Dytiscinae, might be associated with the importance that pre-insemination or post-insemination systems would acquire, the latter being the most complex in the Hydroporinae subfamily, both in females and males, as we will see below.

Then, as mentioned above, the diving beetles are within an arms race and therefore females seem to counteract the sperm competition mechanisms by their cryptic female choice abilities. These adaptations are reflected in both the external and internal genitalia of the male. In external genitalia several species have spines or sawlike structures (Sharp and Muir 1912). On the other hand, it has been found conjugation (Higginson and Pitnick 2011) and/or heteromorphism on sperm morphology (Higginson et al. 2012a). Dytiscidae diving beetles have different degrees of conjugation (i.e. two or more spermatozoa physically unite for transport in a female reproductive tract): simple conjugation (two sperm heads unite), medium conjugation (aggregation of multiple sperm heads) and complex conjugation or “rouleaux”. However, in some cases sperm is found solely too, named as singleton (Higginson et al. 2012b). Apart from co-occurrence with conjugation, diving beetles also show sperm heteromorphism (i.e. the simultaneous production of more than one type of sperm) that is manifested by head shape and sperm length (Higginson et al. 2012a), which in other organisms is associated to sperm competition mechanisms (for a review, see Cordero Rivera and Córdoba-Aguilar 2016).

In addition to the adaptations concerning the internal and external genitalia of both sexes, it has been found that some *Dytiscus* species produce a mating plug in the apex of the female abdomen (Aiken 1992) that remains attached to the female during long periods after fertilisation, a strategy that is believed to be used in male-male competition for paternity.

11.2.4 Sexual Conflict and Genitalia

The change in paradigm that occurred in sexual selection studies in the last decades (Fig. 11.1) was in fact initiated when the relationship between animal genitalia and sexual selection became evident, with the pioneering work by William Eberhard (1985). The recent review of the field has found extensive support for the sexual selection hypothesis as the main driver of genital evolution (Leonard and Córdoba-Aguilar 2010). However, the relative importance of sperm competition and cryptic female choice, and the associated sexual conflicts, remains controversial, and particularly understudied in vertebrates (Brennan and Prum 2015).

One prediction from the sexual conflict hypothesis is that it leads to sexually antagonistic co-evolution at the genital level, where each sex is selected to advance control over mating and fertilisation, and as a consequence there is a co-evolutionary arms race (Brennan and Prum 2015).

The relationship between sexual conflict and genital evolution has been reviewed recently in insects (Simmons 2014), and in-depth discussions exist for several taxa, including water striders (Arnqvist 1997), odonates (Córdoba-Aguilar et al. 2003; Cordero-Rivera and Córdoba-Aguilar 2010) and water beetles (Miller and Bergsten 2014). Therefore, here we concentrate in a few clear examples, and suggestions for future experiments.

Distinguishing between hypotheses of genitalic sexual selection is extremely difficult, due to the interactions between males and females and the fact that the same prediction can be derived from different hypotheses, like sexually antagonistic co-evolution and cryptic female choice (Eberhard 2010). In the context of this review, the most relevant pattern is the diversity and rate of evolution of genitalia when compared with other traits. Genitalia evolves much faster (Eberhard 1985), and this needs an explanation. In the Gerridae several studies have shown that genitalia is under sexual selection, and that the form of particular male sclerites is related to fertilisation success, easily interpreted as the result of variable ability among males in sperm competition, mediated by female phenotype (i.e. cryptic female choice) (Arnqvist and Danielsson 1999). There is also evidence that genitalia may evolve by sexually antagonistic co-evolution (Perry et al. 2017).

In the odonates, there is good knowledge of functional morphology of copulation, especially after the work of Peter Miller (1987a, b). The form of the genital ligula is characterised by the presence of apical and lateral lobes and horns, and by a variable amount of backwards-oriented spines, which are used to trap and remove sperm from the previous mates of the female (reviewed by Córdoba-Aguilar and Cordero-Rivera 2008; Cordero-Rivera and Córdoba-Aguilar 2010). These spines in the intromittent organ could also function as copulatory weapons, known in other insects (Reinhardt et al. 2014), and merit further study. If during copulation males damage the internal genitalia of females, there could be an arms race and sexually antagonistic co-evolution.

In the European genus *Calopteryx*, common in rivers and streams (Fig. 11.3c), this sexual conflict over control of sperm reserves can be experimentally studied by using “hand-pairing” (Opphenheimer and Waage 1987), a technique which allows obtaining even interspecific matings. If females co-evolve with conspecific males at the genital level, heterospecific males should have an advantage when interspecific matings occur because females will show less resistance to them than to conspecific males. This is what Cordero-Rivera (2017b) found when *Calopteryx haemorrhoidalis* and *C. splendens* were hand-paired, and it is the first experimental evidence in odonates for such a sexually antagonistic co-evolution in the genitalia (Fig. 11.11).

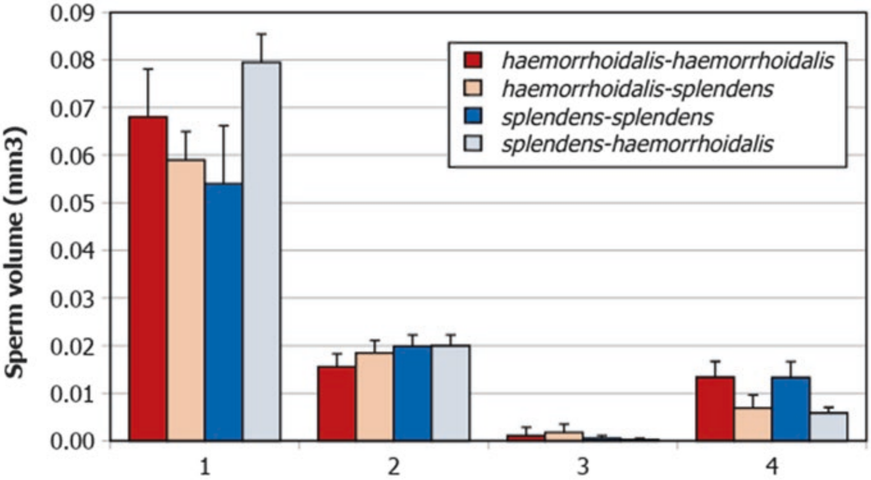


Fig. 11.11 The volume of sperm in the *bursa copulatrix* and spermatheca of double-mated females after conspecific and heterospecific matings (postcopula treatment; the male species is indicated first in the legend), compared to the volume stored by females mated to a conspecific male and then to a conspecific or heterospecific male, but interrupted after 60 movements of stage I, before insemination. The volume of sperm in the *bursa* was reduced by 98–100% in all cases. The volume of the spermatheca in intraspecific matings was reduced by 14% in *Calopteryx haemorrhoidalis* and by 26% in *C. splendens*. In contrast, volume reduction was 63–69% in heterospecific matings. These results indicate that females have more control over spermathecal sperm when mating with a conspecific male (i.e. there is sexually antagonistic co-evolution). Source: Cordero-Rivera (2017b)

11.3 Conclusions and Suggestions for Future Work

Our review of the literature about three groups of aquatic insects is consistent with our working hypothesis about the dimensionality of the habitat as a modulator of male ability to control reproductive decisions. The existence of complex grasping apparatus in some species suggests that sexual conflict is behind the evolution of these characters. We propose that, in the odonates, the family Gomphidae is a priority for future work, given their elaborated male anal appendages (Fig. 11.6). Unfortunately, the study of gomphid behaviour is lagging behind other odonate families, probably because they are rarely seen in mating. In diving beetles, some subfamilies are more affected by the modifications that derive from the pre-copula phase (i.e. Cybistrinae and Dytiscinae), others from the post-copula phase (i.e. Hydroporinae) and other subfamilies that are at a morphological and behavioural intermediate point (Miller and Bergsten 2014). Thanks to this fact, the Dytiscidae beetle family gives us the opportunity to study the sexual conflict and its gradient, in the different phases of sexual behaviour. However, nearly all the phases of reproductive behaviour, and particularly of copulation in this group, require further investigations (Miller and Bergsten 2014).

Other aquatic insects are promising for future work in this field. For instance, in the water bugs of the family Nepidae, male genitalia has a pair of parameres with a hook (Keffer 2004), and we hypothesise that these could have evolved as adaptations to grasp females for copulation. In the Megaloptera, there is good evidence for a trade-off between elaborated weapons and size of nuptial gifts (Liu et al. 2015), and they are another group worth studying from a sexual conflict perspective. The whirling beetles (Gyrinidae) live, as water striders, on the water surface, and are also constrained to a bi-dimensional habitat (although they can also dive). Sexual selection can therefore be intense, at least on some organs (e.g. Fairn et al. 2007). More studies of morphological and ethological adaptations that can be used by males to try to monopolise females and also a detailed analysis of female counter-adaptations are needed to obtain a balanced view of conflict resolution (Ah-King et al. 2014).

In relation to copulation duration, we have good information from the Gerridae and many families of odonates, but for diving beetles information is scarce. Morphological studies have been completed in many genera, but without an ethological perspective the picture is clearly incomplete. The possibility that sexual conflict over mating duration has selected for smaller body size in females, allowing them to breathe directly from the water (Madsen 2012), is a suggestion for future investigations. It must be noted that this hypothesis predicts that females should be smaller at increasing intensity of sexual conflict over mating duration. Species with very long copulations (Aiken 1992) are particularly interesting in this context. Other aquatic insects, like Corixidae, Notonectidae and Aphelocheiridae, some of which obtain the oxygen from the water, should also be studied to detect sexual conflicts.

In some species, sexual conflict has apparently resulted in the evolution of aggressive copulation by males, whose intromittent organ has evolved as a wounding device, resulting in extreme sexual conflict (Reinhardt et al. 2014). The genital ligula in male odonates has a diverse form and commonly is covered by spines, which are thought to be devices to trap and remove rivals' sperm (Córdoba-Aguilar et al. 2003). However, its function as wounding devices has to be studied, and the same can be applied to other aquatic insects (i.e. the aedeagus of *Dytiscus*; see Guignot 1933). Although not an aquatic taxon, the genus *Neotrogla* (Psocodea: Prionoglarididae) from Brazilian caves is an excellent model of study because it shows reversed genitalia, with female penis, male vagina and females that mount males and that control copulations that may last for 40–70 h (Yoshizawa et al. 2014), likely resulting in extreme sexual conflict. The ecological pressures that are behind the evolution of this sex-role reversal might also apply to other taxa.

The field of postcopulatory sexual conflicts, derived from sperm competition and cryptic female choice mechanisms, is another priority for future research. It is known that some odonate females eject sperm after copulation (Fig. 11.9), but this behaviour is so cryptic that probably it is much more common than previously thought. A comprehensive review of this behaviour is needed, and an experimental approach with genetic markers is an absolute priority to know if this behaviour is a consequence of sperm competition (the sperm ejected is the amount removed by the last copulating male; e.g. Lindeboom 1998) or is cryptic female choice in action (Córdoba-Aguilar 2006). Furthermore, do Gerridae females or diving beetles eject sperm after copulation? We could not find any reference to this behaviour in the surveyed literature.

The behaviour of males and females after copulation can also be affected by sexual conflict. We have discussed the strategy of underwater oviposition in female odonates, and the same could be applicable to insects of the water surface. Gerridae females sometimes lay eggs underwater. Is this behaviour related to male disturbance, as expected from sexual conflicts? Or other natural selection pressures, like avoiding egg parasites (e.g. Amano et al. 2008), or the presence of a helping male in tandem (Hirayama and Kasuya 2008), are more relevant? In diving beetles, there is evidence for arms races between male and female genitalia (Miller and Bergsten 2014), and the existence of mating plugs (Aiken 1992) seems easily interpretable as an example of a male adaptation to control fertilisation, which can generate a sexual conflict. If so, mating plugs should be more common in species with high-density populations, where the encounter rate between sexes is high.

The study on sexual selection, sexual conflict and mating behaviour, among others, was based on beliefs and stereotypes that are far from a feminist vision (i.e. equality). Since Darwin proposed that females were timid per se, that idea further fuelled a male-centred stereotype, which even today persists in many minds both in men and women (Ah-King et al. 2014). The influential work of Darwin was used as a justification by contemporary researchers to maintain stereotyped thinking about female behaviour, to such an extent that they came to question the mental abilities of females to choose their mates (Milam 2010). Like the snake that bites its own tail, the assumption that the role of the female in sexual selection or in sexual conflict is merely the one of a secondary protagonist, or not even that, but as a simple spectator leads to the belief that it is difficult to study female genitalia. But that belief loses all its validity with the modern technologies, or just with an unbiased review of the taxonomic literature (e.g. Eberhard 2006). In fact, there are no biological reasons for this lack of studies of female genitalia and behaviour, and the bias does not depend on the gender of the investigator (Ah-King et al. 2014).

We conclude that a comprehensive understanding of sexual conflicts in animals requires the study of both male and female anatomies, as well as their behaviours, avoiding previous assumptions, or stereotypes. Conflict appears when two individuals are involved, a conclusion that a priori seems obvious, since the same word conflict implies two or more individuals, so it does not make sense to study only one part. A balanced study of this field requires a more egalitarian approach, i.e. a feminist view of the science (Ah-King et al. 2014).

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Chapter 12
Paternal Care in Giant Water Bugs

Shin-ya Ohba, José Ricardo I. Ribeiro, and Melania Santer

Abstract We describe general biology of giant water bugs (Heteroptera, Belostomatidae), exclusive paternal care (back-brooding behavior in Belostomatinae and emergent-brooding behavior in Lethocerinae), and recent topics in sexual selection in this family. In the general biology, we introduced phylogenetic relationships of Belostomatidae within Nepomorpha and among Belostomatidae genera, distribution, food, behavior, and general egg morphology. After Smith's evolutionary hypothesis (Smith RL, The evolution of social behavior in insects and arachnids. Cambridge University Press, Cambridge, 1997), feeding habit of Belostomatidae was revealed and the result agreed with his hypothesis. In the exclusive paternal care, we reviewed the role of paternal care, oviposition site selection, and evolution of sexual size dimorphism and its relation to the presence of paternal care. After controlling for phylogenetic signal, it seems that the infanticide phenomenon does not necessarily explain the origin of sexual size dimorphism biased toward females in Belostomatidae, since the ancestor of all Belostomatidae was most likely a non-brooder. Finally, we show the future direction of the study in giant water bugs: coevolution between male and female genitalia in Belostomatidae, allometry for sexual size dimorphism and its disagreement with Rensch's rule, and phylogenetic test of predictions provided by Smith's evolutionary scenario assuming alternative conditions (*Horvathinia* is an emergent-brooder, a back-brooder, or a non-brooder).

Keywords Belostoma · Eggs · Behavior · Freshwater · Evolution

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12.1 General Biology of Belostomatidae

Giant water bugs (Belostomatidae, Heteroptera, Insecta) are classic examples of paternal care systems in arthropods, being shown them in some textbooks (Costa 2006; Royle et al. 2012). They include ca. 150 species distributed throughout the world's subtropical and tropical areas (Lauck and Menke 1961), consisting of eight genera in the subfamily Belostomatinae (*Horvathinia* Montandon, *Hydrocyrius* Spinola, *Limnogeton* Mayr, *Abedus* Stål, *Weberiella* De Carlo, *Belostoma* Latreille, *Appasus* Amyot & Serville, and *Diplonychus* Laporte) and three genera in the subfamily Lethocerinae (*Benacus* Stål, *Kirkaldyia* Montandon, and *Lethocerus* Mayr) (Polhemus 1995; Perez-Goodwyn 2006; Estévez and Ribeiro 2011; Ribeiro et al. 2018). They are found in freshwater habitats such as rice fields, marsh, ponds, lakes, and slow-moving rivers (Cullen 1969; Menke 1979; Mukai et al. 2005). Besides their large bodies, their reproductive biology is unique and well known (Clutton-Brock 1991; Shuster and Wade 2003; Arnqvist and Rowe 2005; Smiseth 2014), which includes female competition and male parental care (Ichikawa 1988, 1990, 1991; Smith and Larsen 1993; Thrasher et al. 2015). In this chapter, we review current knowledge on the function and evolution of paternal care in the giant water bugs. Additional study of giant water bug paternal care in particular, and their mating systems in general, will be an important advance in behavioral ecology. Controlling for body size in males and females via multiple regression, a phylogenetic perspective is given as well as a behavioral approach to discuss the evolution of paternal care. Using a phylogenetic approach is essential because closely related genera could have similar body sizes; that is, the traits could exhibit phylogenetic signal (Morand 1997).

12.2 Distribution and Phylogenetic Relationships of Belostomatidae Within Nepomorpha and Among Belostomatidae Genera

As mentioned, Belostomatinae is a widespread subfamily with the highest number of described genera among the family Belostomatidae. *Abedus* is restricted to the Nearctic Region, Mexico, where there is the largest number of representatives, and to Central America. *Belostoma*, the most diverse genus, occurs in the New World, with the largest number of representatives in South America (Lauck and Menke 1961; Moreira et al. 2011). *Appasus* and *Diplonychus* are distributed throughout Southeast Asia, Africa, India, and Australia (Estévez and Ribeiro 2011). *Hydrocyrius* is restricted to the African continent, and little is known about its biology. *Limnogeton*, restricted to north-eastern Africa, comprises apparently strict predators of snails. Its members bear smooth profemora, lacking sulci, and are thought to be the only representatives of Belostomatidae which do not have middle and posterior legs modified for swimming (Ribeiro et al. 2014). *Weberiella* is monobasic, constituted by *Weberiella rhomboides* (Menke), and is recorded from the states of Amazonas, Mato Grosso and Rondônia in Brazil, as well as French Guyana and Venezuela (Menke 1965; De Carlo 1966; Estévez and Ribeiro 2011). Its members inhabit the surface film of freshwaters exclusively (*kinon* by Fittkau 1977). *Horvathinia* is also monobasic, and it is recorded from southeast and central south of South America (Lauck and Menke 1961; Moreira et al. 2011). The genus comprises only two species, *Horvathinia lenti* De Carlo, and *H. pelocoroides* Montandon (Schnack and Estévez 2005).

Lethocerinae, now reformulated as a subfamily comprising the genera *Benacus* and *Kirkaldyia* (both being monobasic genera), and *Lethocerus* (according to Perez-Goodwyn 2006 and Ribeiro et al. 2018), is a cosmopolitan subfamily, being better represented in the Neotropical region (with about ten recorded species according to Ribeiro et al. 2009 and Perez-Goodwyn 2006). *Kirkaldyia* is distributed throughout Japan, southeastern Asia, China, Taiwan, and Korea, whereas *Benacus* extends from Oriental North America to southward, reaching Honduras, Cuba, and Jamaica (Perez-Goodwyn 2006).

Nepoidea (including Belostomatidae and Nepidae) has been generally considered the most basal branch of Nepomorpha (Mahner 1993; Hebsgaard et al. 2004; Hua et al. 2009), and Spooner (1938) was the first author who formally and intuitively proposed that Belostomatidae and Nepidae are closely related, indicating some morphological similarities. Later on, the conspicuous phallus of representatives of these two families, with the apex fully sclerotized, was highlighted as evidence of such a relationship by Dupuis (1955).

By including modifications or clarifications of both somatic and genitalic characters (including some spermatheca traits), as well as multiple genes (COI, 18S rDNA, and 16S rDNA), Ribeiro et al.'s (2018) comparative study of these genera yielded putative homology hypotheses coded as 104 morphological characters and 1829 aligned characters (Fig. 12.1a). Accordingly, the authors have corroborated the monophyly of Belostomatidae based on the retractable condition of the air straps into the abdomen, eyes somewhat projected laterally with angled borders, and tarsi 2- or 3-segmented, rarely 1-segmented. Lauck and Menke (1961) intuitively subdivided Belostomatidae into three subfamilies based on aspects of male genitalia morphology and in a more critical analysis of other characteristics, such as the condition of the abdominal sternites divided or not by a suture, and the degree of development of tarsal claws of the first pair of legs. Lee (1991) concurred with the decision made by Lauck and Menke (1961) of separating Belostomatidae into the Lethocerinae, Horvathiniinae, and Belostomatinae. However, the restriction of Belostomatidae to such three subfamilies has not been corroborated, and Ribeiro et al. (2018) have suggested the inclusion of *H. pelocoroides* within the subfamily Belostomatinae instead of comprising the monobasic subfamily Horvathiniinae related to the subfamily Belostomatinae (Fig. 12.1a).

Lethocerinae was recovered as a monophyletic group, despite having low support (Ribeiro et al. 2018). The authors suggest that the lateral lobes of segment 7 of abdomen with proximal portions subdivided into sublateral and lateral plates, and the presence of a conspicuous pouch below spermatheca, support Lethocerinae.

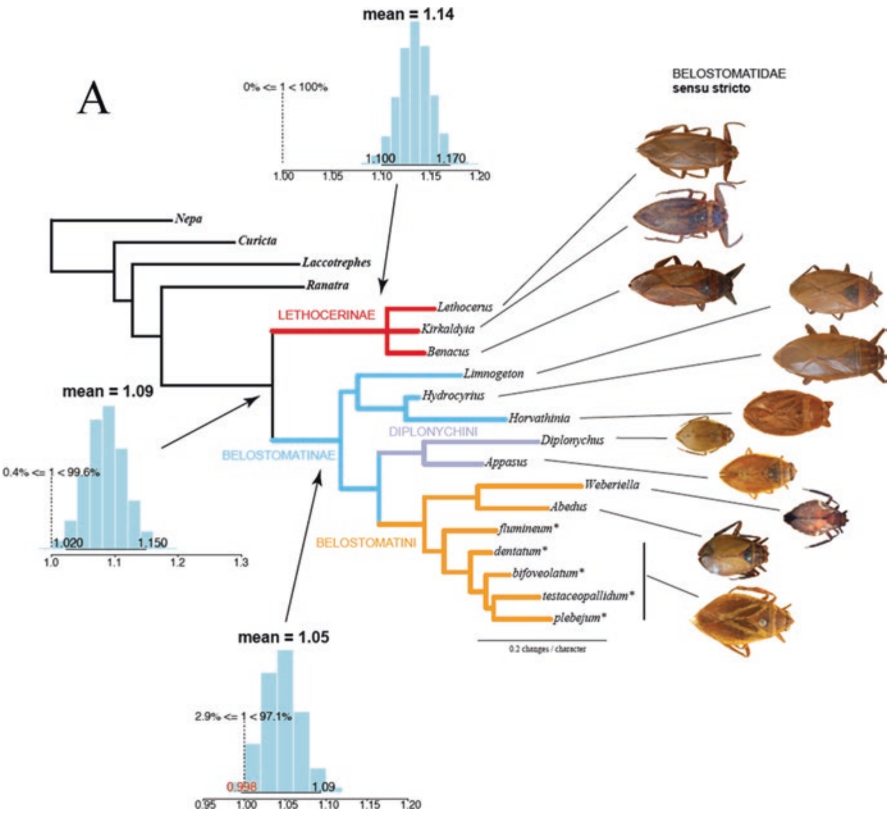

Fig. 12.1 (**a–c**) Phylogeny of Belostomatidae sensu stricto (i.e., without fossils) and evolution of sexual size dimorphism (SSD) in total body length through water bugs. Groups of *Belostoma* species are represented by an asterisk. Outgroups (Nepidae) are in bold. (**a**) Bayesian consensus phylogram including highlighted clades estimated by maximum parsimony and maximum likelihood, with *Appasus*, *Benacus*, and *Kirkladyia* resurrected (based on Ribeiro et al. 2018). Histograms represent the posterior samples of different sexual size dimorphism in body size ancestral reconstructions by Bayesian MCMC method for estimating ancestral states. Values near to the base of histograms are the 95% probability intervals (i.e., 95% HDI). Values smaller than 1.0 are in red. Clades are colored accordingly to proposed classifications. A female-biased size dimorphism is supposed to be found earlier than that in emergent-brooders since this condition is the ancestral state in Belostomatidae. Only 2.9% of the credible values are smaller than 1.0 in the Belostomatinae node. (**b**) Posterior probabilities for evolution of the three-state threshold brooding behavior character in which the underlying model for evolution of the liability (Felsenstein 2012; Revell 2014) is an Ornstein-Uhlenbeck (OU) model with $\alpha = 0.12$ (3.1e-06 − 3.2). The results suggest that the ancestor of all Belostomatidae was a non-brooder, because it had the liability exceeding most likely the non-brooder threshold character state. Mean effective sample sizes (ESSs) for all parameters were higher than 200. Here, *Horvathinia* was considered to be a back-brooder. (**c**) Nonphylogenetic, ordinary least square (OLS) regression analysis in which the Ribeiro et al. (2018) branch lengths were dismissed (i.e., by considering a starlike phylogeny), because the fit of the OLS model was better than regression adopting the Ornstein-Uhlenbeck process (RegOU) and phylogenetic generalized least square (PGLS) models. By comparing SSD in total body length, calculated as $\log_{10}$ (F/M + 0.5), with brooding behavior degrees for each group, we evaluated how

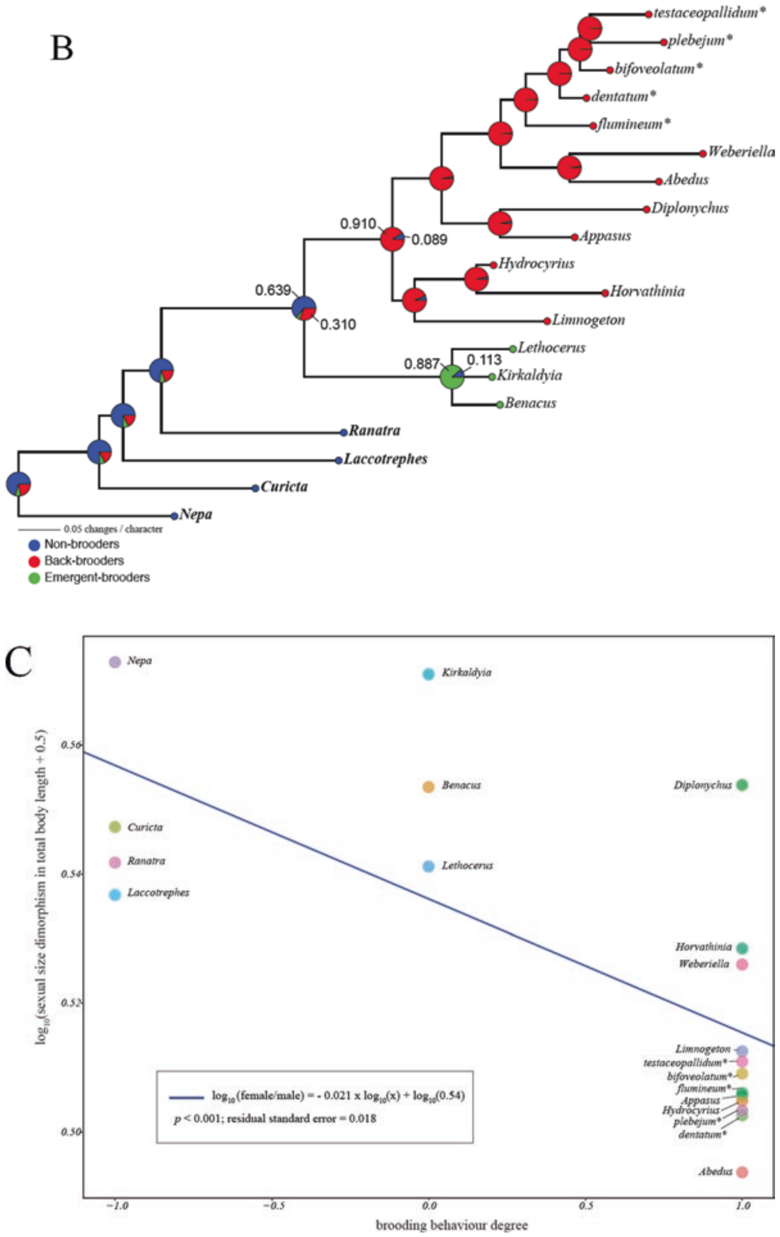

Fig. 12.1 (continued) changes in brooding behavior conditions had contributed to changes in SSD. After controlling for the body size of males and females via multiple regression (not shown), such approach allowed to identify that the intensification of brooding behavior mediated by males is a possible target of selection (according to Davis and Roth 2008), whatever the alternative phylogenetic scenarios have been used (*Horvathinia* was considered to be a back-brooder in this plot). SSD in body length showed strong and highly statistically significant phylogenetic signal ($K = 1.407$; $P < 0.001$)

Despite being monophyletic, Ribeiro et al. (2018) failed to find clear internal relationship in the Lethocerinae clade. Based on a morphological dataset, the authors suggested that *Benacus* and *Kirkaldyia* are supported by the head equal to the anterior portion of pronotum and narrower than its largest width, a homoplastic synapomorphy. *Lethocerus* can be defined by the absence of spines or tubercles on the surface of apex of ventral diverticulum, a homoplastic condition also supported by *Horvathinia*.

Belostomatinae was also characterized based on some symplesiomorphic conditions. For example, Lauck and Menke (1961) and Lee (1991) stressed that the absence of divisions in the abdominal sternites differentiated it from the other subfamilies. However, Ribeiro et al. (2018) have based the monophyly of this subfamily on six unambiguously morphological synapomorphies. The classical male genitalic condition stated by Lauck and Menke (1961) (i.e., phallosoma fused with ventral diverticulum), the apex of second valvulae bearing spines and/or protuberances, and the foretarsi bearing both claws vestigial were some of the traits that supported such a monophyly.

Horvathinia has been accepted in Belostomatinae, and is supported by the abdominal sternites 3–7 divided laterally by weak, suture-like folds into median- and parasternites, a reversal according to Ribeiro et al. (2018). In fact, such recent findings are in conflict with previous hypotheses (Lauck and Menke, 1961; Lee 1991; Mahner 1993) that defined Belostomatinae as having the abdominal sternites 3–7 undivided laterally by weak folds. The resurrected genus *Appasus* (see Polhemus 1995) and *Diplonychus* have been formally recognized as a separate tribe named Diplonychini with strong support. According to Ribeiro et al. (2018), the transverse bridge of basal plate clearly jointed and entire is one of the unambiguously non-homoplastic synapomorphies. The authors still advocated that the differentiation of hemelytrum in the hemelytral membrane appeared independently in some instances in Belostomatidae, being more developed in the clade *Abedus* + *Weberiella*, moderately developed in *Limnogeton*, and completely absent in many species of *Diplonychus*. *Belostoma* was recovered as invalid by Mahner (1993) considering it very conservative and mostly distinguished by its plesiomorphic set of characteristics, such as membrane of hemelytrum distinctly larger than the greatest width of clavus, thus being wrongly considered equivalent to an ancestral Belostomatini. Ribeiro et al. (2018) recovered *Belostoma* as a monophyletic group, based on the presence of fourth segment of the antenna with only one fingerlike projection slightly more bulbous than prolongations of segments 2 and 3, an unambiguous homoplastic synapomorphy. *Abedus* was supported by the presence of straight apex of the ventral diverticulum (fused with phallosoma)—a unique unambiguous non-homoplastic synapomorphy. As with Mahner (1993), *Weberiella* has been supported by Ribeiro et al. (2018) by the lateral margins of abdomen not smooth but interrupted at the borders between the segments (a scalelike abdomen), an unambiguous non-homoplastic apomorphy.

12.3 Support for Smith's Hypothesis (Smith 1997)?

In aquatic environments, a fundamental constraint on the embryo brooding is related to the oxygen availability, since there can be considerable costs to making oxygen available to the whole egg mass (Fernández et al. 2000). Paternal care in Belostomatidae has probably evolved in response to reducing the risk of dehydration and/or increasing egg aeration (Munguía-Steyer et al. 2008; Requena, Munguía-Steyer & Machado 2014). Accordingly, all species studied so far exhibit paternal care for eggs, wherein the females lay on the males' back (Belostomatinae) or on emergent plant stems (Lethocerinae) (Smith 1997). Lethocerinae males (called "emergent-brooders") supply water to the egg mass laid by usually one partner female on the emergent vegetation above the water surface, whereas Belostomatinae males (called "back-brooders") show behavior such as brooding, pumping, or swimming to the water surface, providing oxygen to the egg mass on male's back laid by one or multiple partner females simultaneously (Fig. 12.2) (Smith 1997). Since all other Belostomatinae are back-brooders, we should expect *Horvathinia* to be a back-brooder as well, and describing its brooding behavior has been for many years the "holy grail" of those interested in the reproductive ecology of this group.

Smith (1997) proposed a fascinating hypothesis on the evolution of paternal care in giant water bugs. According to his hypothesis, ancestral species of Belostomatidae

Fig. 12.2 Brooding male of Lethocerinae (*Kirkaldyia deyrolli*) (**a**), a brooding male and a female of Belostomatinae (*Appasus japonicus*) (**b**), and a male brooding two clutches on his back (**c**)

had small body size and they laid the smaller eggs under the water surface. Natural selection acting on body size (through egg size) allowed individuals to explore new food niches, such as large aquatic prey animals. As a result, he suggested that as large females produced larger eggs, the giant water bugs faced a problem: the large eggs have a low surface/volume ratio, which hampers gas exchange in water. Thus, females started laying eggs on the emergent vegetation (in Lethocerinae) or the back of conspecific males (in Belostomatinae), thus resolving the low surface/volume "problem" (Smith 1997).

According to this hypothesis, current Lethocerinae, the largest-bodied subfamily in Belostomatidae, are expected to eat larger vertebrate prey more than other aquatic insects. Lethocerinae species prefer to eat mainly vertebrate animals such as fish and anurans (Smith 1997). For example, *Lethocerus americanus* prefers to eat large fish (Schumann et al. 2012). Some researchers observed *Lethocerus* attacking birds (Hungerford 1919; Menke 1979) and water snakes (Wilson 1958). In recent years, it has also been reported that *Kirkaldya deyrolli* (belonging to the subfamily Lethocerinae) eats snakes (*Rhabdophis tigrinus*, *Amphiesma vibakari*, and *Gloydius blomhoffii*) (Mori and Ohba 2004; Ohba 2012) and turtles (*Mauremys reevesii*) (Ohba 2011) in their natural habitats in Japan. The nymphs possess a claw on the terminal segment of the raptorial foreleg that is crucial for capturing prey. Young nymphs with highly curved claws caught proportionally larger prey than older nymphs with less curved claws. When young nymphs (first to third instars) encounter prey that are larger than themselves, they first hook the claws of their raptorial legs onto the animal, and then use all their legs to pin the larger animals, fully clasping the prey body (Fig. 12.3). The young nymphs are forced to capture prey larger than themselves because smaller prey is less abundant during the hatchling season (Ohba et al. 2008). Older nymphs have an overall well-developed body size, but smaller prey is regularly utilized. Indeed, all *K. deyrolli* nymphs are able to feed on prey of a particular length (around 3 cm). They change catching behavior based on changes in raptorial characteristics to maximize prey resources acquired at each developmental stage (Ohba and Tatsuta 2016).

In contrast, prey size increases as predator nymphs grow in Belostomatinae, *Diplonychus indicus* (Cloarec 1992), *Belostoma oxyurum* (Perez-Goodwyn 2001), and *Appasus japonicus* (Ohba et al. 2008), same as a general predator's rule stating that predators catch prey that are smaller than they are (Nentwig and Wissel 1986; Warren and Lawton 1987). Moreover, Belostomatinae does not digest vertebrates well, because the saliva does not have enzymes capable of digesting protein-rich meals such as vertebrate animals (Swart et al. 2006).

Smith's (1997) hypothesis on the evolution of paternal care in water bugs has been deeply influential in behavioral ecology. Accordingly, he mentioned some predictions about an evident female-biased size dimorphism found across lethocerine lineages. Since appropriate oviposition sites on emergent vegetation may be in short supply, lethocerine females may aggressively compete for access to them, destroying non-filial eggs and opening space for their own eggs (Ichikawa 1990). Infanticide should occur in species in which females are considerably larger than males and thus able to displace the males and destroy the clutch they are caring for (Smith

Fig. 12.3 A first instar of Lethocerinae (*Kirkaldyia deyrolli*) grasping larger vertebrate (tadpole) prey by using all six legs

1997). In species slightly or totally monomorphic in size, infanticides should be rare and multiple clutches should be the rule (Ichikawa 1990; Smith 1997). In the most recent edition of the Alcock's (2013) book, for instance, this hypothesis is explained in detail and illustrated in the chapter on parental care. According to him, in a given moment in the past, belostomatine males were able to return to the aquatic environment probably because individuals were small enough for their eggs to survive in the water, and thus the "infanticide phenomenon" became rare or practically inexistent among them.

This hypothesis on the evolution of sexual size dimorphism (SSD) in water bugs was tested and now seems to be clearly connected to the intensification of paternal care in Belostomatidae, whatever alternative phylogenetic scenario is assumed (assuming *Horvathinia* specimens as being emergent-brooders, back-brooders, or non-brooders) (Ribeiro et al. unpubl. data). Unlike Smith's scenario, a female-biased size dimorphism in total body length is supposed to be found earlier than that in lethocerines (i.e., emergent-brooders) since this condition was more likely to be the ancestral state in Belostomatidae and in other Nepidae lineages. Also, the shift to back-brooding behavior seems to be associated with evolutionary decrease in SSD after controlling for phylogenetic history (Figs. 12.1b, c). Whereas the infanticide phenomenon might occasionally explain the maintenance of the increasing in SSD values among lethocerines, such hypothesized phenomenon does not necessarily explain the origin of SSD biased toward females in Belostomatidae. Assuming the model showed (Fig. 12.1c), the results suggest that the ancestor of all

Belostomatidae was most likely a non-brooder (about 64%). As stressed by Smith (1997), however, oviposition on emergent vegetation seems to be the ancestral state in the family Belostomatidae.

The SSD values greater than one (i.e., biased to females) seem to be otherwise based on the tendency of related Nepidae species to be similar because they share a common history (according to Morand's 1997 ideas) (Table 12.1). Accordingly, this seems to be due to selection-mediating fertility in the females (Andersson 1994; Blanckenhorn 2009). In Belostomatinae, on the other hand, it is known that clutch size on the male dorsum depends both on the quantity of mature ova inside females and on the available area for egg-laying on males (Iglesias et al. 2010). So, Belostomatinae males have acquired a longer body (maybe a wider dorsum as well) than that of females presumably because they are being selected by females to offer a larger surface for egg-laying (but see Iglesias et al. 2012 and Thrasher et al. 2015 to the contrary).

The tendency for the degree of sexual dimorphism to vary with body size (see Fairbairn 1997; Dale et al. 2007; Davis and Roth 2008) refers to an allometric pattern that has been formalized into Rensch's rule (Rensch 1959). Biologists interested in documenting and quantifying this size allometry have plotted log-transformed values of female versus male body length (e.g., Davis and Roth 2008), whereby slopes below 1.0 indicate negative allometry and, in turn, an allometric pattern consistent with Rensch's rule. Accordingly, this means a greater variability in male size among lineages than in female size (Fairbairn 1997). Without phylogenetic correction or any statistical treatment, there seems not to be a tendency for small male back-brooders to be either narrower or shorter than their conspecific females (Fig. 12.4). Conversely, the relationship between female and male size—being represented by total body length—in Belostomatidae seems to be hypoallometric (i.e., slopes smaller than 1.0) (Fig. 12.4b) (Ribeiro et al. unpubl. data). Ultimately, these results provide some evidence that Belostomatidae display allometry for SSD consistent with Rensch's rule. So, this could indicate that a pattern emerges in Belostomatidae which is characterized by a greater variation in male body size than female body size (according to Fairbairn and Preziosi 1994).

12.4 The Role of Paternal Care and Oviposition Site Selection

12.4.1 Belostomatinae

Paternal care of Belostomatinae species plays a role in maintaining oxygen and humidity conditions of their egg masses (Smith 1976a, b, 1997; Munguía-Steyer et al. 2008). Paternal behavior, i.e., brood pumping, brood stroking, and surface brooding, is essential to egg development and survival (Smith 1997). Eggs increase

Table 12.1 Brooding behaviour categories, body size measurements of male and females of the Belostomatidae (sensu Ribeiro et al. 2018), and Nepidae genera *Curicta*, *Laccotrephes*, *Nepa*, and *Ranatra*

Taxa	BC	*N*	Males: TBL (mean ± SD)	Females: TBL (mean ± SD)	SSD (TBL)	SDI (TBL)
Lethocerinae						
Benacus griseus	EB	5	52.5 ± 6.3	57.2 ± 6.4	0.553	0.131
Kirkaldyia deyrolli	EB	11	52.0 ± 2.3	61.6 ± 2.5	0.571	0.178
Lethocerus	EB	71	63.8 ± 9.8	70.4 ± 10.0	0.541	0.101
Belostomatinae						
Abedus	BB	42	28.6 ± 4.1	31.0 ± 7.4	0.494	−0.013
Appasus	BB	57	19.8 ± 4.2	21.4 ± 3.6	0.505	0.015
Belostoma gr. *bifoveolatum*	BB	223	21.2 ± 1.2	21.7 ± 1.2	0.509	0.024
Belostoma gr. *dentatum*	BB	82	36.6 ± 6.2	36.9 ± 5.4	0.502	0.009
Belostoma gr. *flumineum*	BB	28	21.1 ± 2.8	21.7 ± 2.4	0.506	0.015
Belostoma gr. *plebejum*	BB	83	12.3 ± 1.5	12.6 ± 1.5	0.503	0.010
Belostoma gr. *testaceopallidum*	BB	28	29.9 ± 2.4	30.9 ± 2.0	0.511	0.029
Diplonychus	BB	54	16.7 ± 3.4	16.4 ± 2.6	0.554	0.155
Horvathinia	?, unknown brooding behavior category	26	25.9 ± 1.7	27.1 ± 1.6	0.528	0.070
Hydrocyrius	BB	64	56.0 ± 10.2	55.3 ± 10.3	0.506	0.015
Limnogeton	BB	40	48.7 ± 6.0	51.6 ± 4.7	0.513	0.032
Weberiella rhomboides	BB	16	21.0 ± 0.8	22.0 ± 0.8	0.526	0.063
Nepinae						
Curicta	NB	54	20.7 ± 4.8	23.1 ± 5.6	0.547	0.116
Laccotrephes	NB	24	24.3 ± 11.3	27.3 ± 11.6	0.537	0.091
Nepa	NB	10	16.9 ± 0.9	20.4 ± 0.8	0.573	0.183
Ranatrinae						
Ranatra	NB	230	32.4 ± 7.1	35.0 ± 7.4	0.542	0.103

Brooding behavior categories (BC) scored for giant water bug genera

N refers to the number of measurements recorded either in those references cited or based on material examined

Taxa in bold refer to the water bug subfamilies

All measurements are given in millimeters, except for SSD which was calculated as $\log_{10}(F/M) + 0.5$ and SDI which was estimated by taking the ratio of the larger (female) to the smaller sex (male) and subtracting 1

TBL total body length, *SSD* sexual size dimorphism, *SDI* sexual dimorphism index

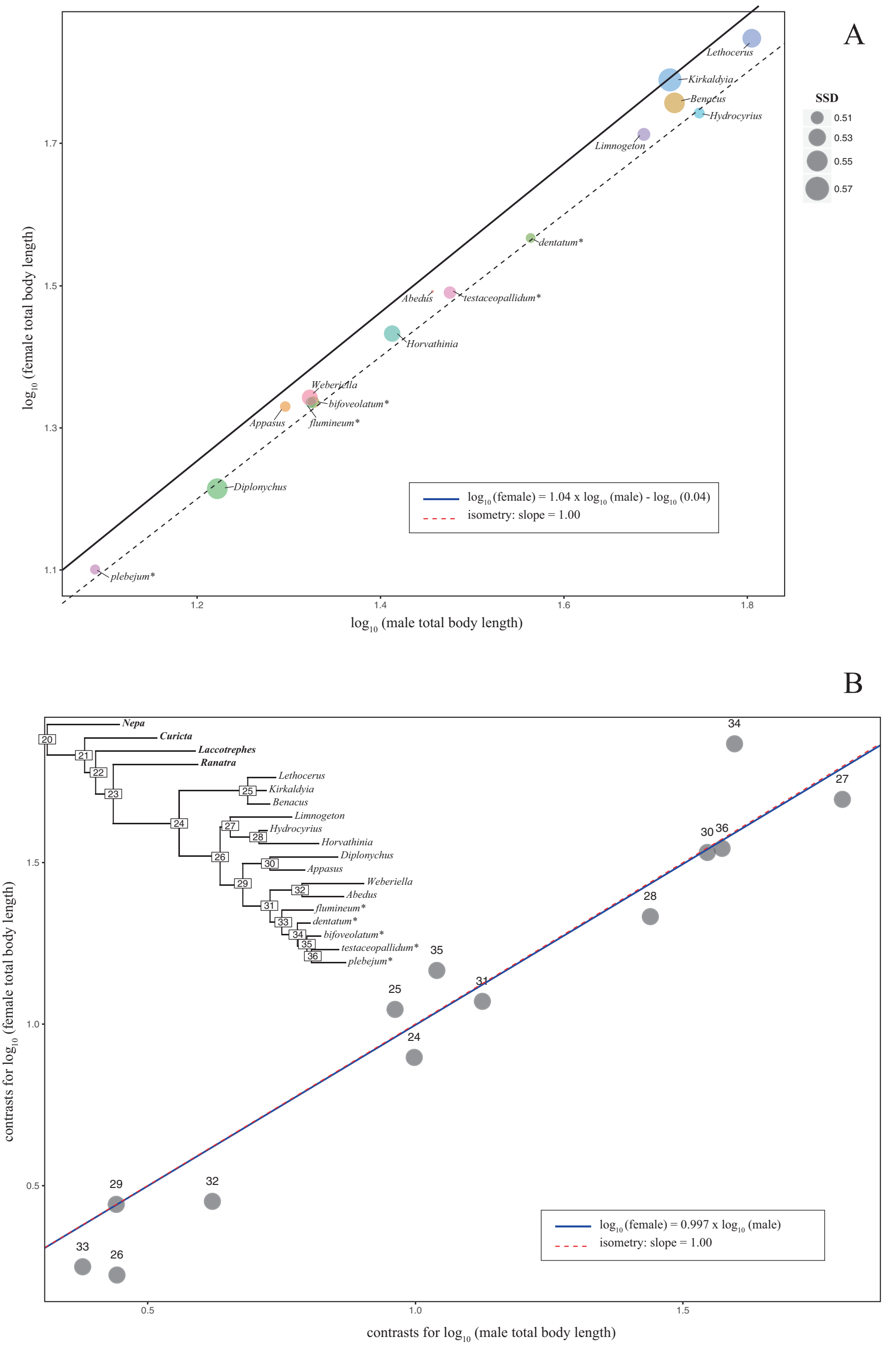

Fig. 12.4 (**a**, **b**) Use of standardized major axis regression to assess allometry for sexual size dimorphism. Groups of *Belostoma* species are represented by an asterisk. (**a**) Log$_{10}$ (female size) versus log$_{10}$ (male size) for each group used in the phylogeny of Belostomatidae (Ribeiro et al. 2018).

in volume by absorbing water through the hydropyle (Madhavan 1974; Venkatesan and Rao 1980). Thus, egg-caring males change brood pumping in response to the growth of the eggs, while non-brooded/submerged eggs suffer lower hatching rate in *Abedus breviceps* Stål (Munguía-Steyer et al. 2008). However, paternal care behavior incurs a cost in terms of foraging efficiency (Crowl and Alexander 1989), mobility (Kight et al. 1995), and longevity (Gilg and Kruse 2003) in *Belostoma flumineum*. Thus, males sometimes remove the egg pad in response to egg pad size (Kight and Kruse 1992) and low-temperature conditions (Kight et al. 2000) and when the males are isolated from the females (Kight et al. 2011). Males with small egg pads are more likely to discard their eggs in autumn (when breeding adults are young) than in spring (Kight et al. 2011). However, there are also studies that did not detect the cost of egg-caring in *Abedus breviceps* in the wild condition (Munguía-Steyer and Macias-Ordonez 2007) and *Belostoma lutarium* in the laboratory condition (Thrasher et al. 2015).

When the females lay egg masses, the mating pairs sometimes repeatedly copulate during a single mating sequence; this is known in many species of Belostomatinae (Smith 1979a, b; Ichikawa 1989). Frequent copulation has been interpreted as an adaptation that reduces sperm competition (Parker 1970; Simmons 2001) and risk of cuckoldry (Smith 1979a). In *A. herberti*, 98% of newly hatched nymphs were attributable to males that had brooded their eggs, indicating that the male's repeated copulation assures his paternity of the eggs (Smith 1979b). However, in *Appasus major* collected from the field, 28.4% of the eggs on the back of males were of other male origin (Inada et al. 2011). These differences between *Abedus* and *Appasus* may be derived from ecological differences between these two species, i.e., differences in cost of brooding. Where costs are higher (less food) selection on paternity assurance may be higher. These possibilities will be interesting subjects for future study.

12.4.2 Lethocerinae

Lethocerinae males supply water to the egg mass laid by the partner female on the emergent vegetation or branch above the water surface (Ichikawa 1988; Smith and Larsen 1993; Macías-Ordóñez 2003). Males supply eggs with water until hatching. As in Belostomatinae, submerged eggs cannot hatch (Ichikawa 1988). In addition to watering, there are two roles of the brooding behavior of *K. deyrolli* males: defense

Fig 12.4 (continued) Such graph illustrates an isometric pattern (test of isometry, $P = 0.0736$, see Warton et al. 2006). Sexual size dimorphism (SSD) in total body length was calculated as $\log_{10}$ (F/M + 0.5). (**b**) Independent contrasts of $\log_{10}$ (female size) versus $\log_{10}$ (male size). The tree topology of Ribeiro et al. (2018) and all available Belostomatidae genera were used. Outgroups (Nepidae) are in bold and were excluded. Such graph illustrates apparently a hypoallometric pattern, which is consistent with Rensch's rule (test of isometry, $P < 0.0001$). Numbers represent the nodes in the tree against infanticidal females (Ichikawa 1990, 1991, 1995) and protection of the egg mass from predators (ants) (Ohba and Maeda 2017). Egg predation by females occurs probably due to the female-biased operational sex ratio during the reproductive season (Ichikawa 1990, 1991, 1993). The brooding males attack the infanticidal females but they may not be able to overcome them because females are larger than males. By destroying the eggs of her competitor, a female can obtain the mating partner and ensure male care of her eggs without having to search for a non-brooding mate within the limited reproductive season (Ichikawa 1990). Egg-caring males stay on the egg mass during night probably protecting the clutch against females (Ichikawa 1995), and shorten the egg period by uniform watering of all eggs, thus regulating the hatching synchronization within an egg mass (Ohba 2002) (Fig. 12.5a). The egg-caring male can protect its eggs from ants by means of physical and chemical defense. In the chemical defense, males release a chemical substance

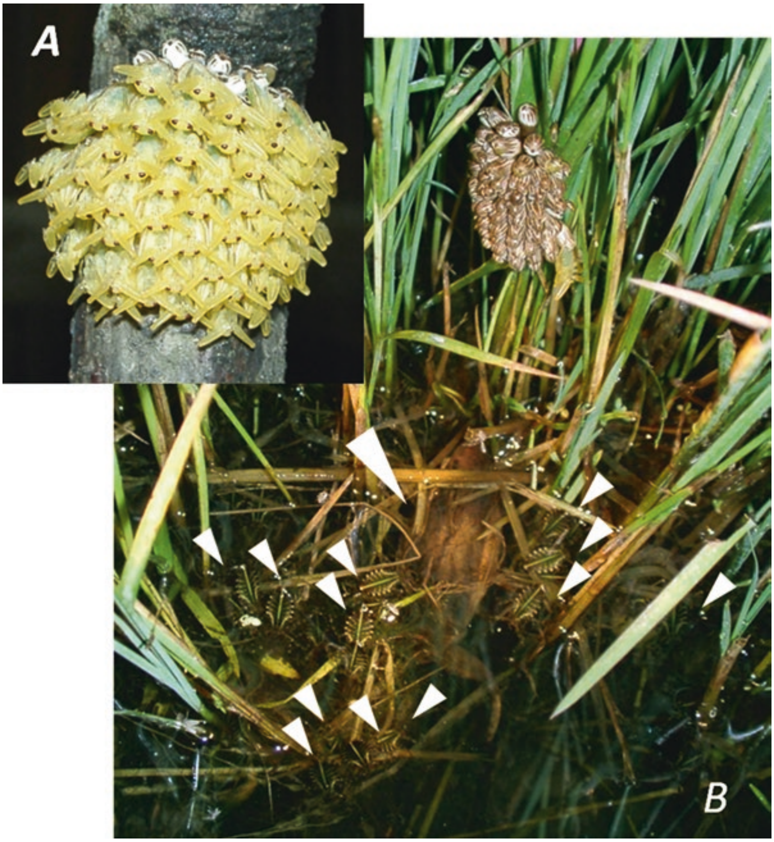

Fig. 12.5 Synchronized hatching between individual eggs in an egg mass (**a**), and aggregated hatchlings (small triangles) under their egg mass and the attendant male in *Kirkaldyia deyrolli* (large triangle) (**b**)

with a grassy smell; this deters ants from attacking the eggs (Ohba and Maeda 2017). After hatching, males were found situated just below the water on the natal substrate, and the first instar nymphs were aggregated around the substrate (Fig. 12.5b). The position and posture of the males were constant during daylight. When disturbed, the attendant males displayed aggressive behavior, brandishing their forelegs toward the source of disturbance. Cannibalistic behavior in the nymphs was well developed 72 h after hatching, when the nymphs had already dispersed from the natal substrate. The suppression of sibling cannibalism in younger nymphs would promote the maintenance of tight nymphal aggregations and consequently extend male care to the first instar stage in this species (Ohba et al. 2006).

12.4.3 Sexual Selection in Paternal Care

Once the male's care for the eggs became indispensable for egg survival, sexual selection may have played a secondary role in the maintenance of paternal care in Belostomatidae. It is hypothesized that male care in animals has evolved under the pressure of sexual selection (Tallamy 2000, 2001; Alonzo 2012; Requena et al. 2014). In addition to offspring survival, male care behavior may enhance reproductive success through increased mating opportunities, because it provides direct benefits to mates, thereby attracting them (Tallamy 2000; Alonzo 2012). Moreover, paternal care can also provide an honest signal of the male's ability to defend offspring (Tallamy 2000, 2001). Therefore, males of species with established paternal care can advertise their parental intent to females (Hoelzer 1989; Kelly and Alonzo 2009). In addition to the harvestmen (Nazareth and Machado 2010, Requena and Machado 2015) and assassin bugs (Thomas and Manica 2005), the sexual selection hypothesis is now supported by two genera of Belostomatinae (Ohba et al. 2016, 2018), belonging to Diplonychini (*Appasus* and *Diplonychus*) (Ribeiro et al. 2018). However, there is little information on the sexual selection hypothesis in other tribes in Belostomatinae and Lethocerinae. In Lethocerinae, the females of *K. deyrolli* do not give the egg-caring males their own eggs without first destroying the eggs of the other female (i.e., by performing infanticide) (Ichikawa 1990, 1991), whereas a male of *L. americanus* was found to attend multiple egg masses (Smith and Larsen 1993). The volume of literature concerning mating systems of Belostomatidae is increasing gradually, but there is not enough information on the relationship between female choice and male care. This information will be essential to understand the evolution of paternal care in Belostomatidae, as well as in other arthropods. During courtship displays, the males of Belostomatidae perform a pumping (push-up) display at the water surface. Males that displayed for longer durations secured more copulations in *Abedus indentatus* (Haldeman) (Kraus 1989). Thus, further work is needed to establish whether push-up displays indicate male parental ability, and whether females discriminate between males based on these displays (Smiseth 2014).

12.5 Future Directions

Studies with Belostomatidae and the evolution of paternal care through its members have raised a variety of curious unanswered questions. (1) May push-up displays used by males that seem to attract females and a variety of sophisticated brooding behaviors found among belostomatines be indeed monitored by females and provide information about male's parental ability? (2) There is no formal test of the predictions of the Smith's hypothesis (Smith 1997) concerning the evolution of body size in Belostomatidae. In Smith's scenario, mean body sizes of emergent-brooders are predicted to be larger than those of back-brooders. Were shifts to back-brooding behavior associated with a decrease in mean body size after correcting for the phylogenetic effect? If so, has the same happened in minimum and maximum values of total body length and greatest width of body? Are the mean ancestral body sizes predicted by Smith correct? Such scenario can now be explored since new phylogenies are being produced. (3) Belostomatine males make extreme efforts that seem to increase paternity. Some *Abedus* species, for example, interrupt ovipositing females frequently to insist on copulating again. So, is there a sexually antagonistic coevolution between male and female genitalia in Belostomatidae? It is possible that the presence of spurs and spines usually seen at the apexes of the second valvulae of Belostomatine females might evolve in response to such male insistence. Likewise, the parameres in the male genitalia of all Belostomatine species seem to be conveniently disassociated from the intromittent phallosoma. The hooklike shape of parameres could facilitate a good interaction with the apex of genital chamber's third valvulae, so that to force females copulate to males.

12.6 Conclusion

We have summarized here important advances in the understanding of paternal care in Belostomatidae. A recent phylogeny has suggested the inclusion of *H. pelocoroides* within the subfamily Belostomatinae instead of comprising the monobasic subfamily Horvathiniinae related to the subfamily Belostomatinae. So, with Belostomatidae subdivided into two subfamilies, a phylogenetic perspective was given associated with a behavioral approach to discuss the evolution of paternal care. After controlling the phylogenetic signal, a female-biased size dimorphism is supposed to be found earlier than that in emergent-brooders since this condition is the ancestral state in Belostomatidae. So, it has been suggested that the ancestor of all Belostomatidae was most likely to be a non-brooder. After controlling for the body size of males and females, we now can identify that the intensification of brooding behavior mediated by males is a possible target of selection, because it seems to be associated with evolutionary decrease in the sexual size dimorphism (SSD) in total body length, whatever the alternative phylogenetic scenarios have been used. Still, the infanticide phenomenon does not necessarily explain the origin of SSD biased toward females in Belostomatidae. Rather, it seems to be based on the tendency of related Nepidae species to be similar because they share a common history.

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Chapter 13
The Aquatic Lepidopterans: A Mysterious and Unknown Fauna

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Abstract The order Lepidoptera is represented by the popular butterflies and moths, and is identified by the presence of scales on the wings with an extraordinary variety of colors and sizes. Although most Lepidoptera are exclusively terrestrial there are some lineages associated with the aquatic environment. Little is known about aspects of the biology and life history of its representatives leading to a gap in scientific knowledge. Thus, we can find aquatic Lepidoptera that have tracheal breathing that can remain outside the water for a limited time, being considered semiaquatic larvae, while larvae with branchial respiration are aquatic while retaining all their submerged larval development. In this chapter, possible evolutionary paths are explored which aquatic lepidopteran larvae had to live in aquatic environments and we examine the incipient studies that address life aspects of these extraordinary animals.

Keywords Moths · Butterflies · Parapoynx · Petrophila · Crambidae · Caterpillar

When we talk about "the unknown tropical fauna," we often mean the animals of which little is known about their role in their habitat. This is considered true for some specimens of Lepidoptera, which spend a part of their lives on aquatic ecosystems.

Lepidoptera is one of the best known groups of insect, due to its exuberance, diversity, and economic importance. The lepidopterans are commonly known as moths and butterflies and can be mostly identified by the presence of scales on their wings and for their wide variety of colors and shape patterns. It is possible to find many studies about these insects in the literature, but most of them are focused on agriculture for their potential as herbivores in plantations or on taxonomic surveys of these holometabolous insects' adult forms. However, little is known about the biology and life history of this order, which leads to a gap in the

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scientific knowledge that mostly affects the species with part of their development in aquatic environments.

Currently, Lepidoptera has about 157,578 described species in the world (Zhang 2011) out of which approximately 740 species (representing 4.7% of the total) are believed to go through an aquatic larval stage (Mey and Speidel 2008). Nevertheless, the aquatic lepidopterans are relevant in aquatic ecosystems and can represent up to 32% of the macroinvertebrate community in a lotic system (Luiza-Andrade et al. 2017).

13.1 Evolution and Adaptation to the Aquatic Life

With the arising and radiation of the angiosperms in the Cretaceous Period, a new food resource became widely available promoting coevolutionary process and adaptive radiations in insect herbivorous including lepidopterans (Mey and Speidel 2008). During this coevolutive events, these insects were capable of exploiting all the parts of a plant and have possibly harnessed the resources of other ecosystems such as aquatic and semiaquatic environments. It is important to highlight that the transition from the aquatic to the semiaquatic life has independently occurred multiple times. Still, it has taken several adaptations to enable these forms of life to explore this new habitat, emphasizing changes in physiology and locomotion (Welch 1919).

As for terrestrial specimens, the respiratory system of the Lepidoptera larvae is formed by spiracles connecting with tracheas and a branched network of tubes that allows the air to flow throughout the body. However, in aquatic ecosystems, besides the tracheal breathing, it is also possible to find some individuals with bronchial breathing. The ones with a respiratory tracheal system are called semiaquatic and can survive out of the water for a certain period. These specimens have hydrophobic bristles throughout the body that cover the entire dorsal surface of the animal that when submerged allow the seizure of air, which is also stored around the respiratory spiracles that allows the animal to perform gas exchange. These characteristics can be observed in detail on the caterpillar of *Paracles klagesi* Rothschild 1910 (Erebidae: Arctiinae) as it has two kinds of bristles: one is thorn shaped (filiform) lying around the respiratory spiracles laterally along its body, and the other is drop shaped (pectiform), and it is located on the dorsal surface; both are hydrophobic (Fig. 13.1).

To feed, the caterpillar submerges. However, it must get back to the water surface periodically. This activity promotes the renewal of the air that is stocked between the tracheal spiracles at the base of the hydrophobic bristles. These spiracles open up in a cavity that has long chitin filaments until the lumen, directly connected to the connection trunk which leads to the trachea (Fig. 13.1). The number, anatomy, and histology of the spiracles vary among the species.

The aquatic species usually have filamentous gills (Fig. 13.2) that can show up at different larval instars varying with the species. Each gill filament has a cavity that connects directly to the hemocele. At the last instars, the gills become more ramified, and each filament will have a main trachea. At the axial position, the gill

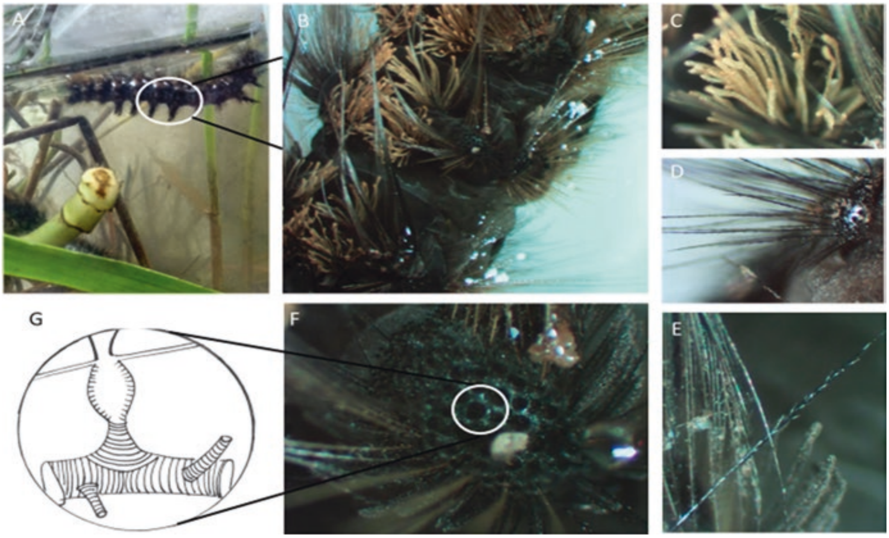

Fig. 13.1 Scheme of the tracheal respiratory system of *Paracles klagesi* based on Welch 1922. (**a**) The submerged larva—the arrow indicates the air bubbles between the bristles; (**b**) detail of the body segments showing the bristles; (**c**) orange drop-shaped bristles; (**d**) filiform bristles on the tracheal spiracle; (**e**) anatomic detail of the filiform bristle; (**f**) tracheal spiracles; (**g**) internal scheme of the tracheal bristle (photographs: **a**–**f** Iasmim De-Freitas)

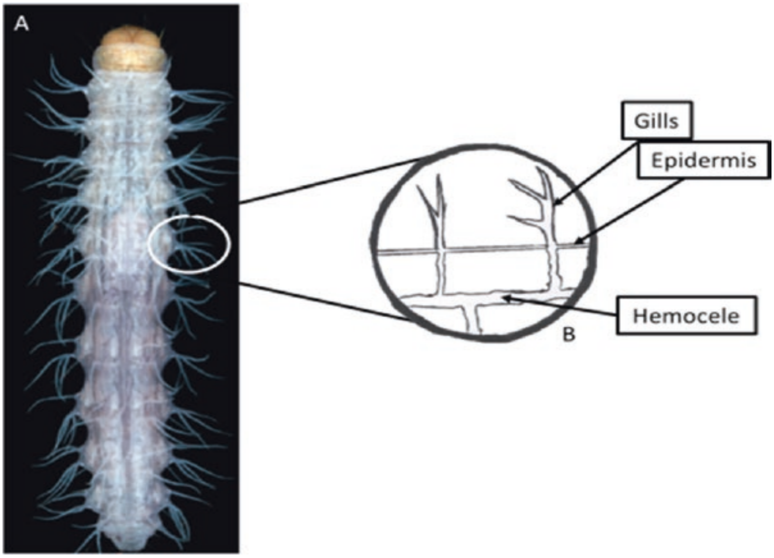

Fig. 13.2 Scheme of the *Usingeriessa onyxalis* branchial respiration based on Welch 1922. (**a**) *Usingeriessa onyxalis* caterpillar in dorsal view; (**b**) internal scheme of a gill (photograph of the aquatic larva: courtesy of M. Alma Solis, Nathan E. Harms, Eugenie Phillips-Rodríguez, Sonja J. Scheffer, Matthew L. Lewis, Daniel H. Janzen, Winnie Hallwachs, and Mark A. Metz; 2018. Aquatic Larvae of Two Acentropines, *Usingeriessa onyxalis* (Hampson) and *Oxyelophila callista* (Forbes) (Lepidoptera: Crambidae), Entomological Society of Washington, 120(1):180–195)

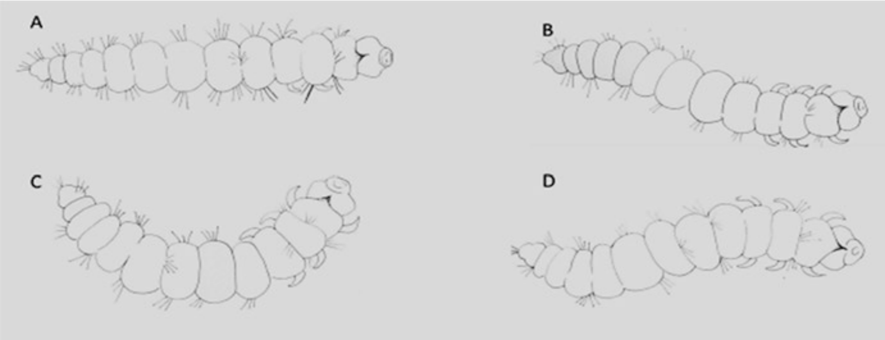

Fig. 13.3 Locomotion scheme. (**a**) Inert caterpillar; (**b**) the beginning of the bending; (**c**) the bending; (**d**) whip effect

filaments, along with the trachea, extend together in fine branches and form the tracheoles (Fig. 13.2).

The locomotion in terrestrial species can be typified mainly as "inchworm," while the aquatic ones developed a mechanism characterized by horizontal movements along the water column, like a whip in the posterior body parts where, initially, the anterior body part is flexed to one side horizontally and with a fast movement that provides the propulsion required to swim (Fig. 13.3).

13.2 Biology and Life History

Erebidae, Nepticulidae, Coleophoridae, Tortricidae, Pyralidae, Cosmopterigidae, Crambidae, and Noctuidae (Hamada et al. 2014; Mey and Speidel 2008; Mccafferty and Minno 1979) are the main families of Lepidoptera that are possible to find in literature with aquatic representatives. However, even though it is known that these species have aquatic larvae, there are not enough studies about their life histories and biological aspects. Having that in mind, some known neotropical exceptions will be presented in the following paragraphs.

The Arctiinae (Erebidae) subfamily has more than 3600 species; the *Paracles* genus has two aquatic representatives: the *Paracles klagesi* Rothschil 1910 and the *Paracles laboulbeni* Bar 1873 (Meneses et al. 2013; Mey and Speidel 2008). The *P. klagesi* aquatic larvae have tracheal breathing and were found in two distinct regions of aquatic environments in Brazilian territory—in lakes near the city of Timon (Maranhão State, 43°01′52.2″W, 05°03′03.3″S) and at "Vereda" lakes of the Neotropical Savanna near the city of Uberlândia (Minas Gerais State, 48°14′02″W, 18°54′52″S). Meneses et al. (2013) observed that the caterpillar eats two types of aquatic macrophytes: *Eichhornia* sp. (Pontederiaceae) and *Cabomba caroliniana* (Cabombaceae). The pupal stage consists of a fiber cocoon which allows buoyancy and is always adhered to a plant (Fig. 13.4). The *P. laboulbeni* caterpillar has tracheal

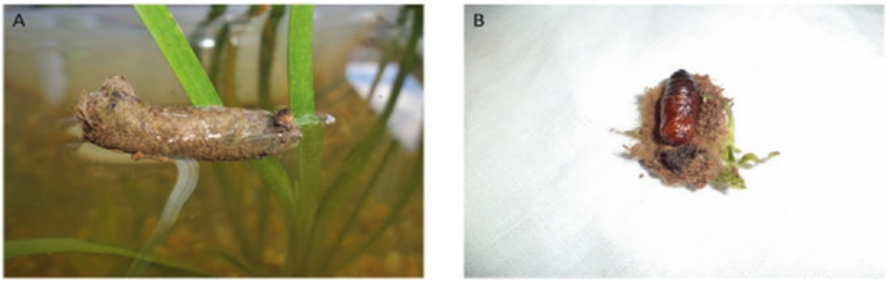

Fig. 13.4 (**a**) The *Paracles klagesi* pupa in its natural environment, with the cocoon made of hydrophobic fibers that allow buoyancy; (**b**) the fiber wrap was taken off so the cocoon cloud be visualized (photographs: **a** and **b** Iasmim De-Freitas)

breathing and eats macrophytes like *Echinochloa spectabilis*, *Hymenachne amplexicaulis*, *Oryza grandiglunis*, and algae of the *Oedogonium* genus (Adis 1983). The larval development varies from 30 to 35 days and the period of the greatest abundance was recorded from May to June, which precedes the rise in water level. However, its abundance is reduced when the water level is low (Adis 1983).

The Crambidae family has about 600 described species (Hamada et al. 2014). Among the species that have an aquatic larval stage, there is the *Niphograpta albiguttalis* Warren 1889, distributed between Argentina and Brazil. Its total development, since the egg to the adult form, lasts about 35 days; the adult females oviposit on the leaves of *Eichhornia crassipes* (Pontederiaceae), primarily in areas where the epidermis has been damaged, which will feed during the five larval instars (Julien 2001). However, despite the *N. albiguttalis* having been considered a biological control agent against the water hyacinth, currently it is considered a plague of *E. crassipes*, because when the oldest larvae eat the leaves, the plants become waterlogged and sink (Canavan et al. 2014).

Other species that have aquatic larvae are *Donacaula forficella* Thunberg 1794 (found in China, Europe, and South Africa); *Nymphula nitidulata* Hufnagel 1767 (found in Europe, Japan, Turkey, Armenia, Russia, and China); *Schoenobius gigantella* Denis and Schiffermüller 1775 (found in Europe and China); *Cataclysta lemnata* Linnaeus 1758 (found in Europe, Morocco, and Iran); and *Elophila nymphaeata* Linnaeus 1758 (found in Europe) (Vallenduuk and Cuppen 2004); however, little is known about their life histories and biology. It is important to highlight that the geographic extension of these species can be higher than it was described.

The eccentric species *Acentria ephemerella* Denis and Schiffermüller 1775 (Crambidae) draws attention for having females with paedomorphosis (the retention of the juvenile or even larval traits into later life), which means that even though they are adults they still live in the aquatic environments and do not develop wings. The most interesting aspect about the *A. ephemerella* happens during its mating because the females need to swim to the surface and put the abdomen above the water surface so that the male can copulate (Vallenduuk and Cuppen 2004). However, this species can only be found in Central Europe. No other species of aquatic lepidoptera with paedomorphosis has been found, even in tropical regions.

The Pyralidae family has about 5000 described species (Hamada et al. 2014). The aquatic larva of the *Parapoynx rugosalis* Moschler 1890 has gills and a study carried out in Costa Rica found that *P. rugosalis* uses a tent made of leaves that protects it from predators; as its development advances this tent is changed (Mueller and Dearing 1994). Another member of the Pyralidae family is the *Samea multiplicalis* Guenee 1854 (Knopf and Habeck 1976) that also has a wide distribution that extends from the Southwest of the United States to Argentina. The average development time for each stage of life of *S. multiplicalis* is 4 days to the eggs; 15.6 days to the larvae; and 5.2 days to the pupa; also, the number of eggs laid by a female in its natural environment was 94 eggs.

Among the most interesting aspects found among the representatives of the Pyralidae family, there is the Californian species *Parargyractis confusali* Walker, which has gills and the females of which go into the water to oviposit between 220 and 296 eggs on submerged rocks. The *P. confusali* larva builds silk chambers in depressions or cracks in the rocks and feeds on resources around them. When the cocoon is packed, it has an outer casing, which has openings for the water circulation (Tuskes 1977).

It is clear that studies on aquatic Lepidoptera are very scarce, being the great majority realized for species in temperate regions. Even though the studies about the biology and natural history of these specimens are almost unknown for tropical environments, it is important to emphasize morphological works (Solis et al. 2018), molecular studies (Park et al. 2014), and studies of biological controls (Hickel et al. 2017). These aspects mentioned above could be the gateway to new research with a focus on aquatic lepidoptera, not only for scientific knowledge but also for the ecological importance they exert as bioindicators (Stoops et al. 1998) and as herbivores (Habeck 1974), and the economic importance as food resources (Ramos-Elorduy 2006; Williams and Williams 2017) and agricultural pests (Mey and Speidel 2008; McGaha 1954). It is known that tropical aquatic environments are constantly polluted by anthropic interference, such as the discharge of urban sewage, the flow of agricultural nutrients, and the waste of confined animals that alter these sensitive environments and that compromise the survival of species that we will not even know.

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Chapter 14
Urban Aquatic Insects

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Abstract The increasing growth of urban areas on natural ecosystems has seriously affected wetlands. Aquatic insects, as key components of urban wetlands, are critically impacted by human environmental changes and practices. The main threats are those derived from the lost, replacement, or fragmentation of natural habitats, ecosystem homogenization, and modification of hydrological, sedimentological, and thermal wetland characteristics due to the surrounding urban matrix. Therefore, understanding the mechanisms by which urbanization processes affect biodiversity, and in particular how the biota responds to alteration of their habitats, is crucial for integrating the environment in proper urban planning. In this chapter we analyze the relationships between aquatic insects and environmental factors, including human influences and threats in urban wetlands. For this purpose, we compiled studies from around the world, especially from the neotropical region, addressing biological patterns and associated environmental processes in urban areas and endeavors. We discerned the main environmental threats and clues for the maintenance of the increase of the insect biodiversity, including the creation of new, man-made, wetlands. In addition, we focus on the importance of insect knowledge as indicators of environmental health in urban wetlands and the promotion of the citizen science to improve their conservation.

Keywords Urbanization · Biodiversity · Ecology · Freshwater · Colonization

14.1 Introduction

An urban area can be defined as a cultural landscape where people live at high densities, and extensive impervious surface areas are occupied by built structures and infrastructure, forming a dynamic patch mosaic whose structure, function, and

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dynamics are determined by coupled human-environment interactions (Pickett et al. 2011; Wu 2014). The process by which urban ecosystems are created is the urbanization (McIntyre 2000), and it has as a consequence transformed pristine natural landscapes to agricultural and suburban, and finally to urban landscapes. These impacts hinge on spatial scales from global and regional (e.g., mosquito population changes in response to global warming (Martin and Lefebvre 1995)), through landscape (e.g., electric lights, fast-moving traffic, replacement of mangroves by docks) down to highly local (e.g., water butt communities, unburied organic matter, wood stored in a warehouse). Yet the highly local is related to the regional and global; for example discarded vehicle tires encourage the spread of mosquitos and transported goods from harbor to harbor carry biota with specific habitat requirements. In addition, a worldwide increasing of infectious diseases associated with wetlands has been related, among other causes with a high human encroachment of natural environments, reductions in biodiversity, and changes in the number of vector breeding sites or in reservoir host distribution (Niemelä and MacDonnell 2011).

The Ramsar Convention's 10th meeting of the Conference of the Contracting adopted Resolution X.27 on Wetlands and urbanization (RAMSAR 2008) recognized that wetlands in urban and peri-urban areas can provide a range of important ecosystem services—benefits to people—but also that in many countries wetlands are increasingly becoming degraded because of spreading urbanization. As a complement of cities' green spaces, wetlands are also considered as blue spaces (Wu 2014). There are several papers dealing extensively with urban wetland ecology, as for example Chadwick et al. (2006), Meyer et al. (2005), Urban et al. (2006), and Walsh et al. (2005) for streams and Hassall (2014) for ponds.

Urban wetlands are ecosystems seriously threatened by the increase of the human population which, in the last decades, have been inclined to favor the growing of urban centers instead of rural areas; in addition, Latin America is one of the regions with the highest projected growth of urban population (De Sherbinin et al. 2009). This trend increases the pressure over the remaining green and blue spaces, as large parcels of land are deeply modified due to the real state pressure. At the same time the increase of the impervious surfaces which locally modify the evapotranspiration regime or increase of air and water pollution is a main driver to reduce availability, quality, and size of urban wetlands.

On the other hand, remaining wetlands are modified in order to fit human uses, practices, and preferences or new ones are made by man for different purposes, as drainage systems, garden, and ornamental and industrial ponds (Hassall 2014). The main threats are those derived from the lost or replacement of natural habitats (by filling, drainage, and excavation), ecosystem homogenization (i.e., decreasing microhabitat diversity through simplification of wetland coasts, reduction of riparian vegetation), and modification of hydrological, sedimentological, and thermal wetland characteristics due to the surrounding urban matrix and the introduction of alien species. These modifications impact negatively all levels of biodiversity and the ecosystem services they provide, implying an amelioration of life quality.

Nowadays, there are an increasing number of studies focusing on the improvement of management practices for urban wetlands and strategies for biodiversity conservation. One of the main objectives of those studies is to improve environmental quality and increase the ecosystem services they provide. Taking into account that insects represent one of the main taxa in any terrestrial or aquatic ecosystem, concurrently studies about the ecological role of the aquatic insects in these ecosystems and their value as biological indicators are ramping.

14.2 Aquatic Insects in Urban Wetlands

Modern cities tend to harbor different kinds of wetlands, natural, modified, and artificial, from rivers, streams, rivulets to ponds, lakes, ditches, dams, and phytotelmata (Fig. 14.1). Almost all main orders of aquatic insects can be potentially inhabitants of urban wetlands, excluding probably those extremely sensitive to environmental impacts as chemical pollution, habitat homogenization, or highly estenoic (i.e., aquatic Mecoptera). Nevertheless, as mentioned before, urbanization generates ecosystem homogenization and we could assume that a particular urban wetland exhibits less species richness than a similar one, non-anthropized, in the same region (Fig. 14.1a, b). Even though cities negatively affect natural wetlands, reducing their number, size, and heterogeneity, there is also a positive effect of human developing, the availability of new artificial wetlands which partially mitigate adverse impacts (Fig. 14.1c) (Schnack et al. 2000; Kadoya et al. 2004; Fontanarrosa et al. 2009; Holtmann et al. 2018). On the other hand, if these new artificial wetlands offer habitat for autochthonous species, we could expect an increase of more generalist or synanthropic species.

Fig. 14.1 Urban wetland diversity. (**a**) Pergamino stream crossing Pergamino city (Buenos Aires province, Argentina), (**b**) Pergamino stream downstream the city (Buenos Aires province, Argentina), (**c**) highway ditch in Avellaneda city (Buenos Aires province, Argentina), (**d**) artificial pond, Japanese Garden (Buenos Aires city), (**e**) artificial pond in a public park (Buenos Aires city, Argentina), artificial shoreline, (**f**) artificial pond in a public park (Buenos Aires city, Argentina), artificial shoreline

Fig. 14.1 (continued)

As aquatic insects mostly have complex amphibiotic life cycles (Fig. 14.2), urbanization impacts on aquatic and terrestrial ecosystems could affect the success of their populations. Interrelation between aquatic, semiaquatic, and terrestrial/aerial developmental stages, as for example adult emergence and maturation, mating, oviposition, and pupae survival, could be seriously affected by urbanization, leading to population losses (Smith et al. 2009). Also for those insects with a complete aquatic life cycle (e.g., several Nepomorpha as Belostomatidae, Corixidae, or Notonectidae) that eventually can fly and disperse through the terrestrial environment (Fig. 14.2a), it is necessary to consider for its conservation the structure of the surrounding terrestrial matrix.

Moreover, several management activities and/or urban infrastructure can act as ecological traps for many animals, especially for insects (Hale et al. 2015) (Fig. 14.3). Ecological traps are structures that can attract adult insects, especially those in dispersal or reproductive movements, as for example several species of Ephemeroptera which are attracted by higher polarization of reflected light of dark and shiny asphalt roads, probably because they use horizontally polarized light to identify ponds as potential oviposition sites (Smith et al. 2009; Malik et al. 2010; New 2015).

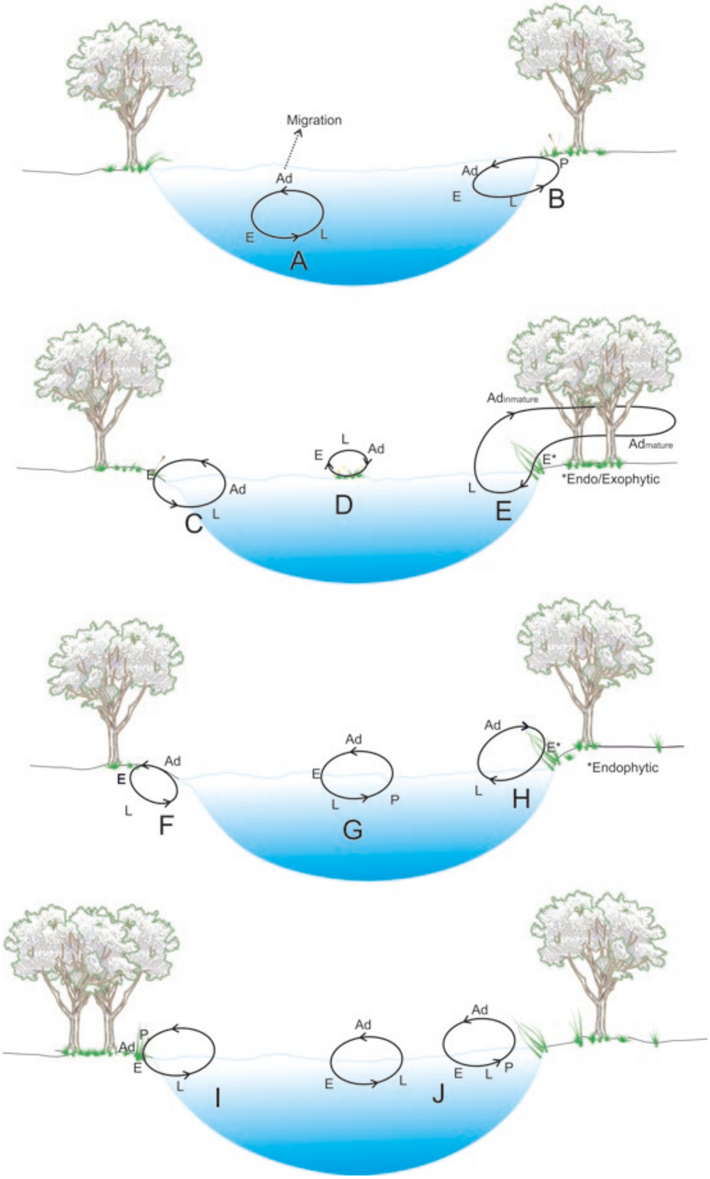

Fig. 14.2 Diagram of general types of aquatic/semiaquatic insect life cycles. E: eggs, L: larvae, P: pupae, Ad: adults. (**a**) Fully aquatic, eventually with migration flights (e.g., Corixidae, Notonectidae, Belostomatidae), (**b**) aquatic with terrestrial/riparian pupae (e.g., Dytiscidae, Gyrinidae, Elmidae), (**c**) aquatic or semiaquatic with riparian/aerial eggs (e.g., Hydrometridae, Gerridae, Belostomatidae only genus *Lethocerus*), (**d**) semiaquatic pleustonic (e.g., Orthoptera), (**e**) aquatic with terrestrial/aerial adults with prereproductive phase flying far from wetland (e.g., several Odonata), (**f**) fully riparian (e.g., Gelastocoridae, Ochteridae, Saldidae), (**g**) aquatic larvae and pupae with eggs over the water surface and terrestrial/aerial adults (e.g., Diptera Culicidae), (**h**) aquatic larvae with endophytic eggs on riparian plants and terrestrial/aerial adults (e.g., several Odonata), (**i**) terrestrial with aquatic larvae (e.g., Megaloptera), (**j**) aquatic with terrestrial/aerial adults (e.g., Odonata Anisoptera with exophytic oviposition, Trichoptera, several Diptera)

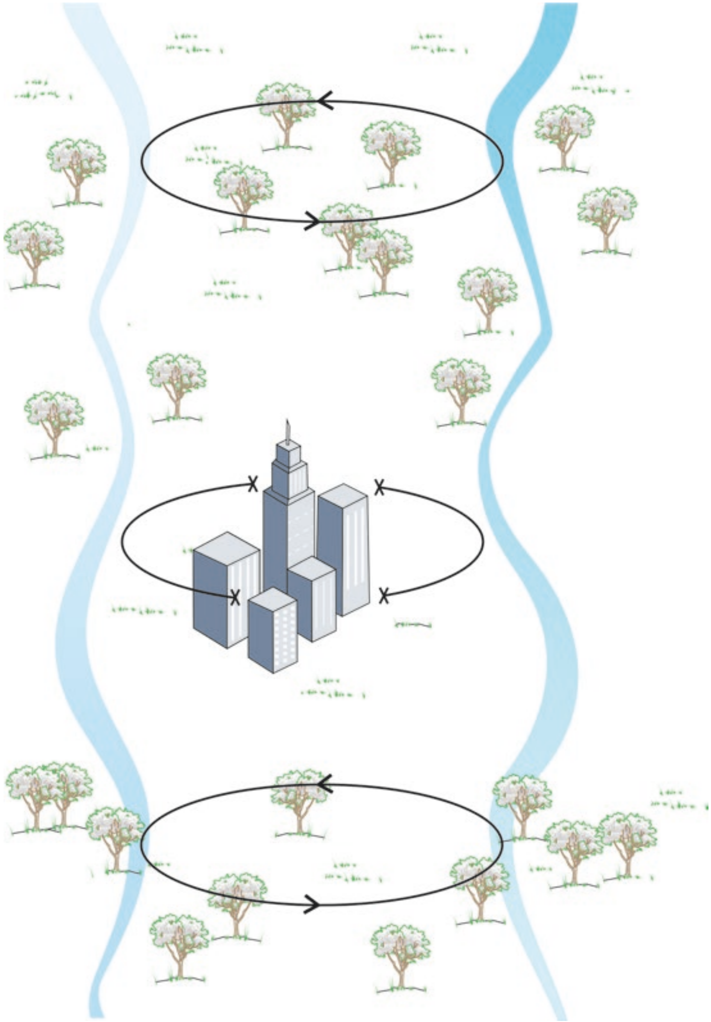

Fig. 14.3 Cities acting as an ecological trap. Diagram showing biota relationship between two different streams and the interference of urban infrastructure. Modified from Smith et al. (2009)

14.3 Main Threats and Impacts

There are a series of common characteristics or processes in urban centers proposed as threats for aquatic insects:

- Habitat fragmentation: Fragmentation reduces wetland size and connectivity and could affect negatively diversity. Wetland fragmentation in cities may be due to different types of human constructions or infrastructure (e.g., roads and buildings). Lost, replacement, or size reduction can be mentioned as a first impact on wetlands and its communities. There are some infrastructure, as bridges or road culverts, that also can act as barriers, mainly for lotic insect migration (Blakely et al. 2006). In addition, loss of connectivity between aquatic and terrestrial habitats, as for example modification of shorelines, could have a critical impact on those taxa with amphibiotic cycles with eggs and/or pupas in an aquatic/terrestrial interphase (Fig. 14.1e, f) (Smith et al. 2009).

- Nevertheless, there are no conclusive evidences about negative effects of wetland fragmentation on insects (Kadoya et al. 2004; Goertzen and Suhling 2013; Talaga et al. 2017). Suitability of habitats is assumed as more relevant than size and connectivity in some studies, perhaps due to the fact that most aquatic insects have a high dispersion capacity (Goertzen and Suhling 2013; Ramos et al. 2017). Whether wetland size could or could not influence insect diversity, there are some indirect environmental characteristics that could be primarily affected by size and shape, as for example shoreline longitude and heterogeneity of riparian vegetation (Samways and Steytler 1996; Kadoya et al. 2004) (Fig. 14.1d–f). Artificial man-made wetlands, as for example dams and road ditches, can host a significant specific diversity (Schnack et al. 2000; Goertzen and Suhling 2013; Ramos et al. 2017; Holtmann et al. 2018) counterbalancing negative impacts of other human constructions (Fig. 14.1c, d). On the other hand, an increase of ß diversity was positively correlated with habitat fragmentation in urban areas because fragmentation increases habitat heterogeneity and promotes edge species (Jones and Leather 2012; Talaga et al. 2017).
- Chemical pollution: Including diffuse, extensive, and continuous emissions deposited through atmospheric pollutants (from industry, traffic-related emissions, etc.) and point sources (as industry deposits, waste deposits, landfills, sewer, etc.). In addition, wetlands can receive pollutant inputs, through stormwater runoff and treated wastewater effluents (Niemelä and MacDonnell 2011; Turpin-Nagel and Vadas 2016). Unlike soil, pollution negative impacts on wetlands are fast and harder to contain, both on running and standing waters. Aquatic insects are negatively affected not only by the chemical itself, but also by alteration produced by it (e.g., changes in oxygen demand, conductivity, pH). Other important sources of water pollution are insecticides, commonly used in cities mostly for pest and mosquitoes' control. Some special ecosystems, as phytotelmata, are greatly threatened by insecticide spraying (Talaga et al. 2017).
- Light pollution: Artificial light is a new stressor for biotic components, recently incorporated by humans in the last 150 years. The attraction potential that artificial lights have over insects is recognized albeit not well known because light does not affect uniformly species and sexes; cities' light pollution can modify photoperiod responses and reduce nightime drift of larval aquatic insects in urban streams by disrupting their circadian rhythms (Henn et al. 2014). These impacts can modify inter- and intraspecific interactions and communities' structures, implying the disruption of ecosystem functioning, for which the term ecological light pollution was coined (Longcore and Rich 2004).
- Resource disruption: Habitat fragmentation, exotic vegetation, and human water consumption can affect negatively resource availability for many insect groups.

For example, differences in the composition of the riparian vegetation can produce changes in leaf litter decomposition, thus modifying the relative abundance among functional feeding groups, or oviposition substrate availability (Frankie and Ehler 1978; Smith 2007; Talaga et al. 2017).

- Urban heat island effect: It has been observed in most cities of the world that air temperatures are significantly higher than in the surrounding rural areas; this alteration of the climate is known as heat island effect. It can be a very complex phenomenon, showing a mosaic of different temperatures according to city design, distribution, and abundance of green spaces and wetlands (New 2015). These differences are not restricted to a specific season in the year, and vary according to the characteristics of the city, such as size and type of buildings (Niemelä and MacDonnell 2011). The causes of this effect are the supplanting of vegetation by impervious surfaces, which reduces evaporation and evapotranspiration (Niemelä and MacDonnell 2011; New 2015). There are several effects of the heat island effect on general urban biodiversity including aquatic communities. Higher temperatures affect the periods of growth and flowering of plants that affect or suppress ecological successions, which modifies the structures of the communities. In addition, the heat island favors the settlement of thermophilic species and alien species from warmer climates.
- Invasive species: Urban populations are fundamental in trade and transport plants and animal alien and/or invasive species and provide opportunities for a range of different introduction pathways (Hassall 2014). There are several examples of deliberated fish introduction in cities' ponds both as ornamental and sports fishing species. These invasive species could have a direct impact on aquatic insects' diversity and abundance, modifying their taxocoenosis (Muzón et al. 2005; Buria et al. 2007). On the other hand, invasive aquatic plants have a negative impact on wetlands, modifying water courses, reducing runoff, replacing native species, etc. (Howard 1999). Nonetheless, the effect of invasive exotic plants is not always detrimental to endemic biodiversity, since many of these plants behave ecologically similar to native plants (Samways 2005). Some species of dragonflies are excluded when invasive exotic trees provide a lot of shade in the habitat, but if the indigenous species are mixed with the native ones, the species do not seem to be affected (Kinvig and Samways 2000).

14.4 Aquatic Insects as Target Taxa for Urban Wetland Restoration and Conservation

As urban wetlands are nowadays considered key ecosystems to improve life quality and cities' sustainability, there are increasing studies focusing on evaluating and monitoring its environmental health, and evaluating the efficiency of recovery and/or conservation practices (Kadoya et al. 2004; Blakely et al. 2006; Hassall 2014; New 2015; Nieto et al. 2017).

Systematic and ecological knowledge of insects from urban wetlands is a major input for monitoring ecosystem health and evaluating best practices to improve biodiversity levels in cities (Morley and Karr 2002). On the other hand, urban insects' knowledge helps the promotion of the citizen science which in turn improves their conservation (Dickinson et al. 2010; Buldrini et al. 2015; Code 2017; Dumakude and Graham 2017).

Aquatic insects have been proposed as a reliable bioindicator group, both in natural and anthropogenic ecosystems. A bioindicator is a species or a group of species, whether animals, plants, or microorganisms, that can live under relatively specific environmental conditions under a narrow range of tolerance to one or more environmental factors of biotic or abiotic origin (Segnini 2003). Their presence in a habitat is informative of a particular state of its environment; they have been used to evaluate the magnitude of the disturbance produced by the human being, to monitor population trends in other species, and to identify and locate areas of high regional biodiversity.

Aquatic macroinvertebrates, particularly insects, are the most used bioindicators to assess environmental health. Many countries have a long history of using macroinvertebrates to monitor the environmental health of aquatic ecosystems. Benthic macroinvertebrates are key components of aquatic food webs that link organic matter and nutrient resources (e.g., leaf litter, algae, and detritus) with higher trophic levels. With the sensitive life stage and relatively long life span, they have the ability to integrate the effects of short-term environmental variations. Besides, these assemblages are made up of many species among which there is a wide range of trophic levels and pollution tolerances, therefore providing strong information for interpreting cumulative effects. Community structure of the assemblages frequently changes in response to environmental disturbances in predictable ways, which is the basis for development of biocriteria to evaluate anthropogenic influences (Li et al. 2010). Since different taxa are found in different geographical areas, biotic indices must be regionally specific.

At present, aquatic macroinvertebrates are the most widely used organisms in the biomonitoring of wetlands impacted by human disturbance (Bonada et al. 2006). It has been shown that, among them, insects are good subrogates, reducing monitoring cost and time (Smith 2007; Simaika and Samways 2012). Furthermore, as mentioned before, several aquatic insects have complex amphibiotic life cycles that could make them good monitors simultaneously on aquatic and terrestrial ecosystems (Kietzka et al. 2016).

There are several insect groups proposed or used as good biomonitors (e.g., Ephemeroptera, Odonata, Plecoptera, Hemiptera, Coleoptera, Diptera, Trichoptera), both together and separately. There are many indexes considering several taxa at once as for example:

- Biotic index, which evaluates community structure and makes use of the indicator species concept without placing undue emphasis on species that do not appear in significant numbers (Hilsenhoff 1977).
- Family biotic index, which requires only family identifications (Hilsenhoff 1988; Pérez and Ramírez Restrepo 2008).

- EPT index, for Ephemeroptera, Plecoptera, and Trichoptera: This index works under the assumption that the higher the water quality of streams, the higher is the specific richness due to the low tolerance of these taxa (Lenat and Penrose 1996; Hepp et al. 2013).

Also, there are indexes that are not based on supra-specific taxa or multi-taxa groups, but rather consider the information at the specific level for a particular group. For example, Odonata species were successfully used to test habitat quality (Dias-Silva et al. 2010; Dutra and De Marco 2015; de Oliveira-Junior et al. 2015; Valente-Neto et al. 2016; Miguel et al. 2017). Also there are several indexes based on odonate species: the Dragonfly Biotic Index, DBI (Simaika and Samways 2009, 2012; Samways and Simaika 2016), the Dragonfly Association Index (Chovanec et al. 2015), and the Odonate River Index, ORI (Golfieri et al. 2016), and the synanthropy level of urban wetlands through the Nuorteva index (Ramos et al. 2017).

Finally, there are some indexes used to describe environmental conditions in order to evaluate taxa diversity, as for example the Habitat Integrity Index (HII), widely used in South America (Nessimian et al. 2008). This index considers a protocol of 12 items that describe several environmental conditions, assessing characteristics that include patterns of land use adjacent to the riparian vegetation, the width of the riparian forest and its state of preservation, the condition of the riparian forest within a radius of 10 m, a description of the type of sediment and presence of retaining debris, the structure and erosion of the banks, the characteristics of the substrate of the stream bed, the aquatic vegetation and debris, and the distribution of rapids, pools, and meanders. Each of these items is scored on a scale of four to six points, and these values are summed and divided by the maximum possible score to provide a final value of 0–1 for the HII, with the highest values indicating the greatest stream integrity (Nessimian et al. 2008; Miguel et al. 2017). Although originally used for birds, the index has been used for many aquatic insects such as Heteroptera (Dias-Silva et al. 2010), Odonata (Miguel et al. 2017), and Trichoptera (Pereira et al. 2012).

14.5 South American Background

Most studies done in urban ecosystems have to do with megacities. The landscape that these ecosystems form is more similar among the cities of the world, regardless of their location, than with the surrounding ecosystem. However, most neotropical cities do not have these characteristics, but they are smaller (Talaga et al. 2017); this can modify the relationship with the surrounding ecosystems and the response of biodiversity. Additionally, there are few studies dealing with the processes that act within urban plots over time, except in studies of environmental impact due to specific sources of contamination with a strong sociological/epidemiological content or in many cases economic.

In the Neotropics, most of the studies are developed in streams (Couceiro et al. 2007; Dias-Silva et al. 2010; Feitosa et al. 2012; Miguel et al. 2017; Hepp et al.

2013; Monteiro-Júnior et al. 2014, 2015; de Oliveira-Junior et al. 2015) and to a lesser extent temporary ponds (Fontanarrosa et al. 2009; Ramos et al. 2017) and phytotelmata (Talaga et al. 2017). These studies are mainly focused on comparison of insects' diversity between urban and rural or pristine environments. There are few studies dealing with the processes that act within urban plots over time, except in studies of environmental impact due to specific sources of contamination with a strong sociological/epidemiological content or in many cases economic.

Surprisingly, studies of urban streams from an ecological point of view are scarce. Morley and Karr (2002) surveyed the world literature published between 1991 and 2001 and found that only 30 papers were concerned with the direct estimation of human effects on the biota in urban streams.

14.6 Wetlands as Promoters of Urban Biodiversity

As urban green spaces, wetlands (blue spaces) are main providers of many important ecological services to local communities (Wu 2014). In fact, among others they can act as flood control, groundwater replenishment, shoreline stabilization, storm protection, sediment and nutrient retention, water purification, and reservoirs of biodiversity. In addition, wetlands are key habitats for the development of educational programs aimed to the general public on natural sciences and also to initiate several citizen science programs. Hassall (2014) proposes a socio-ecosystem approach for the environmental management of urban ponds in order to minimize the arising conflicting priorities over ecological functions and services.

A sustainable urban design (including disciplines like architecture, landscape architecture, civil engineering, and urban planning) urgently needs information inputs from basic and applied research. Nevertheless, in a global context, the knowledge of urban ecosystems is far from being balanced between terrestrial and aquatic ones, being wetlands far less known than terrestrial, as well as their biota (Pickett et al. 2011). Hassall (2014) identifies three main research needs: the roles of design and location of urban ponds in influencing biodiversity, the function of urban wetlands for stormwater and pollution management, and the public perceptions of urban ecosystems and how those perceptions are influenced by interactions with natural systems.

Regarding aquatic insects, and in order to prevent major impacts or to better manage urban wetlands, we need to know not only species inventories, but also life cycle requirements, dispersal traits and patterns, ecological relationships, how species respond to the already urbanization threats, long-term consequences of changing landscapes on population genetics and species persistence, etc. (Smith and Lamp 2008). This kind of information is very uncommon for neotropical taxa, even though there are some important works published in Brazil (e.g., Feitosa et al. 2012; Monteiro-Júnior et al. 2014; Nicasio and Juen 2015; de Oliveira-Junior et al. 2017).

Considering that urbanization impacts on wetlands cause a decrease in their biodiversity, optimizing urban design is crucial for minimizing impacts and promoting biodiversity levels. Several requirements were proposed for the construction of new artificial ponds, which were summarized by Hassall (2014). Goertzen and Suhling (2013) suggest that conservation urban planning in urban centers must focus on a general improvement of habitat structure; for example, they proposed that moderate anthropogenic disturbance can increase habitat diversity and promote species of temporary and pioneer ponds especially at ruderal sites. Increasing biological value of urban wetlands through reduction of impact level, for example restoration of degraded shorelines and banks, removal of invasive alien trees, and recovering of riparian natural vegetation, can significatively increase specific richness, specially insects (Samways and Taylor 2004; Suren and McMurtrie 2005; Samways and Sharratt 2010; Goertzen and Suhling 2013). Also, Goertzen and Suhling (2013) have suggested at the city scale that different pond types regarding water level and succession stage would be beneficial for increasing biodiversity levels. In a similar way, a study carried out by Fontanarrosa et al. (2009) in temporary urban ponds in Buenos Aires found that seasonally irregular filling pattern due to local climatic conditions (humid temperate cities of the Southern Hemisphere) and physical characteristics of ponds (pool depth and area) were most significative to community structure.

Regarding minimizing of impacts, there are several studies around the world on how some threats affect aquatic biodiversity, especially aquatic insects. Management actions or best practices proposed in those studies must be considered for sustainable urban design; the region or the city the proposal is carried out does not matter (Walsh et al. 2005). For example, rehabilitate the natural heterogeneity of riparian ecosystems (Holmes et al. 2008); prevent and manage ecological traps (Hale et al. 2015); for those impacts produced by dark asphalt roads three mitigation measures have been proposed: to keep gravel roads in susceptible areas, to cover it with small-sized white gravel, or paint the asphalt with matte white stripes (Malik et al. 2010). Blakely et al. (2006) studied the effect of culverts as barriers for stream restoration and they found that the constriction of streams by culverts and associated physical barriers should be minimized in order to promote insect oviposition rates and sustain biodiversity levels.

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Chapter 15
The Tinbergen Shortfall: Developments on Aquatic Insect Behavior that Are Critical for Freshwater Conservation

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Abstract Humans have altered biodiversity worldwide, including accelerating species extinctions and loss of ecosystem services. Loss of many species is occurring even before they are collected for study, and researchers have recognized seven knowledge shortfalls that affect biodiversity and its use in conservation. This loss is especially true in aquatic ecosystems highly threatened by human pressures, including habitat transformation and degradation, and water extraction. Here, we propose the "Tinbergen shortfall" in honor of Nikolaas Tinbergen, related to limited knowledge of aquatic insect behavior in tropical regions, and how this shortfall highlights the need to have more knowledge on aquatic insect behavior for improving applied ecology, specifically biomonitoring, as it is the field where aquatic insect behavior information is most often used in measuring water quality, ecological integrity, and conservation. Through a systematized literature search in Web of Knowledge

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database, we showed the limitation of our current knowledge on aquatic insects, behavior, and its use in conservation. We demonstrate a bias toward temperate countries, orders (e.g., Lepidoptera, Orthoptera, and Heteroptera), behavioral topic (feeding behavior), and limited use of aquatic insect behavioral knowledge in conservation science. Although aquatic insects having a long-established history in biomonitoring protocols worldwide, the use of behavior knowledge, such as oviposition and dispersal, is still limited. We emphasize the behavior that proxies can be used in biomonitoring and conservation studies in cases where information is unavailable, and how behavior information can improve recent approaches such as simulation modelling. Aquatic insect behavior can better inform conservation strategies based on scientific evidence, and we use some examples, including the creation and maintenance of protected areas, the reduction of anthropogenic impacts on animal behavior, and the development of specific agendas for animal species or groups of species that are particularly relevant for their value and changes in human behavior. The challenges ahead for biodiversity conservation will require addressing Tinbergen shortfall for aquatic insects and the increase of our understanding about the behavior of our own species in relation to the others.

Keywords Biomonitoring · Insect-human interactions · Anthropogenic impacts · Biodiversity loss · Bioindicators

15.1 Introduction

Species extinctions and imperilment in freshwater ecosystems have increased worldwide due to human impacts that are resulting in the loss of ecosystem services (Dudgeon et al. 2006; Strayer and Dudgeon 2010; Dudgeon 2014). Human activities have resulted in at least 10,000 freshwater species going globally extinct or becoming imperiled (Strayer 2006; IUCN 2017; Vörösmarty et al. 2010). Because each species has specific ecological traits and behaviors, when a species is lost, many ecological traits and behaviors that can be fundamental for ecosystem services and to community structure are also missing (Covich et al. 2004; Luck et al. 2009; Dirzo et al. 2014). Loss of many species is occurring even before they are collected for study. Because most species are not yet formally described (the Linnean shortfall) their ecological and geographical distributions are poorly understood (Lomolino 2004; Whittaker et al. 2005). Knowledge gaps related to the biology of invertebrate species and their importance in freshwater ecosystems are examples of bias, while the lack of cross-ecosystem integration requires much more consideration (Di Marco et al. 2017).

These knowledge gaps affect recommendations and prevent effective conservation actions, and are a cause for increasing concern. Here we summarize several key features. First, the knowledge gap regarding aquatic insects is a major concern as they are highly speciose, and it is a group that plays many important roles in providing material and nonmaterial ecological services. Balian et al. (2008) estimate that the total number of freshwater animal species is about 1,260,000, and aquatic insects are the dominant group (60.4%). Second, the most threatened ecosystems in tropical regions are freshwater rivers, lakes, and wetlands. These ecosystems are losing biodiversity at an alarming rate due to deforestation, habitat degradation, pollution, eutrophication, siltation, impoundments, channelization, flood control, exotic species invasions, overexploitation, fisheries, increasing salinity, and climate change (Dudgeon et al. 2006; Samways et al. 2010; Winemiller et al. 2016; Pelicice et al. 2017).

Improving inclusion of information about little studied but highly important groups is at the heart of global conservation and sustainability strategies. Improvement requires overcoming shortfalls of various types of knowledge. Seven previously proposed shortfalls (Hortal et al. 2015) pinpoint knowledge gaps for species taxonomy (Linnean), distribution (Wallacean), abundance (Prestonian), evolutionary patterns (Darwinian), abiotic tolerances among species' niches (Hutchinsonian), species traits (Raunkiæran), and biotic interactions (Eltonian). These shortfalls are especially valid for determining how aquatic insects are protected and conserved. Here, we propose a new shortfall, the "Tinbergen shortfall" in honor of Nikolaas Tinbergen (one of the founders of modern ethology, and winner of the Nobel Prize, https://www.nobelprize.org/prizes/medicine/1973/tinbergen/facts/). This shortfall relates to limited knowledge of aquatic insect behavior in general in tropical regions. This focus highlights the needs for devoting multidisciplinary studies of aquatic insects' behavior in a broad sense throughout the tropics to solve problems in conservation and biomonitoring. We explore the implication of this shortfall for biodiversity conservation of aquatic insects and propose some avenues for future progress in understanding how insects function in freshwater ecosystems.

Although the link between animal behavior and biodiversity conservation has a long history, it was only recently that these areas were merged into a field termed conservation behavior (see Sutherland 1998; Blumstein and Fernández-Juricic 2004). Since then, there have been advances using behavioral information for captive breeding, species reintroduction, relocation, reducing animal-human conflicts, protected area design, and wildlife management. However, most studies have focused on mammals and birds. Only recently have some studies focused on aquatic invertebrates, and they have shown that understanding behavior can inform better decision-making in conservation (Samways 2007; Samways et al. 2010). Aquatic insect behavioral science is a rapidly developing discipline, and the knowledge generated is highly relevant for conservation and biomonitoring (Heino and Peckarsky 2014). Most initiatives for conservation depend on behavioral data. For instance, to assess the conservation status of a species, it is important to know aspects of its movement and reproduction, because these behaviors are critical parameters for understanding the distribution and abundance of populations and communities, as well as their relationships with spatial, temporal, and environmental variables. Despite their importance, most studies related to conservation of population, communities, and metacommunities in tropical freshwaters are limited in their inferences because of the gaps in knowledge of aquatic insect behavior.

In this chapter, we evaluate trends in conservation literature considering aquatic insect behavior, including insect groups, biological behavioral traits, geography, ecological systems, and level of biological organization that are needed to better comprehend the Tinbergen shortfall. We then explore the implications of having more knowledge of aquatic insect behavior for improving applied ecology. The focus here is on biomonitoring because it is the field where aquatic insect behavior information is most often used in measuring water quality and ecological integrity. Finally, we discuss some challenges on using information on aquatic insect behavior in a conservation context, especially through connecting of animal behavior and conservation (Berger-Tal et al. 2011). We include example of direct and indirect anthropogenic impacts on animal behavior that have consequences for populations and communities, behavior-based management, and behavioral indicators to other processes that are of conservation concern (e.g., use of aquatic insects as bioindicators of water quality).

15.2 The Extent of the Challenge for Filling the Knowledge Gap

Monitoring biases and trends in the literature on insect conservation is crucial to tracking the progress of the discipline. We evaluated trends in the aquatic insect literature that cover aspects of behavior and conservation. We searched the literature using ISI Web of Knowledge database in December 2018, using as keywords the combination of the name of each 31 existing insect orders AND one of the following words related to behavior: “behavior,” “feeding behavior,” “reproductive behavior,” and “breeding behavior.” In the second step, we associate each insect order AND the keywords related to the behavior AND “conservation”. Among the selected papers, the following information was extracted: insect group, country of the study, year, main key words that are selected in the article, type of ecosystem, and full reference.

Supporting our proposal of the Tinbergen shortfall for aquatic insects, we found bias toward geographical region, taxonomic order, environmental system, and behavioral topics in studies involving behavior and conservation. Most studies have been done in temperate countries (United States had the most undertaken), with terrestrial orders (e.g., Lepidoptera, Orthoptera, and Heteroptera), and were about behavioral traits focusing on feeding behavior (Fig. 15.1; Table 15.1—complementary material). Despite some changing trends, studies on behavior of aquatic insects are still poorly connected with conservation science and conservation priorities. Overcoming this challenge may require improving the integration among conservation and behavioral studies on aquatic insects, but more importantly this integration requires strong connection with real-world applications, as

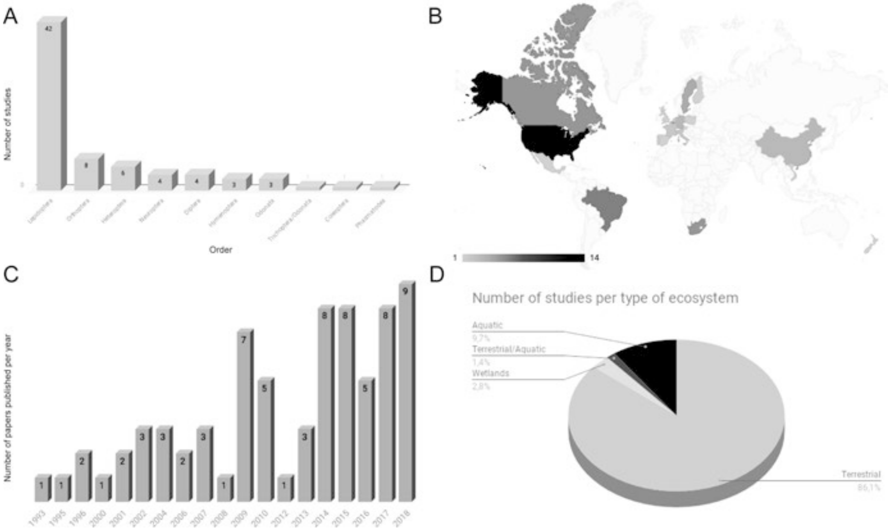

Fig. 15.1 (**a**) Number of studies selected per insect order that assessed topics relating behavior and conservation. (**b**) Number of studies published by country; light and dark colors represent countries with few and large number of papers, respectively. (**c**) Trend in the number of papers published per year. (**d**) Number of studies by ecosystem types

already highlighted by Berger-Tal et al. (2011) for animal behavior and conservation in general.

15.3 Using Behavior Knowledge in Applied Issues: Biomonitoring

Aquatic insects have a long-established history in biomonitoring protocols worldwide, because high biotic diversity responds to various anthropogenic changes, including deforestation, urbanization, toxins, and organic pollution (Rosenberg and Resh 1993; Buss et al. 2015). For example, in lotic systems, anthropogenic impacts that increase water temperature and decrease dissolved oxygen cause a great reduction in species richness of Ephemeroptera, Plecoptera, and Trichoptera (EPT). The effects of anthropogenic changes on species abundance and distribution depend on species-specific tolerances to altered conditions and resources that may ultimately lead to local extinctions. However, we are far from understanding, particularly in the neotropics, how anthropogenic impacts alter species' behaviors, and whether these changes result in fitness reductions that have consequences for populations and communities (Peckarsky et al. 1997; Heino and Peckarsky 2014).

Table 15.1 Number of articles found in the database Web of Science: In dark gray, articles selected in order that have at least one of the key words of behavior

Order	Behavior	Behavior + conservation	Behavior stricto sensu	Feeding behavior	Feeding behavior + conservation	Feeding behavior stricto sensu	Reproductive behavior	Reproductive behavior + conservation	Reproductive behavior stricto sensu	Breeding behavior	Breeding behavior + conservation	Breeding behavior stricto sensu
Archaeognatha	18	0	0	1	0	0	3	0	0	0	0	0
Blattodea	88	3	0	28	1	0	6	0	0	4	0	0
Coleoptera	5360	161	0	1435	30	1	696	20	0	218	17	0
Collembola	227	3	0	52	**0**	0	13	0	0	3	0	0
Dermaptera	87	0	0	11	0	0	12	0	0	3	0	0
Diplura	5	0	0	1	0	0	2	0	0	0	0	0
Diptera	6163	102	0	170	31	0	712	11	0	305	10	2
Embioptera	17	1	0	1	0	0	3	0	0	0	0	0
Ephemeroptera	193	7	0	77	0	0	11	0	0	5	0	0
Grylloblattodea	4	1	0	1	0	0	0	0	0	0	0	0
Hemiptera	2660	39	0	926	16	0	318	3	0	59	0	0
Heteroptera	1197	12	5	297	3	0	178	1	1	18	1	0
Hymenoptera	9668	230	2	1257	35	1	1351	31	0	234	3	0
Isoptera	769	9	0	188	1	0	59	1	0	20	2	0
Lepidoptera	5594	220	38	1576	46	4	629	18	0	129	10	0
Mantodea	68	0	0	14	0	0	11	0	0	1	0	0
Mecoptera	47	0	0	17	0	0	9	0	0	1	0	0
Megaloptera	24	0	0	1	0	0	1	0	0	0	0	0
Neuroptera	233	9	3	58	5	1	23	1	0	3	1	0
Odonata	755	43	2	90	3	0	152	7	0	49	8	2
Orthoptera	1286	26	8	242	3	0	195	4	0	41	6	0
Phasmatodea	24	1	1	2	0	0	4	0	0	1	0	0

Phthiraptera	52	1	0	8	1	0	3	0	0	11	1	0
Plecoptera	158	0	0	54	0	0	9	0	0	0	0	0
Protura	2	0	0	0	0	0	1	0	0	0	0	0
Psocoptera	31	1	0	7	0	0	0	0	0	0	0	0
Siphonaptera	48	0	0	14	0	0	3	0	0	2	0	0
Strepsiptera	30	0	0	0	0	0	7	0	0	0	0	0
Thysanoptera	303	4	0	109	1	0	27	0	0	14	0	0
Trichoptera	256	13	1	77	0	0	9	0	0	0	0	0
Zoraptera	9	0	0	1	0	0	4	0	0	0	0	0
Zygentoma	13	0	0	2	0	0	1	0	0	0	0	0

In light gray, the articles selected in order that had at least one of the key words linked to the behavior plus the word conservation. Blank cells, the articles in order that actually use behavior in conservation matters

The two pathways in which aquatic insect behavioral metrics have been used in conservation and biomonitoring (see Berger-Tal et al. 2011 for animal behavior in general) are (1) behavioral indicators that provide an early warning to population decline or habitat degradation before community responses are evident (e.g., Roque et al. 2018) and (2) behavioral indicators used to monitor water conditions (Rosenberg and Resh 1993). Studies of feeding behavior are also highly relevant and have a long-established application in developing metrics for aquatic ecology and biomonitoring (Merrit et al. 2008; Rosenberg and Resh 1993). The focus on oviposition and dispersal behavior is valuable because these types of behavior affect survival and reproduction (hence recruitment), so providing essential information on population and community dynamics that can improve biomonitoring.

Basic knowledge about behavior is fundamental to better development of biomonitoring and conservation studies. Researchers use animal behavior to track a species' movement, dispersal, and feeding behaviors to decide the best time and place for collecting different species that are effective bioindicators. For example, dragonflies are best sampled on sunny days between 10:00 and 15:00 h, due to their known thermal restrictions (Corbet 2004). Blackflies include important disease vector species and are known to be associated with rapid-flowing waters, so the sampling strategy to study these animals should focus on these habitats. Some species of *Chironomus* (Chironomidae) prefer habitats with low dissolved concentrations and high organic matter, and therefore are effective bioindicators of organic matter pollution (Rosenberg and Resh 1993).

Another key information that behavioral studies can provide to biomonitoring relies on the classical relationship between biodiversity and environment, a cornerstone of biomonitoring. Any change in the environment can affect survivorship, reproduction, and growth. When these effects are scaled up to the community level, distributional changes emerge. Reproduction is a particularly interesting life history aspect that is used to better understand the biodiversity-environment relationship of aquatic insects because adult female insects can select favorable environmental conditions to lay their eggs and increase their offspring's chances of survivorship and population size (Encalada and Peckarsky 2012; Lancaster and Downes 2014; Heino and Peckarsky 2014). Some aquatic insects, such as the damselfly *Calopteryx splendens*, select more oxygenated, fast-flowing water for laying eggs, which significantly increases egg development time while decreasing their mortality, compared to slow-flowing waters (Siva-Jothy et al. 1995). Others species identify suitable structures to lay their eggs, such as protruding substrates (rocks, stems, wood). For example, the number of oviposition sites (protruding rocks) influenced the density of larvae of the mayfly *Baetis rhodani* and a caddisfly *Rhyacophila dorsalis*, whose adults oviposit exclusively on emergent rocks in riffles (Lancaster and Downes 2014). The neonate and mid-stage larva distribution pattern of mayfly *Baetis rhodani* is positively related to egg masses, suggesting a persistence of maternal effects on larval distribution patterns (Lancaster et al. 2011). Damselflies may select specific patches of a water body with certain vegetation structure to oviposit, where larvae will develop (Guillermo-Ferreira and Del-Claro 2011). In the neotropics, oviposition behavior of dragonflies was used to understand the relationship between species richness and forest loss (Rodrigues et al. 2018). The number of species of exophytic and epiphytic (species which lay eggs on the emerged surface of substrates) behavior was positive, but negatively related to riparian forest loss, suggesting that forest loss may favor species with particular oviposition behaviors (Rodrigues et al. 2018). These studies demonstrate that a strong effect of adult behavior on larva distribution and oviposition trait behaviors can be incorporated in ecology and biomonitoring to better understand biodiversity-environment relationships.

The oviposition behavior involves decisions by female insects, such as to stay at their natal sites or to disperse from their natal sites to another site with more suitable environmental conditions. In this way, oviposition behavior and dispersal are interconnected, although the former is a small-scale phenomenon and the latter is related to larger scale regional processes (dispersal between sites). Species dispersal behavior may change the classical biodiversity-environment relationship, an important connection recognized in metacommunity ecology (Leibold et al. 2014; Leibold and Chase 2018). Species may leave a high-quality patch as a result of intense competition and may colonize low-quality patches, and where mortality rates are greater than reproduction rates. The high mortality is overcome by dispersers from high-quality patches (source patches) maintaining populations in the low-quality patches (sink patches). In turn, these source-sink dynamics could mask biodiversity-environment relationship, affecting biomonitoring (Heino 2013). For example, specialist species can be present in low-quality patches not because the conditions and resource levels are suitable in those patches, but as a result of dispersal of individuals from a close high-quality patch. Despite this theoretical perspective, information on dispersal such as the maximum distances, direction, and frequency of movement is unknown for most aquatic insects (Lancaster and Downes 2014). Consequently, dispersal proxies are increasingly being used in biomonitoring and conservation studies such as distance-related measures among sites, dispersal traits, and graph-based approaches (e.g., Erős et al. 2012; Heino 2013). However, a recent study showed that dispersal traits did not predict colonization (Downes and Lancaster 2018), as usually assumed, indicating that much more information is needed regarding this type of behavior.

Although adult aquatic insects can fly and consequently disperse longer distances than larvae, drift is also important at smaller spatial scales, such as the stream reach scale (Downes and Lancaster 2018). Larvae may actively select for microhabitats with specific backgrounds or substrates to occupy (Tavares et al. 2018), which may have effects at macroscale and determine species distribution and community composition. Maternal behavior detected in early instars of *B. rhodani* and *R. dorsalis* is a result of female selection of sites to oviposit but is obscured in later instars (Lancaster and Downes 2014). This result is a consequence of density-dependent mortality of early instar instars, mainly due to predation, and dispersal (drift). These effects of mortality and drift on later instars could mask the environmental-biodiversity relationship, if it is assumed that high-quality habitats are more abundant than low-quality habitats. Drift can be even more important for community patterns than aerial dispersal. In a large-scale experiment (22 km stream length), Downes and Lancaster (2018) demonstrated that larval drift is the main dispersal route used to reach downstream habitats and that dispersal traits frequently used to infer dispersal did not capture colonization ability. These results suggest the need to improve our current knowledge of aquatic insect dispersal to improve conservation planning, restoration, and biomonitoring of aquatic systems (Erős et al. 2012; Heino 2013; Tonkin et al. 2018).

Understanding the behavior of aquatic insects and its application in biomonitoring and conservation is still incipient, particularly in the Neotropical region. This knowledge gap leads to weak or even erroneous conclusions. This means that we need an improvement in information on insect behavior to enhance biomonitoring, with many more studies required on the large number of species despite the difficulties associated with analysis of aquatic insects (e.g., direct observation of larval behavior). For conservation planning and biomonitoring related to accelerating rates of habitat loss, fragmentation, and transformation, we could use some behavioral proxies, such as species traits (e.g., Rodrigues et al. 2018) and distance proxies for dispersal (Tonkin et al. 2018). Alternatively, we could use other approaches to improve conservation planning and to predict future human impacts such as niche modelling (Diniz-Filho et al. 2010). Simulation modelling studies is another interesting tool that can be used to inform conservation and biomonitoring actions (Economo 2011; Siqueira et al. 2014). These models require some biological characteristics to bring the simulations close to reality. Among the required information, dispersal rates and oviposition preferences are particularly important in the case of aquatic insects.

Valente-Neto et al. (2018) used a simulation model to predict biodiversity patterns in a riverine network, and showed the model-predicted observed patterns for the less mobile insects. Despite not knowing the number of eggs and dispersal rates for many aquatic insects, they used two proxies (mean of number of eggs and a dispersal kernel). The same model was also used in a biomonitoring context (Siqueira et al. 2014). We expect that in the near future, we can include more specific behavioral information in modelling approaches and biomonitoring, such as oviposition preferences and maximum dispersal distance, and improve the predictability of biodiversity patterns.

15.4 Using Aquatic Insect Behavior Information in Conservation

In the last decade, many studies have emphasized the key role animal behavior plays in conservation practice. Here we will give some examples of how the understanding of aquatic insect behavior can inform better conservation strategies based on scientific evidence.

The most effective conservation strategy for a target species or group is the creation and maintenance of protected areas. Aquatic insect distribution information has been used in prioritizing areas for protection through systematic planning processes (Nieto et al. 2017). For many reasons, the selection of priority areas for conservation has often used species distribution. As a result, the creation of the protected areas has been strongly based on terrestrial biota, and the threats to these species related to the terrestrial ecosystems (Azevedo-Santos et al. 2018). Because the physical organization of freshwater drainage networks influences the dispersal behavior of aquatic insects (Tonkin et al. 2018), ignoring the spatial relations of aquatic habitats can result in less effective planning of the locations of protected areas for conserving aquatic insect metapopulations and metacommunities in the long term (Erős et al. 2012). The behavior of target species is essential when designing protected areas at the landscape scale. For example, the Serra de São José Wildlife Reserve was created to protect and conserve dragonflies in the Atlantic Forest, and has had considerable success based on the locations of many streams with suitable habitats for these species (Bedê et al. 2015).

Another important strategy for aquatic insect conservation is reducing anthropogenic impacts on animal behavior. When humans alter the environment, the fitness value of existing behavioral strategies changes and can lead to local extinctions. Not only do such impacts affect population dynamics and local extinction, but they also lead to the extinction of behaviors. Anthropogenic effects on gene pools may select certain genes and exclude others that would express unique behaviors or behaviors of interest for ecological services. Moreover, in some species, aquatic insects may exhibit behavioral syndromes or personalities. In these cases, genetic diversity results in different phenotypic traits that are interpreted as a diversity of behavioral patterns among individuals. To lose such behavioral diversity can be compared to lose biodiversity and ecological processes that rely on animal behaviors (see Cordero-Rivera 2017). We may even be successful in conserving a flagship species, but at the same time conservation attempts may exclude certain genes that produce behaviors that are typical for this species. For instance, if we conserve dragonflies, but not their typical oviposition sites or habitat selection behaviors, we lose what makes a dragonfly a dragonfly. In other words, we lose the natural genetic components of entire lineages. Ultimately, such losses may impair the stability of populations and lead to long-term extinction events.

Hence, reducing and mitigating anthropogenic stress on aquatic insect behavior are critical for conservation. Studies have produced some of the information needed for a general framework for conserving biodiversity that is likely to be useful for aquatic insects. First reducing habitat loss should be a top priority for conservation planners because land conversion is still the main reason of biodiversity loss in tropical regions (see Rodrigues et al. 2016; Roque et al. 2018). Strategies that reduce anthropogenic threats to natural systems would benefit aquatic insects. Losses of species are clearly increased by deforestation, habitat degradation and transformation, overexploitation, pollution, eutrophication, siltation, impoundments, flood control, exotic species invasions, fisheries, increasing salinity, and climate change. In general, “macro” conservation initiatives depend less on specific knowledge about aquatic insects, but they are intended to implement general public policies for biodiversity conservation. However, there is no reason to wait for solving the entire

Tinbergen shortfall before conservation action. We can improve conservation strategies as more information on aquatic insects becomes available to avoid wasting effort, money, and time.

It is unrealistic to propose behavioral studies of all aquatic insect species to support conservation strategies. The first reason is the Linnean and Wallacean shortfalls. How could researchers study aquatic insect behavior when many species are still not formally described or have a huge gap in their distribution? In addition, behavioral studies demand considerable fieldwork to assess key variables of an insect species (e.g., movement, reproductive behavior, selection of habitats for oviposition) and there are relatively few insect specialists to carry out these studies (Samways 2018). It is important to develop specific agendas for animal species or groups of species of particular relevance, such as endangered species or key species. In these cases, behavioral studies could be part of specific conservation strategies for sustaining these species.

Human and aquatic insects interact in many positive and negative ways. Behavior manipulation is an important field that can inform conservation strategies to mitigate human and aquatic insect conflicts or booster beneficial interactions. For example, manipulating elements of the landscapes (e.g., adding potential perches, oviposition sites) can attract and readjust the behavior of aquatic insect predators (e.g., dragonflies), which could increase the consume of mosquitos and other insects, reducing potential conflicts between humans and these vectors of diseases (Faithpraise et al. 2014). Controlling insect populations through species-specific manipulation of behavior such as sexual communication, without adversely affecting nontarget species, has a long history in applied entomology, particularly in the context of agriculture (Foster and Harris 1997). Beyond the studies on manipulation of behavior for controlling some species of mosquitos, not much has been done on other aquatic insect groups. The use of behavior manipulation (e.g., applications of sex pheromones for attract sexual patterns) as a strategy to improve the populations of red listed aquatic insects is a completely open avenue.

According to the United Nations Food and Agriculture Organization, almost 50% of the world's economy is based directly and indirectly on the use of biological resources. The sustainable use of the biodiversity and ecosystem services for people is the core of conservation strategies (CBD 2014). People directly use aquatic insects in many different ways (Suter and Cormier 2014), such as for food, robotic inspiration, bioindicators, bio-jewels, and pets. Aquatic insects are also involved in critical ecological services, such as water quality, decomposition, and food web regulation. Some species have nonmaterial value, including art, cinema, folklore, music, literature, and religious activities. So, improving the knowledge on aquatic insect behavior has implications for all these areas. Without greater knowledge of the aquatic insect behavior, the promise of using aquatic insects in a sustainable way to improve human health and conservation will remain largely unfulfilled.

Related areas of study such as ecological restoration need to be integrated in establishing protected areas and other large projects because these activities can contribute enormously to biodiversity conservation and global stability and resilience, especially given the current and projected impacts of land-use changes and climate change (Steffen et al. 2015). There are many initiatives to restore aquatic ecosystems around the world. However, in most cases, aquatic insects are neglected, or they are used only as bioindicators of environmental conditions rather than as integral parts of the entire ecosystem. Although there are few documented cases of captive breeding and reintroductions of aquatic insects, some successful reintroduction attempts (e.g., Hemiptera, see Ahlroth et al. 2003; Odonata, see Dolny et al. 2018; Plecoptera, see Zwick et al. 2011) indicate that these activities can enhance restoration and increase the value of protected areas. Because behavior is central for the adaptation of animals to their environments, understanding the ways that aquatic insect species perceive different environments, and how their learning processes affect changes in behavior, is fundamental in planning the best reintroduction strategies. As an example, studies about spatial learning in dragonflies have shown that they remember their positive and negative experiences in different environments and adjust their future space use accordingly (Eason and Switzer 2006). Captive breeding and reintroduction programs can use this kind of behavioral information to increase the fitness of a species in changing environments. In summary, reducing the Tinbergen shortfall is critical to increasing the success of reintroduction and conservation of aquatic insects.

Human behavior is causing a major loss of biodiversity. Changes in human behavior are necessary to achieve more sustainable relationships between humans and the rest of nature. The success of a conservation program can depend on both our knowledge of behavior of aquatic insects and human actions. Aquatic insects and humans interact in complex ways, so changing the behavior of humans in relation to the insects is among the main challenges for aquatic insect conservation. According to Samways (2018), insect conservation throughout the twenty-first century calls for action and new perspectives: (1) philosophy (establishing the ethical foundation), research, policy, psychology (understanding how to engage humans in insect conservation action), practice (implementation of action), and validation (establishing how well we are doing at conserving insects). In this way, educational programs, insect watching movements, citizen science initiatives (e.g., Nerbonne and Nelson 2004; Buytaert et al. 2014), and monitoring programs of freshwater ecosystems (e.g., Buss et al. 2015) can all help humans to better understand the importance of aquatic insects. Like bird or butterfly watching, aquatic insect watching has a huge potential to reconnect people with nature, and this is currently happening. People are already engaged in observing dragonflies, such as Dragonfly Pond Watch, a volunteer-based project of the Migratory Dragonfly Partnership (MDP)—https://xerces.org/dragonfly-migration/pondwatch/; Dragonfly India Citizen Science movement. Moreover, there are many volunteer programs of aquatic monitoring using insects as bioindicators in place across the world. New communication technologies have boosted the flow of data and knowledge in such initiatives, as the RiuNet, a *Citizen Science* project dedicated to assessing the ecological status of a river reach by following the steps of a standardized protocol available in the RiuNet app (http://www.riunet.net). In this context, we have an unprecedented opportunity to create big collaborative networks around the conservation of aquatic insects.

Species extinction is just the most evident consequence of biodiversity loss. In fact, when a species goes extinct, our planet also loses genes, behaviors, interactions, ecological services, and so on. Beyond the potential consequences for humans already explored in this chapter, the loss of animal behaviors due to anthropogenic impacts led to the "extinction of experiences"—in other words, people are becoming less likely to have direct contact with nature (Soga and Gaston 2016).

New fields such as conservation psychology and personalized ecology which focus on intention-behavior exhibited by people are promising areas that link animal and human behavior toward conservation (Gaston et al. 2018; Simaika and Samways 2018). New perspectives such as "behaviorscape," which integrates landscape ecology, behavior ecology, and biodiversity ecology, provide a solid theoretical framework to understand biodiversity patterns with implication for conservation. However, it has not yet been used for aquatic insects. The challenges ahead for biodiversity conservation will require not only the improvement of the Tinbergen shortfall for aquatic insects but also an increase in our understanding of the behavior of our own species in relation to all the others.

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Chapter 16
Genetic Connectivity in Conservation of Freshwater Insects

Drielly da Silveira Queiroga, Renan Fernandes Moura, and Jessica Ware

Abstract Ecosystems and species are disappearing fast and the conservation of isolated and fragmented landscapes is not enough to maintain healthy populations. However, populations from fragmented and impacted landscapes may be benefited if there are pathways allowing their connection. These pathways enable the exchange of individuals, allowing species to increase their genetic diversity and resilience to stochastic events by recolonization and phenotypic adaptations. In aquatic ecosystems, climate changes and water exploration are impacting the species' capability to disperse among populations and survival. In this scenario, aquatic insects are even more threatened as most of them have terrestrial and aquatic life stages, suffering impacts from both environments. Focusing in this aspect, this chapter aims to provide an initial insight about how population connectivity can be used in conservation strategies as well as methods of measuring genetic connectivity. Here we selected studies with odonates, ephemeropterans, and other aquatic insects to exemplify how river dynamics can influence the direction of gene flow and dispersal patterns of individuals, besides showing the main approaches used in this study area. By contributing to the understanding of this necessary field, we hope to stimulate new researchers to engage in the conservation of aquatic insects.

Keywords Conservation genetics · Endangered arthropods · Entomology · Habitat fragmentation · Molecular markers

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16.1 An Overview

Globally environments are disappearing faster than we can access their diversity. Scientists, environmentalists, and governments have issued dire warnings about biodiversity loss and the consequences of such losses for human health and environment permanence. There are many causes for biodiversity loss ranging from the exploitation of natural resources to the introduction of exotic species and global warming. According to World Wide Fund for Nature (WWF), a rich biodiversity is fundamental for the balance and stability of ecosystems, providing vital ecosystem services such as climate regulation, nutrient and waste management, flood control, coastal protection, provision of food and freshwater, fuel, medicines, building materials, fertile soils, and breathable air. Biodiversity has also a wide potential for economic use, especially for biotechnology. Extinction is a natural fate for any species, and occurs at some background rate; however, anthropogenic activities have increased extinction rates across species, causing catastrophic diversity loss. Preservation is imperative when it comes to aquatic environments given the intimate relationship between water and all living beings. Although aquatic environments are essential to human health, they are often the most exploited environments. Human reliance on freshwater water for consumption, agriculture and industrial purposes, and effluent dilution has resulted in freshwater vulnerability.

Recognizing the main components and dynamics of aquatic environments is the first step to establish conservation strategies. For instance, the spatial arrangement of freshwater systems is widely recognized as a fundamental attribute to be investigated. Freshwater systems are organized in drainage basins, which have distinct geological processes of formation, being composed of interconnected springs, streams, rivers, and lakes along the basin. The water direction and speed are determined by the region's topography, which can create rapids or standing water sites. The basin's arrangement is known as dendritic network, since the interconnection among streams and rivers resembles the design of a tree, with numerous small branches interconnecting and increasing in thickness as they approach to the trunk. When an ecological disturbance occurs, the direction of water flow and the disturbance origin can be used to predict negative impacts along the basins. This information combined with the regional topography can be useful to define conservation strategies within threatened areas.

Other aspects of river basins can help us to predict species diversity. For example, springs and small streams have small volumes of water and low sunlight incidence. As streams interconnect, becoming large rivers, their both the water volume and the sunlight incidence increase. For aquatic insects, the sunlight incidence and structural changes of rivers, as well as the properties of terrestrial surroundings (that may provide microhabitats), are fundamental to determine what species may occur at a given point of the watershed.

Many aquatic insects may increase or decrease in abundance in response to environmental disturbances; these species are known as bioindicators and may be used to evaluate the environmental quality of aquatic ecosystems. Changes in the relative abundance of bioindicator species may be enough to indicate whether a given environment is under stress. Thus, it is imperative to preserve bioindicators as they can alert us before environmental impacts become large enough to extinguish ecologically important species. Unfortunately, bioindicators cannot be used as universal conservation tools as they are an indirect and relatively subjective measuring of environmental quality. So what other approaches can be used to conserve biodiversity? Currently, there are several conservation approaches for aquatic organisms, but the most common practices have serious economical and logistical issues. For instance, protecting regions where threatened populations live is essential, but it is not possible for all populations. Research species conservation programs cost a lot of time and resources, and many species are widely distributed, making it infeasible to be applied for all known threatened populations. Since we are not able to protect all species at the same time, priorities should be established: How do we evaluate which species deserves more attention?

To best determine which species require the most attention, many scientists have turned to genetic tools to identify genetically diverse populations and their relative genetic connectivity. Such studies are fundamental for conservation genetics, that uses genetic analyses for management and conservation purposes. The International Union for Conservation of Nature (IUCN) recommends the preservation of high genetic diversity in populations. High genetic diversity may allow populations to more quickly adapt to environmental changes and reduce their levels of inbreeding—these two features are related to the increase in survival and fitness of natural populations. Thus, high genetic diversity and connectivity among populations—which increase genetic diversity—are one of the most important factors for the preservation of natural populations.

The importance of genetic diversity in the maintenance of natural populations has become more widely studied recently thanks to an increase in the number of conservation genetic studies that seek to combine genetic studies of populations with conservation. Many of these studies focus on understanding the mechanisms that lead to the persistence of a population and how populations respond under some natural or anthropogenic environmental stress. In this sense, this chapter provides some basic concepts to understand the studies that approach genetic connectivity in freshwater environments, focusing mainly on aquatic insects.

16.2 What Is Genetic Connectivity?

Genetic connectivity is the exchange of genetic material among populations of the same species, allowing the genetic diversity maintenance. This exchange occurs through the processes of **dispersion** and **migration**, which are movements performed by individuals or populations (Kool et al. 2013). While migration is characterized by long-distance movements, often related to seasonality—as seen in birds and fishes—dispersal is used more commonly to describe any local movements performed individuals. Dispersion can be directional when an individual goes to a "planned" place, such as its breeding site or randomly when reaching "non-planned" places, other populations, or uninhabited sites. Dispersion allows individuals to reach different populations, but genetic connectivity only occurs through mating between individuals. This reproductive connection among populations is known as **gene flow** and it may increase **genetic diversity** by introducing new alleles into a target population, changing local allele frequencies (Whitlock and Mccauley 1999).

Links among populations may be reduced or prevented due to **barriers**. Barriers are any obstacle to species dispersal. They may be structural or even environmental variations, whether naturally occurring or not. They act by separating populations although sometimes individuals may overcome barriers, resulting in the connection of two or more populations. When a barrier is strong enough, however, that no individual can transpose it, the populations become isolated, causing a genetic diversity loss (Crook et al. 2015).

The importance of gene flow for the maintenance of populations is clear, and measurements of gene flow reflect the evolutionary history of species (Ye et al. 2018). Studies on genetic connectivity have sought to understand the evolutionary processes and natural history of species. This knowledge has helped researchers to develop conservation efforts, and manage endangered species, including the mountain lion, manatee terns and harpies (Castilho et al. 2012). The pressures suffered by species vary among distinct environments, reinforcing the importance of specific studies for each species or environment: freshwater and terrestrial species greatly differ in response to environmental pressures. Within the freshwater habitat, differences occur in water flow, substrate, etc., making each environment relatively unique (Campbell Grant et al. 2007). For terrestrial species, physical structures such as vegetation, mountains, or urbanness may act as barriers to dispersal (Anderson et al. 2010). By contrast, barriers in aquatic environments are physical-chemical (i.e., temperature and water oxygen rate) more often than structural (i.e., waterfalls, dams, or rapids) (McRae 2006).

16.2.1 What Is the Importance of Genetic Connectivity in Aquatic Environments?

In freshwater systems, water speed and depth, and chemistry can act as barriers to organismal dispersion, as well terrestrial environments, that ultimately limit and shape aquatic systems (Phillipsen and Lytle 2013). Barriers may limit movements of organisms among rivers, generating high genetic structuring by isolating certain populations. Connectivity in aquatic systems has four dimensions: (1) longitudinal, throughout the channel; (2) lateral, in floodplain inundation events; (3) vertical, between the water mirror and the other water layers in environments with great depth; and (4) temporal, due to seasonal and stochastic events. Given this, McGlashan and Hughes (2001) suggest three possible scenarios: (1) negligible gene flow among drains over long periods, resulting in strong genetic structuring; (2) moderate gene flow among closely connected adjacent drains; and (3) extensive genetic flow, which reflects a high dispersion potential that can overcome the isolation imposed by drainage structures.

The structure of most basins has a tree pattern, where their trunk and branches form a structure known as a **dendritic network** (Campbell Grant et al. 2007). This structure can be found in many freshwater environments—except in isolated lakes—and is organized hierarchically, from the source (upstream) to the mouth (downstream), following the direction of water flow. This dendritic hierarchy was proposed by Robin L. Vannote et al. (1980), in a theory known as the "River Continuum Concept" (RCC). In the RCC, there are three groups of fluvial gradients, classified by its number of streams confluence: headwaters (stream order 1–3), midreaches (stream order 4–6), and lower reaches (stream order > 6) (Fig. 16.1). Each stream has different characteristics—i.e., variation in shading provided by riparian forests, sediment type, and water volume—that allow us to predict which organisms are expected to occur at each stream point. Since the environmental requirements of organisms vary along a fluvial gradient, RCC theory can be used to predict potential barriers to dispersion. This idea was tested by Meffe and Vrijenhoek (1988) and Hughes et al. (2009); they proposed a model based on RCC to explain the connectivity of aquatic populations called the "Stream Hierarchy Model" (SHM).

Under the SHM, connectivity patterns among populations of riverine species are a consequence of the dendritic arrangement of streams (Hughes et al. 2013). Under this model, populations from distinct sites within the same stream would show higher connectivity than populations present in different streams, but in the same sub-catchment. Subsequently, population connectivity would decrease among distinct sub-catchments and catchments, following a hierarchical dendritic model,

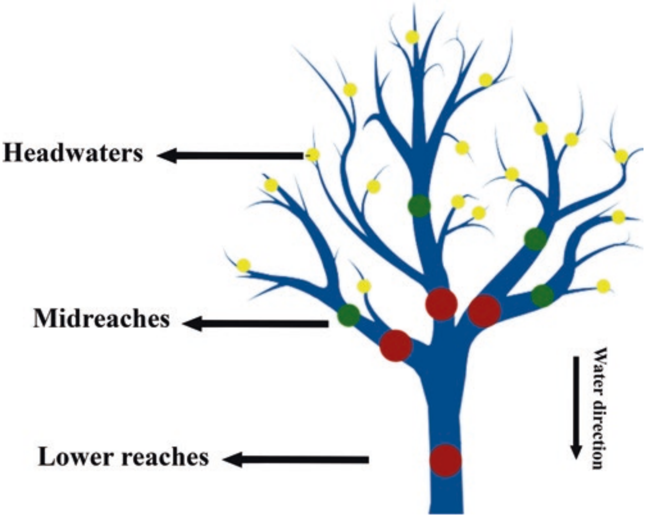

Fig. 16.1 Representation of a watershed in its tree-like dendritic pattern. The hierarchical structure is represented by circles: yellow (headwaters), green (midreaches), and red (lower reaches)

where connectivity decreases as the scales are increased. For instance, shredders—organisms that feed on coarse particulate organic material—are expected to be found in headwaters. These animals are represented by organisms such as mayflies (Ephemeroptera) or stoneflies (Plecoptera) who will feed on fallen leaves, abundant in headwaters and small streams due to riparian vegetation. In bigger streams and rivers, food might not be accessible for these organisms since most organic matter is composed of fine particles that may be taken away by strong water streams (Horne and Goldman 1994). Therefore, as RCC predicts a tree pattern, with habitats of these mayflies and stoneflies connected by large rivers, SHM predict that structural and chemical changes which occur along stream orders will be barriers to the dispersal of aquatic species, rather than the distance or isolation of streams (Keller et al. 2012).

While in lotic systems the main barriers to species distribution are the terrestrial environment between headwaters, waterfalls, and dams; the major barrier in lentic systems is the stratification of water bodies that may occur in deep lakes. Stratification is a phenomenon where different water layers of varying temperatures occur simultaneously, and the less dense layers—those with the highest temperatures—float on the denser ones with a minimum degree of mixing between them. This occurs due to the absence of aquatic currents that mix the surface water (heated by the atmosphere) with the deep water. However, stratification is a dynamic phenomenon and the water layers behave differently every season. In temperate lakes, in the early spring, when temperatures are increasing, the ice layer breaks and the water temperature increases to 4 °C, reducing its density. As summer approaches, air temperature heats surface waters and decreases their density, but deeper water remains cold due to low light incidence. In summer, there is a water layer called **thermocline**, a band of rapid temperature changes, which occurs between **hypolimnion**, the lowest and coldest lake layer, and **epilimnion**, the upper warm layer. During the fall season, the epilimnion and hypolimnion waters start to mix as their temperature equalizes until the winter, where occurs an inverse stratification, with the high-density water on top (Horne and Goldman 1994). These changes directly affect the biota in these environments. Changes in the water temperatures across seasons, for example, limits the occurrence of some species. Changes in this cycle can cause drastic population reductions (bottlenecks), that may result in a loss of genetic diversity and extinction events.

Knowing the main limitations to the dispersion of organisms is fundamental to assess the connectivity between populations. Factors such as mobility capacity, life cycle, environmental dependences, and sensibility can influence the dispersal potential of species and it should be taken into account when planning studies to assess connectivity between populations. There are several techniques for assessing connectivity between populations. However, it is always indicated to combine two or more techniques to increase the accuracy of the results and to decide what techniques are the best will depend on the organism in question. The following is a summary of the two major categories of connectivity assessment techniques seen in most studies.

16.2.2 How Can One Evaluate Connectivity?

There are several methods for estimating connectivity between populations. Since each method has advantages and disadvantages, researchers should choose methods tailored to the organisms and environments to be evaluated. Such methods are grouped into two categories: **direct** and **indirect estimates** (Kool et al. 2013). In direct estimates, individuals or gametes are samples used to estimate gene flow (i.e. Villella et al. 2004). Mark-recapture techniques are common direct approaches (Fig. 16.2); however, they are relatively imprecise about the actual gene exchange between populations (Kool et al. 2013). For example, dispersing individuals may not be successful in finding a mate if they eventually arrive at inadequate habitats that reduce their chances of a successful mating. On the other hand, indirect estimates investigate the allele frequencies between populations. They are commonly used due to its instant response, without the uncertainty of recapture and the need of waiting for individuals to travel between populations. Despite these advantages, indirect measurements have disadvantages: genetic samples assess the outcomes of past connectivity, but recent changes to populations may not be yet detectable (Rosa 2009).

16.2.3 Molecular Markers: What Genetic Analyses Are Used to Evaluate Population Connectivity?

16.2.3.1 Mitochondrial DNA (mDNA)

Mitochondrial genes are maternally inherited by the offspring. The main characteristic of mtDNA markers is their non-Mendelian pattern of inheritance, with low rate of genetic recombination. Polymerase chain reaction (PCR) can be used to

Fig. 16.2 Mark-recapture techniques are used to assess individual's movements among populations. The picture shows an individual from *Erythemis credula* (Libellulidae) marked on its right hindwing

amplify copies of the mtDNA which can be sequenced and analyzed. mtDNA are useful markers to estimate phylogenetic relationships, estimate genetic distance, and discriminate subpopulations and overall biogeographic history.

16.2.3.2 Microsatellites

Microsatellites, also known as short tandem repeats (STRs) or simple sequence repeats (SSRs), are small sequences of DNA (1–6 base pairs), organized in tandem, randomly distributed in the eukaryotic genome. Using a small sample of DNA, microsatellites can be amplified by primers—segments of nucleic acids necessary for the initiation of DNA replication—in a polymerase chain reaction (PCR) technique, where a small and specific region of the genome is amplified by DNA polymerase enzymes. Due to their high frequency, polymorphism, and distribution along the genome of many species, microsatellites are used for tests on recent genetic splits among populations as estimators of genetic distances, discriminating subpopulations, genetic diversity, gene flow, bottleneck effects, hybridism, and individual identification.

16.2.3.3 Single-Nucleotide Polymorphism (SNP)

SNPs reflect the variation in DNA sequences at a single nucleotide in a specific position of the genome. They present low rates of mutation, and are commonly used as genetic markers for population-based, phylogeographic, and phylogenetic studies.

Freshwater Environments

Freshwater environments encompass a wide variety of formations, with different geological history, and biotic and abiotic components. They are divided into three types: lotic, lentic, and wetlands, which are a specific type of lentic system.

Lotic systems have flowing waters and can vary from springs, of few centimeters of deep, to large water bodies such as the Brazilian Amazon River, the biggest river on earth, with 6.992 km in length. Lotic systems can vary in speed, form, and size. Springs and rivers are examples of lotic systems, as are streams, creeks, waterfalls, and rapids. Rivers have unidirectional flow, continuous physical change, high degree of spatial and temporal heterogeneity at all scales, and high habitat variability throughout their orders and bear a specialized biota adapted to live in running water conditions.

Lentic systems are those where the water flows slowly or is completely stopped. They are lakes, lagoons, water puddles, wetlands, and even seasonal pools. They can range from a temporary rainwater pool with few centimeters depth to areas such as the Baikal lake of Russia, with a maximum depth of

1740 m. While lotic systems present a continuous flow that homogenizes the water temperature, lentic systems have a thermal stratification that results in water layers of different temperatures.

Wetlands are areas where the soil is saturated or flooded (permanently or seasonally). The main wetland types are swamps, marshes, bogs, fens, and peatlands. Wetlands occur on every continent and are important to water purification, flood control, and carbon sink. The largest wetlands are the Amazon River basin, the South American Pantanal, the West Siberian Plain, and the Sundarbans in the Ganges-Brahmaputra delta (Fig. 16.3).

Fig. 16.3 An example of lotic system, a stream surrounded by a riparian forest in the Cerrado biome, southeastern, Brazil

16.3 New Approaches in Freshwater Connectivity: Riverscape Genetics

There are many studies aiming to assess how habitat heterogeneity influences genetic structure of populations in terrestrial environments by combining methods from landscape ecology, spatial statistics, and population genetics (Tischendorf and Fahrig, 2000; Alp et al. 2012; Phillipsen et al. 2015). These studies comprise a sub-discipline known as landscape genetics that, more recently, has been expanded to be used in marine environments and defined as "seascape genetics" (Davis et al. 2018). Both landscape and seascape genetics try to explain how specified habitats can increase or decrease the movements of individuals and test whether certain models of individual movements can explain connectivity better than other models.

For river environments, an approach called riverscape genetics (RG) is commonly used. RG combines methods from landscape ecology and population genetics. It seeks to understand processes and factors that interfere in population dynamics to gather information that can be used to develop conservation strategies. Davis et al. (2018) define RG as "an area of study that evaluates the effect of riverscape features on spatial genetic variation." Thus, it evaluates the effect of riverscape features on spatial genetic variation considering the riverscape as a continuum where habitats have permeable boundaries but also discontinuities among patches that can influence river organisms.

Studies in RG use continuous and discrete sampling designs to identify physical barriers and correlations between spatial genetic variation and abiotic factors. Most studies about RG, however, have been focused on discrete barriers such as waterfalls and dams (isolation by barrier hypothesis, i.e. Coleman et al. 2018) and on the physical distance among populations (isolation by distance hypothesis, i.e. Finn et al. 2006). For insects, recent studies concluded that the greatest obstacle to the dispersion of most aquatic insects is distance (Sabando et al. 2011; Short and Caterino 2009; Watanabe et al. 2008, 2010). Although their winged form can overcome most physical barriers, they often fail to travel long distances (Pfeiler and Markow 2017), with the exception of long-distance migrants like the dragonfly *Pantala flavescens* (e.g., Hobson et al. 2012; May 2013). An example of low dispersal is found in the study carried out by Chaput-Bardy et al. (2008) with the damselfly *Calopteryx splendens* (Fig. 16.4), where they found clear isolation by distance among populations. Adults cannot disperse long distances due to their limited flight capacity. By contrast, larvae can disperse greater distances than adults—despite their lower active dispersal capacity—as they are carried by the stream flow.

Fig. 16.4 The damselfly *Calopteryx splendens* (male) defending its territory on water. Photo by Kilodk on pixabay.com

Compiling several studies on riverscape genetics, Davis et al. (2018) evaluated how they have approached riverscape features in distinct aquatic taxa and pointed a few prospects for future studies. They found that studies addressing the effects of natural and anthropogenic barriers commonly seek explanations based on isolation by distance and by barriers to explain genetic diversity, but rarely these two hypotheses alone have fully explained the patterns found. Although their importance is recognized as structuring processes of genetic diversity, there is another kind of isolation that has been used to study certain organisms such as fishes. Isolation by resistance occurs when effects of multiple landscape variables, such as precipitation and temperature, are the main limitations to gene flow among populations. In this scenario, populations can respond to physical-chemical variations as barriers to dispersion more than physical barriers or distance (McRae 2006). Although there are few studies that combine all these approaches (barriers, distance, and resistance), the use of isolation by resistance concept combined with isolation by distance and barriers provides better responses to river systems.

Besides the hypotheses that try to explain connectivity patterns based on potential dispersal limits, there are others that predict the direction of gene flow. Created by Paz-Vinas et al. (2015), the Downstream Increase in Intraspecific Genetic Diversity (DIGD) hypothesis describes the asymmetrical genetic pattern found in many groups of aquatic organisms, predicting gene flow direction and estimating the genetic variation source found in a species population. DIGD suggests that dendritic networks allow asymmetrical gene flow, with the direction of gene exchange between populations usually following the water flow direction, since many species cannot travel against it (Keller et al. 2012).

Certain phenotypes can be selected by specific pressures on populations. When this occurs, organisms usually show strict adaptations that give them advantages to explore local resources better than nonspecialized neighbors, increasing their fitness. Whitehead et al. (2011) observed that living populations of the killifish *Fundulus beteroclitus* had adaptations that allowed them to tolerate pollution. In a stressed environment, these adaptations were mediated by genes related to osmotic shock, by increasing velocity response to these conditions. The link between spatial adaptive genetic variation and riverscape heterogeneity is the focus of gene-environment association (GEA) studies, which aim to find associations between genes and environment conditions.

Although GEA studies have been reporting strong correlations between genes and environment, their main challenge is in the study of wild populations. However, there are problems in assessing adaptations in wild populations regarding the ability of isolating the environmental variables of interest. An alternative to these problems is computer programs that carry out genetic selection simulations, such as LOSITAN (Looking for Selection in a Tangled dataset) (Antao et al. 2008). These programs help to understand adaptive evolution in natural populations by evaluating how dispersal and connectivity affect adaptive genes across populations. This information can be used to elucidate how environmental disturbances (such as biological invasions, diseases) affect natural populations.

An important issue is that GEA studies do not always reflect recent conditions and events. Adaptations settle in populations only after several generations, demanding a large timescale for some species depending on the time between generations. Thus, in many cases, spatial genetic structure of populations can be attributed to ancient historical events, as the Pleistocene glacial cycles or mega-flood events that affected the genetic connectivity among populations (Wong et al. 2004). Geological processes can structure or interrupt connections between populations on an entire river network. Current and past geological processes that affect genetic variation of populations allow us to preserve different species by providing information about the resilience, adaptive capacity, and natural history of populations. To evaluate the importance of past processes, scientists have developed molecular techniques capable of detecting the effects of ancient geological processes on current genetic patterns. Ye et al. (2018) using mDNA and other molecular markers found that the current connectivity patterns in *Metrocoris sichuanensis* (Hemiptera: Gerridae) were established in the last glacial event and did not change until the present. Despite the interesting results of these techniques, most studies have been conducted using fishes, which limits the extrapolation of these results to other aquatic organisms.

Riverscape genetics is a new and specialized study area that uses landscape genetics applied in river studies, but just as every new approach the methods involved are constantly being discussed and improved. Perhaps, the greatest challenge of RG today is to find a way to incorporate the dendritic spatial arrangement of rivers and the water directional movement on its modeling. Although landscape genetics addresses spatial variables, the dendritic arrangement of rivers induces organisms to exhibit dispersion patterns and connectivity that are dependent on the conformation of water bodies, flow, and physicochemical factors, and approaches that focus on these particularities are needed (Eros and Campbell Grant 2015). These particularities have been studied in seascape genetics studies; however, studies focusing on riverine organisms and other organisms than fishes can help us to establish ecological generalizations.

16.4 Genetic Connectivity in the Study of Aquatic Insects

In aquatic environments, there are several ways to use the dispersive potential of a species to approach connectivity, but knowledge regarding behavior and natural history of the involved species is required to evaluate their dispersal ability (Hughes 2007). For instance, it is known that flight is the major dispersal mechanism of winged insects while larvae and species with fully aquatic adult forms apparently move very little within water streams, resulting in significant genetic differentiation. Despite their limited dispersion, aquatic insects can eventually disperse overland. Boersma and Lytle (2014) reported one of these few events in the water bug *Abedus herberti* (Hemiptera: Belostomatidae), a flightless aquatic insect. They argue that even strictly aquatic insects, can have some level of genetic connectivity, as in drought periods in which these insects are compel to disperse overland. Differently, winged insects can travel through barriers, and some species can travel for distances as long as entire countries.

Differences in flight potential are not necessarily related among taxonomic orders. Among Odonata, for instance, there is a clear difference between the flight capability of anisopterans and zygopterans, where anisopterans, with larger bodies and wings, can fly greater distances than zygopterans, overall. Anderson (2009) and Watts et al. (2004) studied two extreme examples of dispersal ability in these groups. Anderson (2009) used mark-recapture techniques to confirm earlier reports of large-scale transoceanic dispersion in *Pantala flavescens* (Anisoptera), suggesting an incredible flight capability for this dragonfly. Conversely, Watts et al. (2004) used microsatellite markers to study the UK populations of the endangered damselfly *Coenagrion mercuriale* (Zygoptera) and found a fine-scale dispersal with high genetic structure among them, where isolation by distance develops within 10 km. While *P. flavescens* is genetically homogeneous among the continental scales due to its increased flight capacity, *C. mercuriale* has a low dispersive potential compared to other Odonata, even other Zygoptera, due to its lower flight capability and vulnerability to habitat fragmentation. This vulnerability to habitat fragmentation makes its dispersive potential relatively short, not exceeding 1.5–2 km. In addition to the high isolation by distance (IBD) (within 10 km) experienced by *C. mercuriale*, fragmentation effects make its populations more isolated than in natural conditions, increasing the risk of extinction.

Fragmentation effects harm aquatic insects as they can use the terrestrial environments as habitats, mating places, and/or corridors for migration, which allows the maintenance of gene flow among populations or subpopulations. Deforestation and land use negatively affect genetic diversity by creating barriers to dispersal and excluding adult habitats. There is a variety of studies addressing these questions, mostly with headwater-specialized insects. Alexander et al. (2011) studied the mayfly *Ephemerella invaria* (Ephemeroptera) in forested and partially deforested headwater catchments in the Mid-Atlantic Region of the Eastern United States. Using molecular markers, they found a strong negative correlation between genetic diversity and deforestation on first-order catchments. As the deforestation rate increases the genetic diversity of *E. invaria* populations decreases, so intact terrestrial environments are necessary to maintain the connectivity among populations that otherwise would be extinct. Extinction events can be followed by recolonizing events performed by survivors, but even so they may cause genetic diversity reduction by excluding populations that could be a source of genetic variation.

Isolation by distance is an important hypothesis to explain the genetic structuring in many aquatic insects as black flies, damselflies, dragonflies, caddisflies, and mayflies. Studying the Japanese caddisfly *Stenopsyche marmorata* (Trichoptera), Yaegashi et al. (2014) combined microsatellite techniques with empirical field observations of flight behavior and spatial distribution and found a significant IBD in populations separated from each other for more than 33 km. This caddisfly generally disperses along the water flow, probably occurring in both larval and adult stages, but occasionally winged adults can disperse among water catchments.

Interestingly, these researchers observed that the lateral dispersion of *S. marmorata* allows the existence of two distinct lineages, separated in upland (regions upper 250 m a.s.l.) and lowland (< 250 m a.s.l.) lineages. The main difference between them is a voltinism (number of generations per year) adaptation mediated by temperature (as we saw on GEA). Upland lineages experience monthly accumulated temperature (MAT) < 90 °C and exhibit univoltine life cycle (one reproductive event per year), whereas lowland lineages experience MAT > 90 °C and bivoltine life cycle (two reproductive events per year). Thus, besides IBD, these differences in life cycles may reduce the gene flow between *S. marmorata* populations, acting as a reproductive barrier.

Strictly aquatic insects are frequently considered to exhibit high isolation among populations from different streams, considering their low capacity of terrestrial dispersion, but that does not always occur. Miller et al. (2002) studied the dispersive potential and gene flow of *Ambrysus thermarum* (Hemiptera: Naucoridae), which has an exclusive aquatic life cycle. To evaluate its dispersive potential, they positioned traps throughout the stream margins to capture adults during dispersal movements between populations, but they did not find any of them. Hence, they did not expect to find genetic any connectivity among populations, but results showed strong genetic similarity among them. Combining these two results and the fact that seasonal streams were common in the study area, the authors concluded that there are consecutive periods of extinction and recolonization in this ephemeral environment, homogenizing the allele frequencies among populations. When there are consecutive extinctions, the new populations only have as source of genetic variation the few individuals that eventually travel between these populations, explaining the low genetic differentiation observed.

Although Miller's findings concerning *A. thermarum* emerged from recent historical events of seasonal streams, there are cases where the natural factors influencing populations are depicted from much older periods. Using mDNA, Baker et al. (2003) investigated the spatial genetic structure of the caddisfly *Cheumatopsyche* sp. (Trichoptera) in Australian streams. They suggest that *Cheumatopsyche* was isolated in small populations during the Pleistocene, but over time there was an expansion of these populations that increased the dispersion and gene flow between them. The gene flow increase caused the high genetic homogenization observed nowadays in a large geographic scale despite distance between them. Another example is the study carried out by Finn et al. (2007) with the giant water bug *Abedus herberti* in Sky Island, USA. Using mDNA as well, they found that *A. herberti* populations are isolated due to the Pleistocene climatic cycles that suppressed the connections among headwater populations. In addition, the increasing rate of climatic warming in this region accelerated the disappearance of ephemeral streams in which this species lives.

Here, we exposed a few examples illustrating how most researchers approach genetic connectivity to study aquatic insects. Hypotheses as IBD have been used to explain dispersion limitation for several taxa. However, as we have seen, the genetic connectivity patterns of each taxon will depend on life history traits and historical events that affect each environment. In addition to these factors, considering historical processes and the health of adjacent habitats is an effective way to investigate connectivity of aquatic insects.

16.5 Perspectives for the Conservation of Aquatic Insects

The importance of aquatic insects for the maintenance of aquatic and terrestrial systems has been defended for a long time. Aquatic insects contribute to many ecological functions and can admit distinct trophic positions, being filterers, collectors, predators, and others. The disappearance of one of these categories unbalances the whole system, reducing the amount of available oxygen in water, as well as affecting the rate of energy transfer. Aquatic insects transfer energy when predated by fishes and other predators, and the energy flow can even travel from the aquatic system to the terrestrial environment benefiting terrestrial predators such as birds, mammalians, and amphibians. For the maintenance of aquatic insects and their ecological functions, several conservation approaches have been developed, aiming most of the time specific species or environments. As we have seen in this chapter, genetic strategies allied with conservation strategies are helping to clarify connectivity patterns of aquatic insects and raised hypotheses that seek to explain their distribution (Frankham et al. 2012). Some hypotheses can be applied to all aquatic insects, such as IBD, and others can vary according to the environment type and the developmental stage of individuals. Even so, it is time to use this knowledge to guide management policies of aquatic and adjacent environments.

Habitat fragmentation, whether occurring directly in the aquatic environment through dams or in the terrestrial environment through deforestation, is the greatest challenge for aquatic insect conservation (Bunn and Arthington 2002). Studies performed by Fagan (2012), Petersen et al. (2004), Alexander et al. (2011), and others showed evidences of habitat fragmentation effects on genetic structure of aquatic insect populations. Even highly dispersive species may encounter barriers to their dispersion, but undoubtedly the most vulnerable species are those with limited dispersive potential. Some of them form naturally isolated populations, which makes them more susceptible to local extinctions. *C. mercuriale*, a threatened damselfly, can disperse only 10 km, but in a continuous open agricultural land its dispersal is reduced to 1.5–2 km. This scenario is not different for *A. herberti*, a naucorid, where populations are highly isolated by the headwater shortening caused by global warming. Climate change would dry completely the mountain headwaters in which *A. herberti* inhabits, causing not only its local extinction and genetic diversity loss but also of many other aquatic species. These studies may serve as a benchmark to define conservation units and should be considered when the implementation of ecological corridors (they increase connectivity among populations) and environmental restorations are necessary.

A novel approach for conserving aquatic insects is to use certain threatened species with a wide distribution as “umbrella species.” It is common for many governments and society in general to not devote much attention to insect conservation, focusing attention on more charismatic groups such as mammals and birds. However, when we focus on aquatic insects it is possible to relate the preservation and health of these organisms to the quality of water and thus to human health. The main taxa associated to this idea are Ephemeroptera, Plecoptera, and Trichoptera (known as EPT); they are used in many rapid protocols that assess the quality of aquatic environments (Elbrecht et al. 2015). They inhabit headwaters and other aquatic environments relatively undisturbed, and can be used to protect a wide variety of other taxa that depend not only on aquatic habitats, but also on the terrestrial ones.

To conclude, the conservation of aquatic insects directly depends on preserving their aquatic systems, which ultimately depicts the most valuable resource for us humans: the water. Nonetheless, all approaches depend on governmental managements and the creation of policies that minimize the human impacts on these systems. Studies that take into account genetic composition of populations for the establishment and maintenance of genetic diversity sources are necessary for biodiversity conservation. However, anthropogenic issues are beyond the directly observed impacts on aquatic systems. As some studies have shown, global temperature is still rising and wildlife is suffering with a fast environmental change that most species are not able to deal with. Freshwater systems are dependent on the water supply in wet seasons for their persistence; thus changes in rainfall regimes in addition to the exploitation of water tables can impact these environments at large scales, affecting the fauna and human needs. In this scenario, it is essential to optimize the natural resource conservation using modern tools, such as genetic markers allied to large-scale public policies that address the diversity loss problem as a real threat to the human health.

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Chapter 17
Aquatic Insects as a Source for Biomimetics

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Abstract Understanding functional principles of materials, structures, sensors, actuators, locomotion, control systems, behavior of aquatic insects is of major scientific interest. On the other hand, this basic knowledge is also highly relevant for technical applications. One of the greatest challenges for today's engineering science is miniaturization. Insects have solved many problems correlated with extremely small size, during their evolution. Zoologists, entomologists, morphologists, neurobiologists have collected a huge amount of information about the structure and function of such living micromechanical systems. This information can be utilized to mimic them for industrial applications. There are following main technology areas, where aquatic insect's solutions may be applied: (1) materials science and technology, (2) surface science, (3) science of adhesives, (4) optics, (5) photonics, (6) sensorics, and (7) robotics. A few selected examples are discussed in this chapter, but having a great number of described aquatic insect species as a source for inspiration, one may expect a lot more ideas from aquatic insects science for biomimetics.

Keywords Cuticle · Bioinspiration · Biomimetics · Functional morphology · Materials · Surfaces · Insecta

17.1 Introduction

Insects have solved a variety of technical problems in their evolution and have evolved a great variety of shapes and structures. Although often intricate and fragile, they can nonetheless deal with extreme mechanical loads. Many functional solutions in insects are based on a variety of ingenious structural solutions. Elaborate cuticular structures, rich sensory equipment of insects including complex eyes, and various receptors (chemo-, hygro-, thermo-, mechanoreceptors, etc.) taken together

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with a compact brain reveal interesting motion control patterns and remarkable behavioral features (Gorb 2011; Gorb and Gorb 2016). Aquatic insects are not an exception: due to their aquatic or amphibiotic habit, they evolved many particularly interesting functional solutions, which are of special interest for biomimetics.

Understanding functional principles of insect materials, structures, sensors, actuators, locomotion patterns, control systems, and behavior is of major scientific interest, since we can learn about their functional principles and biological role. On the other hand, this knowledge is also highly relevant for technical applications. One of the greatest challenges for today's engineering science is miniaturization. Aquatic insects have solved many problems dealing with their small size and amphibiotic life, during their evolution. Zoologists, entomologists, morphologists, and neurobiologists have collected a huge amount of information about the structure and function of such living micromechanical systems. This information can be utilized to mimic them for diverse technical applications.

The following are the main technological areas, where "insect solutions" may be of interest: (1) materials science and technology, (2) surface science, (3) science of adhesives, (4) optics, (5) photonics, (6) sensorics, and (7) robotics (Fig. 17.1). Possible innovations may also appear on the boundary between aquatic entomology and the areas listed above. Only a few selected examples are discussed in this chapter, but having a huge amount of other described aquatic insect species as a source for inspiration one may expect a lot more ideas for biomimetics (Gorb 2011).

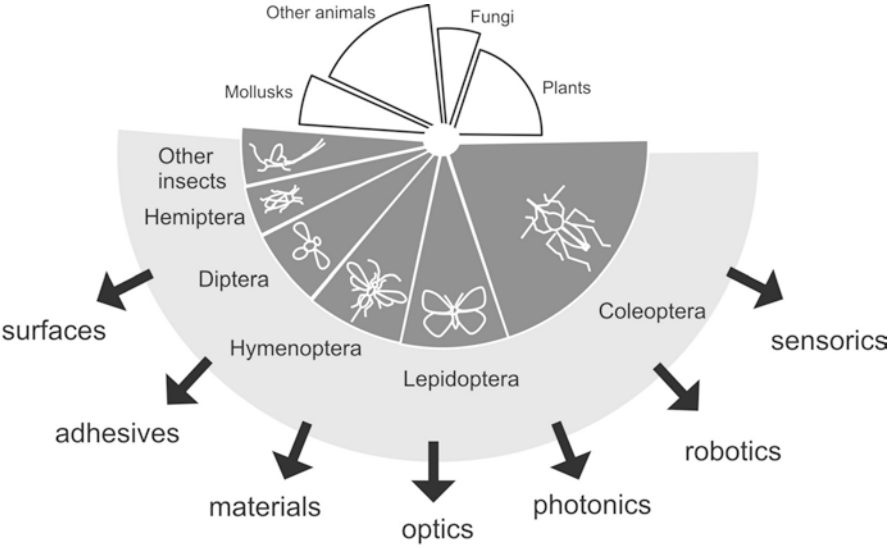

Fig. 17.1 Diagram of insect diversity as a source for biomimetic ideas in various areas of technology (Gorb 2011)

17.2 Materials

The insect exoskeleton is called a cuticle. Being an interface between a living animal and environment, the cuticle of an insect serves many functions. (1) It limits the dimensions of the exoskeleton and is a basis for muscle insertion (mechanical function and locomotion). (2) It is an important element in organism defense against a variety of external factors, such as mechanical stress and dry, wet, cold, or hot environments. (3) It takes part in the transport of diverse epidermal secretions and serves as a chemical reservoir for the storage of metabolic waste products. (4) A variety of cuticular structures are parts of various receptors. (5) The cuticle, its coloration pattern, and chemical components are also important for thermoregulation and are often involved in diverse communication systems. (6) Specialized cuticular protuberances may serve a variety of functions, such as oxygen retention under water, food grinding, and body cleaning (grooming).

Cuticle is a layered composite material (Fig. 17.2a), which consists of two principal components: chitin and protein. Chitin is a structural polymer, found in insects in crystalline form. The structure of chitin molecules and their arrangement are well studied, but the structure of chitin-protein assemblages still remains unknown.

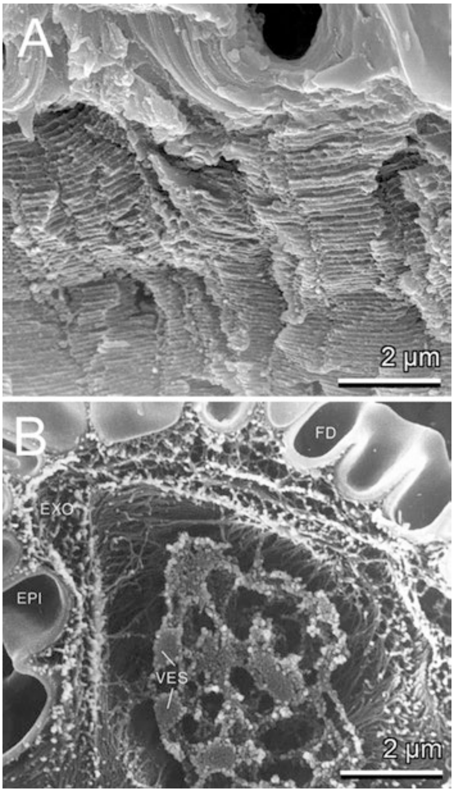

Fig. 17.2 Dragonfly cuticle. (**a**) Fracture through the stiff tanned cuticle of the rear side of the head in the adult dragonfly *Aeshna mixta*, scanning electron microscopy (SEM) (Gorb 2011). Note the layered structure of the exocuticle. (**b**) Neck membrane of the adult damselfly *Ischnura elegans*, SEM (Gorb 2000). Semi-thin Spurr-embedded sections treated with Maxwell's solution, SEM. *EPI* epicuticle, *EXO* exocuticle, *FD* folds, *VES* vesicles

There are three morphs of chitin differing in the molecule packing and polarities of adjacent chains: α-, β-, and γ-chitin (Rudall 1963). The arrangement of molecules usually varies within the different morphs of chitin. All three morphs of chitin are classified as viscoelastic polymers (Hepburn and Chandler 1978). Chitin crystals always occur in insects as bundles of microfibrils of 25–30 Å in diameter. Microfibrils are always associated with protein in a chitin-protein complex. Chitin-bearing cuticular microfibrils have a complex pattern of orientation in the three-dimensional space of the cuticle.

Arthrodial and caterpillar-like cuticles are materials of great flexibility, great extensibility, and reasonable strength. The interaction between chitin fibers and protein matrix is very loose, as has been demonstrated in deformation and fractographic studies. Under tension, these cuticles are visco-plastic and show so-called necking, as do the steel specimens under the same conditions (Hepburn and Chandler 1976). However, there is remarkable variation regarding the extent to which such cuticles can be extended (Vincent and Wood 1972; Vincent and Wegst 2004). There are two types of membranous cuticle organizations found in insects. Highly extensible membranes can extend more than 1000% of their length (Vincent 1981). This cuticle is highly specialized at the molecular level due to its protein composition (Hackman 1975; Hackman and Goldberg 1987). The explanation for such extreme extension ability is the specific alignment of chitin fibers; one can also assume that the protein matrix is not completely bound to the chitin fraction. The second type of membranous cuticle is folding laminated cuticle with a lower degree of extension. This cuticle is found in the neck membranes of dragonflies (Fig. 17.2b) (Gorb 2000).

Resilin is a protein that has its molecular structure in the form of a three-dimensional network of chains having only a few stable cross-links (Andersen 1963, 1964, 1966). These covalent cross-links are fluorescent due to the presence of di- and trityrosine (Andersen and Weis-Fogh 1964). Amino acid composition of resilin from different species is quite similar (Hepburn 1985). Resilin was initially described in the prealar arm and wing-hinge ligaments of the locust *Schistocerca gregaria* and in the pleuro-subalar muscle tendon of the dragonfly *Aeshna grandis*. Meanwhile it has been revealed in different structures of numerous insect species including aquatic dragonfly larvae (Büsse et al. 2017). The resilin-bearing structures usually show recoverable mechanical deformability, so that the resilin-containing cuticle has been called rubberlike cuticle, in contrast to the tanned "solid" cuticle. Resilin can be reversibly extended over 200% of its initial length. Its principal physical properties are its long-range elasticity and lack of either creep or stress relaxation (Weis-Fogh 1960, 1961; Andersen and Weis-Fogh 1964), but Kovalev et al. (2018) recently showed a viscoelastic response of resilin. The resilin-containing structures work as mechanical springs under tension and compression (Rothshild et al. 1975; Frazier et al. 1999; Gorb 2004). Resilin has been revealed in different areas of insect wings (Gorb 1999; Haas et al. 2000a, b; Appel and Gorb 2014), where it presumably prevents material fatigue in folds and promotes wing profile adaptation to aerodynamic situation in flight (Appel et al. 2015; Rajabi et al. 2015, 2016, 2017).

Insect cuticle demonstrates, in different functional systems, a gradient of material properties, which may range from very stiff areas of condyle of joints to membranous areas between leg segments (Gorb 2000). These gradients depend on the fiber density, fiber orientation, polymerization degree of the matrix, and thickness of single layers.

Meanwhile, composite materials are widely spread in various areas of technology. However, the fiber size in technical systems usually remains in the micrometer range and fibers normally have random or preferable orientation within the matrix. Insect cuticle may inspire materials scientists with its helicoidal arrangement of nanofibers in successive layers as it is the case in the exocuticle and with its gradient-like materials properties.

In the last years, many efforts were undertaken to synthesize artificial rubberlike material protein of the cuticle (resilin) (Elvin et al. 2005). There are many areas of potential applications for such a material ranging from medical rubbers to technical sealing systems.

17.3 Surfaces

Aquatic insect surface structures may serve many different functions, such as air retention, food grinding, and body cleaning (Fig. 17.3). Some examples of such surfaces in purely terrestrial and aquatic insects seen in a scanning electron microscope are given in Fig. 17.4.

Because of the structural and chemical complexity of insect surfaces, exact functional principles have been studied for only a few systems. Due to the broad diversity of functions of insect surfaces, inspirations from entomology are currently in focus in a broad range of research topics in engineering sciences: adhesion, friction, wear, lubrication, filtering, sensorics, wetting phenomena, self-cleaning, antifouling,

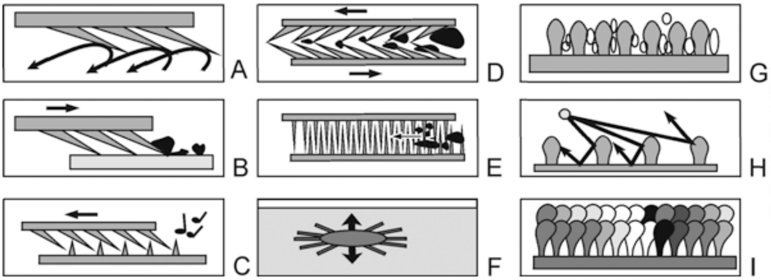

Fig. 17.3 Diagram of functions of cuticular microstructures in aquatic insects. (**a**) Aerodynamically active surfaces in adults. (**b**) Grooming. (**c**) Sound generation. (**d**) Food grinding. (**e**) Filtration devices. (**f**) Hydrodynamically active surfaces. (**g**) Air retention. (**h**) Thermoregulation. (**i**) Body coloration pattern (Gorb 2001, 2011)

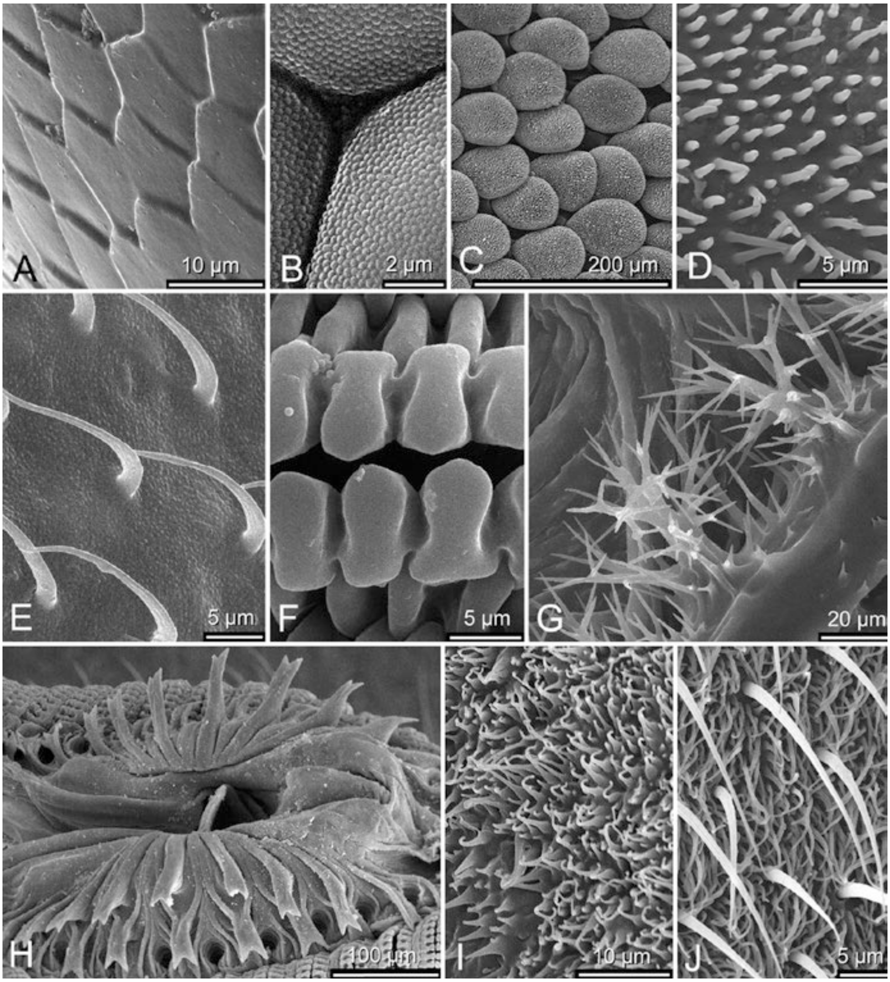

Fig. 17.4 Functional diversity of non-innervated cuticular protuberances in insects, SEM. (**a**) Unspecialized polygonal surface on the tarsus of the scarabaeid beetle *Melolontha melolontha*. (**b**) Ommatidia surface in the calliphorid fly *Calliphora vicina*. (**c**) Scales on the dorsal surface of the elytron in the scarabaeid beetle *Hoplia sp*. (**d**) Same, the surface of a single scale. (**e**) Wing surface in the bibionid dipteran *Bibio ferruginatus*. (**f**) "Pseudotrachea" of the labellum in the *C. vicina*. (**g**) Filter system of the spiracle in the tenebrionid beetle *Tenebrio molitor*. (**h**) Prestomal teeth in the *C. vicina*. (**i**) Plastron in the nepid bug *Ranatra linearis*. (**j**) Air retaining hair coverage in the water strider *Gerris lacustris*

thermoregulation, optics, etc. Since insect surfaces are multifunctional, it makes them even more interesting from the perspective of biomimetics.

One of the challenges in designing moving parts of microelectromechanical devices (MEMS) is the fabrication of joints allowing precise motion of parts about one rotational axis or multiple axes. One problem is the high friction, stiction, and wear rate of joints (Scherge et al. 1999; Komvopoulos 2003). Wear of the interacting surfaces is a consequence of friction, affecting the material's contact points by becoming deformed or being torn away. Friction and wear are strongly correlated processes, by which the points of the surfaces in contact change their topography continuously. Capillary adhesion, due to the presence of a water layer in contact, can account for a great part of the measured friction or lead to the stiction between a contact pair (Scherge et al. 1999). These are critical issues limiting the operational lifetime and negatively influencing the technological potential of MEMS. Conventional methods of lubrication cannot always be used, especially in devices with medical applications. Friction reduction in some man-made mechanical systems is based on the different hardness of elements in contact (Miyoshi 2001; Li et al. 2004), on the use of hydrophobic surfaces, and on applying surface texture, which minimizes the real contact area between two solid surfaces. Ideas from studying surface properties of insect joints, which have stiffer outer layers located on softer ones, specialized microstructure on the contact pair (Fig. 17.5), and particular fiber orientation in the exocuticle, might represent an interesting set of principles towards a solution (Perez Goodwyn and Gorb 2004; Barbakadse et al. 2006).

Aquatic insects move on land, in the air, and in water. The resistance against motion mediated by surrounding media and by mechanical contact with various materials was an evolutionary factor, which contributed to the appearance of many surfaces adapted to reduce such resistance. On the other hand, one always needs friction to generate force, in order to move on a substrate or to overcome the drag caused by friction elsewhere. A living motion system becomes optimized when it is capable of minimizing friction at one end of the system while maximizing it at the other end (Radhakrishnan 1998). In other words, insects, like any other organism, need a combination of maximum friction required for acceleration, deceleration, and maneuvering, combined with minimum friction in joints for economic energy expenditure. Adhesion phenomena can also positively or negatively contribute to the functionality of such a system.

In insect joints working under lower loading forces, but much higher frequencies than vertebrate joints (Wootton and Newman 1979; Gronenberg 1996), the joint surfaces are usually smooth or present a combination of wavy and smooth counterparts (Fig. 17.5a–e). Underlying tissues are penetrated with channels, which are presumably responsible for delivering lubricants into the contact area. The specialized surface structures have been shown to confer friction-reducing properties in insect joints (Perez Goodwyn and Gorb 2004). Technical developments of such contact pairs are realized using laser technology and 3D printing (Vagts et al. 2017, 2018) (Fig. 17.5f, g).

Small bristles, scales, and microtrichia of the wings of flying insects (Bocharova-Messner and Dmitriev 1984) presumably may generate microturbulences around such structures in flight due to building a kind of lubricating layer of air between an airflow and the insect's surface. This could possibly decrease friction during high-speed flight.

Some insect surfaces especially in aquatic species are covered by a superhydrophobic (non-wettable) cuticle, which has an external layer consisting of both cuticle

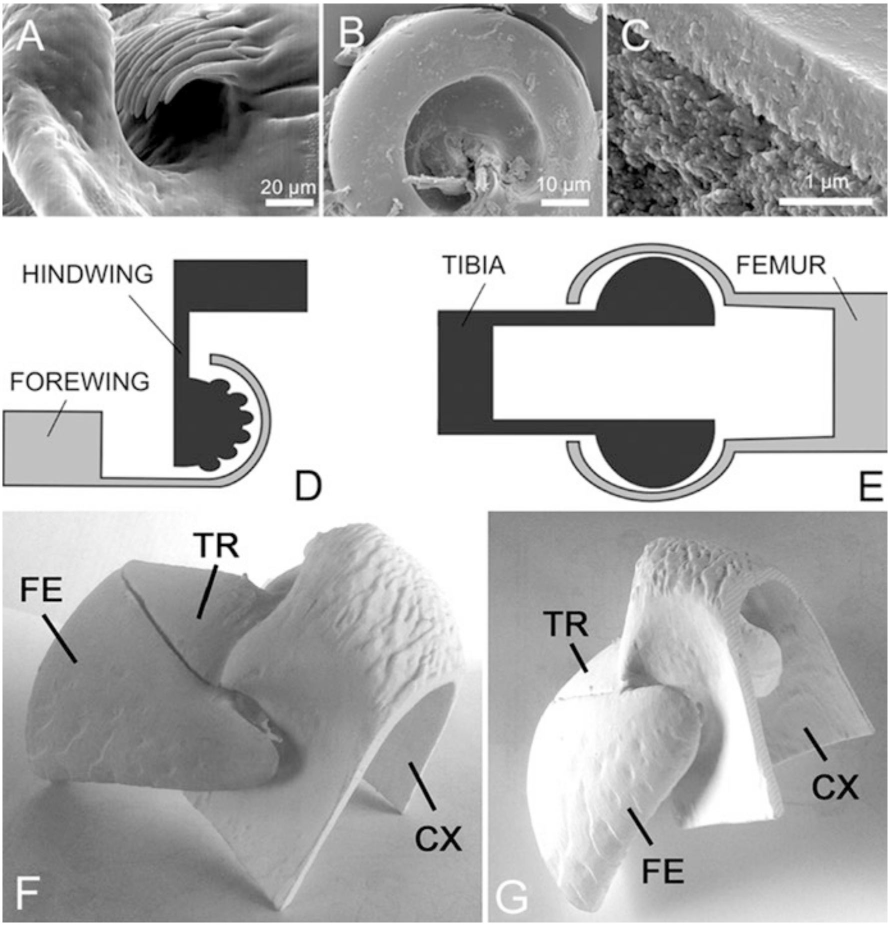

Fig. 17.5 Examples of micro-joints in insects. (**a**) Lateral view of the wing double-wave locking mechanism in the bug *Coreus marginatus* (forewing part), SEM. This joint provides interlocking between both wings on the same body side in the anterior direction allowing them to slide in the medial and lateral directions (Perez Goodwyn and Gorb 2004). (**b**) Medial aspect of the femoro-tibial joint (femoral part) of the leg in the beetle *Melolontha melolontha*, SEM. (**c**) Fracture of the material of the joint in the beetle *M. melolontha*, SEM. (**d**) Diagram of the wing-locking mechanism shown in **a**. (**e**) Diagram of the femorotibial joint shown in **b** and **c**. Constructional and mechanical principles found in such joints can be used to design joints in technical actuators. (**f**, **g**) 3D printed coxo-trochanter-tibial joint of the beetle *Pachnoda marginata* based on the data obtained from the micro-CT scan (Vagts et al. 2017). *CX* coxa, *FE* femur, *TR* trochanter

microstructure and epicuticular waxes. The layer may contain wax projections, with dimensions ranging from hundreds of nanometers to micrometers (Fig. 17.6). The roughness of such surfaces together with their hydrophobic properties decreases wettability, which is reflected in a greater contact angle of water droplets on such surfaces compared to smooth surfaces of the same chemical composition. In some

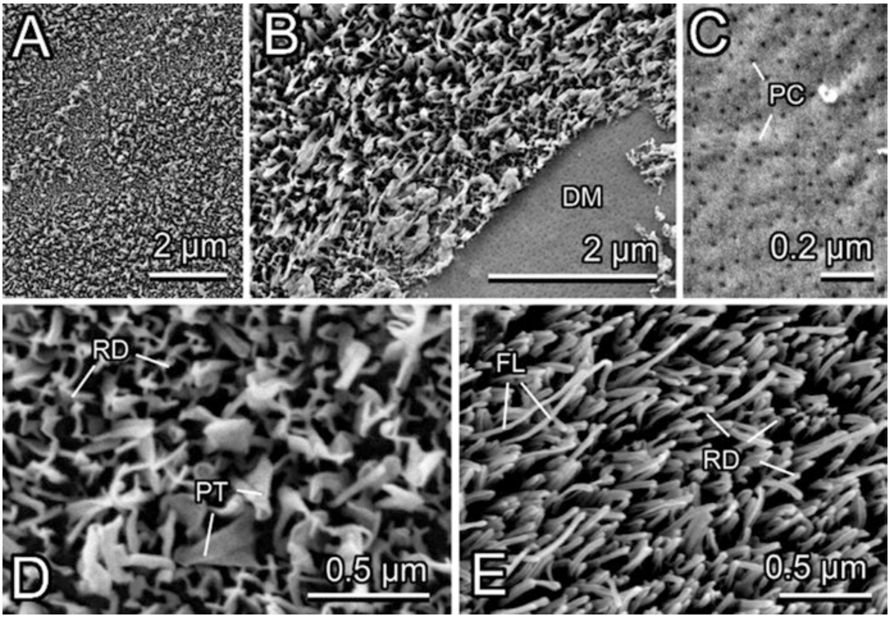

Fig. 17.6 Dorsal wing surface of the adult dragonfly *Calopteryx splendens*, SEM: young mature male surface of wing membrane covered with 3D wax (**a**, **d**, **e**); wing membrane surface with damage (scratches) in wax crystalline layer (**b**, **c**). *DM* damage/scratch, *FL* wax filaments, *PC* porous channels of cuticle, *PT* wax platelets, *RD* wax rods, *WC* wax projections (Gorb et al. 2009)

plant surfaces, this property results in their ability to be cleaned by rolling drops of water (Barthlott and Neinhuis 1997, 1998). Similar insect structures in insects, such as those on wings of representatives of Odonata, Ephemeroptera, and Neuroptera, are extremely non-wettable and self-cleaning (Wagner et al. 1996; Gorb et al. 2009). In addition, these surfaces prevent biofouling under water.

Many aquatic and semiaquatic arthropods have sculptured surfaces involved in holding air underwater for respiration. Such surfaces called plastrons usually contain fields of microtrichia, very small cuticle protuberances (Heckmann 1983). These structures appear convergently in various arthropod taxa, as an adaptation to aquatic environments: Collembola, Lepidoptera, Coleoptera, Heteroptera, Diptera, Araneae, and Diplopoda (Thorpe and Crisp 1947; Hinton 1976; Messner 1988). Some terrestrial insects, such as Aphididae (Auchenorrhyncha), also bear similar structures in the form of bristles, mushroomlike spines, or stigmal plates, which can protect their surfaces from moisture (Heie 1987). In water striders and some spiders, the anti-wetting surfaces of legs and the ventral body side are involved in the locomotion mechanism of walking on water.

Especially interesting are the genera *Halobates* (Gerridae) and *Haloveloides* (Veliidae), the only open seawater dwellers (Perez Goodwyn 2009). Representatives from the genus *Halobates* have outstanding water protection structures. The microtrichia pile is composed of specialized prolongations. Each microtrichium has a

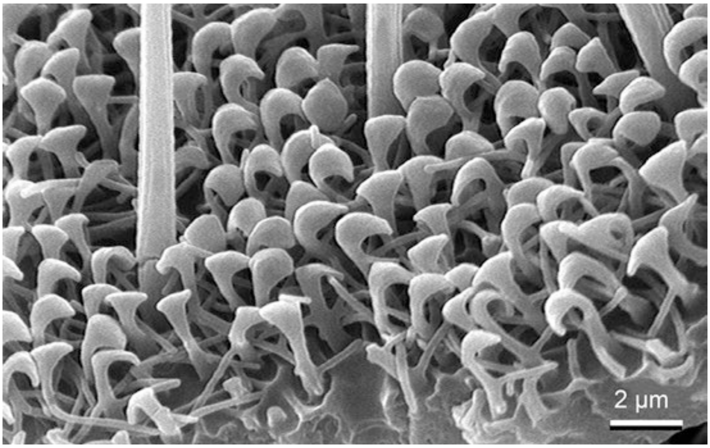

Fig. 17.7 Thoracic microtrichia cover of *Halobates germanicus* (Gerridae), SEM. Note golf club-shaped heads and interlocking extensions between shafts (Perez Goodwyn 2009)

thickened head, which is several times wider than the shaft and usually tilted to one side like in a golf club (Fig. 17.7). On the shaft itself, there are up to four perpendicular branches interlocking the microtrichia, the shafts of which are 0.8–1.1 μm apart. This structure provides effective water protection in case of being submerged, a frequent situation in the open sea (Perez Goodwyn 2009).

Highly specialized areas of cuticle, responsible for sound generation, usually consist of patterns of cuticular plates, seldom of microtrichia fields (Hinton 1970). When these surfaces slide over each other, sound is generated. Such structures have been previously described from elytra, abdomina, and coxae in phylogenetically distantly related arthropod taxa, including bugs Cimicomorpha, Pentatomomorpha, and beetles (Gogala 1984; Palestrini et al. 1987). The sound frequency corresponds to the periodicity of these structures contacting functionally corresponding surfaces and to the speed of sliding. These systems should be, in addition, wear resistant. However, rigorous experiments supporting or rejecting this statement are absent in the literature.

Filtration systems are usually equipped with long bristles. Such systems are well known from mouthparts of aquatic insect larvae. The filtering system of insect spiracles that keeps the tracheae free of dirt particles is composed of branched acanthae. However, in some cases, completely different principles may be involved in the functioning of these systems. The labellum of many dipterans bears so-called pseudotracheae (Gracham-Smith 1930; Elzinga and Broce 1986) whose outgrowths have a complex material structure. Labellum and pseudotracheae are driven by muscles, resilin springs, and hydraulic pressure, enabling a change in the diameter of the filtration sieve, depending on the size of the particles in the food.

Functional surfaces in technical systems have many functional requirements, which can be fulfilled by using principles learned from biology. Figure 17.8 lists reported activities on the implementation of biologically inspired microstructure

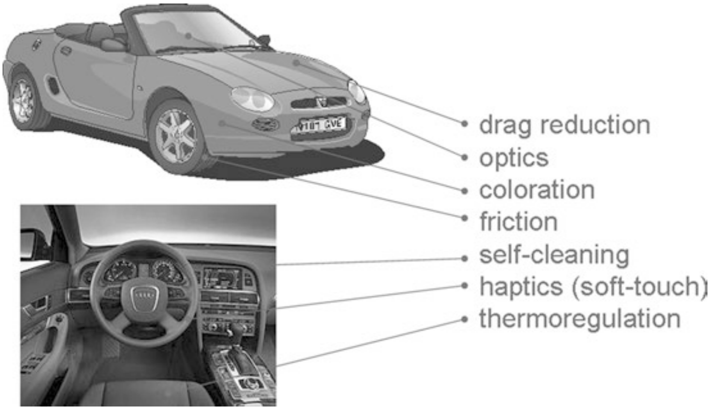

Fig. 17.8 An example from the car industry that applies functional surfaces, where microstructure development uses ideas from biological studies on insects and some other organisms

into product design. Since insects bear a huge variety of such microstructures, many of which have not even been previously described, a systematic approach to insect surface science would be very desirable. The important step in this direction is establishing a database of insect functional surfaces. Furthermore, we need more experimental studies, targeted to answering the relationship between structure at various levels of organization and its function. We believe that enhancing the pool of new ideas from biology will provide a leap in the surface technology of tomorrow.

17.4 Attachment Devices

There is a variety of specialized biological systems that prevent separation of two surfaces. These systems are often called *attachment devices* (Gorb 2001). Some of them are based entirely on mechanical principles, while others additionally rely on the chemistry of polymers and colloids (Scherge and Gorb 2001; Habenicht 2002). There are at least three reasons for using adhesives in biology and in the industry as well: (1) they join dissimilar materials; (2) they improve stress distribution within the joint; and (3) they increase design flexibility (Waite 1983). These reasons are relevant both to the evolution of natural attachment systems and to the design of man-made joining materials.

In general, adhesive-bond formation consists of two phases: contact formation and generation of intrinsic adhesion forces across the joint (Naldrett 1992). The action of the adhesive can be supported by mechanical interlocking between irregularities of the surfaces in contact. Increased surface roughness usually results in an increased strength of the adhesive joint in the glue-based systems due to the increased contact area between the contacting surfaces and the solidified adhesive substance. Strong adhesion is also possible between two ideally smooth surfaces. Adhesive organs, which may be used for attachment to substrates as well as for catching prey, demonstrate a huge diversity among insects due to their structural and chemical properties. Biological adhesion underlies the organization of all living tissues. There is no doubt that many functional solutions have evolved independently in different insect lineages.

Many species of insects are supplied with diverse attachment devices, the morphology depending on the species' biology and particular function, in which the attachment device is involved. The evolutionary background and animal behavior influence the specific composition of attachment systems in each particular species. There are eight fundamental classes of attachment principles found in insects: (1) hooks, (2) lock or snap, (3) clamp, (4) spacer, (5) suction, (6) expansion anchor, (7) adhesive secretions (glue), and (8) friction (Gorb 2001). However, different combinations of these principles also occur in existing attachment structures. Three types of adhesion at the organism level are known: (1) temporary adhesion allowing an organism to attach strongly to the substrate and detach quickly when necessary (see the subsection below about locomotory attachment devices); (2) transitory adhesion permitting simultaneous attachment and movement along the substrate; (3) permanent adhesion involving the secretion of cement. These three types of adhesion do not have the same purpose and use different adhesive systems.

Walking machines usually use suckers to hold onto vertical and overhanging surfaces. A primary disadvantage of this attachment principle is that a very smooth substrate surface is required. A future goal is walking robots capable of walking on a variety of surfaces. Insects can walk rather well on smooth and structured substrata, on inclines, vertical surfaces, and some of them even on the ceiling. One such example is the hairy surface of legs in flies and beetles. This system uses a secretion enabling hairs to attach and detach very quickly to diverse substrata. The hair structure includes a mechanism that delivers the secretion, in extremely small amounts, directly to the contact area (Ishii 1987), and only then, when contact to the substrate is achieved.

Generally, in their evolution, insects have developed two distinctly different mechanisms to attach themselves to a variety of substrates: with smooth pads or with setose/hairy surfaces. Due to the flexibility of the material of the attachment structures, both mechanisms can maximize the possible contact area with the substrate, regardless of their microsculpture. Tenant setae are relatively soft structures (Niederegger et al. 2002). In *Calliphora* flies, their tips are usually compressed, widened, and bent at an angle of about 60° to the hair shaft (Bauchhenss and Renner 1977). Some male beetles possess mushroomlike terminal tips of setae (Fig. 17.9a).

Different forces may contribute to the resulting attachment force: capillary adhesion and intermolecular van der Waals forces. A contribution of intermolecular interaction to the overall adhesion has been shown in experiments on the adherence of beetles (Stork 1980) and beetle setae (Stork 1983) on a glass surface. The presence of claws, decrease of air pressure, decrease of relative humidity, or electrostatic forces do not influence beetle attachment on smooth substrata. In the terrestrial chrysomelid beetles, the resulting attachment force directly depends on the number

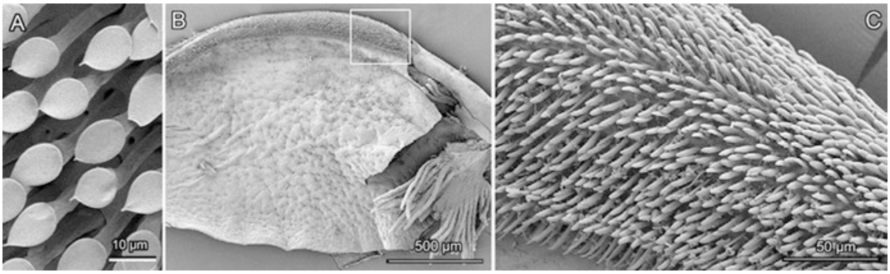

Fig. 17.9 Insect attachment devices, SEM. (**a**) Ventral surface of the tarsus in the male of the terrestrial beetle *Gastrophysa viridula* (Gorb et al. 2007). (**b**, **c**) Underwater attachment structures on the ventral surface of the gills of the mayfly larva *Epeorus assimillis* (Ditsche-Kuru et al. 2010): overview of a whole-gill lamella (**b**); antero-proximal part of the pad (**c**)

of single hairs contacting the surface. The contribution of intermolecular interaction and capillary force has been demonstrated for the fly *Calliphora vicina* in a nanoscale experiment using an atomic force microscope (Langer et al. 2004). Attachment forces increase when the contacting surfaces slide against each other. This may explain why flies placed on a smooth undersurface always move their legs in a lateral-medial direction (Wigglesworth 1987; Niederegger and Gorb 2003). During these movements, setae slide over the surface in order to obtain optimal contact.

The size of single points in hairy attachment devices gets smaller and their density higher as the body mass of the animal group increases (Scherge and Gorb 2001; Arzt et al. 2003). The fundamental importance of contact splitting for adhesion on smooth and rough substrata has been explained by a very small effective elastic modulus of the fiber array (Persson 2003). Adhesion enhancement by division of the contact has also been demonstrated experimentally (Peressadko and Gorb 2004; Gorb et al. 2007). An additional advantage of patterned surfaces is the reliability of contact on various surface profiles and the increased defect tolerance of individual contacts.

In aquatic insects, hairy attachment surface has been observed on the ventral surface of the abdominal gills of the mayfly larvae (Ditsche-Kuru et al. 2010) (Fig. 17.9b, c). These microstructures evolved independently from the leg adhesive pads mentioned above and adhere not only to the smooth stone surfaces, but also to those covered with biofilms.

Hairy leg attachment pads are promising candidates for biomimetics of robot soles adapted for locomotion. Similar principles can be applied to the design of microgripper mechanisms with an ability to adapt to a variety of surface profiles (see paragraph *Robotics* in this chapter). There are very interesting insect adhesive systems combining microstructure and glue, such as the mouthpart apparatus used by rove beetles (genus *Stenus*) to trap the animals they feed on (Betz et al. 2009). The beetles' extended, rod-shaped lower lips have two sticky pads and shoot out like a catapult to capture potential prey (Fig. 17.10a, b). It seems that the adhesive function is based not only on the subdivision of the contact area into many smaller

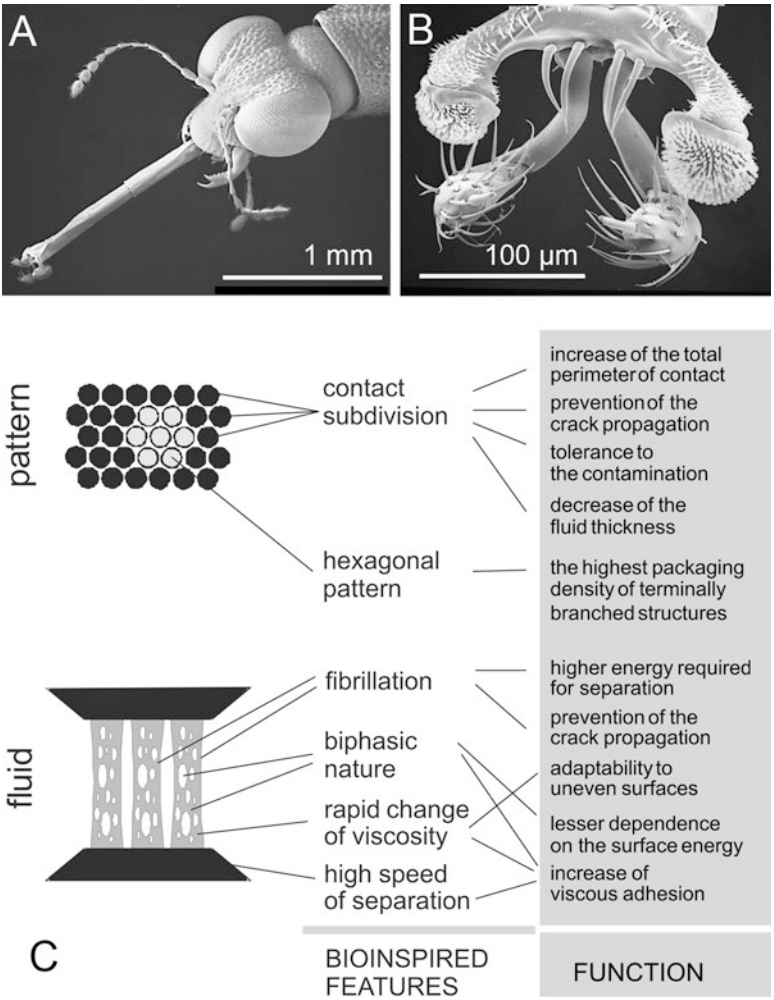

Fig. 17.10 The adhesive capture apparatus of the rove beetle *Stenus comma*. (**a**) SEM image of the head with the protruding lower lip (labium). (**b**) SEM image of the tip of the labium with adhesive pads. (**c**) Summary of the functional principles with biomimetic potential in the system under investigation (Betz et al. 2009)

ones, but also on very special features of the beetle glue itself: (a) fibrillation at the surfaces' separation (energy dissipation mechanism and crack propagation-preventing mechanism), (b) biphasic nature of the glue (universal wettability mechanism), and (c) rapid change of its viscosity (viscose force adhesion mechanism).

The industry of adhesives is presently following three main goals (Hennemann 2000): (1) an increase in the reliability of glued contact; (2) mimicking of natural, environment-friendly glues; and (3) development of mechanisms for application of a minute amount of glue to the surface. An additional challenge is the use of substances and/or mechanisms that allow multiple attachments and detachments and enable attachment to a variety of surfaces. This section clearly demonstrates the strong potential of insect adhesives for inspiring development of technical adhesives that fulfill the listed requirements.

17.5 Optics

Ommatidial gratings are antireflective structures on the eyes of insects, especially those which are nocturnally active (Fig. 17.11). These protuberances are very small (200 nm in diameter) and increase visual efficiency through decreased surface reflection in their density and increased photon capture for a given stimulus condition (Parker et al. 1998; Vukusic and Sambles 2003).

Such a grating is particularly useful on a curved corneal surface, since it increases the transmission of incident light through the cornea compared with a smooth surface. For an increase in transmission and reduced reflection, a continuous matching of the refractive indexes at the boundary of both adjacent materials is very critical. If the periodicity of the grating is smaller than the wavelength of transmitting light, only light of zero order can be reflected or transmitted. For a constant ratio of both materials (cuticle-air) at the boundary between media, the electromagnetic field strength of incoming light is nearly constant (Bernhard et al. 1965). This region, therefore, can be considered as homogenous and an effective refractive index can be given.

Grooming is a very important function for insects that sometimes live in extremely dirty or dusty environments. Their rich sensory equipment of eyes and antennae has to be kept clean in order to respond adequately to external signals. Many insects bear specialized cleaning structures (Schönitzer and Lawitzky 1987;

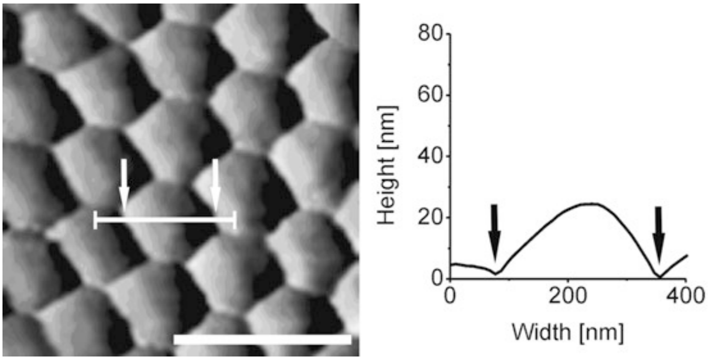

Fig. 17.11 Atomic force microscopic (AFM) error channel image (left) and profile (right) of ommatidia of the moth *Laothoe populi*. White bar marks the region used for measurements of surface profile. The grating borders indicated by arrows in the left picture correspond to the arrows shown in the surface profile diagrams. Scale bar = 500 nm (Peisker and Gorb 2010)

Francouer and Loiselle 1988). Others rely on the micro- and nanostructured surfaces with an antiadhesive function. Ommatidia gratings are a multifunctional surface that employs self-cleaning due to the real contact surface reduction mechanism (Peisker and Gorb 2010).

17.6 Structural Coloration

Structural coloration due to the presence of scales and bristles is well known in insects, such as butterflies (Grodnicky 1988; Ghiradella 1989) and beetles (Schultz and Hadley 1987). For example, scales of some scarabaeid beetles bear additional microtrichia on their surfaces responsible for lusterless appearance of the elytra surface. Scales of some curculionid beetles contain photonic crystals inside (Fig. 17.12). The coloration pattern serves for species and sex recognition, and also for camouflage and mimicry. The most interesting type of structural coloration is called iridescence, which is well known in many insect species (Ghiradella et al. 1972; Huxley 1975).

The iridescence is a result of optical interference within multilayer structures (Ghiradella 1991) that are rather complex in their architecture, and may be incorporated into systems that can produce several different optical effects. Such effects include diffraction-assisted reflection angle broadening (Vukusic et al. 1999, 2000a), all-structural color mixing, and strong polarization effects (Vukusic et al. 2000b).

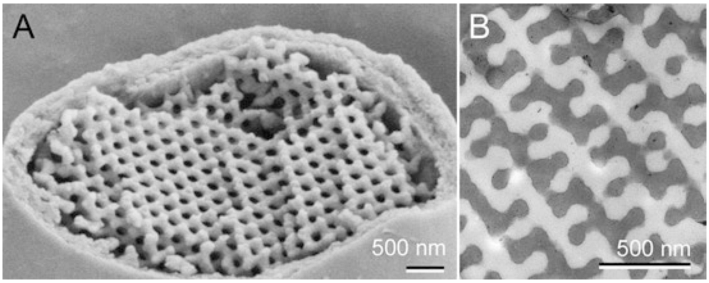

Fig. 17.12 Photonic crystals of the dorsal scalelike hairs in the curculionid beetle *Phyllobius argentatus.* (**a**) SEM micrograph of the cross fracture through the scale. (**b**) Transmission electron microscopy (TEM) micrograph of the oblique ultrathin section of the scale

17.7 Sensorics

Insects carry out flow sensing in various contexts using mechanosensory hairs (Gnatzy and Heusslein 1986) (Fig. 17.13a). The wide variety in hair length and number in insects can be partly explained by the physics of the medium and its interactions with the hair (Humphrey et al. 1993, 2003). For example, filiform hairs provide crickets with a highly sensitive receptor system capable of differentiating air-particle movements in the low-frequency range due to their diverse combinations of directional selectivity, sensitivity, and frequency response.

Crickets also possess composite mechanoreceptors. For example, the coupling of filiform hairs with campaniform sensilla creates a mechanoreceptor with an extended working range (Heusslein et al. 2009). In addition, the composite mechanoreceptor serves as a tactile receptor system superior in its spatial detection range.

The arrangement of hairs also has important sensory effects (Casas and Dangles 2010). The spatially heterogeneous information provided by a transverse flow around a cylinder implies that hairs should be placed all around a cylinder, maximizing the chances to perceive a source coming from any angle (Steinmann et al. 2006). Cricket airflow sensors have recently been a source of inspiration for building artificial airflow sensors (Dijkstra et al. 2005). Design guidelines for building flow-sensing MEMS arrays were also based on biomimetic ideas from studies on the cricket's cerci. A spatial arrangement of MEMS hairs with a large range of angles relative to flow direction on a dedicated platform increases the sensitivity of such sensors. Such design could represent a major advance to the actual mounting of MEMS hairs on a horizontal plate. This is, however, not a trivial task in MEMS fabrication.

In aquatic bugs *Notonecta* (Fig. 17.13b), the superhydrophobic hair coverage keeps stable air layer between the hairs and by this generates a water-layer interface at the body. Vibrations caused by predators or prey can be captured by this interface and effect in deformations in the regions of hair sockets and be further transmitted to the mechanosensory neurons (Mail et al. 2018). Recently, this mechanosensor inspired development of biomimetic sensory device for pressure and flow sensing in underwater applications.

17.8 Robotics

Insect-inspired robotics has strongly developed in the last two decades. Because insects are structurally and functionally complex, a complete technical copy of an animal in hardware and software is not possible (Delcomyn 2004, 2007). There are two different opinions on this matter. Some researchers suggest that as many features of an animal as possible should be incorporated into a robot (Ritzmann et al. 2000, 2004). Other researchers argue that including too many animal-like features into a robot can even impair performance (Yoneda and Ota 2003). Which features of

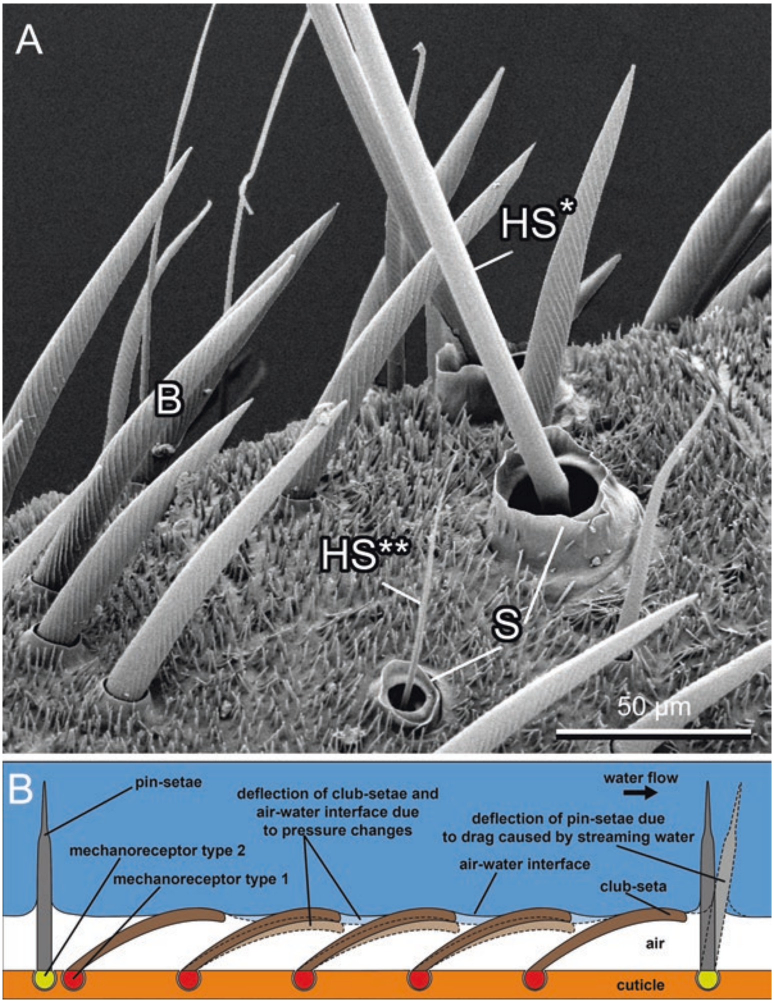

Fig. 17.13 Insect mechanosensors. (**a**) SEM of cercal filiform hairs and campaniform sensilla of the cricket *Gryllus bimaculatus.* Cercus surface showing a filiform hair with a long hair shaft (*HS**) inserted in a large cuticular socket (*S*) and a filiform hair with a very short hair shaft (*HS***) inserted in a small socket (*S*) (Heusslein et al. 2009). (**b**) Proposed *Notonecta* forewing surface function (Mail et al. 2018). An air layer is kept in between the setae. The club setae (dark brown) support the air–water interface. If pressure increases, the air is compressed and the air–water interface is deformed. This deflects the seta (light brown, dashed outline). Mechanoreceptors (red) connected with the cuticle (orange) at the base of each seta should enable monitoring of the setal deflection. The pins (dark gray) most likely penetrate the air–water interface. If so they should be deflected (light gray, dashed outline) by water flow. This deflection most likely is sensed by cuticular mechanoreceptors (yellow). *B* bristles

insects and which aspects of their locomotion are really important for implementation into robot design?

One significant contribution to insect-inspired robotics can be search for nonconventional ways to move parts of the body, for example due to specialized joints, springs, and latches. Work is already in progress on a variety of novel actuators, such as electro-elastomers (Pei et al. 2003) and ionic polymeric-conductor composites (Shahinpoor 2003). Another contribution is the understanding and technical implementation of the concept of the dynamic stability allowing insects to move on land, in the air, or underwater with high speed and to be able to perform strong maneuverability. Especially challenging is locomotion on the wall and ceiling (Daltorio et al. 2005a, b, 2007, 2009). Generally, an incorporation of biomechanical principles into robots has recently contributed to the better performance of these robots (Altendorfer et al. 2001; Witte et al. 2004). The sensory feedback is critical to a fully functional, agile walking robot (Schmitz et al. 2001). This is the least developed area of bioinspired robotics. The reason is that it is difficult to make small and light but effective artificial sensors. Finally, central control of early robots must be changed to more distributed control that is typical for biological systems including insects (Delcomyn 1999; Thor et al. 2018).

Figure 17.14 shows some implementations of insect-based research into robotic systems. Many labs worldwide have designed hexapod robots, but probably the most elaborate ones originate from the Quinn Lab at Case Western Reserve University (Cleveland, USA) (Fig. 17.14a, b). The Prolero, RHex, and Whegs™ series robots utilize a method of locomotion that combines the advantages of wheels and legs (wheel-legs). Wheels are relatively simple and allow a vehicle to move over terrain quickly. Legs allow robots to run on a plain surface, to climb obstacles that are higher than what a wheeled vehicle would be able to climb over, and even to swim. These robots can be equipped with adhesive materials that make them capable of climbing up a glass wall (Fig. 17.14c, d). Structural data on cockroach legs (Frazier et al. 1999) were used to machine insect legs from aluminum blanks, in order to mimic chain-like tarsi capable of optimal grip with various kinds of terrain (Fig. 17.14f, g). In the future, mechanical design of such machines will rely on 3D printing and other additive manufacturing methods (Fig. 17.5f, g). This in turn will allow use of (1) exoskeletons, (2) complex lightweight constructions, and (3) composite materials consisting of different materials and representing sandwiches or lattices at different scales (from macro- and micro- down to the nanoscale). Moreover, using this kind of manufacturing technology may enable direct mimicking of insect constructions obtained through the microcomputed tomography from real insects.

Caterpillar-like locomotion that basically consists of two grippers in the anterior and posterior parts of the body and a set of muscles in between allowing body bending has inspired design of the InspiRatnik robot (Fig. 17.14e). It was recently tested by the company TETRA GmbH (Ilmenau, Germany) for the applications in the 3D environment, such as set of cables or pipes.

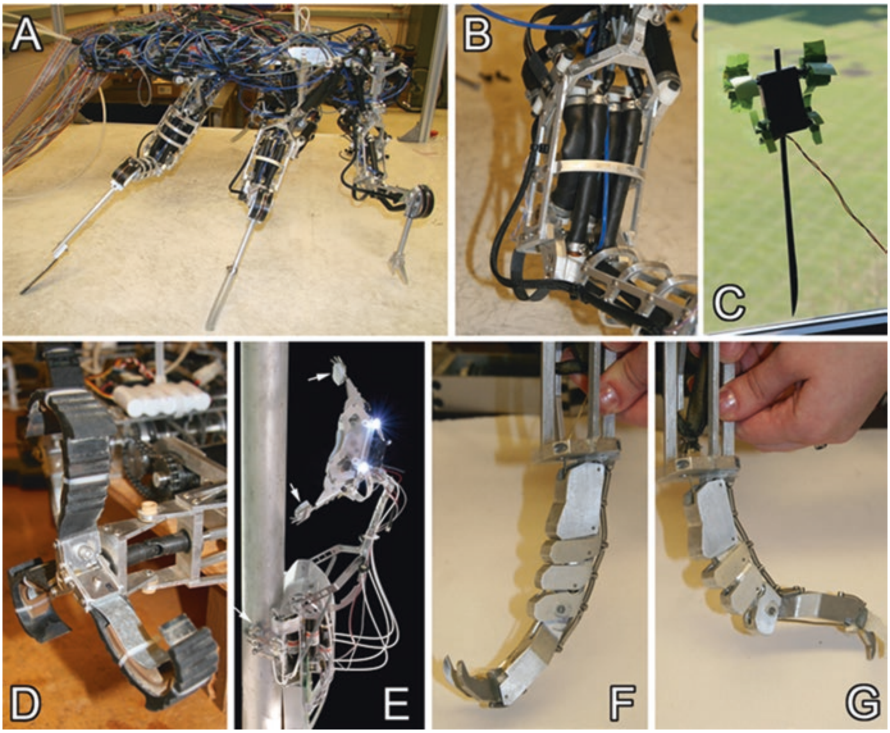

Fig. 17.14 Some examples of insect-inspired robots. (**a**, **b**) Robot with a hexapod kinematics based on studies of the cockroach performed in the Ritzmann Lab in the Biology Department at Case Western Reserve University (CWRU, Cleveland, USA). It has a total of 24° of freedom with five for each front leg, four for the middle legs, and three for the rear legs. (**c**) Climbing Mini-Whegs™ scales vertical glass surfaces using compliant, adhesive feet (Daltorio et al. 2005a, b, 2007, 2009). Like all Mini-Whegs™ robots, it has one drive motor that turns all four wheel-legs in an alternating diagonal gait. (**d**) Legs of the typical Whegs™ robot. (**e**) InspiRatnik robot based on the principle of locomotion of geometrid caterpillars. (**f**, **g**) Gripping leg of the robot based on the inspiration from an insect tarsus. (**a**–**d**, **f**, **g**) Robots built in the Quinn Lab (CWRU, Cleveland, USA). (**e**) Robot built by TETRA GmbH (Ilmenau, Germany)

17.9 Future Perspectives

What can be done to advance the field of insect-inspired biomimetics? First and obviously, additional research on insects will help, not just in the application of biological knowledge to engineering problems, but on the biological systems themselves. Incorporating more biological knowledge into the design of artificial systems will improve their performance, but the fact of the matter is that biologists still do not have a complete understanding of how insect materials are constructed, what their performance is in different situations, how insect locomotion is generated, controlled, regulated, etc. Hence, many technological areas will benefit from additional entomological research.

Additionally, a huge variety of insects and their systems have not been previously studied at all. That is why screening for new interesting systems seems to remain an extremely important research field in the nearest future.

Only few examples of bioinspired systems were tested in order to compare their performance with that of conventional systems or their biological prototypes. The field of biomimetics in general would benefit greatly from the development of a set of standard tests that can be used to evaluate the performance of bioinspired materials and systems. The ultimate objective of biomimetics will be to improve the performance of biologically inspired systems in the real world. Then, it appears to be essential that these systems have to be subjected to real tests of performance. Clearly, the kind of tests will vary from system to system and be different for systems that have different performance objectives.

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