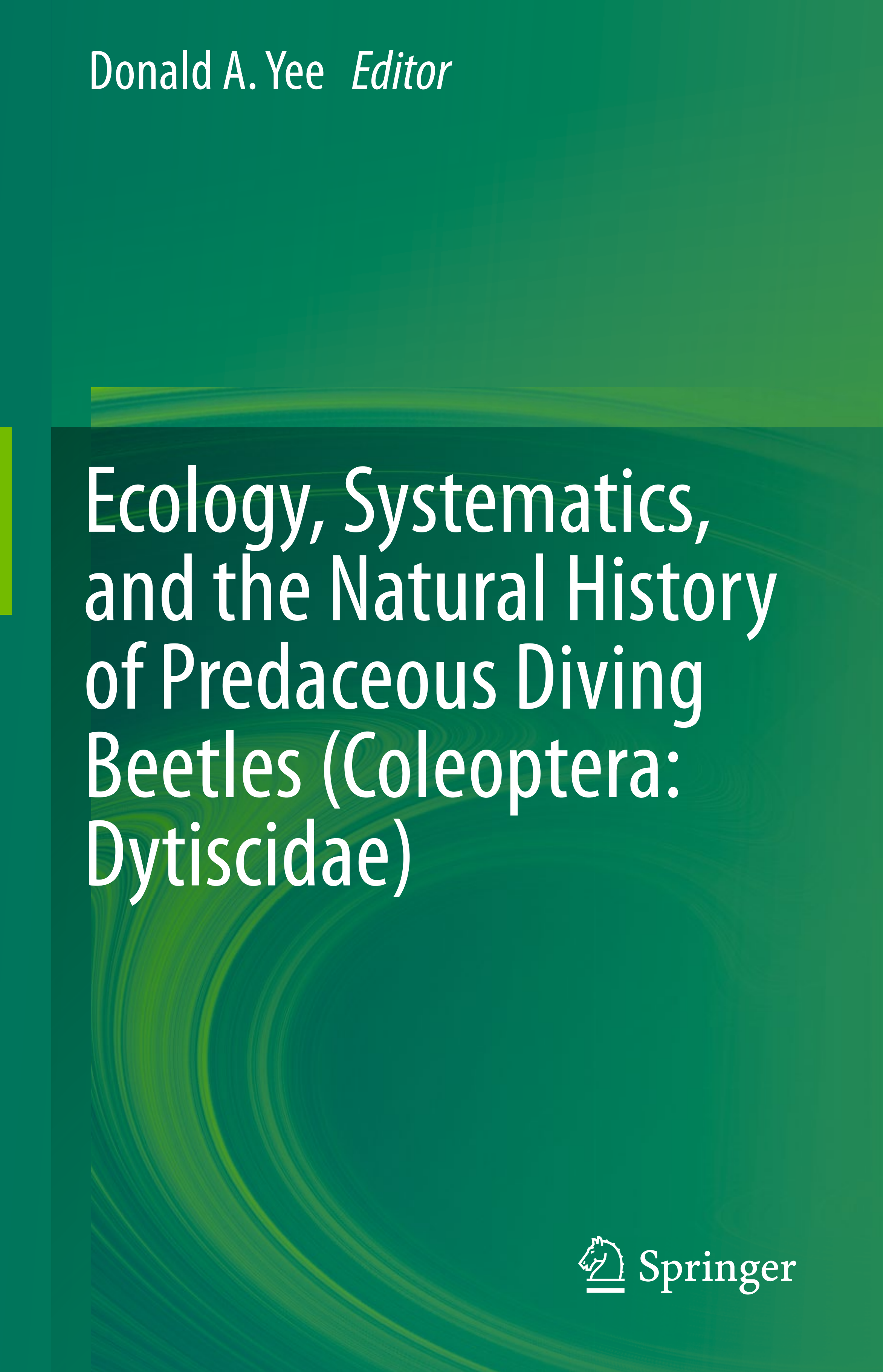
Donald A. Yee *Editor*

Ecology, Systematics, and the Natural History of Predaceous Diving Beetles (Coleoptera: Dytiscidae)



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To Addie, Sebastian, and Ginny
The life so short, the craft so long to learn

Foreword

Books on Diving Beetles

The first multiauthored book restricted to predaceous diving beetles was probably the two-volume set on *Dytiscus* edited by Eugen Korschelt (1858–1946) in 1923 and 1924, and based on research carried out at the German University of Marburg (Korschelt 1923–1924). At the time, anatomy and development were both central topics, which can be seen from the contents of these volumes. More than 60 years later, proceedings from international conferences on predaceous diving beetles and other hydradephagan families started being published regularly as special issues of various scientific journals, including the volumes edited by Wolfe and Roughley (1985), Brancucci and Dettner (1986), and Roughley and Aiken (1990). In spite of the wide variety of topics being dealt with, the main focus of scientific investigations had shifted from the biology of this group to taxonomy and phylogenetics.

In contrast to its predecessors, the volume you now are reading has a more balanced content, presenting up-to-date reviews of, as well as new findings on, predaceous diving beetle biology in most major fields where these fascinating organisms play a major part. In spite of the organism-focus of the new volume, dealing exclusively with various aspects of predaceous diving beetles, i.e., the adephagan family Dytiscidae, it covers many different levels or organization, from molecules (Chap. 6) to community ecology (Chap. 10). The organismic focus of the current book may serve as a valuable counterweight to the ongoing polarization of modern biology favouring more general research in molecular biology or ecology with a wide taxonomic scope. A focus on dytiscids fits my own research profile, so, of outmost modernity or not, I think producing this book is a great thing to do. It is my hope that it will get the status of a standard work within its subject and reach a wide dissemination.

Why Predaceous Diving Beetles?

Diving beetles provide a multidimensional node for different aspects of biology (Chap. 1). As a family of Adephaga they are tightly connected with carabids, and surely the carabidologists have provided some valuable inspiration for us over the years. The fact that dytiscids, in contrast to most other insects, have an adult stage that is truly aquatic has stimulated studies on their unique form and function (Chap. 4). Being aquatic predators, the study of dytiscids connects with aquatic ecology (Chap. 7) and predator–prey studies (Chap. 8). In more evolutionary oriented studies, diving beetles have found a central position especially in studies of sexual conflict (Chap. 5) and migration (Chap. 9). Clearly, diving beetles are more than simple food for fishes and today provide valuable tools for conservation of all kinds of wetlands, a point made clear by Garth Foster in Chap. 11 focusing on conservation aspects.

From Local to Global

I published my first papers on diving beetles in 1978, more than a quarter of a century ago. As often was the case for an entomology rookie, the topic was local faunistics. My fellow ecologists did find faunistics trivial and deprived of theoretical aspects, and wondered how I could allocate valuable research time to such low-life activities. When I later produced an atlas of Swedish diving beetles (Nilsson and Persson 1989), the national interest was so low it had to be published in Switzerland, made possible by the late Michel Brancucci. But that was long before the red-listing business emerged and European governments started to provide support for faunistics via online databases and funding programs (support was available at least for studies of the rarer native, and supposedly most threatened species like *Dytiscus latissimus*).

I have recently donated my collection of dytiscids to the Swedish Museum of Natural History (http://www.nrm.se/), restricting my beetle activities nowadays chiefly to keeping the world catalogue updated. Having achieved a taste for compiling long lists of information, I ended up producing the Dytiscidae parts of the *Catalogue of Palaearctic Coleoptera* edited by Ivan Löbl and Aleš Smetana (Nilsson 2003), the online database *Fauna Europaea*, and the world catalogue of insects (Nilsson 2001). Whereas producing such lists is one thing, keeping them updated is another. After producing a number of annual updates of the Dytiscidae chapter of the palaearctic catalogue, I am now glad that Jiří Hájek has taken over this task (Nilsson and Hájek 2014).

In the age of biodiversity informatics, creating online predaceous diving beetle catalogs compiling national, and when appropriate regional, records for each of the major zoogeographic regions seems achievable. As some coordination seems beneficial, a network including at least one responsible cataloger for each region should be formed. One could argue that such efforts are no longer necessary as this information is already available from global databases like *GBIF*. Still, we need the quality check to get rid of records based on misidentifications and keeping account of the many interesting records that were never entered into the common data sources.

Electronic communication at high speed and more global access to information sources have no doubt levelled out the divergent regional traditions that was such a burden of the old times, providing a hindrance to a universal nomenclature and classification. The concept of e-taxonomy for sure carries a great potential for effective cooperation in providing taxonomic structure beneficial for all. Here the wiki-concept is attractive and is being realized in projects like *WikiSpecies* and *Species-ID*. Once it is more widely used, the more official registers of *ZooBank* will also play a major role in creating a unified taxonomy. The main discussions connected to the development of these platforms include how best to control access to avoid the expression of unqualified opinions and how voluntariness can be combined with full coverage of species information.

World Catalogue Data

The world catalogue of Dytiscidae was generated from an underlying ACCESS taxonomic database constructed by myself (Nilsson 2001). Besides the information given in the catalog, the database now includes body length ranges of each species and latitude plus longitude of each type locality. Information from this database was first used by Joel K. Hallan, then at the Texas A & M University, for his website *Synopsis of the Described Coleoptera of the World*. Hallan's list is valid up to June 2010 and as far as I know has not been updated since. Later, the contents of my database were synchronized with the information already present in the *ITIS* taxonomic database. As *ITIS* is providing data for the *Catalogue of Life*, information from my database is now part of the taxonomic backbone of the web. This includes *GBIF* that now reports 4,343 species of Dytiscidae and 393,125 records of an unknown proportion of them (some confusion here as my own species count for January 1, 2014, reaches only 4,256 extant species, and *GBIF* also cites Wikipedia, saying that "The family has not been comprehensively cataloged since 1920" – I really appreciate that one!). Finally, name lists from my database are to be included in the *Freshwater Animal Diversity Assessment* (FADA) database of freshwater animals of the world (FADA 2013).

The Dytiscidae world catalog is still lacking a bibliographic part, like the one I did add to the noterid equivalent (Nilsson and Vondel 2005). I know that Hans Fery has come a long way towards entering this information into a database, and the early part of it is already, at least to a large part, present in the world catalog of Alois Zimmermann from 1920. But what would one do with a list of more than one thousand works mentioning *Agabus bipustulatus*? Producing such a bibliography of all species names is related to the focus of the online database *Global Names Index* (GNI) that aims at linking together all search strings that refer to the same taxonomic unit. Besides the different ways of writing a species name and synonymy, such a database should also cover misidentifications, and this information could be provided by the bibliography I am talking about. The problem with misidentifications is that they depend on context and cannot be dealt with just by linking different text strings.

As a data provider to more inclusive global projects, the question of how updating of information will be done comes to mind. If the more inclusive projects like *ITIS*, or Thomson Reuter's *Index of Organism Names,* are doing this based on scanning of all new publications, like I think they do, the annual updates I produce seem redundant. Does it matter if this work is carried out by a specialist with some experience of the group in question or not? Do they list the same kind of information as I do? These, and probably a few more, are relevant questions indeed related to the choice of building up specific information structures for Dytiscidae or improving on the more inclusive ones that are already present.

Molecules Rule

Following the general trend, studies of phylogeny within Dytiscidae have quickly, during the last 10 years at most, switched from being based on morphology to being based on DNA. The phylogenetic analysis of the Dytiscidae presented by Kelly B. Miller and Johannes Bergsten in Chap. 3 effectively combines DNA and morphology, including in their data set 6,700 aligned bases and 104 morphological characters from 168 species. The high resolution and generally high branch supports reported in their study would hardly be possible to achieve if using morphological characters only. The barcoding project has so far collected more than 5,000 sequences of 785 species of Dytiscidae in the *BOLD* online database, although only sequences of 417 species are classified as "public" and available for download (December 16, 2013). In *GenBank*, the number of species should be even higher reporting 16,783 nucleotide sequences stored from dytiscids. The most popular species of Dytiscidae being *Agabus bipustulatus* with 604 sequences. The now dominant usage of DNA as the basis for phylogenetic hypotheses is limiting the role of morphology to chiefly as a tool for species delimitation and identification, and in the future visions of the barcoding project, DNA will take over also these aspects. The optimal combination of DNA and morphology as data sources for taxonomy is debated as can be seen in the development of positions known as "DNA taxonomy" or "integrative taxonomy". One thing is sure, molecules are here to stay and purely morphological taxonomy is becoming rarer. Being a pioneer in the study of larval chaetotaxy myself, I cannot deny its potential value for phylogenetic studies, and warmly welcome new developments within the subject as here being presented in Chap. 2 by Yves Alarie and Mariano Michat. Still, as a source of phylogenetic information, it cannot escape from being flooded by the molecules, and barcodes will no doubt be operational also in the identification of larvae of all instars to species.

Synthesis or Filling in the Gaps

Such an enormous mass of information representing the 4,256 extant and named species of Dytiscidae that is now available from various internet sources, I think the time has come to carry out more globally oriented studies. I am not in any way saying that geographically or taxonomically restricted studies are no longer needed. The more recent discovery of a totally unexpected diversity of subterranean predaceous diving beetles in the arid parts of Australia is one example that clearly shows the continuous need for field studies. The need for sampling various rainforest habitats in the tropics before they disappear is another activity that should be given high priority. The challenge of biodiversity informatics is in some way to combine quantity with quality, mining the vast data sources of varying quality in order to establish global patterns of diversity that are robust enough to overcome the noise in the data. Such studies will also provide valuable guidance in where to find the high priority hunting grounds.

Another aspect of biodiversity informatics is that whereas some general structures or scaffolds of great potential use have been established on the web, the details are still to be filled in. Just take a look at the *Tree of Life Web Project*, aimed at providing information on species relationships for all organisms. Actually, absolutely no information is present on relationships within Dytiscidae and the phylogeny provided for the families of Adephaga is by no means up to date. Or consider the *Encyclopaedia of Life,* where every predaceous diving beetle species has its own page, but very few pages carry any information.

In a Book and Everywhere

As the most comprehensive single book on predaceous diving beetles published so far rests in your hands, it is time to contemplate how this mixture of new results and overviews of what already had been achieved can be absorbed into the more inclusive online knowledge systems. It is no longer only a question of science occasionally being popularized in magazines and small booklets. For example, take as an example the new diving beetle phylogeny here presented by Miller and Bergsten (Chap. 3). Will they incorporate their new tree directly into the *Tree of Life* itself? How will the new classification of Dytiscidae they suggest get worked into the taxonomic backbone of the internet? Do such responsibilities follow from authoring or editing scientific literature or are there others that will have assist in this regard? Scientific publication today is linked to an increasing number of registration systems, some optional and some obligatory. In the age of biodiversity, informatics sharing is the key word, and here is a brand new and fully packed book to share!

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Preface

There are nearly 200 families of beetles, with many more families in total among the other insect orders. So to devote a single book to this single family of insects should require an answer to the question, Why dytiscids? My answer is simple: They are cool! Within this context, cool can be defined both scientifically (e.g., one of the most diverse beetle families, ubiquitous in freshwater systems, capable of feeding on a mélange of prey including vertebrates) and aesthetically (streamline shaped, wide variety of colors and behaviors, cultural significance). Also, they are cool for another reason. They are understudied as both an aquatic insect group and as an aquatic predator. Thus, they offer even the casual researcher an opportunity to make significant contributions to the knowledge of their biology, ecology, or evolution. Therefore a book that covers our current understanding of these various aspects of dytiscids, including our gaps in knowledge, seems both timely and warranted.

My hope is that the readers of this book will find it a comprehensive overview of the Dytiscidae, a most ubiquitous and amazing family of aquatic predators. It was partly to satisfy what I perceived as a need for such a book that I began developing this book subsequent to a symposium I organized at the 2010 Entomological Society of America meeting held in San Diego, California. Many of the participants in that symposium were kind enough to prepare chapters for this book (i.e., Yves Alaire, Johannes Bergsten, Patrick Crumrine, Lauren Culler, Margherita Gioria, Siegfried Kehl, Kelly Miller, and Shin-ya Ohba). I am grateful to them, and others (i.e., David Bilton, Garth Foster, Mariano Michat) whom I met in the mean time and graciously accepted my invitation to contribute. I am also thankful to Anders Nilsson, who prepared the Foreword that precedes this chapter. The comprehensive and thoughtful presentations you will find in the following pages are a testament to the authors' passion for science in general and dytiscids in particular. My own history with this group is comparably short, spanning from my post-doctoral position at the University of Calgary in 2007 under Steve Vamosi to the present day. However, even at my first sampling foray into a roadside pond I was struck at the density and variety of adult and larval dytiscids. Once I began to formulate research questions regarding the ecology of these insects I quickly found that a lack of knowledge, especially ecological, was the rule and not the exception for most species. In fact, in their excellent book, *Predaceous Diving Beetles* (*Coleoptera: Dytiscidae*) *of the Nearctic Region*, Larson, Alarie, and Roughley (2000) state:

> *Very little is known about the habitat, life history, or habits of most North America water beetles.*

This statement is apt and can easily apply to dytiscids worldwide. My hope is that this book will help inspire entomologists, ecologists, systematists, and others to make a start to fill in the gaps.

Hattiesburg, MS, USA Donald A. Yee
March 2014

Contents

Chapter 1
An Introduction to the Dytiscidae: Their Diversity, Historical Importance, Cultural Significance, and Other Musings

Donald A. Yee

> *I am surprised what an indelible impression many of the beetles which I caught at Cambridge have left on my mind.*
>
> (Charles Darwin 1887)

Abstract Predaceous diving beetles (Family Dytiscidae) are one of the most fearsome predators in freshwater environments, however most of their biology and ecology remains to be measured. The Dytiscidae exhibit a complex life cycle with both adults and larvae using a variety of aquatic habitats for feeding, reproduction, and intra- and interspecific interactions. Adults are vagile and capable of dispersal across great distances, making them an important component of the terrestrial environment and potentially important for linking various habitats via the movement of energy and materials. Both larvae and adults are predaceous, and the former often possess large curved hollow mandibles that are capable of dispatching large prey, including vertebrates. As predators, they exhibit different hunting behaviors and a full repertoire of chemicals used for defense and communication. Adult dytiscids also display one of the most complex and fascinating examples of sexual selection, with both pre- and post-copulatory mating choice dispersed among different phylogenetic branches of the family. Although the systematics of dytiscids has been of interest for decades, phylogenies are now becoming clearer, allowing us to better understand their dynamic and interesting evolutionary history. These beetles also can instruct us on bigger concepts, like the current focus on conservation both of species and of the habitats that harbor them; to this dytiscids make a good case study. Although often overlooked in the scientific literature compared to other

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aquatic insect groups, their importance in human culture, both past and present, is compelling and worthy of note. With all this, perhaps the most intriguing thing about dytiscids is that we know so little about them.

Keywords Culture • Biodiversity • Darwin • Dytiscidae • Entomophagy • Water beetle • Water tiger

1.1 Dytiscids Past and Present

The pantheon of life is not the sum of mere observations of numbers, like the adding up of so many trading cards or widgets in a collectors case, but instead involves the unique place of each organism on Earth and its rich and often tangled evolutionary past. This book explores the current knowledge of just one family of beetle (among many dozens of families) within one order (among many dozens of orders) within one class (among many dozens of classes) within one phylum (among about 35 phyla of animals) within one of five kingdoms nested within one of the three domains of life. The story of the Dytiscidae, both past and current, is interesting and unique, and it is hoped that the reader will gain a better appreciation of their ecology, natural history, and systematics from the chapters that follow.

Of the approximately three dozen families of aquatic or semi-aquatic beetles, predaceous diving beetles (a.k.a. “diving beetles”, “water beetles”, or “dytiscids”) are a common inhabitant of most freshwater lentic (and sometimes lotic) aquatic systems on Earth (Fig. 1.1). The family name, Dytiscidae, derives from the Greek *dytikos*, meaning “able to dive”, which speaks to their proclivity for submerging in freshwater environments. They occur in almost every type of freshwater (and slightly saline) habitats from large lakes to small plant-held waters (Chap. 7). Many casual and professional scientists have observed adults and larvae when sampling ponds or ditches or other more unlikely places. I myself had the experience of an adult *Cybister* landing in the tailgate of my pickup truck on a summer afternoon, ostensibly thinking that my dark truck bed was a nice refreshing pond. Dytiscids are the most diverse aquatic Coleoptera, with the current number of identified extant species at 4,256 (A. Nilsson 2013, personal communication). However, like most species of life on Earth (and insects in particular), the actual number of living species will exceed this current total, perhaps by thousands of new species. In fact, the recently discovered Australian subterranean fauna of dytiscids (Fig. 1.2, and see Watts and Humphreys 2006, 2009) has added a whole new world of diversity to this group, and it is possible that other untapped areas (including museum drawers) remain to be explored. The subterranean fauna is unique in many ways, especially in regard to adaptation of beetles, like the loss of pigment, eyes, and some swimming adaptations. Beyond the high diversity of dytiscids within and among habitats, they also exhibit high abundance. In agricultural ponds in Alberta, Canada I routinely collected a dozen or more *Graphoderus occidentalis* adults in a single sweep of my D-net! Other authors note similar experiences with bountiful numbers. Adults are distinguished from members of other aquatic beetle families by their highly

Fig. 1.1 An adult *Acilius mediatus* from a pond in southcentral Mississippi, USA. Note the oar-like rear legs fringed with swimming hairs (Photo by Don Yee 2013)

specialized aquatic adaptations, including a rounded body shape with dorsal-ventrally flattening, large natatorial oar-like hind legs, and variable respiratory mechanisms (Chap. 4). These adaptations often are useful for distinguishing them from other aquatic coleoptera, including the Hydrophilidae (water scavenger beetles) and Noteridae (burrowing water beetles). Species in the former family are often collected in association with dytiscids but are less streamlined and often swim with alternating strokes of their crawling legs, whereas the latter family was only recently split from the Dytiscidae, and the two families share many conspicuous morphological features.

One of the first references to dytiscids in the literature appears in the *Systema Naturae* (10th edition, Linnaeus, 1758), although few of the species listed under this family survive under that original set of classifications. Miller and Bergsten in Chap. 3 provide additional history of the scientific literature on dytiscids, although no work of biology can ever be complete without a mention of Charles R. Darwin. As we will see the eminent Englishman also had a few ties to predaceous diving beetles. His earliest recorded scientific work involves dytiscids, which are part of the insect collections he made near Cambridge in early 1829 at the age of 20 (fully 2 years prior to his voyage on HMS Beagle). At this time it is thought that he began to cultivate a keen interest in entomology. The collection records from this time appear in several volumes of British insects by James Francis Stephens (1829). Among other insects, Darwin gathered a variety of dytiscids along with notes on their collections, including

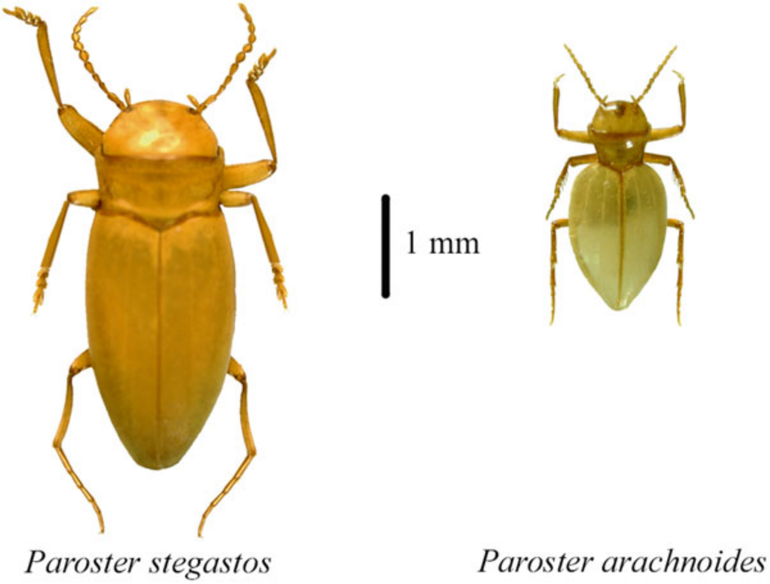

Fig. 1.2 Adult *Paroster stegastos* and *P. arachboides*, species that are part of the recently discovered Australia subterranean fauna of dytiscids. Note the lack of pigment and eyes, and other morphological adaptations to cave living (Photo courtesy of Chris Watts 2014)

Dytiscus conformis ("Near Cambridge, not rare, in 1829"), *Hydaticus hybneri* ("Near Cambridge in 1829"), *Hygrotus scitulus* ("Near Cambridge"), *Hydroporus areolatus* ("Cambridge"), and several *Colymbetes* including *C. agilis* ("In profusion near Cambridge in 1829") (Fig. 1.3). His early fascination with insects, based especially on collecting beetles, has been noted elsewhere, but one cannot help to think that this early exposure whet his appetite for later beetle collecting (e.g., see the quote that starts this chapter and Chap. 6). Charles Darwin did collect dytiscids (and thousands of other specimens) on the 5 year Beagle voyage starting in late December, 1831, including a *Colymbetes signatus* that was caught on board the ship, "45 miles from Cape St. Mary" (Monte Video, Uruguay) (Babbington 1841). Darwin wonders how much farther it would have flown if stronger winds occurred, and perhaps gives us one of our first observation of a dytiscid dispersal event (Chap. 9). Darwin also discovered several new species of dytiscids on that voyage, which were later compiled and published by C.C. Babbington in 1841. After his return, Darwin appeared to lose interest in insects, and focused much effort on various other groups including earthworms, barnacles, and domesticated animals, as they would provide him with details to help him make his eventual case for natural selection. However, he does return to dytiscids later in life, in a case he published involving dispersal of a freshwater bivalve with the aid of a large dytiscid:

> "*On February 18 of the present year, he* [Mr. Walter Drawbridge Crick] *caught a female* Dytiscus marginalis*, with a shell of* Cyclas cornea *clinging to the tarsus of its middle leg.*

Fig. 1.3 Some of the beetles collected by Charles Darwin during his time at Cambridge, England. Note the large dytiscids (perhaps *Cybister* sp.) in the *top* of the *right case*. These and other insects collected by Charles Darwin are on display at the University of Cambridge Zoological Museum (Photo courtesy of Richard Carter 2014)

> *The shell was .45 of an inch from end to end, .3 in depth, and weighed (as Mr. Crick informs me) .39 grams, or 6 grains.*"

This article was published 6 April of 1882, a mere 13 days before his death, and thus represents his last living contribution to science. It is natural for biologists from all fields to try and claim Darwin for their own, either because of his effort, if even fleeting, on their study organism or because of how his work speaks to their current set of questions. Thus, it is of some satisfaction to this author that one could say that his scientific career began and ended with dytiscids.

1.2 Nature Red in Tooth and Claw…and Mandible

When Alfred Tennyson (1809–1982) wrote his famous poem (*Nature, Red in Tooth and Claw*, 1850) he may not have imagined that it would serve as a touchstone to summarize many of the ideas put forth by Charles Darwin in *On the Origin of Species* (1859). However, that phrase, the title to Tennyson's poem about his struggle with his religious faith in the presence of a personal tragedy, has come to encapsulate the very struggle for existence that Darwin outlined in his thesis on natural selection. Dytiscids, as predators, perfectly reflect this struggle (for themselves and their unfortunate prey). Most larvae, including the larger forms (e.g., *Dytiscus*) known as "water

Fig. 1.4 The head of a *Dytiscus* sp. larva, showing the large curved hollow mandibles, stemmata (simple eye spots), and palps. The feeding appendages are powerful enough to restrain and kill tadpoles and fish (Photo courtesy of Neil Phillips 2013)

tigers", are equipped with large hollow curved mandibles (Fig. 1.4), that easily pierce invertebrate and vertebrate (including human) flesh. They also feed on one another, and therefore aptly conform for the struggle within a species as well. Within the aquatic world of a fishless farm pond or a roadside ditch, the *Dytiscus* larvae is the great white shark or African lion, seizing upon unexpecting prey in a flash of blood and writhing bodies. However, this is not the scale at which we often imagine ourselves, and therefore we may lose sight of the significance of these predators to their prey. Imagine for a minute a larval *Dytiscus* as large as a cheetah. After ignoring the limitations that oxygen consumption demands or the structural qualities that chitin imposes, such a predator would likely surpass the most horrible nightmare that Hollywood could conjure up! Even the chewing and slashing mouthpart of the "Xenomorph" of the *Alien* movie franchise would fail to compare to the piercing and sucking mouthparts of a formidable *Dytiscus* larvae writ large! Such nightmares are all too real for many aquatic prey, including many vertebrates like tadpoles and fish (Chap. 8). However, these predators have received considerably less attention than other predatory taxa in lentic systems, but they are no doubt as important.

I am willing to bet that most researchers feel that their particular study organism is underrepresented in the scientific literature and simultaneously underappreciated by the general public. Although the latter is difficult to quantify, evidence for the former condition is not difficult to find to verify (or refute) that point of view. With this in mind I gathered evidence to show that indeed dytiscids are one of the most neglected aquatic insect groups, even among the aquatic Coleoptera and aquatic predators. Using the online search engine Web of Science™ (Thomas Reuters) I gathered citation records for various aquatic insect taxa over the last two decades

(1994 to January 2014). I focused on family names for many aquatic groups (e.g., Culicidae, Dytiscidae, Hygrobiidae, Nepidae) but used the ordinal level for others (Plecoptera, Odonata, Trichoptera, Megaloptera) (Fig. 1.5). I used orders for some groups when they were essentially entirely aquatic. I searched using the "Topic" field, as restricting to publication titles may miss important work where the group was included, but not the major focus (e.g., community ecology studies or broad phylogenies). I also determined the approximate number of species present in each group using various sources. I then divided the total citations over the past 20 years by the number of species in each group to generate an Index of Effort (IE). Values of IE that exceed 1 would indicate more publications than species present (i.e., high effort), whereas values <1 would suggest fewer publications than species (i.e., less effort). There are pros and cons with such an approach, as some groups may receive high effort because of a few important taxa or because some species are of particular interest (e.g., of medical or agricultural importance). Also, this approach is skewed toward more modern interests, and as some groups have ebbed and flowed in scientific focus over the past centuries, this approach may not capture historical interest. It also ignores books and monographs, although they are never as common as journal publications for any group. Finally, this approach will ignore work in journals not covered in Web of Science™, particularly many museum publications or those not written in English. However, I contend that this approach is a good place to start. From the data gathered I wished to know three things. How much scientific effort have dytiscids received compared to other aquatic taxa? How much effort have dytiscids received compared to other aquatic beetles? How much effort have dytiscids received compared to other aquatic predators?

Dytiscids were found in 552 publications (Fig. 1.5), and with the more than 4,200 species had a IE of 0.130. Larson et al. (2000) list about 500 citations in their work on Nearctic dytiscids, so the publications I found seems a reasonable comparison, as they also include citations back to the eighteenth century and included many published in non-English sources. Of those 552 publications, the majority are related to taxonomy or systematics, which should not be surprising, although it does speak to the general lack of knowledge in other areas (e.g., ecology). Of the 45 aquatic groups considered, their IE value placed them near the bottom (34th), between two less diverse aquatic beetle families (i.e., Helophoridae and Dryopidae) (Fig. 1.5). The only other common aquatic group below them are the Tipulidae (Order Diptera, "crane flies") at IE = 0.05. All the other groups lower in IE than dytiscids are aquatic beetles, many of low diversity. Some of the higher diversity aquatic insect groups received much more effort. In fact, considering that dytiscids are one of the most speciose families of aquatic insects they rate only about 1 publication per every ten species, whereas mosquitoes have more than two publications per species (Family Culicidae, IE = 2.16). Other families, like mayflies (Order Ephemeroptera, IE = 0.89), midges (Family Chironomidae, IE = 0.54), and the dragon/damselflies (Order Odonata, IE = 0.45) also have done much better (Fig. 1.5). Compared to other aquatic beetles, here too Dytiscids had a much lower score, especially when one considers that they are the most diverse aquatic beetle family. Many of the groups with higher IE scores had relatively low number of species, with the

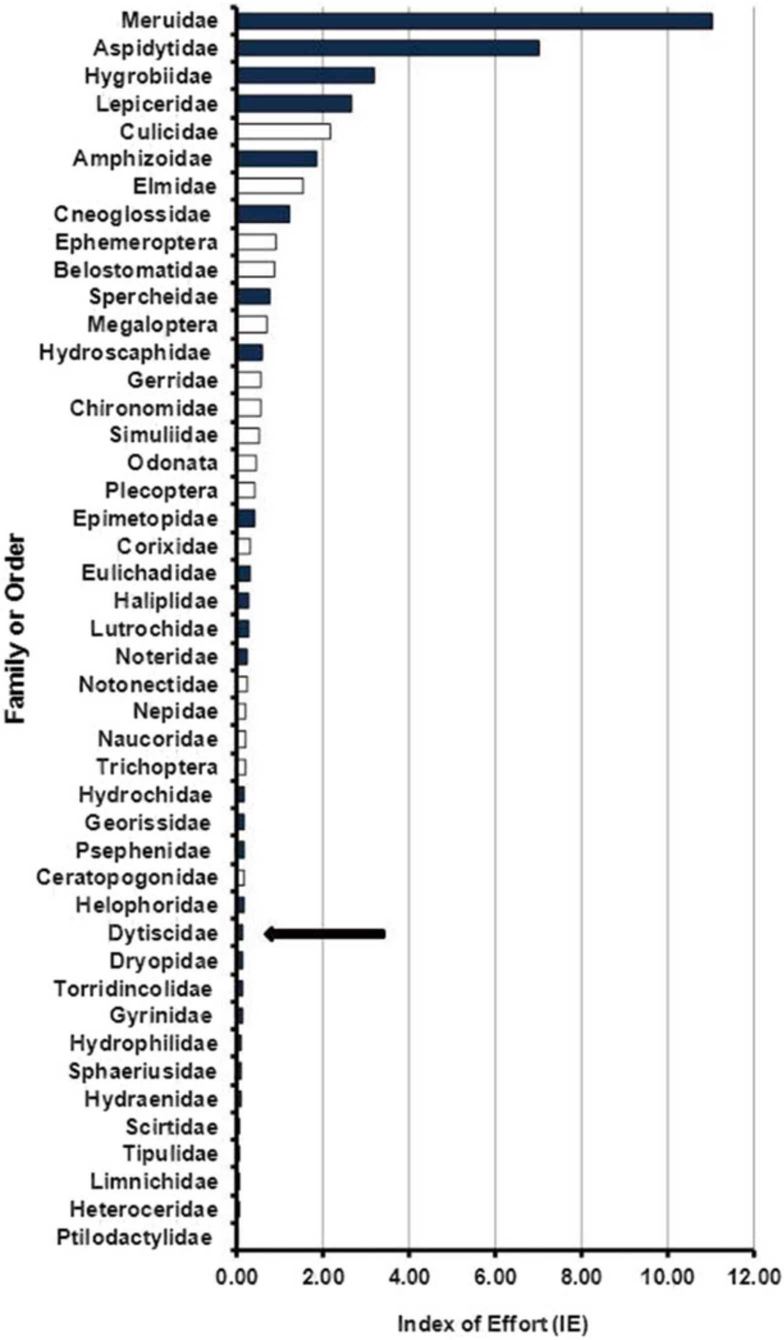

Fig. 1.5 The Index of Effort (*IE*) for various aquatic insect taxa. IE is defined as the number of scientific publications noted in Web of Science™ from 1994 to 2014 using the family or order names divided by the number of species in each group. Values greater than 1 would indicate that there is more than one publication per species within that taxonomic group. *Bars* in *black* are for aquatic beetles whereas *white bars* represent other aquatic insect taxa. The Dytiscidae is noted with an *arrow*

highest IE score achieved by Meruidae (“comb-clawed cascade beetles”) with only 1 species and 11 publications! Perhaps because of their high diversity other families of beetles did not fare very well overall, so dytiscids were not the exception. For instance, Hydrophilidae (second highest number of species at ~2,800) had an IE = 0.11, and both Hydraenidae (“minute moss beetles”, IE = 0.08) and Sciritidae (“marsh beetles”, IE = 0.06) with over 1,000 species each had IE numbers much lower (Fig. 1.5). Of these however only the Hydrophilidae have aquatic larvae and adults, a trait shared with dytiscids, and thus one could argue that they serve as the only true comparison in this regard. Finally, of the aquatic predatory groups, predaceous diving beetles were the lowest ranked, far behind dragon/damselflies, Nepidae (Order Hemiptera, “water scorpions”), Belostomatidae (Order Hemiptera, “giant water bugs”), and the Megaloptera (“dobsonflies” and allies). Thus, based on this examination, it seems clear even given their high species diversity and prominence as aquatic predators that dytiscids are neglected in the scientific literature. I attempted to confirm this examination of the scientific literature by searching for the order or family names in the search engine Google™ and recording the number of pages that were returned. This would essentially find how many times the taxa appeared in both academic and non-academic sites and may serve as a loose proxy for public interest. The numbers were very comparable to the academic publication search, with Dytiscidae returning 367,000 pages, compared to more popular taxa including Chironomidae (540,000 pages), Odonata (734,000), Culicidae (1,010,000), Ephemeroptera (1,550,000), and Plecoptera (1,640,000). Two of the major groups returned fewer pages than dytiscids, the Ceratopoginadae (226,000) and Trichoptera (277,000). In general, reference to other aquatic beetle families were found on fewer than 100,000 pages (e.g., Meruidae 5,300 pages). Thus, the lack of interest for dytiscids seems to extend to the general public as well.

1.3 Cultural Notes

There are many wonderful accounts of how insects have permeated into the folklore and mythology of many different societies, both past and present. The scarab beetle in ancient Egypt, the dragonfly in Japan, and the plagues of locust and flies to the Ancient Hebrews are perhaps primary examples of how insects have shaped many cultures worldwide. Oddly enough, there have been reports of plagues of predaceous diving beetle adults in Queensland, Australia (Johnson 2011; Prain 2011). The presence of dytiscids in myths is rare, although Powell (1900) does document a creation myth among the Cherokee. The mythology centers around the creation of the world, and a water beetle plays a prominent role. Powell writes,

> “*Beetles are classed together under a name which signifies “insects with shells.” The little water-beetle or mellow-bug (*Dlneutes discolor*) is called Dâyuni'sï, “beaver’s grandmother,” and according to the genesis tradition it brought up the first earth from under the water…They* [the animals] *wondered what was below the water, and at last Dâyuni’sï… offered to go and see if it could learn. It darted in every direction over the surface of the water, but could find no firm place to rest. Then it dived to the bottom and came up with*

> *some soft mud, which began to grow and spread on every side until it became the island which we call the earth.*"

Many different insects have also worked their way into less dramatic and more common place positions, such as everyday western phrases ("Busy as a bee", "Nit picking") or popular culture (e.g., movies like "Them" 1950 and "The Fly", 1958). Dytiscids have not, as of yet, played a major role in popular culture, but they have nonetheless been part of various cultures and do occasionally make their way into our everyday lives. Although this is not an exhaustive description of their cultural significance, it provides an introduction.

In an interesting (if not bizarre) cultural connection, several different insect types, including dytiscids, are used by east African girls to stimulate breast development (Kutalek and Kassa 2005). This practice has a long history, and appears widespread in rural Ethiopia, Tanzania, and Uganda. Specifically, girls collect the beetles, known as *yewha inat* or "mother of water" in Tanzania (e.g., *Rhantus capensis, Hydaticus wittei*) from local aquatic habitats during daily chores and are then placed against the girl's nipple until they bite. Upon biting they also release defensive compounds from prothoracic and pygidial glands (Chap. 6). After several days the breast is said to be slightly swollen and the year or so after this event the breasts are reported to grow larger. The purpose of this to allow prepubescent girls the chance to feel more adult, however there is no scientific evidence that this practice delivers the desired results. Oddly enough, young boys in the Njnombe region use the beetles in the exact same way, although they do so to reduce breast growth that may occur during puberty prior to an increase in testosterone levels. In other areas, such as Zimbabwe, boys let the beetles bite their tongues so they may learn to whistle. It appears then that these beetles do not discriminate in helping each sex get an advantage over the other.

Moving away from the warm regions of Africa, dytiscids, like most insects, are not abundant in polar or near-polar regions, however several species do exist in seasonally high numbers in Greenland. These include *Hydroporus moria* and *Colymbetes dolabratus*. The adults and larvae are active during the brief summer, and often feed on chironomids and other small invertebrates. Perhaps because of their prevalence in the relatively barren aquatic systems in Greenland they do seem to have made their way into local folklore. Böcher (1988), citing older sources, reports that native Greenlanders were afraid of *C. dolabratus* specifically, whom they referred to as either "Pamiortooq" (larvae) and "Minngoq" (adults). Their fear lay in being injured when the beetles would attack and destroy their bowels after accidently drinking them in water from local sources. To combat this, locals would introduce amphipods (i.e., *Gammarus locusta*) into "infested" waters, where upon a war between these arthropods would result and would end in the eventual destruction of both (Böcher 1988). This folklore still remains in Greenland today (L. Culler, personal communication) although it seems to be more about getting bitten when swimming in waters with dytiscids rather than having one's bowels destroyed.

Fig. 1.6 A veritable dytiscid feast. Fried *Cybister japonicus*, served in a Cantonese restaurant in China, garnished with parsley and orchid flower (Photo courtesy of Manfred Jäch 2003)

Although Greenlanders are wary of accidentally consuming dytiscids, there are many reports of dytiscids as food for direct human consumption. This entomophagy (dytisciphagy?) is especially prominent in southeast Asia, including China (Jäch and Easton 1998), New Guinea (Gressitt and Hornabrook 1977), and Thailand (Chen et al. 1998). Hoffman (1947) reported on dytiscids (*Cybister* sp.) and hydrophilids being sold and consumed in Canton (now Guangzhou), China. He states,

> "*Beetles of these two families are very commonly eaten in Kwangtung Province and in other places where Cantonese dwell. Although usually kept in separate containers customers very frequently buy some of each family. They care less for the hydrophilids and consequently they are cheaper than the dytiscids…The elytra, legs, and certain other chitinous parts are discarded when eating.*"

Half a century later Jäch and Easton (1998) and Jäch (2003) published similar accounts of the practice and Jäch (2003) specifically provides a firsthand account of eating *Cybister japonicus* in a local restaurant (Fig. 1.6),

> "*This species turned out to be rather tasteless, except for the flavor of garlic and other spicy ingredients that had been added. In contrast to* Hydrophilus [Hydrophilidae], *the chitinous structures are not soft, but more or less as prickly as in living specimens, and the abdomen does not contain notable quantities of soft tissue. I tried to eat one specimen, and although I had partly swallowed it, I felt myself forced to spit the majority on the table in front of me (which is not regarded as rude behavior in China, where table manners are quite different from those in the West).*"

He also comments that eating these aquatic beetles is based on tradition, and not economics, as this area of China is quite prosperous, and most of the beetles are reared locally and not wild caught. He ends by noting that the popularity of eating aquatic beetles is waning, perhaps as China continues to modernize. Several sources suggest that the goal of consumption may not be just for nutrition, as the beetle also are seen as having anti-diuretic attributes, and thus are perceived to have medicinal value (Hoffman 1947; Pemberton 1999). Other cultures also use dytiscids (e.g., *Cybister tripunctatus*) in traditional medicine (e.g., African cultures, Kutalek and Kassa 2005).

Ingestion of dytiscids by humans is much older, even outside of southeast Asia. Roust (1967) reports the findings of examinations of 186 human fecal droppings (coprolites) from caves in the desert southwest in the United States. The specimens were assumed to be prehistoric based on several lines of evidence, and although there appears to have been no radio carbon dating conducted on the samples, other artifacts collected in the caves by others seem to confirm the antiquity of this site (e.g., Heizer and Krieger 1956). Besides an abundance of plant material, the remains contained fish bones, mammal teeth, and bird feathers and egg shell, and also included insect parts. Specifically the remains of a large dytiscid. Roust writes,

> "… *undigested remains of the predaceous water beetle* Cybister explanatus *found in seven (9.46%) of the specimens. Of interest is the fact that no heads of any of these beetles were found, indicating that they were either bitten or torn off prior to ingestion, without chewing, of the whole beetle.*"

This is not the only account of ingestion of these large aquatic beetles in the Americas. In the past, ancient cultures in area of present day Mexico also consumed aquatic beetles, including *Cybister*, which was termed "Atopinan" and described as, "*a marsh grasshopper of a dark colour and great size, six inches long and two broad (!)*" (Smith 1807). Clearly the size of this animal is a gross exaggeration, although consumption of these beetles is not! In their review of the caloric content of almost 100 insects consumed in Mexico, Ramos-Elorduy and Pino (1989) cite earlier works regarding the use of *Cybister* (as known as *cucarachas de agua*, "water roaches"!) as food, specifically their consumption by being eaten roasted with salt or as an ingredient in tacos. These authors list that larvae, pupae, and adults are consumed. They further report that *Rantus* (*Rhantus*) sp. adults contain 4,015.0 kcal/1,000 g, a number comparable to many other beetles examined and much higher than many grains tested (e.g., corn 3,640 kcal/1,000 g) or other animals (e.g., chicken 1,646 kcal/1,000 g or cod 3,888 kcal/1,000 g) (Ramos-Elorduy and Pino 1989). The consumption of predaceous diving beetle adults need not be limited to those areas with a tradition of consuming them, as there are companies that provide them for sale all over the world (Fig. 1.7). The practice of the prehistoric North Americans in removing the heads seems to be another case of ancient wisdom, as even the commercial producers of dytiscids suggest removing the head before consumption.

Although dytiscids are merely viewed as food by some cultures, in other locations dytiscids are kept as pets. Specifically, the tradition of keeping insects, including dytiscids exists in Japan (S. Obha, personal communication, Fig. 1.8) and Hong Kong (Jäch and Easton 1998), and based on some accounts were also kept in many parts of Europe (i.e., *Cybister*, Wesenberg-Lund 1943 reported in Balke et al. 2004). In Japan specifically the practice of keeping insects as pets, especially beetles, is long-standing, and various methods exist for purchasing insects, including vending machines (Kawahara and Pyle 2013.) The large beetles that are often at the center of

Fig. 1.7 Canned predaceous diving beetle adults sold for human consumption. Each of these 15 g cans sells for about $6.00 U.S. plus shipping, and as the label indicates, they are cooked and dehydrated and then dusted with barbeque sauce. The instructions indicate to remove the "outer wings" and that everything except the head can be consumed (Photo courtesy of Thailandunique 2013)

Fig. 1.8 The interior of a store in Osaka, Japan that specializes in selling insect husbandry supplies and live insects as pets. Such stores are common throughout Japan and often offer a wide range of Coleoptera, including dytiscids for sale (Photo courtesy of Hideyuki Suzuki 2013)

this pet trade are held in high esteem, and an entire industry has blossomed around keeping them as pets, including companies that specialize in producing rearing materials, cages, and other accessories for the discerning beetle owner. Related to their use as entertainment, there is an account by Pemberton (1990) who describes the use of large dytiscids in a game of chance. The game requires some people willing to wager a small amount of money, an oval metal tank of water, some prizes, and a live adult *Cybister japonicus*, a species found throughout the region. The game is called *mul bag gae nori*, or the "water beetle game", for reasons that will become obvious. The game is similar to roulette, but instead of a ball that randomly lands within slots along the spinning wheel, here an adult *Cybister japonicus* is allowed to swim and come to rest in one of many vertical flanges that are positioned slightly above the 3–4 cm water level. If the beetle enters or touches a slot then the player wins the corresponding prize (if any) placed along the outer edges of the tank. The prizes are often of low cost (e.g., small toys, candy) but so is the cost to play. On a related note, Pemberton (1990) also mentions that *mul bang gae* ("water beetle") is also a nickname used for a fat man, likely owing to a similarity to the beetle's round shape.

1.4 Final Words

I hope that the readers of this book will find it a comprehensive overview of this ubiquitous and amazing family of aquatic predators. The authors of these chapters have more than a hundred years of combined publishing experience with this family, a fact that hopefully comes out in the comprehensive and thoughtful presentations you will find in the following pages. In each chapter you will find Future Directions that should serve as a starting point for new and less traveled avenues of research. I would add my own suggestion as well, specifically that those who study insects in aquatic systems in particular should take the time to identify and catalog these insects in their community studies. I've met several researchers at scientific meetings who simply ignore them or "lump" species of dytiscids into higher taxonomic groups. Their reasons are varied, but often hinge on a frustration with identification or a general lack of knowledge compared to other aquatic groups (e.g., Odonata). Given the dearth of species-level keys for most dytiscid larvae this is not surprising (Chap. 2), but this should instead be a call to action in producing more keys. In his Forward to this book, Anders Nilsson suggests that the future of taxonomy will likely be focused on molecular approaches, which, if it reaches fruition, should provide a boon to work with larval dytiscids. It is my hope that the book you now have before you will help to mitigate this deficiency and spur interest and new research on this fascinating group of insects.

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Chapter 2
Bridging Ecology and Systematics: 25 Years of Study of Larval Morphology of World Dytiscidae

Yves Alarie and Mariano C. Michat

> *In Nature's infinite book of secrecy*
> *A little I can read*
>
> (William Shakespeare, Antony and Cleopatra, I,2,87)

Abstract Although the Dytiscidae are among the most common insect inhabitants of freshwaters, knowledge of their larval morphology is scant throughout the world. The identification of larvae is a continuing problem because the literature available to accomplish this is scattered, limited to certain groups, outdated, difficult to use, or non-existent. Recent studies have demonstrated the taxonomic and phylogenetic value of chaetotaxy in studying larval Dytiscidae. Study of body sensilla (setae and pores) were shown to be useful and important both for diagnosis and study of phylogenetic relationships among taxa. The fact that all these studies were conducted separately over a period of more or less 25 years does not however facilitate comparison among taxa. This chapter synthesizes these studies into a more comprehensive approach, which should facilitate comparison among the dytiscid subfamilies. A corollary objective of this chapter is to exemplify how knowledge of dytiscid larvae and an ability to identify them has the potential to make the wealth of characters present in the larval stage available for ecological study.

Keywords Bioindicator • Chaetotaxy • Dytiscidae • Hydradephaga • Larval morphology

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2.1 Introduction

Coleoptera is the largest order of the Kingdom Animalia, comprising a quarter of all known animal species (Gullan and Cranston 2010). The order is represented in almost every non-marine habitat on Earth. It includes many of the most beneficial and destructive insects known, yet an enormous amount of basic taxonomy and biological study is necessary to raise our understanding of this group to the level attained in most other insect orders. The current state of coleopteran taxonomy is uneven in several ways, with many large geographical, developmental, and taxonomic gaps (Stehr 1991).

Although the state of knowledge of adult beetle taxonomy varies widely across taxa, our knowledge of coleopteran larvae is generally poor. Most beetle larvae are unidentifiable to species, even though the larval stage typically lasts longer than the adult stage and often has the greatest impacts on humans and the environment. As Holometabola, beetle larvae are under differing selection pressures compared to adults and as such show quite different morphological features. As a different expression of the same genotype, each larval instar represents an ontogenetic stage with its own characters, each being important in determining taxa, reconstructing phylogenies, and building classifications.

With some 4,200 described species (Nilsson 2001, 2003, 2004; Nilsson and Fery 2006) the beetle family Dytiscidae represents one of the largest and most commonly encountered groups of aquatic insects. Up until recently, however, the identification of their larvae was a regular and continuing problem for many because the literature available to accomplish this was widely scattered, limited to certain groups, outdated, difficult to use, or non-existent (Larson et al. 2000). Moreover, larval descriptions were usually lacking or, where present, inadequate because of lack of comparative precision and detail. In part because of this, and also to develop a system useful for phylogenetic analysis, a system of nomenclature of larval chaetotaxy was devised for most Dytiscidae subfamilies but the Hydrodytinae: Agabinae and Colymbetinae (Alarie 1995, 1998), Copelatinae (Michat and Torres 2009), Coptotominae (Michat and Alarie 2013), Dytiscinae (Alarie et al. 2011), Hydroporinae (Alarie et al. 1990; Alarie and Harper 1990; Alarie 1991; Alarie and Michat 2007a), Laccophilinae (Alarie et al. 2000, 2002a), Lancetinae (Alarie et al. 2002b), and Matinae (Alarie et al. 2001). The fact that all these studies were conducted separately over a period of more or less 25 years does not facilitate comparison among taxa. The main purpose of this chapter therefore is to synthesize these studies into a more comprehensive approach, which should facilitate comparison among the dytiscid subfamilies.

Dytiscid larvae are predaceous and attack a wide variety of aquatic organisms. As such they have an important impact in the dynamics of freshwater ecosystems. A corollary objective of this chapter is to exemplify how knowledge of dytiscid larvae and an ability to identify them has the potential to make the wealth of characters present in the larval stage available for ecological study.

2.2 General Morphology of Dytiscidae Larvae

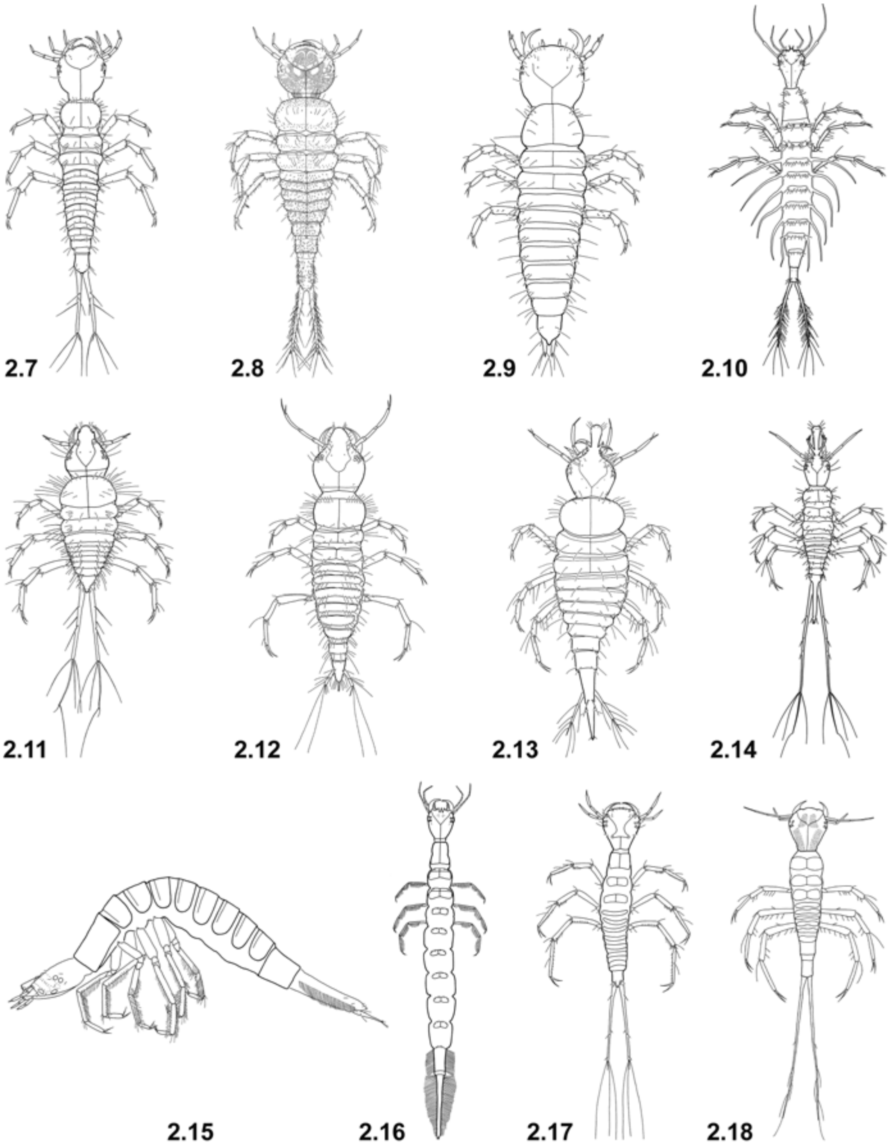
Dytiscid larvae are campodeiform with a strongly sclerotized head capsule and prognathous mouthparts. The body is variously shaped, usually elongate and fusiform, generally widest at level of metathorax or middle abdomen (Figs. 2.1–2.18). The dorsal surface of the body is usually distinctly sclerotized whereas the ventral surface is mostly membranous with sclerotized plates, if present, restricted to the most posterior segments. Sclerites are usually more pigmented than the rest of the body. Color patterns occur on the head capsule and terga of most taxa. More information on their general morphology can be found in Chap. 4 of this book.

The head capsule is strongly sclerotized and variable in shape (triangular, subquadrate, subrectangular, subtrapezoidal, rounded or pyriform (Figs. 2.19–2.24). It is divided above by a Y-shaped epicranial suture, which delimits a frontoclypeal region and two lateral epicranial plates (=parietals). An occipital suture may be present, which crosses the back of the head capsule, intersecting the stem of the epicranial suture (Fig. 2.19). The anterior margin of the frontoclypeus is usually moderately arcuate, but in some groups (e.g., the Hydroporinae) it extends anteriorly forming a median projecting lobe called the nasale (Figs. 2.23 and 2.24). The first instar of most taxa possesses a pair of spine-like tubercules or egg-bursters (*ruptor ovi* of Bertrand (1972)) usually located on the posterior half of the frontoclypeus (Figs. 2.19, 2.21 and 2.23). Each parietal bears an antennal fossa and six stemmata (absent in subterranean taxa). The antennae are elongate and are comprised of four antennomeres (Figs. 2.25–2.28). The antennomere III apically bears a sensory process, which may be short and non-apparent (Fig. 2.26) or elongate, sometimes as long as the antennomere IV (Fig. 2.28). The mandibles are well developed, narrow and falcate and in most taxa are grooved mesally as an adaptation for a liquid mode of feeding (Fig. 2.29). The maxilla usually consists of a small basal cardo, a larger stipes, a palp of three palpomeres borne on a palpifer, and a palpiform galea (Figs. 2.30 and 2.31). The galea is reduced or lacking among the Hydroporinae (Figs. 2.32 and 2.33). In some hydroporine larvae, the cardo is fused to the stipes (Fig. 2.33). There has been considerable confusion about the number of maxillary palpomeres, with the basic number of segments being three. However, the palpifer may appear to be a basal palpomere, and some Dytiscinae larvae have a secondary segmentation, which increases the apparent number of palpomeres (Fig. 2.37). Finally, the labium consists of three major parts; the basal postmentum, the apical prementum (sometimes called the mentum), and a pair of labial palps attached to the prementum by a small palpiger (Figs. 2.38–2.39). In basic form, the labial palp is composed of two palpomeres except for some Hydroporinae (e.g., *Vatellus* Sharp, *Paroster* Sharp), which have one and three, respectively.

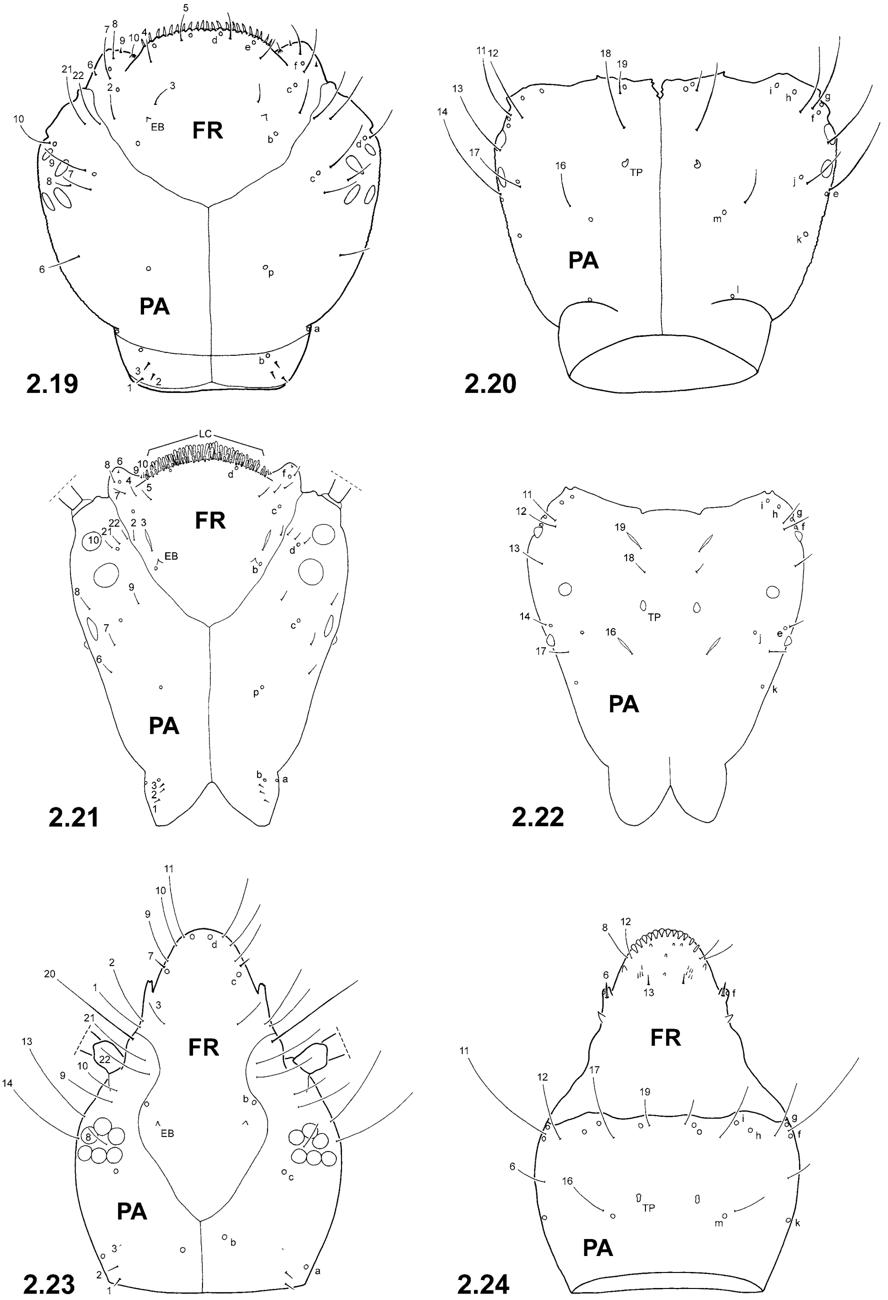
The thorax consists of three segments, the pro-, meso- and metathorax, each of which bears a pair of articulated legs (Figs. 2.1–2.18). Each segment has a large tergite and, in most specimens, a pair of smaller laterotergites associated with each leg attachment. Each tergum is usually divided at the midline by a narrow ecdysial suture (e.g., Fig. 2.7). The ventral region of the thorax is membranous except for a

Figs. 2.1–2.3 Dorsal habitus of selected Dytiscidae: (2.1) *Agabus*/*Ilybius* sp.; (2.2) *Cybister fimbriolatus*; (2.3) *Dytiscus* sp. (Courtesy of Dr. Steve Marshall, University of Guelph, ON, Canada)

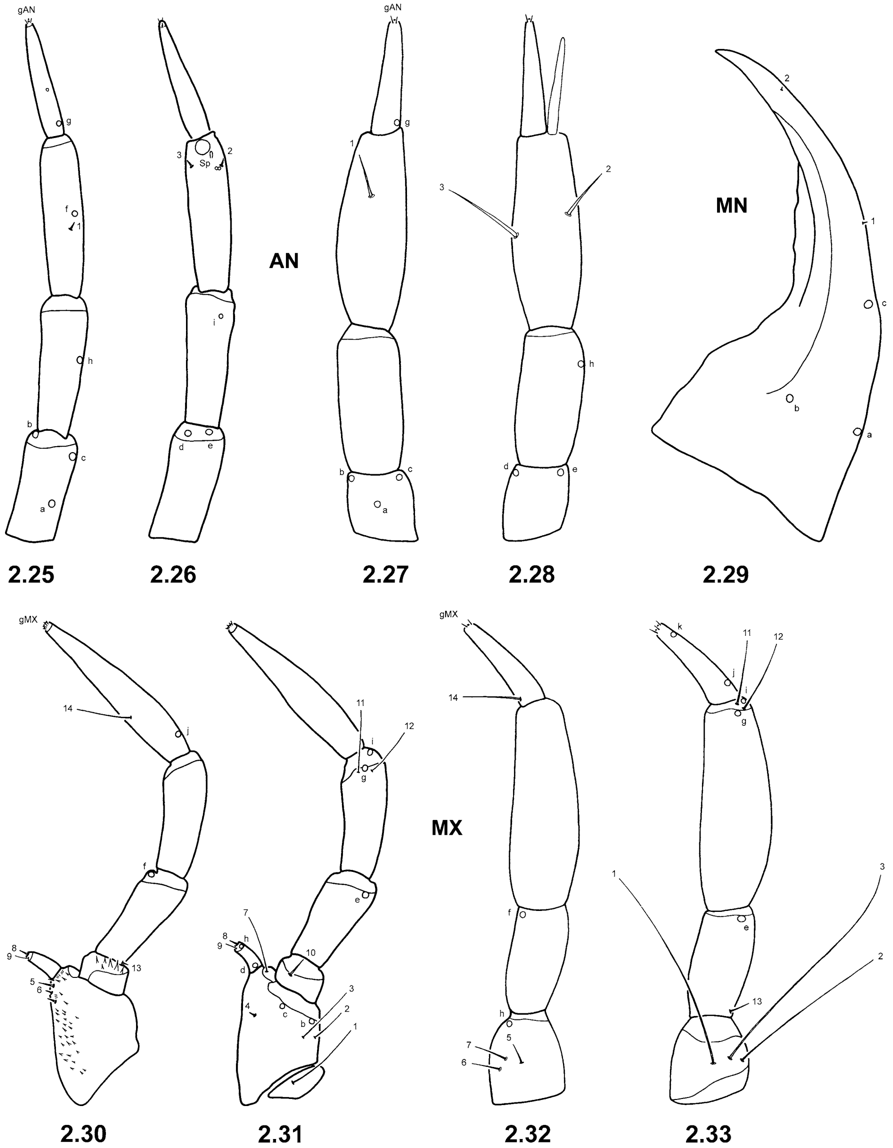
Figs. 2.4–2.6 Dorsal habitus of selected Dytiscidae: (2.4) *Hydrovatus pustulatus*; (2.5) *Laccophilus* sp.; (2.6) *Neoporus undulatus* (Courtesy of Dr. Steve Marshall, University of Guelph, ON, Canada)



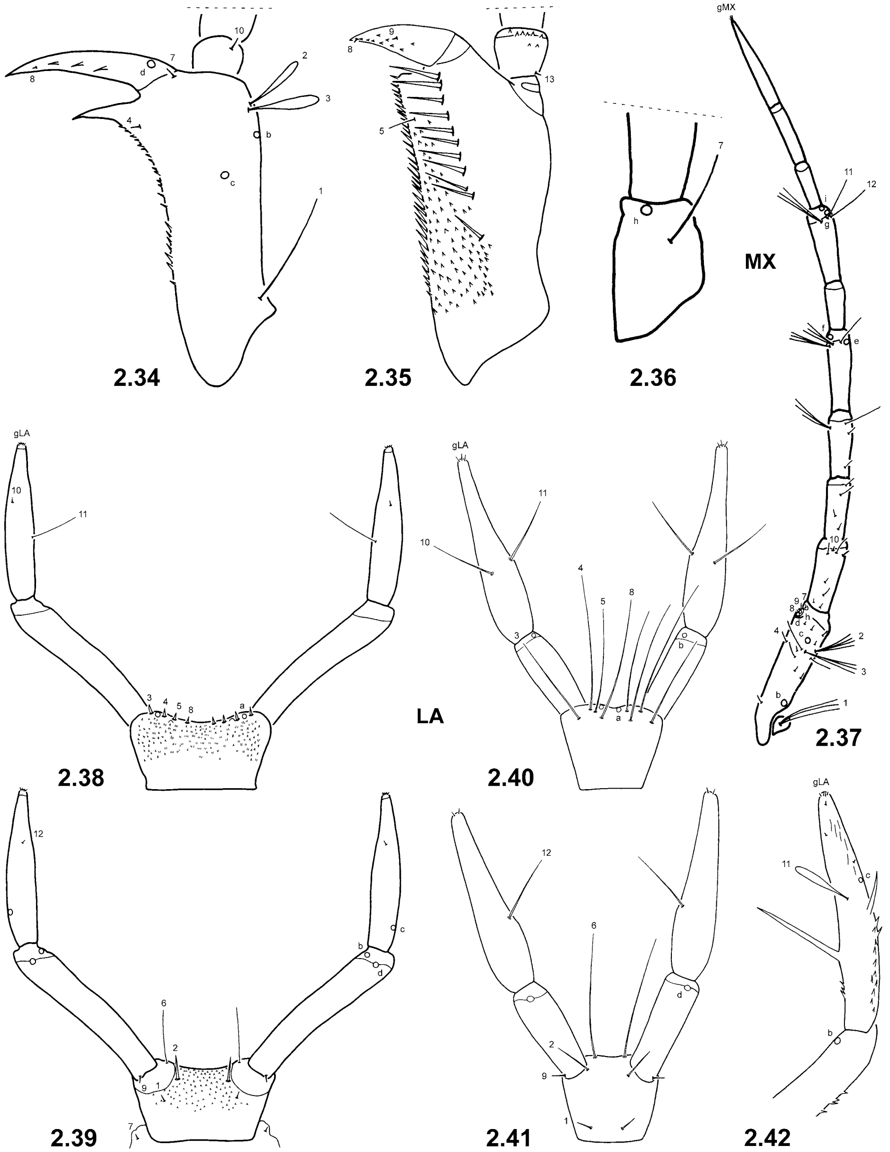
Figs. 2.7–2.18 First instars of selected species of Dytiscidae, dorsal view: (2.7) *Leuronectes curtulus*; (2.8) *Bunites distigma*; (2.9) *Copelatus longicornis*; (2.10) *Coptotomus longulus lenticus*; (2.11) *Amarodytes duponti*; (2.12) *Celina parallela*; (2.13) *Pachydrus obesus*; (2.14) *Derovatellus lentus*; (2.15) *Thermonectus succinctus*; (2.16) *Megadytes glaucus*; (2.17) *Laccophilus obliquatus*; (2.18) *Lancetes marginatus*



Figs. 2.19–2.24 Distribution of ancestral setae and pores on the cephalic capsule of first instars of selected species of Dytiscidae: (2.19–2.20) *Rhantus calileguai*, (2.19) dorsal surface, (2.20) ventral surface; (2.21–2.22) *Acilius semisulcatus*, (2.21) dorsal surface, (2.22) ventral surface; (2.23–2.24) *Anodocheilus maculatus*, (2.23) dorsal surface, (2.24) ventral surface. *EB* egg burster, *FR* frontoclypeus, *LC* lamellae clypeales, *PA* parietale, *TP* tentorial pit; numbers and lowercase letters refer to primary setae and pores, respectively (See Table 2.1 for list of setae and pores)



Figs. 2.25–2.33 Distribution of ancestral setae and pores on the head appendages of first instars of selected species of Dytiscidae: (2.25–2.26) *Leuronectes curtulus*, (2.25) right antenna, dorsal surface, (2.26) left antenna, ventral surface; (2.27–2.28) *Liodessus flavofasciatus*, (2.27) right antenna, dorsal surface, (2.28) left antenna, ventral surface; (2.29) *Leuronectes curtulus*, right mandible, dorsal surface; (2.30–2.31) *Leuronectes curtulus*, (2.30) right maxilla, dorsal surface, (2.31) left maxilla, ventral surface; (2.32–2.33) *Liodessus flavofasciatus*, (2.32) right maxilla, dorsal surface, (2.33) left maxilla, ventral surface. *AN* antenna, *MN* mandible, *MX* maxilla, *Sp* spinula; numbers and lowercase letters refer to primary setae and pores, respectively (See Table 2.2 for list of setae and pores)



Figs. 2.34–2.42 Distribution of ancestral setae and pores on the head appendages of first instars of selected species of Dytiscidae: (2.34) *Eretes australis*, stipes, ventral surface; (2.35) *Acilius semisulcatus*, stipes, dorsal surface; (2.36) *Desmopachria concolor*, stipes, dorsal surface; (2.37) *Megadytes glaucus*, left maxilla, ventral surface; (2.38–2.39) *Leuronectes curtulus*, labium, (2.38) dorsal surface, (2.39) ventral surface; (2.40–2.41) *Liodessus flavofasciatus*, labium, (2.40) dorsal surface, (2.41) ventral surface; (2.42) *Eretes australis*, labial palpomere 2, dorsal surface. *LA* labium, *MX* maxilla; numbers and lowercase letters refer to primary setae and pores, respectively (See Table 2.2 for list of setae and pores)

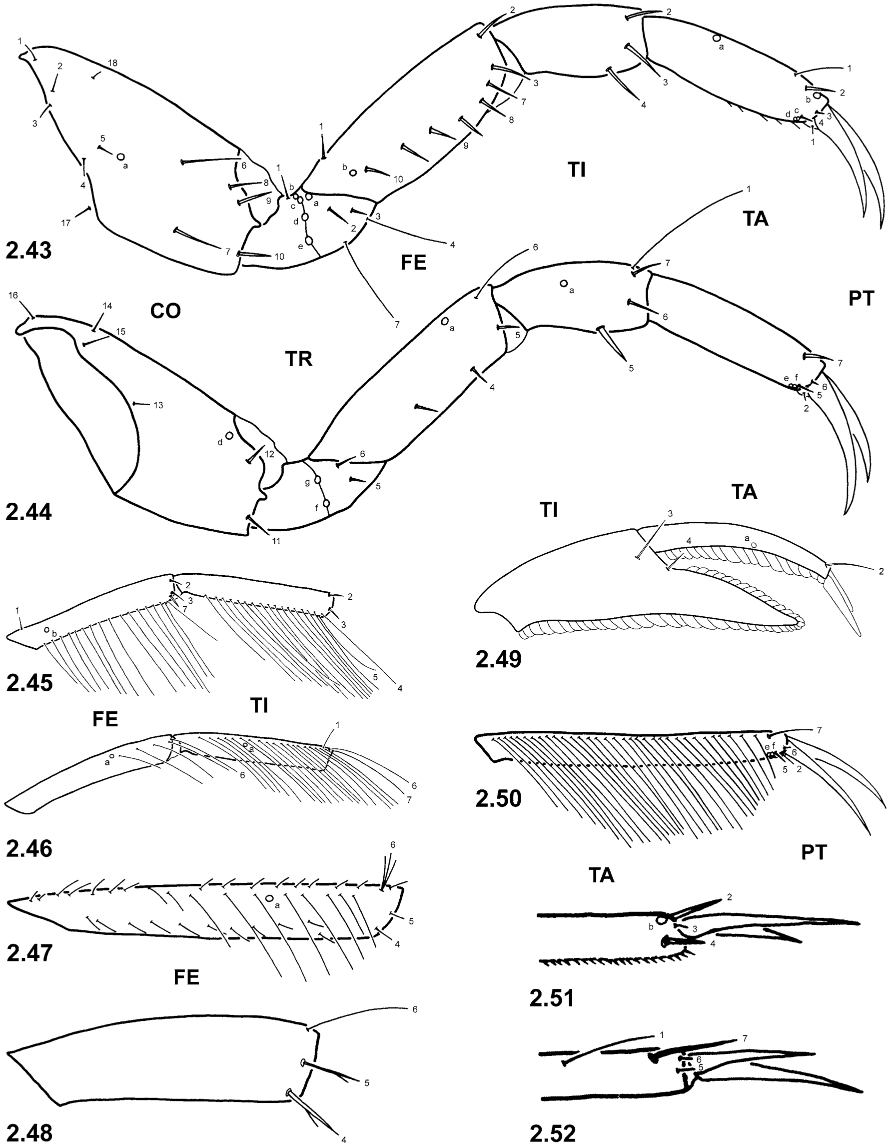
small sclerotized plate or presternum on the prothorax of some groups. One pair of spiracles is usually present on the lateral margin of the mesothorax in the third instar larva. The legs are usually long and slender, the prothoracic legs shortest, the meso- and metathoracic pairs progressively longer and are 6-segmented (sensu Lawrence 1991). The coxa and femur are the longest, and the trochanter the smallest segment (Figs. 2.43 and 2.44). The tarsal claws are usually unequal in length.

The abdomen is subcylindrical and consists of eight visible segments; segments 1–7 more or less similar in form, segment 8 variously modified for respiration (Figs. 2.1–2.18). Each segment has the dorsum consisting of a large median plate, which extends laterally slightly over the pleura. The tergal plate of segment 8 is usually extending posteriorly well beyond the origin of the urogomphi forming a prolongation of the segment called the siphon (e.g., Figs. 2.11–2.14). The ventral surface of the abdominal segments is variously sclerotized. Eight pairs of spiracles are present on the abdomen. The first seven pairs, which are present only in the third instar, are usually located laterodorsally on, or proximad to, the tergal plates. The spiracles on segment 8 are borne dorsally at the apex of the siphon, these being the only spiracles functional throughout the larval stage. The abdominal segment 8 bears a pair of terminal (or subterminal) articulated urogomphi (Figs. 2.1–2.18). These consist of one (e.g., Figs. 2.7 and 2.8) or two (e.g., Figs. 2.11–2.14) segments.

2.3 Chaetotaxy Analysis: Methodological Approach

The term ‘chaetotaxy’ is derived from two Greek words: ‘chatite’ = long hairs; and ‘taxis’ = arrangement (Gordh and Headrick 2001) and refers to the arrangement, nomenclature, or classification of setae distributed over the insect body (Nichols and Schuh 1989). As pointed out by Solodovnikov (2007), however, in the literature on beetle larvae, which considers chaetotaxy in sufficient detail (e.g., Thomas 1957; Ashe and Watrous 1984; Bousquet and Goulet 1984; Wheeler 1990; Lawrence 1991; Kovarik and Passoa 1993; Makarov 1996; Kilian 1998), the system of characters known as ‘larval chaetotaxy’ is sometimes understood more broadly to include a number of other structures such as cuticular extensions (e.g., microtrichia, setiferous tubercles, scales, spines). As defined in the context of this chapter, however, chaetotaxy is understood more narrowly as a system of setae and pores (sensillum placoidum).

The larval chaetotaxy system of the Dytiscidae developed over the past 25 years is a complex of setae and pores demonstrating some patterns in their distribution, similar to the analogous systems of designations originally described for the Carabidae (Bousquet and Goulet 1984). All these systems are based on comparative examination of a certain sample of taxa for evaluating stable versus variable elements of chaetotaxy, finding homologous structures among them, and providing those with a system of designations. Hypotheses of homology were based mainly on the criterion of similarity in position (Wiley 1981) dealing with subsets (i.e., subfamilies). This was based mainly on the assumption that, at lower taxonomic levels, it is possible to determine homology with great precision using stable subpatterns of



Figs. 2.43–2.52 Distribution of ancestral setae and pores on the legs of first instars of selected species of Dytiscidae: (2.43–2.44) *Copelatus longicornis*, metathoracic leg, (2.43) anterior surface, (2.44) posterior surface; (2.45–2.46) *Hydaticus tuyuensis*, metafemur and metatibia, (2.45) anterior surface, (2.46) posterior surface; (2.47) *Megadytes carcharias*, metafemur, posterior surface; (2.48) *Hydrovatus caraibus*, metafemur, posterior surface; (2.49) *Matus bicarinatus*, protibia and protarsus, anterior surface; (2.50) *Megadytes fallax*, metatarsus, posterior surface; (2.51–2.52) *Thermonectus succinctus*, apex of metatarsus, (2.51) anterior surface; (2.52) posterior surface. *CO* coxa, *FE* femur, *PT* pretarsus, *TA* tarsus, *TI* tibia, *TR* trochanter; numbers and lowercase letters refer to primary setae and pores, respectively (See Table 2.3 for list of setae and pores)

sensilla distribution. At the present time, chatetotaxy systems were provided for all dytiscid subfamilies except the Hydrodytinae: Agabinae and Colymbetinae (Alarie 1995, 1998), Copelatinae (Michat and Torres 2009), Coptotominae (Michat and Alarie 2013), Dytiscinae (Alarie et al. 2011), Hydroporinae (Alarie et al. 1990; Alarie and Harper 1990; Alarie 1991; Alarie and Michat 2007a), Laccophilinae (Alarie et al. 2000, 2002a), Lancetinae (Alarie et al. 2002b), and Matinae (Alarie et al. 2001).

The value of the nomenclatural system of chaetotaxy that was derived for the Dytiscidae is enhanced because it differentiates the primary setae and pores (found in the first instar) from the secondary ones, which are added in the later two instars. There is an overall primary pattern, which is widespread among taxa, though it is modified in a variety of groups. This generalized pattern is consistent enough to be used for phylogenetic analysis and yet sufficiently variable to allow for taxonomic distinction. In addition to this, secondary setae and pores added through the ontogenetic development of the larva often show specific variation in number, position, and size that may also serve taxonomic and phylogenetic purposes.

The notation of primary setae and pores of larval Dytiscidae presented in this chapter was based on the study of first instars of selected taxa belonging to different tribes and genera. Larvae of other hydradephagan families (e.g., Amphizoidae, Paelobiidae, Gyrinidae, Haliplidae, and Noteridae) were also examined for any significant differences in distribution of primary setae and pores within this group of taxa to ensure that the ground-plan pattern developed could be extrapolated to related taxa. Descriptions of larval structures were based on specimens cleared either in 10 % KOH or lactic acid and mounted on standard glass slides with either Euparal or Hoyer's medium. Microscopic examination at magnifications of 40–800× was done using an Olympus BX50 compound microscope equipped with Nomarsky differential interference optics. In these systems, each seta is coded by two capital letters corresponding to the first two letters of the name of the structure on which it is located (e.g., AB, last abdominal segment; AN, antenna; CO, coxa; FR, frontoclypeus; LA, labium) and a number. Pores are coded in a similar manner, except that the number is replaced by a lower case letter.

In the larval chaetotaxy systems proposed for the Dytiscidae, the primary setae and pores were subdivided into two categories: **ancestral**, i.e., those associated with the ancestral pattern (recognized and homologized in most or all of examined taxa), and **additional**, i.e., those evolved secondarily in the first instar (generally restricted to a genus or tribe). Only the setae and pores associated with the ancestral pattern are coded here.

2.4 Ground Plan Pattern of Primary Setae and Pores of the Dytiscidae

Analyses of the primary setae and pores of larval structures such as the head capsule, head appendages, legs, last abdominal segment, and urogomphus have been provided for all dytiscid subfamilies but the Hydrodytinae (c.f., references above).

Primary setae and pores are generally easily recognized for most species owing to their similar distribution pattern on the body parts. For some species, however, the homology of some setae and pores may be difficult owing to (1) the presence of additional setae and (or) pores, which could confuse their identification, (2) loss of setae and (or) pores, which disrupts the distribution pattern, and (3) the drastic change of position of setae and (or) pores caused in general by an important modification of the sclerite (e.g., the elongation of the frontoclypeus of the Hydroporinae into a nasale or the variability of the relative elongation of the last abdominal segment into a siphon). The system of primary setae and pores, as defined below for the family Dytiscidae, has a great potential as a source of significant systematic data. The vast number of coded setae (137) and pores (70) and their associated states provide a complex pattern of modification useful at recognizing taxa, at reconstructing phylogeny, and at building classification. The characterization of the ground plan pattern of primary setae and pores on selected structures of the Dytiscidae is based on a reconstructed, or generalized, species bearing all primary setae and pores.

2.4.1 Cephalic Capsule

Fifty-two sensilla (32 setae and 20 pores) are coded on the cephalic capsule of the Dytiscidae. These sensilla are illustrated in Figs. 2.19–2.24 and they are listed in Table 2.1.

2.4.1.1 Frontoclypeus

Thirteen setae (FR1, FR2, FR3, FR4, FR5, FR6, FR7, FR8, FR9, FR10, FR11, FR12, FR13) and five pores (FRb, FRc, FRd, FRe, FRf) compose the basal number of primary sensilla on the frontoclypeus. Except for setae FR1, FR11, FR12, and FR13, which are restricted to the subfamily Hydroporinae (Figs. 2.23 and 2.24), pore FRe, which is only found in the Colymbetinae (Fig. 2.19), Lancetinae, and some Dytiscinae (*Dytiscus* L. and *Hyderodes* Hope) and Laccophilinae (*Neptosternus* Sharp), and setae FR4 and FR5, which are lacking in the Hydroporinae, all other setae (FR2, FR3, FR4, FR6, FR7, FR8, FR9, FR10) and pores (FRb, FRc, FRd, FRf) are generalized within the Dytiscidae with few exceptions (members of *Notaticus* Zimmermann and *Eretes* Laporte (Dytiscinae), *Laccornis* Gozis (Hydroporinae) and Hyphydrini (Hydroporinae) are the only dytiscids where (1) pore FRf, (2) seta FR13 and (3) pore FRb are lacking respectively). It is worth noting that the ventroapical margin of the frontoclypeus is also characterized by the presence of a row of typical sensilla [*lamellae clypeales* of Bertrand (1972)] (Figs. 2.19, 2.21 and 2.24). These sensilla have not been included in the ground plan pattern of the frontoclypeus owing to their great variability (both in number and shape).

Table 2.1 Ancestral setae and pores on the head capsule of first instars of Dytiscidae subfamilies

Setae/pores	AGA	COL	CPL	COP	DYT	HYD	LAC	LAN	MAT
FR1	0	0	0	0	0	1	0	0	0
FR2	1	1	1	1	1	1	1	1	1
FR3	1	1	1	1	1	1	1	1	1
FR4	1	1	1	1	1	0	1	1	1
FR5	1	1	1	1	1	0	1	1	1
FR6	1	1	1	1	1	1	1	1	1
FR7	1	1	1	1	1	1	1	1	1
FR8	1	1	1	1	1	1	1	1	1
FR9	1	1	1	1	1	1	1	1	1
FR10	1	1	1	1	1	1	1	1	1
FR11	0	0	0	0	0	1	0	0	0
FR12	0	0	0	0	0	1	0	0	0
FR13	0	0	0	0	0	0/1	0	0	0
FRb	1	1	1	1	1	0/1	1	1	1
FRc	1	1	1	1	1	1	1	1	1
FRd	1	1	1	1	1	1	1	1	1
FRe	0	1	0	0	0/1	0	0/1	1	0
FRf	1	1	1	1	0/1	1	1	1	1
PA1	1	1	1	1	1	1	1	1	1
PA2	1	1	1	1	1	1	1	1	1
PA3	1	1	1	1	1	1	1	1	1
PA6	1	1	1	1	1	1	1	1	1
PA7	1	1	1	1	1	0	1	1	1
PA8	1	1	1	1	1	1	1	1	1
PA9	1	1	1	1	1	1	1	1	1
PA10	1	1	1	1	1	1	1	1	1
PA11	1	1	1	1	1	1	1	1	1
PA12	1	1	1	1	1	1	1	1	1
PA13	1	1	1	1	1	1	1	1	1
PA14	1	1	1	1	1	1	1	1	1
PA16	1	1	1	1	1	1	1	1	1
PA17	1	1	1	1	1	1	1	1	1
PA18	1	1	1	1	1	0	1	1	1
PA19	1	1	1	1	1	1	1	1	1
PA20	0	0	0	0	0	1	0	0	0
PA21	1	1	1	1	1	1	1	1	1
PA22	1	1	1	1	1	1	1	1	1
PAa	1	1	1	1	1	1	1	1	1
PAb	1	1	1	1	1	1	1	1	1
PAc	1	1	1	1	1	1	0/1	1	1
PAd	1	1	1	1	1	0/1	1	1	1
PAe	1	1	1	1	1	0/1	1	1	1
PAf	1	1	1	1	1	1	1	1	1
PAg	1	1	1	1	1	1	1	1	1
PAh	1	1	1	1	1	1	1	1	1

(continued)

Table 2.1 (continued)

Setae/pores	AGA	COL	CPL	COP	DYT	HYD	LAC	LAN	MAT
PAi	1	1	1	1	1	1	1	1	1
PAj	1	1	1	1	1	0/1	1	1	1
PAk	1	1	1	1	1	1	1	1	1
PAl	1	1	1	1	0/1	0	1	1	1
PAm	1	1	1	1	0/1	1	1	1	1
PAo	1	1	1	1	0/1	1	1	1	1
PAp	1	1	1	1	1	0	1	1	1

AGA Agabinae, *COL* Colymbetinae, *CPL* Copelatinae, *COP* Coptotominae, *DYT* Dytiscinae, *HYD* Hydroporinae, *LAC* Laccophilinae, *LAN* Lancetinae, *MAT* Matinae, *FR* frontale, *PA* parietale, *0* absent, *1* present

2.4.1.2 Parietale

Nineteen setae and 15 pores form the ancestral system of the parietale. The basal half of the sclerite bears five setae (PA1, PA2, PA3, PA6, PA7) and four pores dorsally (PAa, PAb, PAc, PAp), and three setae (PA14, PA16, PA17) and five pores (PAe, PAj, PAk, PAl, PAm) ventrally. The distal portion of the parietale bears six setae (PA8, PA9, PA10, PA20, PA21, PA22) and one pore (PAd) dorsally, and five setae (PA11, PA12, PA13, PA18, PA19) and five pores (PAf, PAg, PAh, PAi, PAo) ventrally. The primary sensilla found on this portion of the head capsule show an extremely consistent pattern within the Dytiscidae except for setae PA6 and PA18, and pores PAl and PAp, which are lacking within the Hydroporinae (Figs. 2.23 and 2.24). Pores PAm, PAo and PAl are also lacking in some genera of the dytiscine tribe Aciliini (Fig. 2.24). Hydroporine larvae are also the only dytiscid in which seta PA20 is present and pores PAd, PAe and PAj are either present or absent (Figs. 2.23 and 2.24).

2.4.2 Head Appendages

Thirty-one setae, 26 pores and three setal groups are coded on the head appendages. The sensilla observed are illustrated in Figs. 2.25–2.42 and their positions are listed in Table 2.2.

2.4.2.1 Antenna

The primary sensilla (three setae, nine pores and a sensillum group) observed on the dytiscid antenna show an extremely consistent pattern among the subfamilies studied (Figs. 2.25–2.26). This system is composed of five pores on antennomere I (ANa, ANb, ANc, ANd, ANe), two pores on antennomere II (ANh, ANi), three setae (AN1, AN2, AN3) and one pore (ANf) on antennomere III, and one lateral pore (ANg) and

Table 2.2 Ancestral setae and pores on the head appendages of first instars of Dytiscidae subfamilies

Setae/pores	AGA	COL	CPL	COP	DYT	HYD	LAC	LAN	MAT
AN1	1	1	1	1	1	1	1	1	1
AN2	1	1	1	1	1	1	1	1	1
AN3	1	1	1	1	1	1	1	1	1
ANa	1	1	1	1	1	1	1	1	1
ANb	1	1	1	1	1	1	1	1	1
ANc	1	1	1	1	1	1	1	1	1
ANd	1	1	1	1	1	1	1	1	1
ANe	1	1	1	1	1	1	1	1	1
ANf	1	1	1	1	1	0/1	0/1	1	1
ANg	1	1	1	1	1	1	1	1	1
ANh	1	1	1	1	1	0/1	1	1	1
ANi	1	1	1	1	1	0	0	1	1
MN1	1	1	1	1	1	1	1	1	1
MN2	1	1	1	1	1	1[a]	1	1	1
MNa	1	1	1	1	1	1	1	1	1
MNb	1	1	1	1	1	1	1	1	1
MNc	1	1	1	1	1	1	1	1	1
MX1	1	1	1	1	1	1	1	1	1
MX2	1	1	1	1	1	1	1	1	1
MX3	1	1	1	1	1	1	1	1	1
MX4	1	1	1	1	1	0/1	1	1	1
MX5	1	1	1	1	1	0/1	0/1	1	1
MX6	1	1	0	1	0/1	0/1	0/1	1	1
MX7	1	1	1	1	1	1	1	1	1
MX8	1	1	1	1	1	0/1	1	1	1
MX9	1	1	1	1	1	0/1	1	1	1
MX10	1	1	1	1	1	0/1	1	1	1
MX11	1	1	1	1	1	1	1	1	1
MX12	1	1	1	1	1	1	1	1	1
MX13	1	1	1	1	1	1	1	1	1
MX14	1	1	1	1	1	1	1	1	1
MXb	1	1	1	1	1	0	1	1	1
MXc	1	1	1	1	1	0	1	1	1
MXd	1	1	1	1	1	0	1	1	1
MXe	1	1	1	1	1	1	1	1	1
MXf	1	1	1	1	1	1	1	1	1
MXg	1	1	1	1	1	1	1	1	1
MXh	1	1	1	1	1	1	1	1	1
MXi	1	1	1	1	1	1	1	1	1
MXj	1	1	1	1	1	1	1	1	1
MXk	0	0	0	0	0	1	0	0	0
LA1	1	1	1	1	1	1	1	1	1
LA2	1	1	1	1	1	1	1	1	1
LA3	1	1	1	1	1	0/1	0/1	1	1
LA4	1	1	1	1	1	1	1	1	1

(continued)

Table 2.2 (continued)

Setae/pores	AGA	COL	CPL	COP	DYT	HYD	LAC	LAN	MAT
LA5	1	1	1	1	1	1	1	1	1
LA6	1	1	1	1	1	1	1	1	1
LA7	1	1	1	1	0	1	1	1	1
LA8	1	1	1	1	0/1	1	1	1	1
LA9	1	1	1	1	1	1	1	1	1
LA10	1	1	1	0	1	0/1	0	1	1
LA11	1	1	1	1	1	1	1	1	1
LA12	1	1	1	0	1	0/1	0	1	1
LAa	1	1	1	1	1	1	1	1	1
LAb	1	1	1	1	1	0/1	1	1	1
LAc	1	1	1	1	1	0	1	1	1
LAd	1	1	1	1	1	0/1	1	1	1

AGA Agabinae, *COL* Colymbetinae, *CPL* Copelatinae, *COP* Coptotominae, *DYT* Dytiscinae, *HYD* Hydroporinae, *LAC* Laccophilinae, *LAN* Lancetinae, *MAT* Matinae, *AN* antenna, *LA* labium, *MN* mandible, *MX* maxilla, *0* absent, *1* present

[a]Coded as MNd in Alarie (1991)

a setal group composed of 2–3 small apical setae and possibly a pore (gAN) on antennomere IV. Antennomere III is also characterized by the presence/absence of a ventroapical spinula (Fig. 2.26). Laccophilinae and Hydroporinae are unique among the Dytiscidae in that here the pore ANi is lacking and the pore ANf is either present or absent (Figs. 2.27–2.28). Within the Hydroporinae pore ANh is either present or absent among genera.

2.4.2.2 Mandible

Two setae (MN1, MN2) and three pores (MNa, MNb, MNc) are coded on the mandible of every dytiscid species known as larva (Fig. 2.29). Seta MN1 is more difficult to homologize in Cybistrini (Dytiscinae) owing to the presence of several additional setae, whereas seta MN2 is minute and pore-like in most Hydroporinae.

2.4.2.3 Maxilla

Fourteen primary setae, ten primary pores and one setal group are coded on the maxilla of the Dytiscidae (Figs. 2.30 and 2.31). One seta (MX1) is either found on the cardo (where present) or the stipes. Six setae (MX2, MX3, MX4, MX5, MX6, MX7) and two pores (MXb, MXc) are the basal number of sensilla on the maxillary stipes. Two setae (MX8, MX9) and 2 pores (MXd, MXh) appear on the galea (except in Hydroporinae and Cybistrini where they are either absent (Fig. 2.32) or located on the stipes (Fig. 2.37)). Five setae, five pores, and a setal group occur on the palpus: one seta (MX10) on palpifer; one seta (MX13) and two pores (MXe, MXf) on palpolmere I; two setae (MX11, MX12) and two pores (MXg, MXi) on palpomere II; one seta (MX14), one pore (MXj) and a setal group (gMX) on palpomere III. This generalized pattern is fairly consistent within the family except for the subfamily Hydroporinae and several members of the subfamily Dytiscinae. Indeed the primary pores MXb, MXc, and MXd and to a lesser extent setae MX4 and MX10 are lacking within the Hydroporinae, which is likely correlated with the absence or reduction of the galea, an unusual feature within the Dytiscidae (Alarie and Michat 2007a) (Figs. 2.32 and 2.33). Unique features observed in some Dytiscinae are: (1) the presence of several elongate and spine-like setae along the dorsal margin of the stipes (Aciliini and Eretini) (Fig. 2.35); (2) the presence of several additional setae on the stipes, palpifer and palpi in the Cybistrini (Fig. 2.37); (3) setae either multifid (Cybistrini) (Fig. 2.37) or lanceolate (Eretini) (Fig. 2.34). It is worth noting that either of setae MX5 and MX6 or both are sometimes lacking (e.g., Dytiscinae (Aciliini and Eretini), Copelatinae, Laccophilinae (*Neptosternus*) and Hyphydrini (Fig. 2.36)). The primary pore MXk is restricted to the Hydroporinae (Fig. 2.33).

2.4.2.4 Labium

Twelve primary setae, four primary pores, and one setal group are coded on the labium (Figs. 2.38 and 2.39). The prementum is characterized by the presence of seven setae (LA1, LA2, LA3, LA4, LA5, LA6, LA8) and one pore (LAa). Four setae, three pores, and a setal group appear on the labial palpus: one small seta (LA9) and two pores (LAb, LAd) on palpomere I; three setae (LA10, LA11, LA12), a setal group (gLA), and one pore (LAc) on palpomere II. Setae LA10 and LA12 are lacking in the Coptotominae, Laccophilinae, and Vatellini, and are most often minute and very difficult to see in the Agabinae, Colymbetinae, Copelatinae, Dytiscinae, and Lancetinae (Figs. 2.38 and 2.39). Pore LAc is consistently lacking within the Hydroporinae (Figs. 2.40 and 2.41). Larvae of Eretini and members of the tribe Cybistrini (Dytiscinae) differ from all other Dytiscidae in that here the seta LA11 is lanceolate (Fig. 2.42) and the setae LA2, LA6 and LA11 are multifid, respectively. It is worth stressing that the seta LA8 is sometimes absent within some members of the subfamily Dytiscinae (*Notaticus*, *Dytiscus* and *Megadytes carcharias* Griffini) and that the seta LA3 is absent in some Hydroporinae (Hydrovatini, Methlini) and Laccophilinae (Laccophilini). The pores LAb and LAd are absent in members of the hydroporine tribes Hyphydrini and Vatellini, respectively.

2.4.3 Legs

Sixty-nine sensilla (51 setae and 18 pores) are coded on the leg of the Dytiscidae. These sensilla are illustrated in Figs. 2.43–2.52 and they are listed in Table 2.3.

Table 2.3 Ancestral setae and pores on the legs of first instars of Dytiscidae subfamilies

Setae/pores	AGA	COL	CPL	COP	DYT	HYD	LAC	LAN	MAT
CO1	1	1	1	1	1	1	1	1	1
CO2	1	1	1	1	1	1	1	1	1
CO3	1	1	1	1	1	1	1	1	1
CO4	1	1	1	1	1	1	1	1	1
CO5	1	1	1	1	1	1	1	1	1
CO6	1	1	1	1	1	1	1	1	1
CO7	1	1	1	1	1	1	1	1	1
CO8	1	1	1	1	1	1	1	1	1
CO9	1	1	1	1	1	1	1	1	1
CO10	1	1	1	1	1	1	1	1	1
CO11	1	1	1	1	1	1	1	1	1
CO12	1	1	1	1	1	1	1	1	1
CO13	1	1	1	1	1	1	1	1	1
CO14	1	1	1	1	1	1	1	1	1
CO15	1	1	1	1	1	1	1	1	1
CO16	1	1	1	1	1	1	1	1	1
CO17	1	1	1	1	1	1	1	1	1
C018	1	1	1	1	1	1	1	1	1
COa	1	1	1	1	1	0/1	1	1	1
COd	1	1	1	1	1	1	1	1	1
TR1	1	1	1	1	1	1	1	1	1
TR2	1	1	1	1	0/1	0/1	1	1	1
TR3	1	1	1	1	1	0	1	1	1
TR4	1	1	1	1	1	1	1	1	1
TR5	1	1	1	1	1	1	1	1	1
TR6	1	1	1	1	1	1	1	1	1
TR7	1	1	1	1	1	1	1	1	1
TRa	1	1	1	1	1	1	1	1	1
TRb	1	1	1	1	1	1	1	1	1
TRc	1	1	1	1	1	1	1	1	1
TRd	1	1	1	1	1	1	1	1	1
TRe	1	1	1	1	1	1	1	1	1
TRf	1	1	1	1	1	1	1	1	1
TRg	1	1	1	1	1	1	1	1	1
FE1	1	1	1	1	1	1	1	1	1
FE2	1	1	1	1	1	1	1	1	1
FE3	1	1	1	1	1	1	1	1	1
FE4	1	1	1	1	0/1	1	1	1	1
FE5	1	1	1	1	0/1	1	1	1	1
FE6	1	1	1	1	1	1	1	1	1
FE7	1	1	1	1	1	1	1	1	1
FE8	1	1	1	1	1	1	1	1	1
FE9	1	1	1	1	1	1	1	1	1
FE10	1	1	1	1	1	1	1	1	1
FEa	1	1	1	1	1	0/1	1	1	1

(continued)

Table 2.3 (continued)

Setae/pores	AGA	COL	CPL	COP	DYT	HYD	LAC	LAN	MAT
FEb	1	1	1	1	1	1	1	1	1
TI1	1	1	1	1	1	1	1	1	1
TI2	1	1	1	1	1	1	1	1	0/1
TI3	1	1	1	1	1	1	1	1	1
TI4	1	1	1	1	1	1	1	1	1
TI5	1	1	1	1	1	1	1	1	1
TI6	1	1	1	1	1	1	1	1	0/1
TI7	1	1	1	1	1	1	1	1	1
TIa	1	1	1	1	1	1	1	1	1
TA1	1	1	1	1	1	1	1	1	1
TA2	1	1	1	1	1	1	1	1	1
TA3	1	1	1	1	1	1	1	1	1
TA4	1	1	1	1	1	1	1	1	1
TA5	1	1	1	1	1	1	1	1	1
TA6	1	1	1	1	1	1	1	1	1
TA7	1	1	1	1	1	1	1	1	1
TAa	1	1	1	1	1	1	1	1	1
TAb	1	1	1	1	1	1	1	1	1
TAc	1	1	1	1	0/1	1	1	1	1
TAd	1	1	1	1	0/1	1	1	1	1
TAe	1	1	1	1	0/1	1	1	1	1
TAf	1	1	1	1	0/1	1	1	1	1
PT1	1	1	1	1	0/1	1	1	1	1
PT2	1	1	1	1	0/1	1	1	1	1

AGA Agabinae, *COL* Colymbetinae, *CPL* Copelatinae, *COP* Coptotominae, *DYT* Dytiscinae, *HYD* Hydroporinae, *LAC* Laccophilinae, *LAN* Lancetinae, *MAT* Matinae, *CO* coxa, *FE* femur, *PT* pretarsus, *TA* tarsus, *TI* tibia, *TR* trochanter, *0* absent, *1* present

2.4.3.1 Coxa

Eighteen setae and two pores compose the basal number of primary sensilla on the coxa (Figs. 2.43 and 2.44). Eleven small setae (CO1, CO2, CO3, CO4, CO5, CO13, CO14, CO15, CO16, CO17, CO18) and one pore (COa) appear on the proximal portion of the segment. Seven setae (CO6, CO7, CO8, CO9, CO10, CO11, CO12) and one pore (COd) appear on the distal portion. This pattern is quite uniform within the taxa studied. The only differences observed are the absence of pore COa in Pachydrini (Hydroporinae), and the relative positions of setae CO6 and CO7 and pore COd.

2.4.3.2 Trochanter

Seven setae and seven pores are coded on the Dytiscidae trochanter (Figs. 2.43 and 2.44). One seta (TR1) and one pore (TRb), and two hair-like setae (TR4, TR7) appear on the dorsal and ventral margin respectively. The anterior surface is composed of two setae (TR2, TR3) and four pores (TRa, TRc, TRd, TRe) whilst the posterior surface is characterized by the presence of two setae (TR5, TR6) and two pores (TRf, TRg). The seta TR3 is lacking within the Hydroporinae, whilst the seta TR2 is either present or absent amongst the Dytiscinae and the Hydroporinae.

2.4.3.3 Femur

Ten setae and two pores characterize this segment (Figs. 2.43 and 2.44). Seven setae (FE1, FE2, FE3, FE7, FE8, FE9, FE10) and one pore (FEb) appear on the anterior surface of the segment. Three setae (FE4, FE5, FE6) and one pore (FEa) are coded on the posterior surface. Setae FE4 and/or FE5 are lacking in some Dytiscinae (Aciliini, Aubehydrini, Dytiscini and Hydaticini) (Fig. 2.46), whilst pore FEa is absent in some tribes of Hydroporinae (e.g., Bidessini, Hydrovatini, Hyphydrini, Laccornini, and some Hydroporini) (Fig. 2.48). It is worth noting that the Dytiscinae larvae are characterized by the presence of a variable number of additional hair-like natatory setae along both the anteroventral and posterodorsal margins of the femur (Figs. 2.45 and 2.46) and that seta FE6 is multifid within the tribe Cybistrini (Fig. 2.47).

2.4.3.4 Tibia

Seven setae and one pore are coded on the tibia (Figs. 2.43 and 2.44). Three setae (TI2, TI3, TI4) are on the anterior surface and four setae (TI1, TI5, TI6, TI7) and one pore (TIa) are on the posterior surface. Setae TI2 and/or TI6 are absent in some Matinae (Fig. 2.49). The ventral margin of the tibia is characterized by the presence of spinulae, which are generally more strongly developed on the protibia. Larvae of *Matus* Aubé (Matinae) are unique in that regard by the presence of characteristic feather-like spinulae on pro- and mesotibiae (Fig. 2.49). Larvae of the Dytiscinae are characterized by the presence of a row of additional natatory setae on posterodorsal and anteroventral surfaces (Figs. 2.45 and 2.46).

2.4.3.5 Tarsus

Seven setae and six pores are coded on the tarsus (Figs. 2.43 and 2.44). Three setae (TA2, TA3, TA4) and two pores (TAc, TAd) occur on the anterior surface and four setae (TA1, TA5, TA6, TA7) and two pores (TAe, TAf) are found posteriorly. Two other pores (TAa, TAb) are inserted dorsally. The individual pores of the pairs TAc/TAd and TAe/TAf are generally present (except within the tribe Aciliini (Dytiscinae) (Figs. 2.51 and 2.52)) but very difficult to distinguish in some taxa because they are positioned close together and because the ventral margin of the tarsus is generally marked by a pronounced thickening of the marginal spinulae. The pore TAb is also very difficult to locate because of both its apical position and the presence of setae TA2 and TA7. The seta TA1 is generally inserted dorso-apically, and is extremely short and hair-like in some taxa. Members of the tribe Cybistrini (Dytiscinae) are characterized by a row of additional natatory setae on the posterodorsal surface (Fig. 2.50).

2.4.3.6 Pretarsus

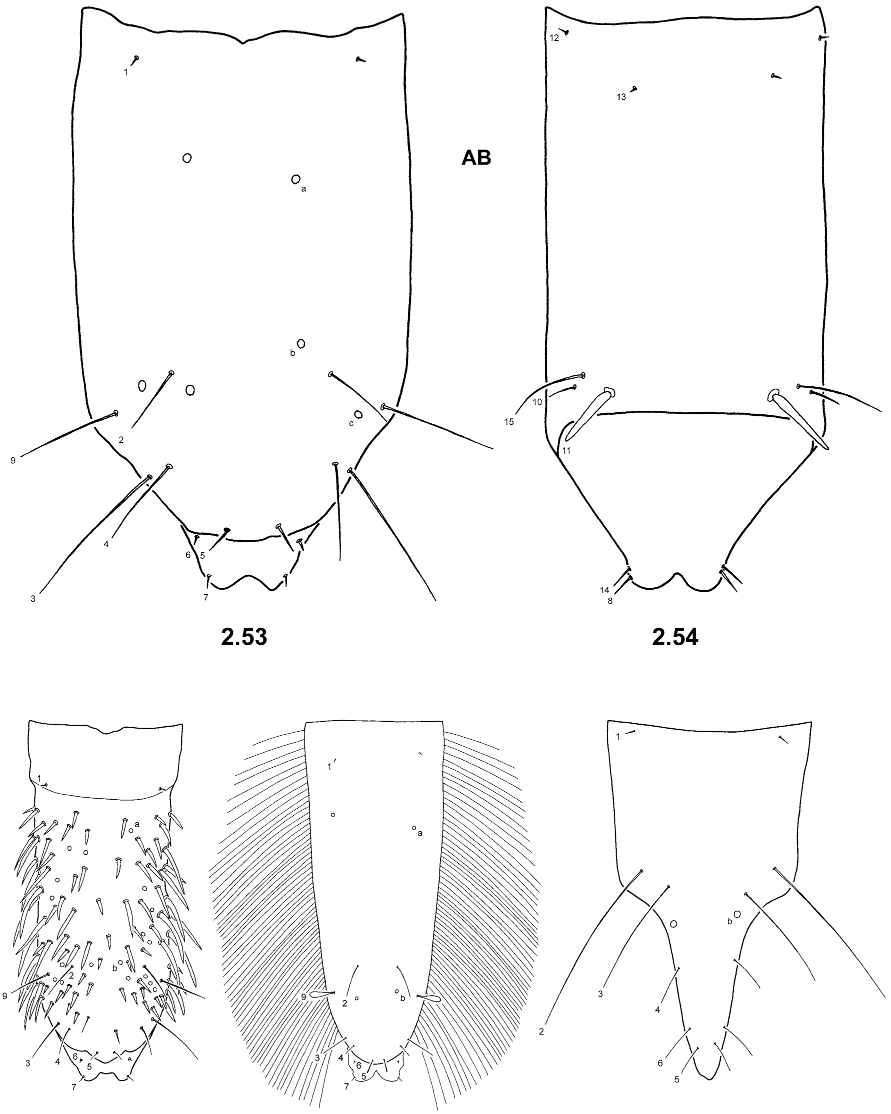
Two short spiniform setae are located basally on the ventral surface of the pretarsus (Figs. 2.43 and 2.44), except within the tribe Aciliini (Dytiscinae) (Figs. 2.51 and 2.52). These may be overlooked easily and incorporated into the row of spinulae of the tarsus.

2.4.4 Last Abdominal Segment

The ground plan pattern of primary setae and pores on the last abdominal segment of the Dytiscidae is illustrated in Figs. 2.53 and 2.54 and the sensilla observed are listed in Table 2.4. Fifteen setae and three pores have been coded. Three minute setae (AB1, AB12, AB13) and one pore (ABa) occur on the anterior portion of the segment. The remaining 12 setae and two pores are inserted posteriorly. Setae AB2, AB3, AB4, AB5, AB6, and AB7 along with pores ABb and ABc are dorsal. Their relative distribution varies among taxa more than likely in correlation to the relative elongation of the segment posteriorly (i.e., siphon). Setae AB8, AB9, AB10, AB11, AB14 and AB15 are ventral although seta AB9 may be more dorsally articulated in some taxa. Because of their small size, marginal position, and spine-like appearance, setae AB7, AB8 and AB14 (=pore ABd within the Hydroporinae) are often extremely difficult to distinguish from the spine-like microsculptures of the siphon. The primary setae AB2, AB6, AB7, AB8, AB13, AB14 and AB15, and the primary pores ABa and ABc are either present or absent amongst the Dytiscinae, Coptotominae, Hydroporinae and Laccophilinae (Figs. 2.56 and 2.57). Larvae of all Dytiscinae are characterized by the presence of several additional elongate hair-like (natatory) setae along the lateral margin (Fig. 2.56). Larvae of Aciliini and Eretini (Dytiscinae) are unique amongst the Dytiscidae in having the seta AB9 lanceolate (Fig. 2.56). Larvae of Matinae, Cybistrini, and some Colymbetinae (*Bunites* Spangler, *Meladema* Laporte, *Neoscutopterus* J. Balfour-Browne) are characterized by the presence of numerous additional setae (Fig. 2.55).

2.4.5 Urogomphus

The primary sensilla (eight setae and three pores) observed on the urogomphus also show an extremely consistent pattern within the family Dytiscidae. They are represented in Figs. 2.58–2.66 and listed in Table 2.4. Their relative distribution relies upon



2.53 2.54

2.55 2.56 2.57

Figs. 2.53–2.57 Distribution of ancestral setae and pores on the last abdominal segment of first instars of selected species of Dytiscidae: (2.53–2.54) *Rhantus calileguai*, (2.53) dorsal surface, (2.54) ventral surface; (2.55) *Bunites distigma*, dorsal surface; (2.56) *Eretes australis*, dorsal surface; (2.57) *Anodocheilus maculatus*, dorsal surface. AB, abdominal segment 8; numbers and lowercase letters refer to primary setae and pores, respectively (See Table 2.4 for list of setae and pores)

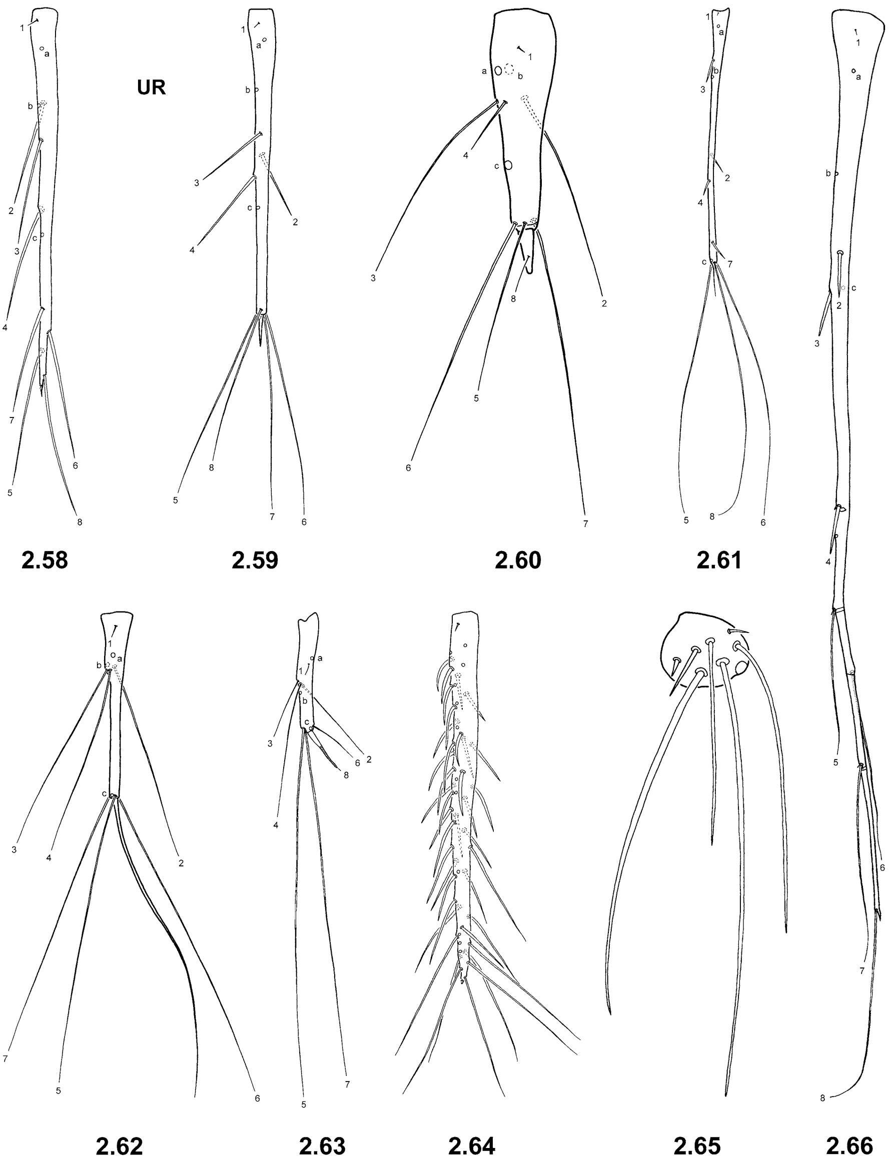
Table 2.4 Ancestral setae and pores on the last abdominal segment and the urogomphus of first instars of Dytiscidae subfamilies

Setae/pores	AGA	COL	CPL	COP	DYT	HYD	LAC	LAN	MAT
AB1	1	1	1	1	1	1	1	1	1
AB2	1	1	1	1	1	0/1	1	1	1
AB3	1	1	1	1	1	1	1	1	1
AB4	1	1	1	1	1	1	1	1	1
AB5	1	1	1	1	1	1	1	1	1
AB6	1	1	1	1	0/1	1	1	1	1
AB7	1	1	1	1	1	0/1	1	1	1
AB8	1	1	1	1	1	0/1	1	1	1
AB9	1	1	1	1	1	1	1	1	1
AB10	1	1	1	1	1	1	1	1	1
AB11	1	1	1	1	1	1	1	1	1
AB12	1	1	1	1	1	1	1	1	1
AB13	1	1	1	0	0/1	1	1	1	1
AB14	1	1	0	1	1	1[a]	0/1	1	1
AB15	1	1	1	1	1	0/1	0/1	1	1
ABa	1	1	1	1	1	0/1	1	1	1
ABb	1	1	1	1	1	1	1	1	1
ABc	1	1	1	0	0/1	0/1	0/1	1	1
UR1	1	1	1	1	1	1	1	1	1
UR2	1	1	1	1	1	1	1	1	1
UR3	1	1	1	1	1	1	1	1	1
UR4	1	1	1	1	1	1	1	1	1
UR5	1	1	1	1	1	1	1	1	1
UR6	1	1	1	1	1	1	1	1	1
UR7	1	1	1	1	1	1	1	1	1
UR8	1	1	1	1	1	0/1	1	1	1
URa	1	1	1	1	1	1	1	1	1
URb	1	1	1	1	0/1	0/1	1	1	1
URc	1	1	1	1	0/1	1	1	1	1

AGA Agabinae, *COL* Colymbetinae, *CPL* Copelatinae, *COP* Coptotominae, *DYT* Dytiscinae, *HYD* Hydroporinae, *LAC* Laccophilinae, *LAN* Lancetinae, *MAT* Matinae, *AB* last abdominal segment, *UR* urogomphus, *0* absent, *1* present

[a] Pore ABd in Hydroporinae

the shape of the urogomphus, which is either one- (e.g., Figs. 2.58, 2.64–2.66) or two-segmented (e.g., Figs. 2.59–2.63). These sensilla are subdivided into three groups. A proximal group is composed of a small spine-like seta (UR1) and a pore (URa) near the base of the urogomphus. Both may be overlooked depending upon the shape of the siphon. The median group is composed of three spine-like setae (UR2, UR3, UR4) and one pore (URb). These setae are variably articulated among taxa. The distal group of primary urogomphal sensilla is composed of four setae (UR5, UR6, UR7, UR8) and one pore (URc). Seta UR8 is inserted on the urogomphomere 2 in Copelatinae (Fig. 2.60) and Hydroporinae (Figs. 2.62–2.63). In some hydroporines (*Canthyporus* Zimmermann, *Laccornellus* Roughley & Wolfe, *Hydrovatus* Motschulsky) it is absent



Figs. 2.58–2.66 Distribution of ancestral setae and pores on the left urogomphus of first instars of selected species of Dytiscidae: (2.58) *Rhantus antarcticus nahueli*, dorsal surface; (2.59) *Leuronectes curtulus*, dorsal surface; (2.60) *Copelatus longicornis*, dorsal surface; (2.61) *Laccophilus obliquatus*, dorsal surface; (2.62) *Laccornellus lugubris*, dorsal surface; (2.63) *Celina parallela*, dorsal surface; (2.64) *Bunites distigma*, dorsal surface; (2.65) *Megadytes glaucus*, ventral surface; (2.66) *Lancetes marginatus*, dorsal surface. *UR* urogomphus; numbers and lowercase letters refer to primary setae and pores, respectively (See Table 2.4 for list of setae and pores)

(Fig. 2.62). Pores URb and/or URc are lacking within the Cybistrini (Fig. 2.65) and some Hydroporinae (URb in *Desmopachria* Babington). Larvae of some Dytiscinae (Dytiscini, Hyderodini) differ from other Dytiscidae by the presence of elongate hair-like (natatory) setae along the outer margin. Several Colymbetinae are characterized by the presence of numerous additional spine-like setae (Fig. 2.64).

2.5 Larval Chaetotaxy and Ontogeny

The value of the nomenclatural system of chaetotaxy that was derived for the Dytiscidae over the past 25 years is enhanced because it differentiates the primary setae and pores from the secondary ones that are added through the ontogenetic development of the larva. Secondary setae often show specific variation in number, position, and size that may also serve taxonomic and phylogenetic purposes. This is best illustrated by comparing the secondary chaetotaxy of the legs of selected species of the subfamily Hydroporinae.

The Hydroporinae is a large, heterogeneous grouping of minute to small dytiscid species (adult length 1.00–7.10 mm) comprised of about 100 genera worldwide (Nilsson 2001). In terms of primary setae and pores, the Hydroporinae legs show a generally consistent pattern including 50 setae and 18 pores (Table 2.3). Larvae of Hydroporinae, however, are quite variable in regard to both the number and the shape of secondary setae. Indeed, some species (e.g., *Oreodytes babai* (Satô) and *O. quadrimaculatus* (Horn) (tribe Hydroporini)) are characterized by the presence of secondary spine-like setae, which may vary both in position and number. Other species, such as *Hygrotus farctus* (Horn) (tribe Hygrotini) and *Hyphydrus ovatus* (L.) (tribe Hyphydrini) differ from both these species in that here a variable number of elongate and hair-like setae (which are deemed to play a role at enhancing the swimming propensity and as such are called ‘natatory setae’) are added in addition to the secondary spine-like setae. We stress that these natatory setae may also vary both in number and position. Larvae of *H. farctus* can easily be distinguished from those of *H. ovatus* by the much lower number of natatory setae. Moreover, both species may readily be distinguished in that the natatory setae are only located on the tibiae and tarsi in the former one compared to the femora, tibiae, and tarsi in *H. ovatus*. One of the most intriguing character states in regards to the secondary leg chaetotaxy of the Hydroporinae, however, can be found within the tribe Pachydrini. Indeed, larvae of the genus *Pachydrus* Sharp differ from any other member of the Hydroporinae in that here the secondary natatory setae are all articulated along the ventral margin of the femora.

2.6 Bridging Ecology and Systematics

Knowledge of insect larvae and an ability to identify them is important to anyone concerned with natural ecosystems and related subjects; yet the larva, undoubtedly, is the most important ecological and biological phase of insect life history. One item of practical significance related to this is that association of larvae with adults has the potential to make the wealth of characters present in the larval stage available for ecological study. This was well illustrated by a recent study emphasizing the functional role of the larvae of *Graphoderus liberus* (Say) (Dytiscinae) in Canadian Shield lakes recovering from acidification (Arnott et al. 2006, also see Chaps. 7 and 10 in this book).

Regional acidification of aquatic habitats has provided insights on direct and indirect effects of disturbance on food webs and information factors influencing recovery, once a disturbance is removed (Yan et al. 2003). The consequences of acidification for the aquatic biota are severe and include decreased population abundance or local extirpation of many species (Baker and Christensen 1991). Macroinvertebrate and fish assemblages are shaped by acidification when acid-sensitive species are lost or reduced in abundance and acid-tolerant species flourish (McNicol et al. 1995; Carbone et al. 1998; Ledger and Hildrew 2005). Arnott et al. (2006) examined the distribution of aquatic beetle assemblages in 29 lakes of varying pH resulting from historical acid deposition. In many of those lakes, fish populations had been lost because of acid deposition originating from nearby metal smelters. One of their objectives was to determine if water beetle predation could pose a barrier to recovery of other components of the food web, such as crustacean zooplankton. Whereas a weak relationship between pH and water beetle richness was observed, the ability to identify dytiscid larvae allowed Arnott et al. (2006) to recognize that in the Canadian Boreal Shield fishless lakes, larvae of *G. liberus* are abundant and can have high feeding rates on crustacean zooplankton decreasing both its richness and diversity. It is worth stressing that an ability to identify the larvae of *G. liberus* assisted in providing evidence that this species thrives in the absence of fish and plays an important role in structuring recovering crustacean zooplankton communities, which could prevent ultimate recovery of aquatic food webs.

2.7 Summary and Future Directions

The study of the larval morphology of the Dytiscidae over the past 25 years demonstrated that a combination of careful attention to detail, thorough consideration of understudied character sets, and appropriate application of phylogenetic theory and methodology can lead to significant advances in our understanding of biodiversity. Such research has demonstrated the power of larval morphology, with its inherent chaetotaxic analysis, as a tool for testing hypotheses of phylogenetic relationships not only of the Dytiscidae (e.g., Alarie et al. 2000, 2001, 2002a, b, 2011; Michat 2006, 2010; Michat and Alarie 2009) but also of other Hydradephaga (Paelobiidae: Alarie et al. 2004; Aspidytidae: Alarie and Bilton 2005; Meruidae: Alarie et al. 2011). Such studies demonstrated that larval structures could be used in phylogenetic reconstruction as a surrogate to adult structures, which have been the traditional cornerstone of systematic biology and subsequent classifications (see Chap. 3 in this book). It is generally held that the more characters support a clade, the more plausible is the hypothesis that the clade represents a natural group

(DeSalle and Brower 1997). A more rigorous and stable classification will result from combining different characters from many life stages (Williamson 1992; Wiley 1981). When a phylogenetic hypothesis is supported by several independent lines of evidence, we gain confidence in it as an estimate of phylogenetic history. There is a relative increase in the probability of a tree being true if separate hypotheses of phylogeny from various data sets are congruent with one another. It is an analogue to an increase in statistical power (Lanyon 1993). Thus far, many established views concerning the taxonomic structure of the Dytiscidae have been challenged (e.g., Alarie and Michat 2007b; Michat et al. 2007). The continued analyses of larvae of these taxa and those of related groups may possibly lead to a revision of our views on how they are taxonomically organized.

One item of practical significance in studying larval morphology is that association of aquatic beetle larvae with adults has the potential to make the wealth of characters present in the larval stage available for ecological and evolutionary study. From an applied viewpoint, the many aquatic ecologists who employ dytiscid beetles in their studies are now in a position to interpret their results from an evolutionary perspective. A central tenet emerging from historical analyses of the evolution of morphology is that hypotheses about how these general patterns are generated may only be tested within an explicit phylogenetic framework, which has been the main output of the research conducted on the larval morphology of the beetle family Dytiscidae over the past recent years.

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Chapter 3
The Phylogeny and Classification of Predaceous Diving Beetles

Kelly B. Miller and Johannes Bergsten

> *The phylogenetic system may be regarded for inherent reasons as the general reference system of biology.*
>
> Willi Hennig (translated from German)

Abstract The phylogenetics and higher (family-group) classification of extant members of the beetle family Dytiscidae (Coleoptera), or predaceous diving beetles, is reviewed and reassessed. A phylogenetic analysis of the family is presented based on 168 species of diving beetles and 9 outgroup taxa from Gyrinidae, Noteridae, Amphizoidae and Paelobiidae. All currently recognized dytiscid subfamilies and tribes are represented, most by multiple genera and species. Data include 104 morphological characters and approximately 6,700 aligned bases from 9 DNA sequence fragments from *cytochrome c oxidase I* (COI) and *II* (COII), *histone III* (H3), *16S rRNA* (16S), *12S rRNA* (12S), *arginine kinase* (argkin), *RNA polymerase II* (RNA pol II), *elongation factor 1 alpha* (Ef1α), and *wingless* (wnt). Parsimony and Bayesian analyses were conducted. The topology of the parsimony tree (consensus of 13 equally parsimonious solutions) exhibits numerous anomalies inconsistent with convincing morphological features and the Bayesian results and has, generally, relatively poor bootstrap support for major clades. The Bayesian topology is more consistent with major morphological features and has strong support

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for most clades, and conclusions are based primarily on this estimate. Major higher-level phylogenetic relationships with strong support include: (1) monophyly of Dytiscidae Leach, (2) Matinae Branden sister to the rest of Dytiscidae, (3) Agabinae Thomson + Colymbetinae Erichson, (4) Hydrodytinae Miller + Hydroporinae Aubé, (5) Dytiscinae Leach + Laccophilinae Gistel + Cybistrini Sharp + Copelatinae Branden, (6) monophyly of the subfamilies Matinae, Colymbetinae, Copelatinae, Coptotominae Branden, Lancetinae Branden, Laccophilinae (including *Agabetes* Crotch), Agabinae (support weaker than in other subfamilies) and Hydroporinae (monophyly of Hydrodytinae not tested), (7) paraphyly of Dytiscinae with Cybistrini sister to Laccophilinae (with strong support) and this clade sister to other Dytiscinae, and (8) monophyly of both Agabini (*Agabus*-group of genera) and Hydrotrupini Roughley (*Hydrotrupes* Sharp and the *Platynectes*-group of genera). Major conclusions regarding tribes within Hydroporinae include: (1) monophyly of the tribes Vatellini Sharp, Methlini Branden, Hydrovatini Sharp, Hygrotini Portevin, Hyphydrini Gistel (without *Pachydrus* Sharp) and Bidessini Sharp (including *Peschetius* Guignot, *Hydrodessus* J. Balfour-Browne and *Amarodytes* Régimbart) (monophyly of Laccornini Wolfe and Roughley and Pachydrini Biström, Nilsson and Wewalka not tested), (2) Pachydrini is a problematic, long-branched taxa resolved here as sister to Hydrovatini but with weak support, (3) Hydroporini monophyletic except for *Laccornellus* Roughley and Wolfe and *Canthyporus* Zimmermann, (4) *Laccornellus* and *Canthyporus* together monophyletic and sister to Hydroporinae except Laccornini. Four groups are resolved within Hydroporini exclusive of *Laccornellus* + *Canthyporus* corresponding to the *Deronectes*-, the *Graptodytes*-, the *Necterosoma*- and the *Hydroporus*-groups of genera. The classification of Dytiscidae is revised with the following taxonomic changes: (1) Hydrotrupini is recognized as a tribe of Agabinae including the genus *Hydrotrupes* and the *Platynectes*-group of genera (**new status**), (2) the genus *Rugosus* García is moved from Colymbetinae to Copelatinae (**new placement**), (3) Cybistrini is elevated from tribe rank within Dytiscinae to subfamily of Dytiscidae (**new rank**), (4) Hyderodini Miller is placed as a junior synonym of Dytiscini (**new synonymy**), (5) *Laccornellus* and *Canthyporus* are removed from Hydroporini and placed in their own tribe, Laccornellini (**new tribe**), (6) the following family group names are resurrected from synonymy with Hydroporini and placed as subtribes within Hydroporini, Deronectina Galewski (for the *Deronectes*-group of genera, **new status**), Siettitiina Smrž (for the *Graptodytes*-group of genera, **new status**), Sternopriscina Branden (for the *Necterosoma*-group of genera, **new status**), and Hydroporina (for the *Hydroporus*-group of genera, **new status**), (7) Carabhydrini Watts is placed as a junior synonym of Sternopriscina (**new synonymy**), and (8) *Hydrodessus*, formerly *incerta sedis* with respect to tribe, is placed in Bidessini (**new placement**). Each subfamily, tribe and subtribe is diagnosed and its taxonomic history discussed.

Keywords Phylogenetics • Taxonomy • Classification • Water beetles • Evolution

3.1 Introduction

3.1.1 History of Dytiscidae Systematics

The 10th edition of the *Systema Naturae* (Linnaeus 1758) included *Dytiscus* Linnaeus among the 25 original genera of Coleoptera with 15 species, though several of these are today not recognized as closely related to Dytiscidae. Continued taxonomic work in the early nineteenth century included descriptions of numerous new taxa by many workers, but especially Aubé (1838), Crotch (1873), Sahlberg (1873) and Régimbart (1879). Numerous more isolated or regional treatments added quite a few new species during this time as well.

Certainly the most significant advance in the history of predaceous diving beetle taxonomy and a very early effort at a phylogenetic classification was by David Sharp, the eminent British coleopterist (Sharp 1882). In this monumental work, he treated the entire family and presented a very early evolutionary understanding of dytiscids. He included about 1,140 species, a great many of which are still recognized, and his concepts at or near the genus rank have largely withstood the tests of time, new taxa, changing theories and practice, and additional data. However, his higher taxonomic subdivisions, although deeply influential and persisting well into the twentieth century, have in recent years been shown, with a few exceptions, to not generally reflect the phylogeny. His higher classification divided the family Dytiscidae into series, tribes, and groups. His two series, *Dytisci Fragmentati* and *Dytisci Complicati*, were based on whether the metepisternum is separated from the mesocoxal cavity by the mesepimeron and metepisternum (the former) or reaches the mesocoxal cavity (the latter). His *Dytisci Fragmentati* included beetles in the currently recognized families Paelobiidae Erichson and Noteridae Thomson, but also two diving beetle groups, Vatellini Sharp (all now placed in a tribe of the subfamily Hydroporinae Aubé) and Laccophilini Gistel (all now in a tribe of the subfamily Laccophilinae). All other diving beetles (and the group now recognized as the family Amphizoidae LeConte) were placed in the series *Dytisci Complicati. Dytisci Complicati* included the "groups" Cybistrini, Dytiscini, and three tribes: Hydroporides, Colymbetides, and Hydaticides, each with several groups. Sharp's concepts of higher groups strongly reflected the emphasis at that time on only one or a few characters for hypothesizing relationships as well as on a gradual evolutionary progression towards "perfection," with cybistrines, in his opinion, near the apex.

The period between Sharp's *magnum opus* and the development of cladistics (Hennig 1966) was marked by the addition of great numbers of new species and genera, largely within the received higher classification. Standing out as the most influential workers in this period were Maurice Régimbart (1895, 1899) (contemporary with David Sharp), Alois Zimmermann (1919, 1920, 1930, 1931, 1932, 1933, 1934) and his coauthor, Leopold Gschwendtner (Zimmermann and Gschwendtner 1935, 1936, 1937, 1938, 1939), and Félix Guignot (1947, 1959a, b, 1961), each of whom also had numerous smaller works. In fact the combined works by Sharp and Régimbart add up to 71 % of the new Dytiscidae names in the period 1870–1909, and the combined productivity of Zimmermann and Guignot include 50 % of the new names in the period 1910–1961 (Nilsson 2008). Paelobiidae (Hygrobiidae during this time) and Amphizoidae were separately recognized as their own families during this period, but Noteridae remained treated as a group within predaceous diving beetles.

Post-Hennigian understanding of diving beetle phylogeny and classification began mainly with Burmeister (1976) who was strongly influenced by Hennig. Burmeister focused especially on characters of the female reproductive tract (Burmeister 1976, 1980, 1990), and resulted in further clarification of this system and a few classification changes including placement of *Agabetes*, previously in Colymbetinae, within Laccophilinae (following Nilsson (1989)) and recognition of Copelatinae as a group separate from Colymbetinae. Other influential morphological cladistic analyses of higher dytiscid taxa in the post-Hennigian period included those by Wolfe (1985, 1988), Beutel (1993, 1994), and Ruhnau (1986) who refined the classifications of several groups including changes to tribal classification within Hydroporinae, elevation of Lancetinae from Colymbetinae and other results. Beutel and Roughley (1987) presented more definitive evidence that Noteridae is not a close relative of Dytiscidae (with Amphizoidae and Paelobiidae closer to Dytiscidae than Noteridae), and few workers since have continued to recognize noterids as a dytiscid subfamily (but see, for example, Pederzani 1995).

Morphological evidence presented in a cladistic framework continued, and Miller (2000, 2001) summarized many of the known data and conducted some of the first, comprehensive cladistic analyses and revisions to the classification. His work included synonymy of Aubehydrinae with Dytiscinae (Miller 2000) and elevation of Copelatinae, Coptotominae, Matinae, and Agabinae from tribes within a demonstrably non-monophyletic Colymbetinae *sensu auctorum* (Miller 2001). A new subfamily, Hydrodytinae, was also erected (Miller 2001, 2002b). Most recent developments have included comprehensive molecular analyses (Ribera et al. 2002, 2008) or molecular and/or morphological analyses of certain, larger groups (e.g., Balke and Ribera 2004; Balke et al. 2004a, b; Miller 2003; Miller et al. 2007b, 2009a; Ribera et al. 2004).

Other prominent modern developments in dytiscid taxonomy include addition of large numbers of new species with over 4,200 valid species now known (Nilsson 2008; personal communication 2014), and probably many more awaiting collection and description from traditional habitats and bioregions. Nilsson-Örtman and Nilsson (2010) predicted a total species richness of around 5,400 species, mainly resulting from an increase of species with small body-size from the Neotropical, Oriental, and Australian regions. Many large genera (e.g., *Copelatus*, *Laccophilus*) await comprehensive revision that will probably result in description of new species. Recent discovery of new faunas in subterranean, phytotelmatic, hygropetric, and terrestrial habitats will likely result in continued increase in species numbers as these habitats become better collected. Dramatic progress on the larval life stage has been made (especially by Alarie and collaborators, e.g., Alarie 1995, 1998; Alarie et al. 1990, 1997, 1998, 2000, 2001b, 2002a, b, 2011; Alarie and Butera 2003; Alarie and Harper 1990; Alarie and Hughes 2006; Alarie and Michat 2007) (see Chap. 2 in this book). Finally, a particularly useful modern world catalog of taxon names (Nilsson 2001, 2003, 2004; Nilsson and Fery 2006) has standardized names and made the nomenclature accessible. The last world catalog was by Zimmermann (1920) and had become seriously out-of-date. Nilsson (2001) not only brought together an updated world catalog for the twenty-first century following the last ICZN code of nomenclature, but also embraced the latest phylogenetic results and scrutinized and consistently treated every original description since Linnaeus. This resulted in, among other things, a substantial number of reinterpreted years of publications. It is today the most highly cited work on Dytiscidae since its publication (Google Scholar). The most recent development is the improved digital dissemination of taxonomic information with all predaceous diving beetle taxon names now in the Integrated Taxonomic Information System based on Nilsson's (2001) work and subsequent updates.

3.1.2 Overview of Current Diving Beetle Classification

Diving beetle reclassification has made progress in recent years, though mainly within subfamilies or tribes. Rather than clarifying relationships among tribes and families, these analyses have tended to illuminate problems with these relationships instead. Ten or eleven dytiscid subfamilies are currently recognized (Larson et al. 2000; Miller 2001; Nilsson 2001). The largest, by far, is Hydroporinae, which includes 10 tribes and over half the total species diversity in Dytiscidae (Fig. 3.1). Hydroporinae, as currently defined, is convincingly monophyletic (Miller 2001), but the tribes within it may not be, especially Hydroporini, which is a large, heterogeneous assemblage of genera. Dytiscinae is a subfamily well-supported by morphological characters from both adults and larvae (Alarie et al. 2011; Miller 2000, 2001), but recent molecular analyses have, in some cases, not recovered it as monophyletic with Cybistrini resolved elsewhere (Ribera et al. 2002, 2008). Other tribes within the group are seemingly monophyletic, but there is some ambiguity especially about their relationships with each other (Alarie et al. 2011; Miller 2000, 2001, 2003; Ribera et al. 2002, 2008). Laccophilinae is a large subfamily, mainly because of the inclusion of two very large genera, *Laccophilus* and *Neptosternus*, with several other smaller genera. Placement of *Agabetes* as sister to all other laccophilines was proposed by Burmeister (1990) based on attributes of the female reproductive tract that was confirmed by Miller (2001) as well as Alarie et al. (2002b) based on larval characters, but disputed by Ribera et al. (2008).

Each of the remaining dytiscid subfamilies comprise taxa formerly placed in Colymbetinae. Lancetinae includes only the monophyletic genus *Lancetes*, with representatives in Australia and temperate or high elevations in South America (Ríha 1961; Ruhnau and Brancucci 1984; Watts 1978; Zimmermann 1924). Coptotominae also includes only a single distinctive genus, *Coptotomus*, with a few species restricted to North America. The three genera in Matinae, *Matus*, *Batrachomatus*, and *Allomatus*, are together apparently monophyletic (Alarie and

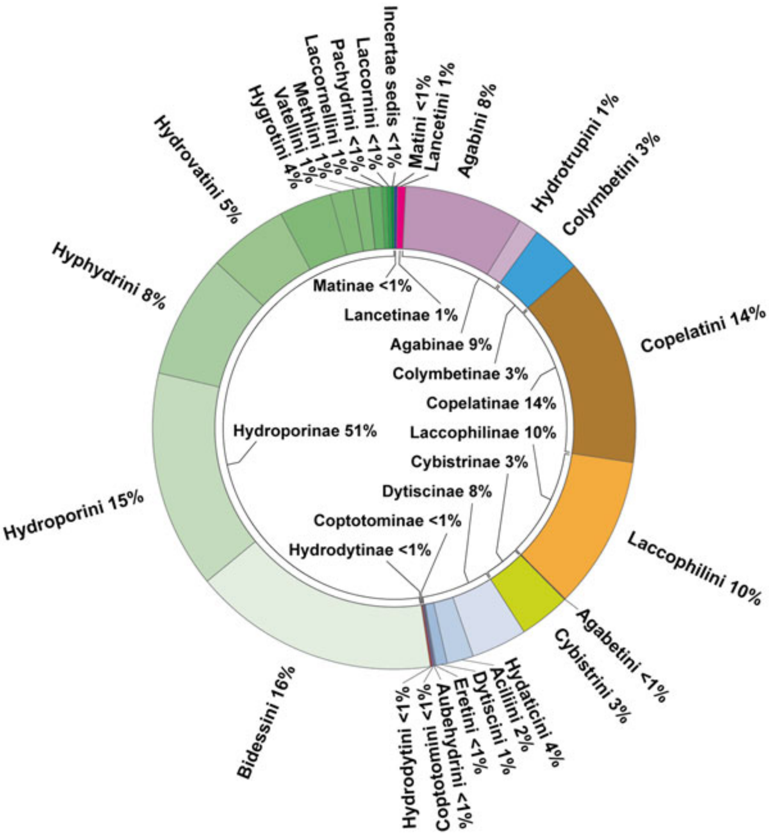

Fig. 3.1 The relative species richness of tribes and subfamilies into which the ~4,200 species of Dytiscidae are divided

Butera 2003; Alarie and Watts 2003; Miller 2000), but have an unusual disjunct distribution with *Matus* in eastern North America and the other two genera in Australia. Copelatinae includes an extremely large number of primarily tropical species in several genera, with *Copelatus* and *Exocelina* among the largest dytiscid diversifications (Balke et al. 2007). The most recently described dytiscid subfamily, Hydrodytinae, includes species previously placed in the copelatine genus, *Agaporomorphus*, and is comprised of only two genera and a few, rare species (Miller 2002b). Agabinae, closely associated with Colymbetinae historically, includes a large number of primarily Holarctic genera and species but with several assigned genera found in the Neotropics, southeast Asia and Australia. *Hydrotrupes* was given its own subfamily by Roughley (2000), Hydrotrupinae, based largely on evidence from larva features presented by Beutel (1994). This genus was historically placed in Agabinae, and was placed back into that subfamily by Miller (2001). Larval characters have shown some support for this conclusion as well (Alarie et al. 1998). *Hydrotrupes* has been placed together with the "austral" agabines in some analyses

(Ribera et al. 2004, 2008). Finally, what remains of the subfamily Colymbetinae under its modern definition (Miller 2001) is still quite a large group of several genera with one, *Rhantus*, very large, heterogeneous and found worldwide.

Although many of the currently recognized dytiscid subfamilies and tribes appear to be demonstrably monophyletic, relationships among these groups remain ambiguous or poorly supported, with few exceptions. Not only is diving beetle classification in need of a more well-founded phylogenetic hypothesis, but a better understanding of the phylogeny will dramatically enhance work on the evolution of dytiscid diversity, sexual selection, chemical evolution, biogeography, and evolutionary ecology, among other pursuits. The goal of this project is to establish, to the extent possible, a comprehensive phylogeny of extant diving beetles with broad taxon and data sampling and to revise the classification based on it, as needed, with emphasis on the family-group taxa.

3.2 Material and Methods

3.2.1 Taxon Sampling

3.2.1.1 Ingroup

One-hundred and sixty-eight species of diving beetles were included in the analysis (Table 3.1). All currently recognized subfamilies and tribes are represented, most by multiple exemplars. A single exemplar each is included for Hydrodytinae, Agabetini, Aubehydrini, Laccornini, Pachydrini, and Carabhydrini. Ninety-five dytiscid genera (~60 % of the total) are represented.

3.2.1.2 Outgroup

Representatives from Amphizoidae, Paelobiidae, Noteridae, and Gyrinidae are included as outgroups (Table 3.1). Trees were rooted using Gyrinidae based on evidence that they may be sister to Hydradephaga (Ribera et al. 2002).

3.2.2 DNA

Whole genomic DNA was extracted using Qiagen DNEasy kit (Valencia, California, USA) and the animal tissue protocol. Thoracic muscle tissue was taken from large specimens and extracted. Smaller specimens were extracted by removing the abdomen and placing the remaining portion of the specimen in buffer. The portions of the specimens remaining after extraction were retained for vouchering. Vouchers and DNAs are deposited in the Museum of Southwestern Biology Division of

Table 3.1 Taxa used in phylogenetic analysis of Dytiscidae, collecting data, KBMC voucher numbers, and GenBank accession numbers for DNA sequences

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Gyrinidae			*Spanglerogyrus albiventris*	KBMC Spal472	United States, Alabama, Conecuh Co., 23 km SE Evergreen along CR42, 31°20.059′N 86°47.641′W, 62 m, 12 May 2006, KB Miller, leg., KBM1205063	JX477995 --- JX477914	JX478084 JX478172 JX477836	KJ548470 KJ548857 ---
Gyrinidae			*Dineutus ciliatus*	KBMC Dici474	United States, Alabama, Conecuh Co., 18.5 km SE Evergreen along CR42, 31°21.38′N 86°50.761′W, 92 m, 12 May 2006, KB Miller, leg., KBM1205062	JX477971 --- JX477893	JX478060 JX478148 JX477829	--- KJ548821 ---
Gyrinidae			*Gyrinus elevatus*	KBMC Gyel494	Australia, New South Wales, Tuross River, 5 km W Bodalla, 36°8.7′S 149°59.083′E, 39 m, 2 Nov 2000, KB Miller, leg., KBM0211003	JX477977 --- JX477898	JX478066 JX478154 JX477831	KJ548430 --- ---

Noteridae	*Hydrocanthinae Hydrocanthus*	KBMC Hcsp570	Zambia, Northwestern Province, stream ~4 km NW Ikatu, 11°30.268′S 24°22.747′E, 1,384 m, 7 Nov 2007, KB Miller, leg., KBM07110702	KJ548275 KJ548381 KJ548798	--- KJ548630 KJ548720	KJ548490 KJ548872 ---
Noteridae	*Noteridae Notomicrus*	KBMC Ncsp642	Venezuela, Amazonas, Communidad Cano Gato, Rio Sipapo, 4°58.838′N 67°44.341′W, 95 m, 16 Jan 2009, KB Miller, leg., VZ09011601	KJ548279 KJ548385 KJ548802	--- --- KJ548724	KJ548493 --- ---
Noteridae	*Noterus clavicornis*	KBMC Nocl503	Italy, Sardinia, Nuoru Prov., nr Bultei, 40°25.613′N 9°5.149′E, 262 m, 16 Apr 2006, KB Miller, leg., KBM1604064	JX477985 KJ548358 JX477904	JX478073 JX478161 JX477834	KJ548457 --- ---
Noteridae	*Tonerus wheeleri*	KBMC Tosp639	Venezuela, Amazonas, Tobogan de la Selva, 5°23.207′N 67°36.922′W, 125 m, 14 Jan 2009, KB Miller, leg., VZ09011401	KJ548278 KJ548384 KJ548801	KJ548556 KJ548633 KJ548723	KJ548492 --- ---

(continued)

Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Amphizoidae			*Amphizoa lecontei*	KBMC Amle58	United States, Colorado, Garfield Co., Rifle Falls State Park, East Rife Creek, 10 Aug 2000, KB Miller, leg., KBM100800	KJ548196 AY071771 KJ548745	KJ548509 --- ---	KJ548409 EU677585 EU677662
Paelobiidae			*Hygrobia hermanni*	KBMC Haho504	Italy, Sardinia, Nuoru Prov., nr Bultei, 40°25.613′N 9°5.149′E, 262 m, 16 Apr 2006, KB Miller, leg., KBM1604064	JX477982 KJ548326 JX477902	JX478071 JX478159 ---	KJ548431 KJ548826 KJ548151
Dytiscidae	Agabinae	Agabini	*Agabini Ilybius*	KBMC Agsp411	United States, Louisiana, Briarwood Preserve, 32°7.9′N 92°59.205′W, 2 Jun 2002, KB Miller, leg., AJA0206021	KJ548194 KJ548304 KJ548743	KJ548507 KJ548576 KJ548657	KJ548407 KJ548813 ---
Dytiscidae	Agabinae	Agabini	*Agabus didymus*	KBMC Pmsp730	Italy, Sardinia, Nuoru Prov., 4.5 km SE Bottidda, 40°20.332′N 9°1.785′E, 200 m, 16 Apr 2006, KB Miller, leg., KBM1604063	KJ548286 KJ548392 KJ548809	--- --- KJ548727	--- --- ---

Dytiscidae	Agabinae	Agabini	*Agabus disintegratus*	KBMC Agdi412	United States, New Mexico, Hidalgo Co., Coronado Natl. For., Cloverdale Cr., 15 May, MF Whiting, leg.	KJ548192 KJ548302 KJ548741	KJ548505 KJ548574 KJ548655	--- KJ548811 ---
Dytiscidae	Agabinae	Agabini	*Agabus tristis*	KBMC Agtr60	United States, Colorado, Summit Co., Bogan Flats, 39°26.7′N 106°19.9′W, 2784 m, 6 Aug 2000, KB Miller, leg., KBM0608001	KJ548195 KJ548305 KJ548744	KJ548508 KJ548577 KJ548658	KJ548408 --- AF392003
Dytiscidae	Agabinae	Agabini	*Ilybiosoma cordatum*	KBMC Agco57	United States, Colorado, Garfield Co., Rifle Falls State Park, East Rife Creek, 10 Aug 2000, KB Miller, leg., KBM100800	KJ548191 KJ548301 KJ548740	KJ548504 KJ548573 ---	KJ548405 --- KJ548141
Dytiscidae	Agabinae	Agabini	*Ilybiosoma seriatum*	KBMC Agse413	United States, Utah, Utah Co., Diamond Fork Cyn, river approx 2 mi from turnoff, 29 Apr 2002, DC Ames, leg.	KJ548193 KJ548303 KJ548742	KJ548506 KJ548575 KJ548656	KJ548406 KJ548812 KJ548142
Dytiscidae	Agabinae	Agabini	*Ilybius fraterculus*	KBMC Ilfr409	United States, Utah, Utah Co., Goshen Ponds, 14 Jul 2000, JA Robertson, leg.	KJ548236 KJ548342 KJ548771	KJ548533 KJ548603 KJ548691	KJ548440 --- ---

(continued)

Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Dytiscidae	Agabinae	Agabini	*Ilybius gagates*	KBMC Ilga12	United States, New York, Tompkins Co., pond 10 km S Caroline, 10 Sep 1999, KB Miller, leg., KBM1009992	--- --- KJ548772	KJ548534 --- KJ548692	--- --- AF392002
Dytiscidae	Agabinae	Agabini	*Ilybius subaeneus*	KBMC Ilsu64	United States, Colorado, Summit Co., Homestake Creek, 39°24.617′N 106°25.35′W, 2798 m, 6 Aug 2000, KB Miller, leg., KBM0608002	KJ548237 KJ548343 KJ548773	KJ548535 KJ548604 ---	KJ548441 --- AF392029
Dytiscidae	Agabinae	Hydrotrupini	*Agabini Platynectes*	KBMC Pysp457	French Guiana, Kaw Mt Res, Amazone Lodge, 4°33′N °12.66′W, 8 Feb 2005, KB Miller, leg., KBM0802051	KJ548256 KJ548365 KJ548784	KJ548543 KJ548618 KJ548707	--- KJ548852 ---
Dytiscidae	Agabinae	Hydrotrupini	*Agametrus humilis*	KBMC Ansp760	Venezuela, Merida State, Bailadores, 8°14.393′N 71°48.672′W, 1862 m, Cascada Bailadores, stream margins, Short et al, leg., VZ09-0718-02A	--- KJ548294 KJ548733	--- KJ548568 KJ548647	KJ548398 --- KJ548138

Dytiscidae	Agabinae	Hydrotrupini	*Agametrus nitens*	KBMC Atsp759	Costa Rica, Cartago Province, Tapanti National Park, Kiri Lodge Trail, small stream in secondary forest, 17 Aug 2010, Short and Gustafson, legs, CR10-0317-SG1	--- KJ548293 KJ548732	--- KJ548567 KJ548646	KJ548397 --- KJ548137
Dytiscidae	Agabinae	Hydrotrupini	*Hydrotrupes palpalis*	KBMC Hppa371	United States, Oregon, Lane County, Seal Rock, seeps along cliff at beach, 44°30.217′N 124°4.9′W, 1 Sep 2001, KB Miller, leg., KBM01090101	KJ548223 KJ548331 KJ548764	KJ548526 KJ548596 KJ548678	KJ548435 --- KJ548154
Dytiscidae	Agabinae	Hydrotrupini	*Platynectes decemnotatus*	KBMC Plde130	Australia, Victoria, Stoney Creek, 5 km E Meeniyan, 38°35.733′S 146°4.5′W, 25 m, 30 Oct 2000, KB Miller, leg., KBM3010004	JX477993 --- JX477913	JX478082 JX478170 ---	--- --- ---
Dytiscidae	Colymbetinae	Colymbetini	*Carabdytes upin*	KBMC Crup251	Papua New Guinea, Eastern Highlands Province, Crater Mtn Research Area, Miamafu Village, 8 Jul 2001, KB Miller, leg., FW0807011	KJ548208 KJ548317 KJ548756	KJ548519 KJ548588 KJ548666	KJ548421 KJ548820 KJ548149

(continued)

Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Dytiscidae	Colymbetinae	Colymbetini	*Colymbetes fuscus*	KBMC Clsp476	Italy, Sardinia, Nuoru Prov., nr Bultei, 40°25.613′N 9°5.149′E, 262 m, 16 Apr 2006, KB Miller, leg., KBM1604064	KJ548205 KJ548314 KJ548753	KJ548516 KJ548585 KJ548664	KJ548419 KJ548818 KJ548147
Dytiscidae	Colymbetinae	Colymbetini	*Colymbetes infuscatus*	KBMC Cbin410	United States, Utah, Utah Co., Payson, Payson Lakes, Box Lk., 15 Sep 2004, S Bybee, leg.	KJ548203 KJ548312 KJ548751	KJ548514 KJ548583 KJ548663	KJ548416 KJ548816 KJ548146
Dytiscidae	Colymbetinae	Colymbetini	*Colymbetes paykulli*	KBMC Cbpa59	United States, Colorado, Summit Co., Homestake Creek, 39°24.617′N 106°25.35′W, 2,798 m, 6 Aug 2000, KB Miller, leg., KBM0608002	KJ548204 KJ548313 KJ548752	KJ548515 KJ548584 ---	--- --- AF392005
Dytiscidae	Colymbetinae	Colymbetini	*Hoperius planatus*	KBMC Hopl453	United States, Delaware, New Castle Co., Frenchtown Woods Natural Area, 23 May 2004, AEZ Short, leg. AS-04-065	KJ548222 KJ548330 KJ548763	KJ548525 KJ548595 KJ548677	--- KJ548829 KJ548153

Dytiscidae	Colymbetinae	Colymbetini	*Meladema coriacea*	KBMC Mdco475	Italy, Sardinia, Nuoru Prov., river upstream from Lake Flumendosa, 39°58.943′N 9°24.722′E, 785 m, 18 Apr 2006, KB Miller, leg., KBM1804063	KJ548246 KJ548354 ---	KJ548539 KJ548612 ---	KJ548452 KJ548845 KJ548166
Dytiscidae	Colymbetinae	Colymbetini	*Neoscutopterus angustus*	KBMC Nean25	United States, New York, Tompkins Co., McLean Bog, 26 May 2000, KB Miller, leg., KBM2605002	KJ548249 KJ548357 ---	KJ548540 KJ548613 KJ548703	--- --- AF392035
Dytiscidae	Colymbetinae	Colymbetini	*Rhantus atricolor*	KBMC Rhat10	United States, Arizona, Cochise Co., Rucker Canyon, 31°45.067′N 109°22′W, 26 Apr 2000, KB Miller, leg., KBM2604001	KJ548257 KJ548366 KJ548785	KJ548544 KJ548619 KJ548708	--- KJ548854 KJ548169
Dytiscidae	Colymbetinae	Colymbetini	*Rhantus binotatus*	KBMC Rhbi3	United States, Arizona, Cochise Co., Rucker Canyon, 31°45.067′N 109°22′W, 26 Apr 2000, KB Miller, leg., KBM2604001	KJ548258 KJ548367 KJ548786	KJ548545 KJ548620 KJ548709	KJ548465 KJ548855 AF392040

(continued)

Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Dytiscidae	Colymbetinae	Colymbetini	*Rhantus calidus*	KBMC Rhca262	Peru, Madre de Dios, Explorers Inn, 12°50.208′S 69°17.603′W, 10 Dec 2003, KB Miller, leg., KBM1012031	KJ548259 KJ548368 KJ548787	KJ548546 KJ548621 ---	KJ548466 --- KJ548170
Dytiscidae	Colymbetinae	Colymbetini	*Rhantus sinuatus*	KBMC Rhsi17	United States, New York, St Lawrence Co., Macomb Twp, Fish Cr Marsh, 44°28.333′N 75°33.8′W, 23 May 2000, KB Miller, leg., KBM2305001	KJ548260 KJ548369 KJ548788	KJ548547 KJ548622 KJ548710	KJ548467 --- AF392041
Dytiscidae	Colymbetinae	Colymbetini	*Rhantus validus*	KBMC Rhsp408	Chile, Prov. Llanquihue, Rio Blanco nr Cascadas, 21 Dec 2001, Whiting, Ogden, Terry, leg.	KJ548261 KJ548370 KJ548789	KJ548548 KJ548623 ---	KJ548468 KJ548856 KJ548171
Dytiscidae	Copelatinae	Copelatini	*Agaporomorphus silvaticus*	KBMC Apsy268	Peru, Madre de Dios, Posadas Amazonas, 12°48.133′N 69°17.983′W, 13 Dec 2003, KB Miller, leg., KBM13120301	KJ548198 KJ548307 ---	KJ548510 KJ548579 KJ548660	KJ548412 --- KJ548144

Dytiscidae	Copelatinae	Copelatini	*Copelatus distinctus*	KBMC Cpdi9	United States, Arizona, Santa Cruz Co., Hanshaw Cr., Patagonia, 31°27.25′N 110°43.283′W, 27 Apr 2000, KB Miller, leg., KBM2704001	KJ548207 KJ548316 KJ548755	KJ548518 KJ548587 KJ548665	KJ548420 KJ548819 KJ548148
Dytiscidae	Copelatinae	Copelatini	*Exocelina australiae*	KBMC Cpau126	Australia, New South Wales, 6 km SW Braidwood, 35°29.867′S 149°44.15′E, 2 Nov 2000, KB Miller, leg., KBM0211001	KJ548206 KJ548315 KJ548754	KJ548517 KJ548586 ---	--- --- AF392006
Dytiscidae	Copelatinae	Copelatini	*Lacconectus andrewsi*	KBMC Lsan768	India, Maharashtra, Amboli, 15°55.843′N 73°57.836′E, 3 Oct 2004, KB Miller, leg., KBM0310041	KJ548185 KJ548298 KJ548737	--- --- ---	KJ548400 --- KJ548139
Dytiscidae	Copelatinae	Copelatini	*Lacconectus regimbarti*	KBMC Lsre769	India, Karnataka, forest stream 30 km E Udupi, 04 Oct 2004, KB Miller, leg.	KJ548186 KJ548299 KJ548738	KJ548501 KJ548571 KJ548650	KJ548401 --- KJ548140

(continued)

Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Dytiscidae	Copelatinae	Laccornini	*Laccornis difformis*	KBMC Ladi16	United States, New York, St Lawrence Co., Macomb Twp, Fish Cr Marsh, 44°28.333′N 75°33.8′W, 23 May 2000, KB Miller, leg., KBM2305001	KF575591 KF575544 KF575363	KF575484 KF575441 KF575406	--- KJ548835 AF392030
Dytiscidae	Coptotominae	Coptotomini	*Coptotomus lenticus*	KBMC Ctle11	United States, New York, Tompkins Co., Ithaca, 42°26.433′N 76°29.8′W, 10 Nov 1999, KB Miller, leg., KBM1009991	KJ548209 KJ548318 KJ548757	KJ548520 KJ548589 KJ548667	--- --- AF392007
Dytiscidae	Coptotominae	Coptotomini	*Coptotomus venustus*	KBMC Ctsp530	United States, Alabama, Monroe Co., 3 km E Owassa, 31°29.791′N 86°51.184′W, 99 m, 11 May 2006, KB Miller, leg., KBM1105064	KJ548271 KJ548377 KJ548794	KJ548553 KJ548626 KJ548717	--- KJ548866 ---

Dytiscidae	Cybistrinae	Cybistrini	*Cybister Cybister*	KBMC Cysp757	Venezuela: Amazonas State, 4°58.838′N 67°44.341′W, 95 m, Communidad Cano Gato on Rio Sipapo, 16 Jan 2009, Short, Miller, Camacho, Joly and Garcia, legs. VZ09-0116-01X	KJ548182 KJ548291 ---	KJ548497 KJ548566 ---	KJ548396 --- ---
Dytiscidae	Cybistrinae	Cybistrini	*Cybister marginicollis*	KBMC Cyma416	Ghana, Volta Region, road between Nkwanta and Odumase, 8°15.537′N 0°26.562′E, 210 m, 15 Jun 2005, KB Miller, leg., KBM1506051	KJ548210 KJ548319 DQ813748	DQ813682 DQ813785 KJ548668	KJ548422 --- DQ813719
Dytiscidae	Cybistrinae	Cybistrini	*Cybister puncticollis*	KBMC Cypu21	Bolivia, Beni, Prov. Cercado, 2.8 km SW Trinidad, 14°50.017′S 64°55.867′W, 17 Jun 1999, KB Miller, leg., KBM1706991	KJ548211 KJ548320 KJ548758	DQ431201 KJ548590 KJ548669	KJ548423 --- AF392009
Dytiscidae	Cybistrinae	Cybistrini	*Cybister tripunctatus*	KBMC Cytr102	Australia, Victoria, 10 km E Corryong, 36°10.683′S 148°2.867′E, 5 Nov 2000, KB Miller, leg., KBM0511001	KJ548212 KJ548321 ---	DQ813687 DQ813789 ---	KJ548424 --- AF392010

(continued)

Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Dytiscidae	Cybistrinae	Cybistrini	*Megadytes fraternus*	KBMC Mefr300	Paraguay, Dpt. Alto Paraguay, Ea. Choroveca, 29 Nov 2002	KJ548247 KJ548355 DQ813764	DQ813698 DQ813800 KJ548701	KJ548453 KJ548846 DQ813728
Dytiscidae	Cybistrinae	Cybistrini	*Megadytes robustus*	KBMC Mero254	Peru, Madre de Dios, boat landing nr Infierno, 12°43.493′S 69°13.043′W, 14 Dec 2003, KB Miller, leg., KBM1412031	KJ548248 KJ548356 DQ813768	DQ813702 DQ813803 KJ548702	KJ548454 KJ548847 DQ813731
Dytiscidae	Cybistrinae	Cybistrini	*Onychohydrus scutellaris*	KBMC Onsc107	Australia, Victoria, 18.6 km W Casterton, 37°35.95′S 141°9.75′E, 11 Nov 2000, KB Miller, leg., KBM1111001	KJ548253 KJ548362 DQ813770	DQ813704 DQ813805 KJ548705	KJ548461 --- DQ813733
Dytiscidae	Cybistrinae	Cybistrini	*Spencerhydrus latecinctus*	KBMC Spla123	Australia, Victoria, 25 km W Casterton, 10 Jun 2000, KB Miller, leg., CHS Watts, leg.	KJ548264 KJ548372 DQ813771	DQ813705 DQ813806 ---	KJ548471 KJ548858 AF392043
Dytiscidae	Cybistrinae	Cybistrini	*Spencerhydrus pulchellus*	KBMC Sppu108	Australia, Western Australia, Byenup Lagoon, Oct 2000, CHS Watts, leg.	KJ548265 KJ548373 DQ813772	DQ813706 DQ813807 KJ548713	KJ548472 KJ548859 DQ813734

Dytiscidae	Cybistrinae	Cybistrini	*Sternhydrus atratus*	KBMC Stat165	Australia, Queensland, Townsville, 27–30 Nov 2001, G. Svenson, leg.	KJ548252 KJ548361 DQ813769	DQ813703 DQ813804 ---	KJ548460 --- DQ813732
Dytiscidae	Dytiscinae	Aciliini	*Aciliini Aethionectes*	KBMC Aesp659	Cameroon, Centre Region, Mbam Djerem Park, Ganga Camp, 60 km SE Tibati, 5°59.857′N 12°52.668′E, 19 Mar 2009, KB Miller, leg., KBM19030902	KJ548280 KJ548386 ---	KJ548557 --- KJ548726	KJ548494 KJ548875 ---
Dytiscidae	Dytiscinae	Aciliini	*Acilius abbreviatus*	KBMC Acab72	United States, Idaho, Fremont Co., Forest pool on N Big Spring Loop Rd., 44°30.372′N 111°16.56′W, 1,957 m, 16 Sep 2000, KB Miller, leg., DLG1609001	KJ548188 KF979078 KF978972	KJ548502 KF978924 KJ548652	KJ548403 --- KF979001
Dytiscidae	Dytiscinae	Aciliini	*Acilius semisulcatus*	KBMC Acse7	United States, New York, Tompkins Co., pond 10kmS Caroline, 12 Oct 2000, KB Miller, leg., KBM2310002	KJ548189 KF979085 DQ275323	DQ275307 KF978933 KJ548653	--- --- AF391999

(continued)

Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Dytiscidae	Dytiscinae	Aciliini	*Aethionectes apicalis*	KBMC Aeop406	South Africa, Eastern Cape Province, Dwesa NP, 24 Jan 2005, J Bergsten, leg.	KJ548190 KF979088 KF978975	KJ548503 KF978937 KJ548654	KJ548404 --- ---
Dytiscidae	Dytiscinae	Aciliini	*Graphoderus liberus*	KBMC Grli69	United States, New York, Tompkins Co., Ringwood Preserve, 19 Sep 2000, KB Miller, leg., KBM1909001	KJ548218 KF979094 DQ813759	DQ813693 DQ813795 KJ548674	KJ548429 --- AF392016
Dytiscidae	Dytiscinae	Aciliini	*Sandracottus bakewelli*	KBMC Saba90	Australia, Northern Territory, Ormiston, CHS Watts, leg.	KJ548262 KF979104 KF978986	KJ548549 KF978953 KJ548711	--- --- KF979014
Dytiscidae	Dytiscinae	Aciliini	*Sandracottus dejeani*	KBMC Sade328	India, Maharashtra, 16°34.992′N 73°35.221′E, 1 Oct 2004, KB Miller, leg., KBM0110041	KJ548263 KJ548371 KJ548790	KJ548550 KF978954 KJ548712	KJ548469 --- KJ548172
Dytiscidae	Dytiscinae	Aciliini	*Thermonectus basillaris*	KBMC Thba210	United States, New York, Schuyler Co., Texas Hollow, 42°24.73′N 76°47.58′W, 358 m, 12 Sep 2002, KB Miller, leg., KBM120902	KJ548266 KF979108 KF978991	DQ431223 KF978958 ---	KJ548473 KJ548860 KF979017

Dytiscidae	Dytiscinae	Aciliini	*Thermonectus nigrofasciatus*	KBMC Thni5	United States, Arizona, Cochise Co., Rucker Canyon, 31°45.067′N 109°22′W, 26 Apr 2000, KB Miller, leg., KBM2604001	KJ548267 --- KF978995	KJ548551 --- KJ548714	KJ548474 KJ548861 AF392047
Dytiscidae	Dytiscinae	Aubehydrini	*Notaticus fasciatus*	KBMC Nofa52	Bolivia, Beni, Prov. Cercado, 9.5 km N Trinidad, 14°46.567′S 64°58′W, 17 Jun 1999, KB Miller, leg., KBM1706992	KJ548250 KJ548359 FJ796545	DQ431220 KJ548614 ---	--- --- AF392036
Dytiscidae	Dytiscinae	Dytiscini	*Dytiscus marginalis*	KBMC Dymg168	Sweden, Västerbotten, Täfteåhalvön, 31 May 2003, J Bergsten, leg.	KJ548214 KJ548323 DQ813757	DQ813691 DQ813793 KJ548671	KJ548425 KJ548823 DQ813725
Dytiscidae	Dytiscinae	Dytiscini	*Dytiscus verticalis*	KBMC Dyve24	United States, New York, Tompkins Co., Ithaca, 42°26.433′N 76°29.8′W, 26 May 2000, KB Miller, leg., KBM2605001	KJ548215 KJ548324 DQ813758	DQ813692 DQ813794 ---	KJ548426 KJ548824 AF392012
Dytiscidae	Dytiscinae	Dytiscini	*Hyderodes crassus*	KBMC Hdcr238	Australia, Western Australia, 6 km S Pinjarra, 10 Mar 2003, CHS Watts, leg.	KJ548219 KJ548327 KJ548761	KJ548523 KJ548593 ---	KJ548432 --- KJ548152

(continued)

Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Dytiscidae	Dytiscinae	Dytiscini	*Hyderodes shuckardi*	KBMC Hdsh104	Australia, Victoria, 20 km W Cowwarr, 38°0.867′S 146°32.05′E, 7 Nov 2000, KB Miller, leg., KBM07110001	KJ548220 KJ548328 DQ813760	DQ813694 DQ813796 KJ548675	KJ548433 KJ548827 AF392018
Dytiscidae	Dytiscinae	Eretini	*Eretes australis*	KBMC Erau103	Australia, South Australia, 15 km N Kingston, 34°5.833′S 140°21′E, 12 Nov 2000, KB Miller, leg., KBM1311001	KJ548216 KF979073 FJ796506	FJ796579 KF978919 KJ548672	KJ548427 --- FJ796547
Dytiscidae	Dytiscinae	Eretini	*Eretes griseus*	KBMC Ergr105	Hong Kong, Lantau Ishland, S of Mui Wo, Ngau Kwu Wani, artificial pond, 19 Nov 2000, J. Bergsten, leg.	KJ548217 KJ548325 KJ548760	KJ548522 KJ548592 KJ548673	KJ548428 KJ548825 KJ548150
Dytiscidae	Dytiscinae	Hydaticini	*Hydaticus aruspex*	KBMC Hyar68	United States, New York, Schuyler Co., Texas Hollow, 42°24.73′N 76°47.58′W, 358 m, 6 Sep 2000, KB Miller, leg., KBM0609001	KJ548230 KJ548337 FJ796507	FJ796580 FJ796627 KJ548685	KJ548436 --- AF392019

Dytiscidae	Dytiscinae	Hydaticini	*Hydaticus cinctipennis*	KBMC Hyci20	United States, New York, St Lawrence Co., Macomb Twp, Fish Cr Marsh, 44°28.333′N 75°33.8′W, 23 May 2000, KB Miller, leg., KBM2305001	KJ548231 KJ548338 FJ796512	FJ796586 FJ796633 KJ548686	--- --- AF392021
Dytiscidae	Dytiscinae	Hydaticini	*Hydaticus exclamationis*	KBMC Hyex400	South Africa, Eastern Cape Province, 2 km N Sterkstroom, 31°30.233′S 26°32.160′E, 1414 m, 20 Jan 2005, J Bergsten, leg.	KJ548232 KJ548339 FJ796517	FJ796592 FJ796639 KJ548687	KJ548437 KJ548832 FJ796554
Dytiscidae	Dytiscinae	Hydaticini	*Hydaticus fabricii*	KBMC Hyfa119	Philippines, Borocay, 11°57′N 121°56′E, 26 Sep 2000, JB2609001	KJ548233 KJ548340 FJ796518	FJ796593 FJ796640 KJ548688	KJ548438 KJ548833 AF392022
Dytiscidae	Dytiscinae	Hydaticini	*Hydaticus subfasciatus*	KBMC Hysu23	Bolivia, Dpto. Santa Cruz, Prov. Chiquitos, 2.7 km S San Jose, 17°52.333′S 60°44.467′W, 27 Jun 1999, KB Miller, leg., KBM2706991	KJ548234 --- FJ796539	FJ796618 FJ796662 KJ548689	--- --- FJ796574

(continued)

Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Dytiscidae	Dytiscinae	Hydaticini	*Hydaticus xanthomelas*	KBMC Hyxa67	Bolivia, Dpto. Santa Cruz, Prov. Velasco, 1.5 km SE San Ignacio, 16°23.4′S 60°57.217′W, 24 Jun 1999, KB Miller, leg., KBM2406991	KJ548235 KJ548341 FJ796544	FJ796624 FJ796668 KJ548690	KJ548439 KJ548834 AF392028
Dytiscidae	Hydrodytinae	Hydrodytinin	*Hydrodytes opalinus*	KBMC Hzsp734	Venezuela: Amazonas State, 4°58.838′N 67°44.341′W, 95 m, Communidad Cano Gato on Rio Sipapo, 16 Jan 2009, Short, Miller, Camacho, Joly and Garcia, legs. VZ09-0116-01X	KJ548284 KJ548390 KJ548807	KJ548560 KJ548638 ---	--- --- KJ548176
Dytiscidae	Hydroporinae	Bidessini	*Bidessini Amarodytes*	KBMC Arsp282	Peru, Madre de Dios, Explorers Inn, 12°50.208′S 69°17.603′W, 12 Oct 2003, KB Miller, leg., KBM1012031	KF575580 KF575533 KF575352	KF575474 KF575431 ---	--- --- ---

Dytiscidae	Hydroporinae	Bidessini	*Bidessini Amarodytes*	KBMC Arsp283	Peru, Madre de Dios, Explorers Inn, 12°50.208′S 69°17.603′W, 10 Nov 2003, KB Miller, leg., KBM1012031	KJ548199 KJ548308 KJ548747	KJ548511 KJ548580 KJ548661	KJ548413 --- ---
Dytiscidae	Hydroporinae	Bidessini	*Bidessini Anodocheilus*	KBMC Adsp696	Venezuela, Amazonas, ca 15 km S Puerto Ayacucho, 5°30.623′N 67°36.109′W, 110 m, 14 Jan 2009, KB Miller, leg., VZ09011403	KJ548282 KJ548388 KJ548805	KJ548558 KJ548636 ---	--- --- KJ548175
Dytiscidae	Hydroporinae	Bidessini	*Bidessini Hypodessus*	KBMC Hosp695	Venezuela, Amazonas, Communidad Cano Gato, Rio Sipapo, 4°58.838′N 67°44.341′W, 95 m, 16 Jan 2009, KB Miller, leg., VZ09011601	KJ548281 KJ548387 KJ548804	--- KJ548635 ---	--- --- ---
Dytiscidae	Hydroporinae	Bidessini	*Bidessini Liodessus*	KBMC Ldsp755	Zambia, Northwestern Province, stream and meadow ~4 km NW Ikatu, 11°30.268′S 24°22.747′E, 1384 m, 7 Nov 2007, KB Miller, leg., KBM07110702	KJ548181 KJ548290 KJ548730	KJ548496 --- ---	KJ548395 --- ---

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Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Dytiscidae	Hydroporinae	Bidessini	*Bidessini Neobidessus*	KBMC Nesp698	Venezuela, Apure St., 7°38.660′N 69°18.004 W, 90 m, btwn "La Ye" and Bruzual, 18 Jan 2009, Short, Garcia, Camacho, legs., VZ09-0118-03x	KJ548283 KJ548389 KJ548806	KJ548559 KJ548637 ---	--- --- ---
Dytiscidae	Hydroporinae	Bidessini	*Bidessonotus inconspicuus*	KBMC Biin82	United States, New York, Elmira, Aug 2001, KB Miller, leg.	KJ548201 KJ548310 KJ548749	KJ548513 KJ548582 ---	KJ548415 KJ548815 ---
Dytiscidae	Hydroporinae	Bidessini	*Hydroporini Hydrodessus*	KBMC Husp735	Venezuela: Amazonas State, 4°58.838′N 67°44.341′W, 95 m, Communidad Cano Gato on Rio Sipapo, 16 Jan 2009, Short, Miller, Camacho, Joly and Garcia, legs. VZ09-0116-01X	KJ548285 KJ548391 KJ548808	KJ548561 KJ548639 ---	--- --- ---
Dytiscidae	Hydroporinae	Bidessini	*Limbodessus compactus*	KBMC Lbco272	Australia, Victoria, 10 km E Lakes Entrance, 34°48.133′S 148°29.617′E, 31 Oct 2000, KB Miller, leg., KBM3110001	KJ548240 KJ548346 KJ548775	KJ548536 KJ548607 ---	KJ548444 --- KJ548161

Dytiscidae	Hydroporinae	Bidessini	*Liodessus affinis*	KBMC Liaf132	United States, New York, Tompkins Co., Ringwood Preserve, 10 Apr 2001, KB Miller, leg., KBM1005011	KF575592 KF575545 KF575364	KF575485 KF575442 ---	KJ548450 --- ---
Dytiscidae	Hydroporinae	Bidessini	*Peschetius nodieri*	KBMC Peno438	Ghana, Volta Region, Kyabobo National Park border, on road from Koue Village, Togo Border, 8°31.218′N 0°36.153′E, 225 m, 14 Jun 2005, KB Miller, leg., KBM1406051	KJ548255 KJ548364 KJ548783	KJ548542 KJ548617 ---	--- KJ548850 ---
Dytiscidae	Hydroporinae	Bidessini	*Peschetius quadricostatus*	KBMC Pequ345	India, Maharashtra, 16°34.992′N 73°35.221′E, 1 Oct 2004, KB Miller, leg., KBM0110041	KF575599 KF575552 ---	KF575492 KF575449 ---	--- KJ548851 ---
Dytiscidae	Hydroporinae	Bidessini	*Uvarus spretus*	KBMC Uvsp289	Costa Rica, Heredia, nr Puerto Viego, La Selva Biological Station, 10°25′N 84°0′W, 23 Feb 2004, KBM2302041	KJ548268 KJ548374 KJ548791	KJ548552 KJ548624 KJ548715	KJ548475 --- ---

(continued)

Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Dytiscidae	Hydroporinae	Hydroporini	*Antiporus blakei*	KBMC Anbl541	Australia, Victoria, grassy roadside pool nr Carranballac, 03 Oct 2002, 37°42.758′S 142°45.868′E, KB Miller, leg.	KF575614 KF575566 KF575385	KF575503 KF575463 KF575423	KJ548483 --- KF575526
Dytiscidae	Hydroporinae	Hydroporini	*Antiporus femoralis*	KBMC Anfe100	Australia, New South Wales, 6 km SW Braidwood, 35°29.867′S 149°44.15′E, 12 Nov 2000, KB Miller, leg., KBM0211001	KF575579 KF575532 KF575351	KF575473 KF575430 ---	KJ548410 --- KF575512
Dytiscidae	Hydroporinae	Hydroporini	*Barretthydrus geminatus*	KBMC Bage544	Australia, New South Wales, Deva River, 20 km NW Moruya, 35°53.046′S 144°58.756′E, 1 Oct 2002, KB Miller, leg., KBM0110021	KJ548272 KJ548378 KJ548795	FR733550 KJ548627 ---	KJ548485 KJ548869 ---
Dytiscidae	Hydroporinae	Hydroporini	*Carabhydrus nigrinus*	KBMC Cani144	Australia, Tasmania, Dentention River, 0.2 km W Montumana, 27 Nov 2000, CHS Watts, leg.	KJ548202 KJ548311 KJ548750	--- --- ---	--- --- ---

Dytiscidae	Hydroporinae	Hydroporini	*Chostonectes gigas*	KBMC Chgi444	Australia, Victoria, nr Carranballac, 37°42.758′S 142°45.868′E, 3 Oct 2002, KB Miller, leg., KBM0310021	KF575582 KF575535 KF575354	KF575476 KF575433 KF575399	KJ548418 --- KF575513
Dytiscidae	Hydroporinae	Hydroporini	*Chostonectes nebulosus*	KBMC Chne545	Australia, South Australia, Victoria R. at Williamstown, 12 Oct 2002, 34°40.372′S 138°53.448′E, KB Miller, leg.	KF575616 KF575568 KF575387	KF575504 KF575465 KF575425	KJ548486 --- ---
Dytiscidae	Hydroporinae	Hydroporini	*Deronectes aubei*	KBMC Deau758	France: Pyr. Or. W Ptrats de Mollo, Torr. Parcigoule, 100 m, 13 Aug 2001	--- KJ548292 KJ548731	AF309326 --- KJ548645	--- --- ---
Dytiscidae	Hydroporinae	Hydroporini	*Deronectes latus*	KBMC Dnla560	Sweden, Västerbotten, Umeå, Bölesholmarna, 6 Aug 2001, J Bergsten, leg.	KJ548274 KJ548380 KJ548797	--- KJ548629 KJ548719	KJ548488 KJ548870 ---
Dytiscidae	Hydroporinae	Hydroporini	*Deronectes moestus*	KBMC Dcmo514	Italy, Sardinia, Nuoru Prov., river upstream from Lake Flumendosa, 39°58.943′N 9°24.722′E, 785 m, 18 Apr 2006, KB Miller, leg., KBM1804063	KF575609 KF575561 KF575380	KF575500 KF575458 KF575419	KJ548480 KJ548865 ---

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Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Dytiscidae	Hydroporinae	Hydroporini	*Ereboporus naturaconservatus*	KBMC Ebna538	United States, Texas, Terrell Co., Caroline Sp., 19 May 2007, Denton and Gibson, legs.	KF575613 KF575565 KF575384	KF575502 KF575462 KF575422	--- KJ548868 KF575525
Dytiscidae	Hydroporinae	Hydroporini	*Graptodytes ignotus*	KBMC Gpig575	Italy, Sardinia, Sassari Prov., 8 km N Aggius, 40°56.271′N 9°1.113′E, 521 m, 15 Apr 2006, KB Miller, leg., KBM1504064	KF575619 KF575571 KF575390	KF575507 KF575467 KF575427	KJ548491 KJ548873 KF575528
Dytiscidae	Hydroporinae	Hydroporini	*Haideoporus texanus*	KBMC Hite536	United States, Texas, Comal Co., Comal Springs Run 3, 8 Nov 2006, Gibson, leg.	KF575612 KF575564 KF575383	--- KF575461 KF575421	KJ548482 --- ---
Dytiscidae	Hydroporinae	Hydroporini	*Heterosternuta pulcher*	KBMC Hepu136	United States, New York, Tompkins Co., Fall Cr., Ithaca, 15 Sep 1999, KB Miller, leg.	KF575585 KF575538 KF575357	KF575478 --- KF575401	KJ548434 --- ---

Dytiscidae	Hydroporinae	Hydroporini	*Hydrocolus paugus*	KBMC Hlpa133	United States, New York, Tompkins Co., pond 10 km S Caroline, 16 May 2001, KB Miller, leg., KBM1005012	KF575586 KF575539 KF575358	KF575479 KF575436 KF575402	--- --- KF575515
Dytiscidae	Hydroporinae	Hydroporini	*Hydroporini Porhydrus*	KBMC Posp754	Italy, Sardinia, Nuoru Prov., Giara di Gestuari, 39°44.141′N 8°59.924′E, 589 m, 19 Apr 2006, KB Miller, leg., KBM1904061	KJ548180 KJ548289 ---	--- --- KJ548644	--- --- ---
Dytiscidae	Hydroporinae	Hydroporini	*Hydroporini Sanfilippodytes*	KBMC Sasp78	United States, Arizona, Santa Cruz Co., Santa Cruz River nr Beyerville, 31°25.233′N 100°55.25′W, 27 Apr 2000, KB Miller, leg., KBM2704002	KF575601 KF575554 KF575372	KF575494 KF575451 KF575413	--- --- KF575520
Dytiscidae	Hydroporinae	Hydroporini	*Hydroporus angustatus*	KBMC Hyan549	Russia, Volgograd Obl., Krasnoslobodsk, pond, 15 May 2001, J Bergsten, leg.	KF575624 KF575576 KF575395	KF575511 KF575471 ---	--- --- ---
Dytiscidae	Hydroporinae	Hydroporini	*Hydroporus obscurus*	KBMC Hyob550	Sweden, Västerbotten, Normjöle Kläppudden, 28 Jul 2001, J Bergsten, leg.	--- KJ548393 KJ548810	KJ548562 KJ548640 KJ548728	--- --- ---

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Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Dytiscidae	Hydroporinae	Hydroporini	*Hydroporus palustris*	KBMC Hypa548	Sweden, Härjedalen, Rogen, Hundviken, 30 Jun 2001, J Bergsten, leg.	KF575623 KF575575 KF575394	KF575510 KF575470 ---	--- --- ---
Dytiscidae	Hydroporinae	Hydroporini	*Hydroporus umbrosus*	KBMC Hyum551	Sweden, Västerbotten, Normjöle Kläppudden, 28 Jul 2001, J Bergsten, leg.	KJ548287 KJ548394 ---	KJ548563 KJ548641 ---	--- --- KJ548177
Dytiscidae	Hydroporinae	Hydroporini	*Megaporus hamatus*	KBMC Mpha96	Australia, New South Wales, 6 km SW Braidwood, 35°29.867′S 149°44.15′E, 2 Nov 2000, KB Miller, leg., KBM0211001	KF575593 KF575546 KF575365	KF575486 KF575443 KF575407	KJ548455 --- KF575517
Dytiscidae	Hydroporinae	Hydroporini	*Megaporus howittii*	KBMC Meho547	Australia, Victoria, pond ~25 km S Casterton, 37°39.289′S 141°14.380′E, 3 Oct 2002, KB Miller, leg.	KF575617 KF575569 KF575388	KF575505 KF575466 ---	KJ548487 --- ---

Dytiscidae	Hydroporinae	Hydroporini	*Nebrioporus clarki*	KBMC Nbcl513	Italy, Sardinia, Nuoru Prov., river upstream from Lake Flumendosa, 39°58.943′N 9°24.722′E, 785 m, 18 Apr 2006, KB Miller, leg., KBM1804063	KF575608 KF575560 KF575379	KF575499 --- KF575418	KJ548479 KJ548864 KF575523
Dytiscidae	Hydroporinae	Hydroporini	*Nebrioporus rotundatus*	KBMC Nbro563	United States, New York, Tompkins Co., Ithaca, 21 Jun 2001, KB Miller, leg.	KF575618 KF575570 KF575389	KF575506 --- KF575426	KJ548489 KJ548871 ---
Dytiscidae	Hydroporinae	Hydroporini	*Necterosoma susanna*	KBMC Ntsu443	Australia, New South Wales, Deva River, 20 km NW Moruya, 35°53.046′S 144°58.756′E, 1 Oct 2002, KB Miller, leg., KBM0110021	KF575595 KF575548 KF575367	KF575488 KF575445 KF575408	KJ548456 --- KF575518
Dytiscidae	Hydroporinae	Hydroporini	*Necterosoma undecimlineatum*	KBMC Ntwa95	Australia, New South Wales, nr Brogo Dam, 36°32.067′S 149°46.7′E, 1 Nov 2000, KB Miller, leg., KBM0111001	KF575596 KF575549 KF575368	KF575489 KF575446 KF575409	KJ548459 --- ---

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Table 3.1 (continued)

						12S	COI	Arg Kin
						16S	COII	RNA Pol II
Family	Subfamily	Tribe	Taxon title	Voucher	Locality	H3	Ef1a	Wnt
Dytiscidae	Hydroporinae	Hydroporini	*Neoporus mellitus*	KBMC Npme532	United States, Alabama, Conecuh Co., 23 km SE Evergreen along CR42, 31°20.059′N 86°47.641′W, 62 m, 12 May 2006, KB Miller, leg., KBM1205063	KF575610 KF575562 KF575381	KF575501 KF575459 KF575420	KJ548481 KJ548867 KF575524
Dytiscidae	Hydroporinae	Hydroporini	*Oreodytes congruus*	KBMC Orco62	United States, Colorado, Pitkin Co., Crystal River nr Marble, 39°4.25′N 107°12.4′W, 1,315 m, 2 Aug 2000, KB Miller, leg., KBM0208001	KF575597 KF575550 KF575369	KF575490 KF575447 KF575410	KJ548462 KJ548849 KF575519
Dytiscidae	Hydroporinae	Hydroporini	*Oreodytes quadrimaculatus*	KBMC Orqu543	United States, Oregon, Lane Co., Heceta Head, Devils's Elbow, Cape Cr., 01 Sep 2001, KB Miller, leg.	KF575615 KF575567 KF575386	--- KF575464 KF575424	KJ548484 --- KF575527

Dytiscidae	Hydroporinae	Hydroporini	*Oreodytes scitulus*	KBMC Orsc63	United States, Colorado, Pitkin Co., Crystal River nr Marble, 39°4.25′N 107°12.4′W, 1,315 m, 2 Aug 2000, KB Miller, leg., KBM0208001	KF575598 KF575551 KF575370	KF575491 KF575448 KF575411	KJ548463 --- ---
Dytiscidae	Hydroporinae	Hydroporini	*Paroster gibbi*	KBMC Psgi775	NCBI	--- AY353842 EF670098	FR732548 --- ---	--- --- ---
Dytiscidae	Hydroporinae	Hydroporini	*Psychopomporus felipi*	KBMC Hysp731	United States, Texas, Val Verde Co., San Felipe Springs, Del Rio, 15 Aug 2008, Foley, leg.	KF575622 KF575574 KF575393	--- --- ---	--- --- ---
Dytiscidae	Hydroporinae	Hydroporini	*Rhithrodytes sexguttatus*	KBMC Rrse508	Italy, Sardinia, Nuoru Prov., 4.5 km SE Bottidda, 40°20.332′N 9°1.785′E, 200 m, 16 Apr 2006, KB Miller, leg., KBM1604063	KF575605 KF575557 KF575376	KF575497 KF575455 KF575415	KJ548477 KJ548862 KF575521

(continued)

Table 3.1 (continued)

						12S	COI	Arg Kin
						16S	COII	RNA Pol II
Family	Subfamily	Tribe	Taxon title	Voucher	Locality	H3	Ef1a	Wnt
Dytiscidae	Hydroporinae	Hydroporini	*Stictonectes optatus*	KBMC Scop512	Italy, Sardinia, Nuoru Prov., river upstream from Lake Flumendosa, 39°58.943′N 9°24.722′E, 785 m, 18 Apr 2006, KB Miller, leg., KBM1804063	KF575607 KF575559 KF575378	KF575498 KF575457 KF575417	KJ548478 KJ548863 KF575522
Dytiscidae	Hydroporinae	Hydroporini	*Stictonectes rufulus*	KBMC Scru511	Italy, Sardinia, Nuoru Prov., river upstream from Lake Flumendosa, 39°58.943′N 9°24.722′E, 785 m, 18 Apr 2006, KB Miller, leg., KBM1804063	KF575606 KF575558 KF575377	--- KF575456 KF575416	--- --- ---
Dytiscidae	Hydroporinae	Hydroporini	*Stictotarsus roffii*	KBMC Stro26	United States, Arizona, Santa Cruz Co., Santa Cruz River nr Beyerville, 31°25.233′N 100°55.25′W, 27 Apr 2000, KB Miller, leg., KBM2704002	KF575603 KF575555 KF575374	KF575495 KF575453 KF575414	--- --- ---

Dytiscidae	Hydroporinae	Hydroporini	*Hydroporus dorsalis*	KBMC Sudo554	Sweden, Hälsingland, Övre Tälningsån, 2 Jul 2000, J Bergsten, leg.	KF575625 KF575577 KF575396	KF575507 KF575472 ---	--- --- ---
Dytiscidae	Hydroporinae	Hydrovatini	*Hydrovatus parallelipennis*	KBMC Hvsp458	Ghana, Volta Region, road between Nkwanta and Odumase, 8°15.537′N 0°26.562′E, 210 m, 15 Jun 2005, KB Miller, leg., KBM1506051	KJ548229 KJ548336 KJ548770	KJ548532 KJ548602 KJ548684	--- --- KJ548159
Dytiscidae	Hydroporinae	Hydrovatini	*Hydrovatus pustulatus*	KBMC Hvpu446	United States, New York, Tompkins Co., Pond 1 km SW Danby, 370 m, 42°20.825′N 26°29.233′W, 23 Sep 2002, KB Miller, leg.	KF575590 KF575543 KF575362	KF575483 KF575440 ---	--- --- ---
Dytiscidae	Hydroporinae	Hydrovatini	*Hydrovatus rufoniger*	KBMC Hvru559	Hong Kong: Lamna Island, Sok Kwu Wan: pond, 18 Sep 2000, J Bergsten, leg.	KJ548273 KJ548379 KJ548796	--- KJ548628 KJ548718	--- --- ---
Dytiscidae	Hydroporinae	Hydrovatini	*Queda youngi*	KBMC Quyo455	Peru, Madre de Dios, boat landing ~20 km S Infierno, nr Puerto Maldonado, 14 Dec 2003, KB Miller, leg.	KF575600 KF575553 KF575371	KF575493 KF575450 KF575412	--- KJ548853 ---

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Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Dytiscidae	Hydroporinae	Hygrotini	*Coelambus compar*	KBMC Htco365	United States, Wyoming, Natrona Co., salty pool, Sand Draw nr Waltman, 43°03.384′N 107°12.106′W, 17 Aug 2002, 1,821 m, KB Miller, leg.	KJ548224 KJ548332 KJ548765	KJ548527 KJ548597 KJ548679	--- --- KJ548155
Dytiscidae	Hydroporinae	Hygrotini	*Coelambus diversipes*	KBMC Htdi360	United States, Wyoming, Natrona Co., Teapot Cr. ~10kmS Midwest, 43°19.204′N 106°14.311′W, 1,534 m, 9 Aug 2002, KB Miller, leg.	KJ548225 KJ548333 KJ548766	KJ548528 KJ548598 KJ548680	--- --- KJ548156
Dytiscidae	Hydroporinae	Hygrotini	*Coelambus impressopunctatus*	KBMC Htim80	United States, Colorado, Mesa Co., Buzzard Cr., pond, 2 May 2000, KB Miller, leg., KBM0205001	KJ548226 KJ548334 KJ548767	KJ548529 KJ548599 KJ548681	--- --- ---

Dytiscidae	Hydroporinae	Hygrotini	*Coelambus salinarius*	KBMC Htsa366	United States, Wyoming, Natrona Co., ~12 km S Midwest, salt pool, 43°17.633′N 106°16.375′W, 9 Aug 2002, KB Miller, leg.	KJ548228 KJ548335 KJ548769	KJ548531 KJ548601 KJ548683	--- --- KJ548158
Dytiscidae	Hydroporinae	Hygrotini	*Herophydrus inquinatus*	KBMC Hpin578	Namibia, Skeleton Coast NP, Uniab River, pools, 20°13.017′S 13°12.603′E, 14 May 2004, KB Miller, leg., KBM1405041	KF575620 KF575572 KF575391	KF575508 KF575468 KF575428	--- --- KF575529
Dytiscidae	Hydroporinae	Hygrotini	*Herophydrus rohani*	KBMC Hpsp574	Zambia, Northwestern Province, stream and meadow ~4 km NW Ikatu, 11°30.268′S 24°22.747′E, 1,384 m, 7 Nov 2007, KB Miller, leg., KBM07110702	KJ548276 KJ548382 KJ548799	KJ548554 KJ548631 KJ548721	--- --- KJ548173
Dytiscidae	Hydroporinae	Hygrotini	*Hygrotini Herophydrus*	KBMC Hhsp752	Ghana, Volta Region, road between Nkwanta and Odumase, 8°15.537′N 0°26.562′E, 210 m, 15 Jun 2005, KB Miller, leg., KBM1506051	KJ548178 --- ---	KJ548495 KJ548564 KJ548642	--- --- KJ548136

(continued)

Table 3.1 (continued)

						12S	COI	Arg Kin
						16S	COII	RNA Pol II
Family	Subfamily	Tribe	Taxon title	Voucher	Locality	H3	Ef1a	Wnt
Dytiscidae	Hydroporinae	Hygrotini	*Hygrotus acaroides*	KBMC Htac370	United States, Alabama, Conecuh Co., 13 km E Evergreen along Hwy 31, Old Town Cr., 31°27.037′N 86°49.81′W, 53 m, 11 May 2006, KB Miller, leg., KBM1105061	KF575589 KF575542 KF575361	KF575482 KF575439 KF575405	--- --- KF575516
Dytiscidae	Hydroporinae	Hygrotini	*Hygrotus decoratus*	KBMC Htdc582	Sweden, Öland, Borgholm, Runsten, pond, 7 July 2005, 6287995 1550690, J. Geijer leg. BMNH744139.	KJ548277 KJ548383 KJ548800	KJ548555 KJ548632 KJ548722	--- --- KJ548174
Dytiscidae	Hydroporinae	Hygrotini	*Hygrotus sayi*	KBMC Htsa34	United States, New York, Tompkins Co., Ithaca, 42°26.433′N 76°29.8′W, 15 Sep 1999, KB Miller, leg., KBM1509991	KJ548227 --- KJ548768	KJ548530 KJ548600 KJ548682	--- --- KJ548157

Dytiscidae	Hydroporinae	Hyphydrini	*Desmopachria convexa*	KBMC Dpco81	United States, New York, St Lawrence Co., Macomb Twp, Fish Cr Marsh, 44°28.333′N 75°33.8′W, 23 May 2000, KB Miller, leg., KBM2305001	KF575584 KF575537 KF575356	KF575477 KF575435 ---	--- --- ---
Dytiscidae	Hydroporinae	Hyphydrini	*Desmopachria portmanni*	KBMC Dppo139	United States, Arizona, Cochise Co., Bear Cr. Huachuca Mts, 31°22.796′N 110°21.814′W, 9 May 2003, KB Miller, leg., KBM0905031	KJ548213 KJ548322 KJ548759	KJ548521 KJ548591 KJ548670	--- KJ548822 ---
Dytiscidae	Hydroporinae	Hyphydrini	*Hyphydrini Pachydrus*	KBMC Pasp761	Venezuela, Zulia St, 9°51.883′N 72°43.285′W, 96 m, btwn Machiques and Tukuko, 29 Jan 2009, Short, Garcia, Camacho, legs. VZ09-0129-03X	KJ548183 KJ548295 KJ548734	KJ548498 KJ548569 ---	--- --- ---
Dytiscidae	Hydroporinae	Hyphydrini	*Hyphydrus congoanus*	KBMC Hysp753	Zambia, Northwestern Province, Zambeze Source, 11°22.09′S 24°17.917′E, 1501 m, 6 Nov 2007, KB Miller, leg., KBM06110701	KJ548179 KJ548288 KJ548729	--- KJ548565 KJ548643	--- --- ---

(continued)

Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Dytiscidae	Hydroporinae	Hyphydrini	*Hyphydrus elegans*	KBMC Hpel440	Australia, Northern Territory, 5 km S Alice Springs, 23°44.74′S 133°52.048′E, 8 Oct 2002, KB Miller, leg., KBM0810022	KF575587 KF575540 KF575359	KF575480 KF575437 KF575403	--- KJ548830 ---
Dytiscidae	Hydroporinae	Hyphydrini	*Hyphydrus esau*	KBMC Hhsp643	Zambia, Copperbelt Province, nr Chimfunshi Wildlife Orphanage, ~40 km NW Chingola, 12°21.69′S 27°32.52′E, 1271 m, 1 Nov 2007, KB Miller, leg., KBM01110701	--- --- KJ548803	--- KJ548634 KJ548725	--- KJ548874 ---
Dytiscidae	Hydroporinae	Hyphydrini	*Hyphydrus excoffieri*	KBMC Hpex441	China: Yunnan, 4 km S Shisong, veg. rich lake, 11 Sep 2000, J Bergsten, leg.	KF575588 KF575541 KF575360	KF575481 KF575438 KF575404	--- KJ548831 ---
Dytiscidae	Hydroporinae	Hyphydrini	*Hyphydrus signatus*	KBMC Hhsi450	Namibia, Skeleton Coast, Oasis Spring, 14 May 2004, 19°26.746′S 12°49.301′E, KB Miller, leg.	KJ548221 KJ548329 KJ548762	KJ548524 KJ548594 KJ548676	--- KJ548828 ---

Dytiscidae	Hydroporinae	Hyphydrini	*Microdytes svensoni*	KBMC Mysv765	India, Karnataka, forest stream 30 km E Udupi, 4 Oct 2004, KB Miller, leg.	KF575578	---	---
						KF575531	---	---
						KF575350	KF575397	---
Dytiscidae	Hydroporinae	Laccornellini	*Canthyporus hottentottus*	KBMC Cnho772	NCBI	---	AJ850585	---
						AJ850333	---	---
						EF670118	---	---
Dytiscidae	Hydroporinae	Laccornellini	*Canthyporus nebulosus*	KBMC Cnne773	NCBI	---	AJ850587	---
						AJ850335	---	---
						EF670117	---	---
Dytiscidae	Hydroporinae	Laccornellini	*Canthyporus parvus*	KBMC Cnpa774	NCBI	---	EF056596	---
						EF056668	---	---
						EF056553	---	---
Dytiscidae	Hydroporinae	Laccornellini	*Laccornellus copelatoides*	KBMC Lccp771	NCBI	---	AY334247	---
						AY334131	---	---
						EF056578	---	---
Dytiscidae	Hydroporinae	Laccornellini	*Laccornellus lugubris*	KBMC Lclu770	NCBI	---	AJ850668	---
						AJ850421	---	---
						EF670227	---	---
Dytiscidae	Hydroporinae	Methlini	*Celina hubbelli*	KBMC Cehu442	United States, New York, Tompkins Co., Jennings Pond. 1 km SW Danby, 370 m, 42°20.825′N 76°29.233′W, 3 Sep 2002, KB Miller, leg.	KF575581	KF575475	KJ548417
						KF575534	KF575432	KJ548817
						KF575353	KF575398	---

(continued)

Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Dytiscidae	Hydroporinae	Methlini	*Celina imitatrix*	KBMC Ceim533	United States, Alabama, Monroe Co., 3 km E Owassa, 31°29.791′N 86°51.184′W, 99 m, 11 May 2006, KB Miller, leg., KBM1105064	KF575611 KF575563 KF575382	--- KF575460 ---	--- --- ---
Dytiscidae	Hydroporinae	Methlini	*Methles cribratellus*	KBMC Mtcr459	Ghana, Volta Region, road between Nkwanta and Odumase, 8°15.537′N 0°26.562′E, 210 m, 15 Jun 2005, KB Miller, leg., KBM1506051	KF575594 KF575547 KF575366	KF575487 KF575444 ---	--- --- ---
Dytiscidae	Hydroporinae	Vatellini	*Derovatellus lentus*	KBMC Dele762	Venezuela, Monagas State, S Maturin, morichal margin, 9°36.591′N 63°8.295′W, 45 m, 2 Feb 2010, Short, Garcia, legs. VZ10-0202-01B	KJ548184 KJ548296 KJ548735	KJ548499 KJ548570 KJ548648	--- --- ---

Dytiscidae	Hydroporinae	Vatellini	*Vatellus bifenestratus*	KBMC Vabi452	Peru, Madre de Dios, Explorers Inn, 12°50.208′S 69°17.603′W, 10 Dec 2003, KB Miller, leg., KBM1012031	KF585004 KF585005 KF585003	KF585006 KF585007 ---	KJ548476 --- ---
Dytiscidae	Hydroporinae	Vatellini	*Vatellus haagi*	KBMC Vaha448	Bolivia, Sta Cruz Prov., San Ignacio, 13 Jan 2004, G Svenson, leg.	KJ548269 KJ548375 KJ548792	--- --- KJ548716	--- --- ---
Dytiscidae	Hydroporinae	Vatellini	*Vatellus pilacaudus*	KBMC Vapi449	Peru, Madre de Dios, Explorers Inn, 12°50.208′S 69°17.603′W, 10 Dec 2003, KB Miller, leg., KBM1012031	KJ548270 KJ548376 KJ548793	--- KJ548625 ---	--- --- ---
Dytiscidae	Laccophilinae	Agabetini	*Agabetes acuductus*	KBMC Abac15	United States, New York, St Lawrence Co., Macomb Twp, Fish Cr Marsh, 44°28.333′N 75°33.8′W, 23 May 2000, KB Miller, leg., KBM2305001	KJ548187 KJ548300 KJ548739	DQ112634 KJ548572 KJ548651	KJ548402 --- AF392048

(continued)

Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Dytiscidae	Laccophilinae	Laccophilini	*Australphilus saltus*	KBMC Apsa373	Australia, Victoria, Brodribb River at Sardine Creek, nr Orbost, 37°30.85′S 148°32.617′E, 22 Nov 2000, KB Miller, leg., KBM2211001	KJ548197 KJ548306 KJ548746	DQ112635 KJ548578 KJ548659	KJ548411 --- KJ548143
Dytiscidae	Laccophilinae	Laccophilini	*Laccophilini Laccodytes*	KBMC Lmsp764	Venezuela, Monagas State, S Maturin, morichal margin, 9°36.591′N 63°8.295′W, 45 m, 2 Feb 2010, Short, Garcia, legs. VZ10-0202-01B	--- KJ548297 KJ548736	KJ548500 --- KJ548649	KJ548399 --- ---
Dytiscidae	Laccophilinae	Laccophilini	*Laccophilini Laccodytes*	KBMC Lysp376	Peru, Madre de Dios, Explorers Inn, 12°50.208′S 69°17.603′W, 10 Dec 2003, KB Miller, leg., KBM1012031	--- KJ548353 KJ548780	DQ112651 --- KJ548700	KJ548451 KJ548844 ---
Dytiscidae	Laccophilinae	Laccophilini	*Laccophilini Neptosternus*	KBMC Nrsp379	India, Karnataka, Agumbe Ghats, 13°29.852′N 75°4.221′E, 9 Oct 2004, KB Miller, leg., KBM09100401	KJ548251 KJ548360 KJ548781	DQ112652 KJ548615 KJ548704	KJ548458 KJ548848 KJ548167

Dytiscidae	Laccophilinae	Laccophilini	*Laccophilus horni*	KBMC Laho378	United States, Arizona, Cochise Co., Bear Cr. Huachuca Mts, 31°22.796′N 110°21.814′W, 9 May 2003, KB Miller, leg., KBM0905031	KJ548238 KJ548344 ---	DQ112644 KJ548605 KJ548693	KJ548442 KJ548836 KJ548160
Dytiscidae	Laccophilinae	Laccophilini	*Laccophilus maculosus*	KBMC Lama4	United States, New York, Tompkins Co., Ithaca, 42°26.433′N 76°29.8′W, 23 Oct 2000, KB Miller, leg., KBM2310001	KJ548239 KJ548345 KJ548774	DQ112647 KJ548606 KJ548694	KJ548443 KJ548837 AF392031
Dytiscidae	Laccophilinae	Laccophilini	*Philodytes umbrinus*	KBMC Pdum355	Namibia, Skeleton Coast NP, spring at mouth of Khumib River, 18°52.66′S 12°25.539′E, 13 May 2004, KB Miller, leg., KBM1305042	KJ548254 KJ548363 KJ548782	DQ112653 KJ548616 KJ548706	KJ548464 --- KJ548168
Dytiscidae	Lancetinae	Lancetini	*Lancetes angusticollis*	KBMC Lcan301	Argentina, Santa Cruz Province, ARG0001011	KJ548241 KJ548347 KJ548776	--- KJ548608 KJ548695	KJ548445 KJ548838 KJ548162

(continued)

Table 3.1 (continued)

Family	Subfamily	Tribe	Taxon title	Voucher	Locality	12S 16S H3	COI COII Ef1a	Arg Kin RNA Pol II Wnt
Dytiscidae	Lancetinae	Lancetini	*Lancetes lanceolatus*	KBMC Lcla91	Australia, Victoria, Sheepwash Lagoon 10 km E Yea, 37°10.267′S 145°31.733′E, 8 Nov 2000, KB Miller, leg., KBM0811001	JX477983 KJ548348 DQ813761	DQ813695 DQ813797 ---	KJ548446 KJ548839 AF392032
Dytiscidae	Lancetinae	Lancetini	*Lancetes marginatus*	KBMC Lcma302	Argentina, Buenos Aires Prov., La Escondida, Bragado, Jan 2002	KJ548242 KJ548349 KJ548777	KJ548537 KJ548609 KJ548696	--- KJ548840 KJ548163
Dytiscidae	Lancetinae	Lancetini	*Lancetes nigrofasciatus*	KBMC Lcni390	Peru, 9°43 S 77°28 W, ~11,500′, 29 Mar 2000, MW Hastriter	KJ548243 KJ548350 KJ548778	--- KJ548610 KJ548697	KJ548447 KJ548841 KJ548164
Dytiscidae	Lancetinae	Lancetini	*Lancetes varius*	KBMC Lcva196	Chile, Rio Hollenberg, 25 km S Poerto Natales, 14 Nov 2001, L Ström, leg.	KJ548244 KJ548351 DQ813762	DQ813696 DQ813798 KJ548698	KJ548448 KJ548842 DQ813726
Dytiscidae	Lancetinae	Lancetini	*Lancetes waterhousei*	KBMC Lcwa303	Argentina, Buenos Aires Prov., La Escondida, Bragado, Jan 2004	KJ548245 KJ548352 KJ548779	KJ548538 KJ548611 KJ548699	KJ548449 KJ548843 KJ548165

Dytiscidae	Matinae		*Batrachomatus daemeli*	KBMC Bada129	Australia, New South Wales, Tuross River, 5 km W Bodalla, 36°8.7′S 149°59.0833′E, 39 m, 2 Nov 2000, KB Miller, leg., KBM0211003	KJ548200 KJ548309 KJ548748	KJ548512 KJ548581 KJ548662	KJ548414 KJ548814 KJ548145
Dytiscidae	Matinae		*Matus bicarinatus*	KBMC Mabi2	United States, New York, St Lawrence Co., Macomb Twp, Fish Cr Marsh, 44°28.333′N 75°33.8′W, 23 May 2000, KB Miller, leg., KBM2305001	JX477984 --- JX477903	JX478072 JX478160 ---	--- --- AF392033

"---" are fragments not acquired or analyzed

Arthropods (MSBA, K.B. Miller). The molecular data include nine genes, *16S rRNA* (16S), *12S rRNA* (12S), *cytochrome c oxidase I* (COI), *cytochrome c oxidase II* (COII), *elongation factor 1α* (Ef1α), *arginine kinase* (AK), *histone III* (H3), *RNA polymerase II* (RNApol), and *wingless* (wnt). Not all fragments were sequenced for all taxa. In particular, the nuclear protein-coding genes did not amplify or sequence for all taxa (except H3, which amplified well for most diving beetles) (Table 3.1). The 3′ end of the fragment of COI and the 5′ and 3′ ends of COII include partial leucine and lycine tRNA coding regions. These were trimmed off because of considerable ambiguity in alignment. DNA fragments were amplified using PCR with TaKaRa Amplitaq (Applied Biosystems, Foster City, CA, USA) on an Eppendorf Mastercycler ep gradient S Thermal Cycler (Eppendorf, Hamburg, Germany). Amplification conditions were similar to those used by Miller et al. (2007b, 2009a) and Miller and Bergsten (2012). Contamination was investigated using negative controls, and PCR products were examined using gel electrophoresis. Products were purified using ExoSAP-IT (USB-Affymetrix, Cleveland, OH, USA) and cycle sequenced using ABI Prism Big Dye (v3.1; Invitrogen, Fairfax, VA, USA) using the same primers used to amplify. Sequencing reaction products were purified using Sephadex G-50 Medium (GE Healthcare, Uppsala, Sweden) and sequenced using an ABI 3130xl Genetic analyzer (Applied Biosystems, Foster City, CA, USA) in the Molecular Biology Facility at the University of New Mexico. Gene regions were sequenced in both directions. Resulting sequence data were examined and edited using the program Sequencher (Genecodes 1999). Five hydroporine taxa amplified a paralogous Ef1α copy (see Miller and Bergsten 2012), and these fragments were discarded. Many of the data were acquired during previous projects (Bergsten and Miller 2007; Miller 2003; Miller and Bergsten 2012; Miller et al. 2007b, 2009a). In a few cases (notably for species in *Laccornellus* and *Canthyporus*) data were acquired from GenBank (Table 3.1). New sequences were deposited in GenBank (Table 3.1).

3.2.3 Morphology

Characters used in this analysis derive from several previous compilations of data (Miller 2000, 2001, 2003, 2005, 2009; Miller et al. 2007b, 2009a, 2006) and those sources should be consulted for more thorough descriptions of the characters and states. Characters and character states are described in the Appendix and character coding for each species is presented in Table 3.2.

3.2.4 Analysis

3.2.4.1 Alignment

Several markers are length-invariant among these taxa (H3, COII, COI, EF1α) and alignments of these were unambiguous. Wingless exhibited length variability associated with three-base-pair, (or multiple of three-base-pair) indels. Gyrinidae

Table 3.2 Morphological data used in combined phylogenetic analysis of Dytiscidae

	00000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000011111
	00000000011111111112222222222333333333344444444445555555555666666666677777777778888888888999999999900000
	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234
	+ + + +
Spal472 Spanglerogyrus albiventris	–0000010110110000001000?0???000000000-001100000000010000000001010011010001000000--00---000-00000000001
Dici474 Dineutus ciliatus	–0000010210010000000000?0???000000000-000000000000010000000001010012010001000000--00---000-00000000001
Gyel494 Gyrinus elevatus	–0000010210110000000000?0???000000000-000000000000010000000001010012010001000000--00---000-00000000001
Ncsp642 Notomicrus sp.	110000100011100000000?0?1???000000000-001100000000010010000000010010000011100000011000---000-00000100000
Tosp639 Tonerus wheeleri	11000000001010000000000?1???000000000-001100000000010010000000020010000011000000001000---000-00000100000
Nocl503 Noterus clavicornis	11000000001010000000000?1???000000000-001110000000010010000000020010000011000000001000---000-00000100000
Hcsp570 Hydrocanthus sp.	11000000001010000000000?1???000000000-001110000000010010100000020010000011000000001000---000-00000100000
Haho504 Hygrobia hermanni	00000010000110000011000?0???0000000012001100000000010010000000020010000002000000011000001000-00000000000
Amle58 Amphizoa lecontei	01000010000100000001000?0???0000000010001100000000010010000000020010000002000000011000001000-00000000000
Mabi2 Matus bicarinatus	1110000100011000101001000100000000000-001100001000021100000000010100000002000000011000001000-00001000000
Bada129 Batrachomatus daemeli	1110000100011000101001000100000000000-001100001000021100000000010100000002000000011000001000-00001000000
Abac15 Agabetes acuductus	1100000100011000001001000100000000000-001100000000021100000011020010000003200000011011001000-00000000000
Laho378 Laccophilus horni	11000001000000000000110?0???000000000-001100000000021100001000021050000013200000011021000000-01000000000
Lama4 Laccophilus maculosus	1100000100000000000011000100000000000-001100000000021100001000021050000013200000011021000000-01000000000
Apsa373 Australphilus saltus	1100000100000000000011000100000000000-001100000000021100001000021050000013200000011021000000-01000000000
Pdum355 Philodytes umbrinus	11000001000000000000110?0???000000000-001100000000021100001000021050000013200000011021000000-01000000000
Nrsp379 Neptosternus sp.	11000001000000000000110?0???000000000-001100000000021100000000021050000013200000011021000000-01000000000
Lmsp764 Laccodytes sp.	11000001000000000000110?0???000000000-001100000000021100000000021050000013200000011021000000-01000000000
Lysp376 Laccodytes sp.	11000001000000000000110?0???000000000-001100000000021100000000021050000013200000011021000000-01000000000
Ctle11 Coptotomus lenticus	1100000100011000001001000100000000000-001100000000021100000001020010000003001000011000000000-00000000000
Ctsp530 Coptotomus venustus	11000001000110000010010?0???000000000-001100000000021100000001020010000003001000011000000000-00000000000
Apsy268 Agaporomorphus silvaticus	11000001000110000010010?0???000000000-0011000000001200000000010100100001040000000110000---00-01000000000
Cpau126 Exocelina australiae	1100000100011000001001000100000000000-001100000001120000000001020010000103000000011000000110-11000000000
Cpdi9 Copelatus distinctus	1100000100011000001001000100000000000-001100000001120000000001020010000103000000011000000110-11000000000

(continued)

Table 3.2 (continued)

	00000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000011111 00000000011111111112222222222333333333344444444445555555555666666666677777777778888888888999999999900000 12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234 + + + +
Lsan768 Lacconectus andrewsi	1100000100011000001001000100000000000-001100000000112000000000102001000010300000011000000110-11000000000
Lsre769 Lacconectus regimbarti	1100000100011000001001000100000000000-001100000000112000000000102001000010300000011000000110-11000000000
Hzsp734 Hydrodytes opalinus	1100000100011000001001010010000000000-0???0000000001200000000010000100????301000011000000000-00000000000
Ladi16 Laccornis difformis	1100000100001010001001010011000000000-101100000000002000000000102001001000301000011000000000-00000000000
Cehu442 Celina hubbeli	1100000100011010001001010011000100100-1011000000000020000000001020010010003010000-1000000000-00000000000
Ceim533 Celina imitatrix	1100000100011010001001010011000100100-1011000000000020000000001020010010003010000-1000000000-00000000000
Mtcr459 Methles cribratellus	11000001000010100010010?0???000100100-1011000000000020000000001020010010003010000-1000000000-00000000000
Lclu770 Laccornellus lugubris	11000001000010100010010?0???000000000-1011000000000021000000001020010010003210000-0000000001000000000000
Lccp771 Laccornellus copelatoides	11000001000010100010010?0???000000000-1011000000000021000000001020010010003210000-0000000001000000000000
Cnne773 Canthyporus nebulosus	11000001000010100010010?0???000000000-1011000000000021000000001020010010003010000-0000000001000000000000
Cnpa774 Canthyporus parvus	11000001000010100010010?0???000000000-1011000000000021000000001020010010003010000-0000000001000000000000
Cnho772 Canthyporus hottentottus	11000001000010100010010?0???000000000-1011000000000021000000001020010010003010000-0000000001000000000000
Anbl541 Antiporus blakei	1100000100001010001001010011000000000-1011000000000011000000001020010010003010000-0000000001000000000000
Anfe100 Antiporus femoralis	1100000100001010001001010011000000000-1011000000000011000000001020010010003010000-0000000001000000000000
Bage544 Barretthydrus geminatus	11000001000010100010010?0???000000000-1011000000000011000000001020010010003010000-0000000001000000000000
Cani144 Carabhydrus nigrinus	11000001000010100010010?0???000000000-1011000000000011000000001020010010003010000-0000000001000000000000
Psgi775 Paroster gibbi	11000001000010100010010?0???000000000-1011000000000011000000001020010010003010000-0000000001000000000000
Chgi444 Chostonectes gigas	1100000100001010001001010011000000000-1011000000000011000000001020010010003010000-0000000001000000000000
Chne545 Chostonectes nebulosus	11000001000010100010010?0???000000000-1011000000000011000000001020010010003010000-0000000001000000000000
Dcmo514 Deronectes moestus	11000001000010100010010?0???000000000-1011000000000011000000001020010010003010000-0000000001000000000000
Dnla560 Deronectes latus	11000001000010100010010?0???000000000-1011000000000011000000001020010010003010000-0000000001000000000000
Deau758 Deronectes aubei	11000001000010100010010?0???000000000-1011000000000011000000001020010010003010000-0000000001000000000000
Ebna538 Ereboporus naturaconservatus	11000001000010100010010?0???000000000-1011000000000011000000001020010010003010000-0000000001000000000000
Hysp731 Psychopomporus felipi	11000001000010100010010?0???000000000-1011000000000011000000001020010010003010000-0000000001000000000000
Posp754 Porhydrus sp.	11000001000010100010010?0???000000000-1011000000000011000000001020010010003010000-0000000001000000000000

Gpig575 Graptodytes ignotus	11000001000010100010010?0???000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Hepu136 Heterosternuta pulcher	1100000100001010001001010011000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Hite536 Haideoporus texanus	11000001000010100010010?0???000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Hyan549 Hydroporus angustatus	11000001000010100010010?0???000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Hyob550 Hydroporus obscurus	11000001000010100010010?0???000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Hypa548 Hydroporus palustris	11000001000010100010010?0???000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Hyum551 Hydroporus umbrosus	1100000100001010001001010011000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Meho547 Megaporus howitti	11000001000010100010010?0???000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Mpha96 Megaporus hamatus	1100000100001010001001010011000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Nbro563 Nebrioporus rotundatus	1100000100001010001001010011000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Nbcl513 Nebrioporus clarki	11000001000010100010010?0???000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Npme532 Neoporus mellitus	11000001000010100010010?0???000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Ntsu443 Necterosoma suzannae	11000001000010100010010?0???000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Ntwa95 Necterosoma wallastoni	1100000100001010001001010011000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Orco62 Oreodytes congruus	1100000100001010001001010011000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Orqu543 Oreodytes quadrimaculatus	11000001000010100010010?0???000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Orsc63 Oreodytes scitulus	11000001000010100010010?0???000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Rrse508 Rhithrodytes sexguttatus	11000001000010100010010?0???000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Scop512 Stictonectes optatus	11000001000010100010010?0???000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Scru511 Stictonectes rufulus	11000001000010100010010?0???000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Stro26 Stictotarsus roffi	1100000100001010001001010011000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Sudo554 Hydroporus dorsalis	11000001000010100010010?0???000000000-1011000000000110000000010200100100030100000-0000000001000000000000
Hlpa133 Hydrocolus paugus	11000001000010100010010?0???000000000-1011000000000100000000010200100100030100000-0000000001000000000000
Sasp78 Sanfilippodytes sp.	11000001000010100010010?0???000000000-1011000000000100000000010200100100030100000-0000000001000000000000
Vabi452 Vatellus bifenestratus	11000001000010110000010?0???010000000-1011000000000110000000010200100100030100000-0000000001000010000000
Vaha448 Vatellus haagi	11000001000010110000010?0???010000000-1011000000000110000000010200100100030100000-0000000001000010000000
Vapi449 Vatellus pilacaudus	11000001000010110000010?0???010000000-1011000000000110000000010200100100030100000-0000000001000010000000
Dele762 Derovatellus lentus	11000001000010110000010?0???010000000-1011000000000110000000010200100100030100000-0000000001000010000000
Husp735 Hydrodessus sp.	11000001000010100010011?0???000000000-1011000000000100000000010200100100030100000-0000000001000000000000

(continued)

Table 3.2 (continued)

	00000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000011111
	00000000011111111112222222222333333333344444444445555555555666666666677777777778888888888999999999900000
	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234
	+ + + +
Peno438 Peschetius nodieri	11000001000010100010011?0???000000000-1011000000000100000000010200101100030100000-0000000001000100000000
Pequ345 Peschetius quadricostatus	11000001000010100010011?0???000000000-1011000000000100000000010200101100030100000-0000000001000100000000
Arsp282 Amarodytes sp.	11000001000011100010011?0???000000000-1011000000000100000000010200101100030100000-0000000001000100000000
Arsp283 Amarodytes sp.	11000001000011100010011?0???000000000-1011000000000100000000010200101100030100000-0000000001000100000000
Biin82 Bidessonotus inconspicuus	11010001000011100010011?0???000000000-1011000000000100000000010200101001030100000-0000000001000100000000
Lbco272 Limbodessus compactus	11000001000011100010011?0???000010000-1011000000000100000000010200101101030100000-0000000001000100000000
Liaf132 Liodessus affinis	11010001000011100010011?0???000000000-1011000000000100000000010200101101030100000-0000000001000100000000
Ldsp755 Liodessus sp.	11010001000011100010011?0???000000000-1011000000000100000000010200101101030100000-0000000001000100000000
Adsp696 Anodocheilus sp.	11010001000011100010011?0???000000000-1011000000000100000000010200101101030100000-0000000001000100000000
Nesp698 Neobidessus sp.	11010001000011100010011?0???000000000-1011000000000100000000010200101001030100000-0000000001000100000000
Uvsp289 Uvarus spretus	1100000100001110001001110011000000000-1011000000000100000000010200101101030100000-0000000001000100000000
Hosp695 gen. nr. Hypodessus sp.	11000001000011100010011?0???000000000-1011000000000100000000010200101101030100000-0000000001000100000000
Htac370 Hygrotus acaroides	1100010100001010001001010011000010000-1011000000000100000000010200100100030100000-0000000000-00000001000
Htdc582 Hygrotus decoratus	11000101000010100010010?0???000010000-1011000000000100000000010200100100030100000-0000000000-00000001000
Htsa34 Hygrotus sayi	1100010100001010001001010011000010000-1011000000000100000000010200100100030100000-0000000000-00000001000
Htco365 Hygrotus compar	11000001000010100010010?0???000010000-1011000000000100000000010200100100030100000-0000000001100000000000
Htdi360 Hygrotus diversipes	11000001000010100010010?0???000010000-1011000000000100000000010200100100030100000-0000000001100000000000
Htim80 Hygrotus impressopunctatus	1100000100001010001001000011000010000-1011000000000100000000010200100100031100000-0000000001100000000000
Htsa366 Hygrotus salinarius	11000101000010100010010?0???000010000-1011000000000100000000010200100100030100000-0000000001100000000000
Hpsp574 Herophydrus rohani	11000101000010100010010?0???000010000-1011000000000100000000010200100100030100000-0000000000-00000001000
Hpin578 Herophydrus inquinatus	11000101000010100010010?0???000010000-1011000000000100000000010200100100030100000-0000000000-00000001000
Hhsp752 Herophydrus sp.	11000101000010100010010?0???000010000-1011000000000100000000010200100100030100000-0000000000-00000001000
Hvpu446 Hydrovatus pustulatus	1100010100001010011001000011000010100-1011000000000100100000000200100100032000000-0000000000-00000000000
Hvsp458 Hydrovatus parallelipennis	11000101000010100110010?0???000010100-1011000000000100100000000200100100032000000-0000000000-00000000000
Hvru559 Hydrovatus rufoniger	11000101000010100110010?0???000010100-1011000000000100100000000200100100032000000-0000000000-00000000000

Quyo455 Queda youngi	11000101000010100110010?0???000010000-1011000000000100100000000200100100030100000-0000000000-0000000000
Hpel440 Hyphydrus elegans	110001010000101000100101001100001 0000-10110000000000000000000010200000100030100000-000000000100000000000
Hpex441 Hyphydrus excoffieri	11000101000010100010010?0???000010000-10110000000000000000000010200000100030100000-000000000100000000000
Hhsi450 Hyphydrus signatus	11000101000010100010010?0???000010000-10110000000000000000000010200000100030100000-000000000100000000000
Hysp753 Hyphydrus congoanus	11000101000010100010010?0???000010000-10110000000000000000000010200000100030100000-000000000100000000000
Hhsp643 Hyphydrus esau	11000101000010100010011?0???000010000-10110000000000000000000010200000100030100000-000000000100000000000
Pasp761 Pachydrus sp.	110001010000101001100111001100001 0000-1011000000000000000000001020000010003010000011000000000-0000000000
Dpco81 Desmopachria convexa	11000101000010100010011?0???000010000-10110000000000000000000000200000100030100000100000000010000000010000
Dppo139 Desmopachria portmanni	11000101000010100010011?0???000010000-10110000000000000000000000200000100030100000100000000010000000010000
Mysv765 Microdytes svensoni	11000101000010100010010?0???000010000-10110000000000000000000010200000100030100000100000000010000000000000
Hppa371 Hydrotrupes palpalis	11000001000110000010010?0???000000001200110000000002110010000000001000000300000001100000 1000-0000000000
Plde130 Platynectes decemaculatus	11000001000110000010010?0???00000000120011000000000211001000100200100000030000000110000 01000-0000000000
Pysp457 Platynectes sp.	11000001000110000010010?0???00000000120011000000000211001000100200100000030000000110000 01000-0000000000
Atsp759 Agametrus nitens	11000001000100000010010?0???00000000120011000000000211001000100200100000030000000110000 01000-0000000000
Ansp760 Agametrus humilis	11000001000110000010010?0???00000000120011000000000211001000100200100000030000000110000 01000-0000000000
Ilfr409 Ilybius fraterculus	110000010001100000100100010000100000110011000000000211001000000100000000030000110110000 01000-0000000000
Ilsu64 Ilybius subaeneus	110000010001100000100100010000100000110011000000000211001000000100000000030000110110000 01000-0000000000
Ilga12 Ilybius gagates	110000010001100000100100010000000000120011000000000211001000100100100000030000110110000 01000-0000000000
Agsp411 Ilybius sp.	11000001000110000010010?0???00000000120011000000000211001000100100100000020000001110000 01000-0000000000
Agdi412 Agabus disintegratus	11001001000110000010010?0???00000000120011000000000211001000100100100000020000001110000 01000-0000000000
Agco57 Ilybiosoma cordatum	11000001000110000010010?0???00000000120011000000000211001000100100100000020000001110000 11000-0000000000
Agse413 Ilybiosoma seriatum	11000001000110000010010?0???00000000120011000000000211001000100100100000020000001110000 11000-0000000000
Agtr60 Agabus tristis	11001001000110000010010?0???00000000120011000000000211001000100100100000020000001110000 01000-0000000000
Pmsp730 Agabus didymus	11000001000110000010010?0???00000000120011000000000211001000000100100100020000000110000 00000-0000000000
Crup251 Carabdytes upin	11000001000110000010010?0???10000000120011000010000211000000000200000000030000000110000 01000-0000000000
Rhsi17 Rhantus sinuatus	11000001000110000010010?0???10000000100011000010000211000000100100000000020010000110001 01000-0000000000
Rhca262 Rhantus calidus	11000001000110000010010?0???10000000120011000010000211000000000200000000020010000110001 01000-0000000000
Rhat10 Rhantus atricolor	110000010001100000100100010010000000010001100001000021100000000010000000002001000011000101000-0000000000
Rhbi3 Rhantus binotatus	110000010001100000100100010010000000010001100001000021100000000010000000002001000011000101000-0000000000

(continued)

Table 3.2 (continued)

	00000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000011111
	00000000011111111112222222222333333333344444444445555555555666666666677777777778888888888999999999900000
	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234
	+ + + +
Rhsp408 Rhantus validus	11000001000110000010010001001000000010001100001000021100000000010000000002001000011000101000-00000000000
Cbin410 Colymbetes infuscatus	11000001000100000010010?0???1000000010001100001000021100000000010000000002001000011000101000-00000000000
Cbpa59 Colymbetes paykulli	11000001000100000010010?0???1000000010001100001000021100000000010000000002001000011000101000-00000000000
Clsp476 Colymbetes fuscus	11000001000100000010010?0???1000000010001100001000021100000000010000000002001000011000101000-00000000000
Nean25 Neoscutopterus angustus	11000001000100000010010?0???1000000010001100001000021100000010010000000002001000011000101000-00000000000
Mdco475 Meladema coriacea	11000001000110000010010?0???1000000010001100001000021100000000010000000002001000011000101000-00000000000
Hopl453 Hoperius planatus	11000001000110000010010001001000000010001100001000021100000000010000000002001000011000101000-00000000000
Lcan301 Lancetes angusticollis	11000001000110000010010?0???0000000112001100011000021100000001021000001003100000011000001000-00000000000
Lcla91 Lancetes lanceolatus	11000001000110000010010001000000000112001100011000021100000001021000001003100000011000001000-00000000000
Lcma302 Lancetes marginatus	11000001000110000010010?0???0000000112001100011000021100000001021000001003100000011000001000-00000000000
Lcni390 Lancetes nigrofasciatus	11000001000110000010010?0???0000000112001100011000021100000001021000001003100000011000001000-00000000000
Lcva196 Lancetes varius	11000001000110000010010?0???0000000112001100011000021100000001021000001003100000011000001000-00000000000
Lcwa303 Lancetes waterhousei	11000001000110000010010?0???0000000112001100011000021100000001021000001003100000011000001000-00000000000
Spla123 Spencerhydrus latecinctus	01000001000100001010010?0???0000000011001100001100021101010100010000011005200000011000---000-00000000110
Sppu108 Spencerhydrus pulchellus	01000001000100001010010?0???0000000011001100001100021101010100010000011005200000011000---000-00000000110
Cyma416 Cybister marginicollis	01000001000100000010010?0???0000000011001100111100021101010100010040011005200000011000---000-00000000110
Cypu21 Cybister puncticollis	01000001000100000010010001000000000011001100111100021101010100010050011005200000011000---000-00000000110
Cytr102 Cybister tripunctatus	01000001000100000010010001000000000011001100111100021101010100010050011005200000011000---000-00000000110
Cysp757 Cybister sp.	01000001000100000010010001000000000011001100111100021101010100010050011005200000011000---000-00000000110
Mefr300 Megadytes fraternus	01000001000100000010010?0???0000000011001100111100021101010100010020011005200000011100---000-00000000110
Mero254 Megadytes robustus	01000001000100000010010?0???0000000011001100111100021101010100010020011005200000011100---000-00000000110
Onsc107 Onychohydrus scutellaris	01000001000100000010010?0???0000000011001100011100021100010100010000011005200000011000---000-00000000110
Stat165 Sternhydrus atratus	01000001000100000010010?0???0000000011001100011100021100010100010000011005200000011000---000-00000000110
Dymg168 Dytiscus marginalis	01000011000100000010010001001000000010010100011000021110000000010010011005200000011000---000-00000000000
Dyve24 Dytiscus verticalis	01000011000100000010010001001000000010010100011000021110000000010010011005200000011000---000-00000000000

Hdcr238 Hyderodes crassus	01000001000110000010010?0???100000000-0100000110000211100000100100100110052000000011000---000-00000000000
Hdsh104 Hyderodes shuckardi	01000001000110000010010?0???100000000-0100000110000211100000100100100110052000000011000---000-00000000000
Nofa52 Notaticus fasciatus	01000001000000000110010?0???000000000-0100000010100211100000001200000110052000000011000---000-00000000000
Hyar68 Hydaticus aruspex	01000001000100000010010?0???000000000-0100000010100211000000001200000110052000000011000---000-00000000000
Hyci20 Hydaticus cinctipennis	01000001000100000010010?0???000000000-0100000010100211000000001200000110052000000011000---000-00000000000
Hyex400 Prodaticus exaratus	01000001000100000010010?0???000000000-0100000010100211000000001200000110052000000011000---000-00000000000
Hyfa119 Prodaticus fabricii	01000001000100000010010?0???000000000-0100000010100211000000001200000110052000000011000---000-00000000000
Hysu23 Prodaticus subfasciatus	01000001000100000010010?0???000000000-0100000010100211000000001200000110052000000011000---000-00000000000
Hyxa67 Prodaticus xanthomelas	01000001000100000010010?0???000000000-0100000010100211000000001200000110052000000011000---000-00000000000
Erau103 Eretes australis	01000001000110000010010?0???000000000-0100000012100211000000000200000110052000000011000---000-00000000000
Ergr105 Eretes griseus	01000001000110000010010?0???000000000-0100000012100211000000000200000110052000000011000---000-00000000000
Grli69 Graphoderus liberus	01000001000100000010010?0???000000000-0100000012100211000010001200000110052000000011000---000-00000000000
Acab72 Acilius abbreviatus	0100000100010000000100100010000000000-0100010012100211000010001200000110052001000011000---000-00000000000
Acse7 Acilius semisulcatus	0100000100010000000100100010000000000-0100010012100211000010001200000110052001000011000---000-00000000000
Thba210 Thermonectus basillaris	01000001000100000010010?0???000001000-0100010012100211000010001200000110052000000011000---000-00000000000
Thni5 Thermonectus nigrofasciatus	01000001000100000010010?0???000001000-0100010012100211000010001200000110052000000011000---000-00000000000
Aeop406 Aethionectes optatus	01000001000100000010010?0???000000000-0100000012100211000010001200000110052001000011000---000-00000000000
Aesp659 Aethionectes sp.	01000001000100000010010?0???000000000-0100000012100211000010001200000110052001000011000---000-00000000000
Saba90 Sandracottus bakewelli	01000001000100000010010?0???000000000-0100000012100211000010001200000110052001000011000---000-00000000000
Sade328 Sandracottus dejeani	01000001000100000010010?0???000000000-0100000012100211000010001200000110052001000011000---000-00000000000

“-” indicates inapplicable data, “?” indicates missing data. Characters are non-additive except those marked with “+”

specimens had introns in RNA polymerase II (at positions 269–345) and *Agaporomorphus silvaticus* (Apsy268) had an intron in arginine kinase (at positions 244–298), which were removed. These were aligned using MUSCLE (Edgar 2004) and the default parameters and then adjusted manually as needed to conserve open reading frame. 16S and 12S are each much more length variable, and these were aligned using MUSCLE (Edgar 2004) and the default parameters.

3.2.4.2 Parsimony

Parsimony analysis was done in TNT (Goloboff et al. 2008). The morphological characters 2, 12, 56, 61, 94, 98, 99 and 104 were treated as additive. Tree searches began by generating trees using 30 random addition sequences. These trees were then swapped using tree bisection-reconnection, sectorial search (with the default parameters in TNT), and 30 iterations of tree-drifting (Goloboff 1999). Shortest trees found were then imported into WinClada (Nixon 2002) for examination of topologies, optimization of character states and calculation of the consensus. Bootstrap values were calculated in NONA as implemented in WinClada using 1,000 bootstrap iterations and saving the consensus of each iteration.

3.2.4.3 Bayesian

Bayesian analysis was done in MrBayes 3.2 (Ronquist et al. 2012). We used a partitioned model with all parameters of the model, except topology and branch length, unlinked, and estimated separately. Partitioning scheme followed Miller et al. (2009a) with 1st, 2nd and 3rd codon positions separated into partitions but the same positions merged across nuclear and mitochondrial protein-coding genes, respectively. Mitochondrial ribosomal 12S and 16S were merged and together given a separate partition. A gamma distributed rate variation parameter (Γ) and a proportion of invariable sites (I) were allotted the model for each partition. The substitution rate matrix was not selected *a priori* but estimated using reversible-jump MCMC for each partition across all 203 possible but reversible 4×4 nucleotide models (Huelsenbeck et al. 2004). The morphological data were analysed under a Markov K model (Lewis 2001)+Γ, with the same characters as in the parsimony analysis treated as ordered and accounting for the bias that only parsimony informative characters were scored. Three separate MCMC runs, each with one cold and three incrementally heated chains ($T=0.1$) were distributed across eight cores of two 2.8 GHz Quad-Core Intel Xeon processors (Mac Pro; L2 Cache 12 Mb per processor: memory: 4 GB 800 MHz DDR2 FB-DIMM) and run for 20 million generations. We used a parsimony tree as a starting tree for the chains, and sampled the cold chains every 1,000th generation. The average deviation of split frequencies, PSRF, ESS, and statistical graphics provided by MrBayes 3.2, and Tracer 1.5 (Rambaut and Drummond 2007), was used to assess mixing and convergence of runs. A burn-in of 25 % was discarded before the remaining sampled trees from the three runs were pooled and a majority-rule consensus tree calculated.

3.3 Results

Thirteen equally parsimonious trees were found of length 46737 (CI = 13, RI = 42) with the consensus of these shown in Fig. 3.2. The consensus is well resolved with few clades collapsed. Support for less-inclusive groupings (genera, tribes) is relatively strong, but support for relationships among the tribes and subfamilies is very low. All of the "backbone," more-inclusive groupings (relationships among tribes and/or subfamilies) are supported by less than 50 % bootstrap values (Fig. 3.2).

The three separate runs for the Bayesian analysis converged satisfactory and the joint tree samples resulted in the close-to fully resolved majority-rule consensus tree in Fig. 3.3. The ingroup, Dytiscidae, was monophyletic (posterior probability, pp = 1.0) and the clade Amphizoidae + Paelobiidae (pp = 1.0) was resolved as its sister group (pp = 1.0). The family Noteridae, containing some of the longest terminal branches in the analysis, was monophyletic (pp = 1.0) and resolved as a sister group to the clade with Amphizoidae, Paelobiidae, and Dytiscidae (pp = 1.0). Within Dytiscidae, the subfamily Matinae was resolved with high support (pp = 0.99) as the sister lineage to remaining Dytiscidae. Matinae apart, the rest of Dytiscidae consist of five well supported major groupings but where the relative relationship between each other is tentative due to the moderate support. The well supported higher-level groups are (1) Agabinae + Colymbetinae (pp = 0.96), (2) Hydroporinae + Hydrodytinae (pp = 1.0), (3) Dytiscinae + Laccophilinae + Cybistrini + Copelatinae (pp = 0.96), (4) Coptotominae (pp = 1.0), and (5) Lancetinae (pp = 1.0). The tentative resolution of these five groups places Lancetinae as sister to Agabinae + Colymbetinae (pp = 0.62), Coptotominae as sister to Hydroporinae + Hydrodytinae (pp = 0.63), and Lancetinae + Agabinae + Colymbetinae as sister to the remaining Dytiscidae (pp = 0.62) apart from Matinae. Seven of the ten subfamilies were highly supported as monophyletic (all with pp = 1.0): Matinae, Colymbetinae, Copelatinae, Coptotominae, Lancetinae, Hydroporinae and Laccophilinae. Hydrodytinae had only a single sampled species and hence its monophyly not tested, but it was not nested in any other subfamily. The two exceptions were Agabinae with only moderate support (pp = 0.72) and Dytiscinae recovered as paraphyletic as discussed in detail below.

The parsimony and Bayes analyses differ considerably in relative support (with much of the parsimony tree poorly supported) and topology. The parsimony tree includes several unexpected results that conflict dramatically with morphology, traditionally recognized groups, and the Bayesian analysis including placement of *Hydrodytes* (Hydrodytinae) among the outgroups, non-monophyly of Agabinae, the sister group relationship between certain Australian Hydroporini and *Canthyporus*, the nesting of *Laccornellus* among the *Deronectes*-group of genera, and non-monophyly of Methlini with *Methles* nested among certain Australian Hydroporini. Because of this, and because the MrBayes analysis is very well supported in general our preferred conclusions about relationships are based on this estimate of the phylogeny (Figs. 3.3, 3.4, and 3.5). Our discussion centers on this topology, and support values for particular conclusions are based on the Bayesian estimate.

Fig. 3.2 Strict consensus of 13 most parsimonious cladograms from combined analysis of morphology and DNA sequence data (length of trees = 46,737, CI = 13, Ri = 42). Numbers at branches are bootstrap values. *Upper right inset* tree is one of 13 parsimony trees with branch lengths proportional to character state changes mapped using "fast" (ACCTRAN) optimization

Fig. 3.2 (continued)

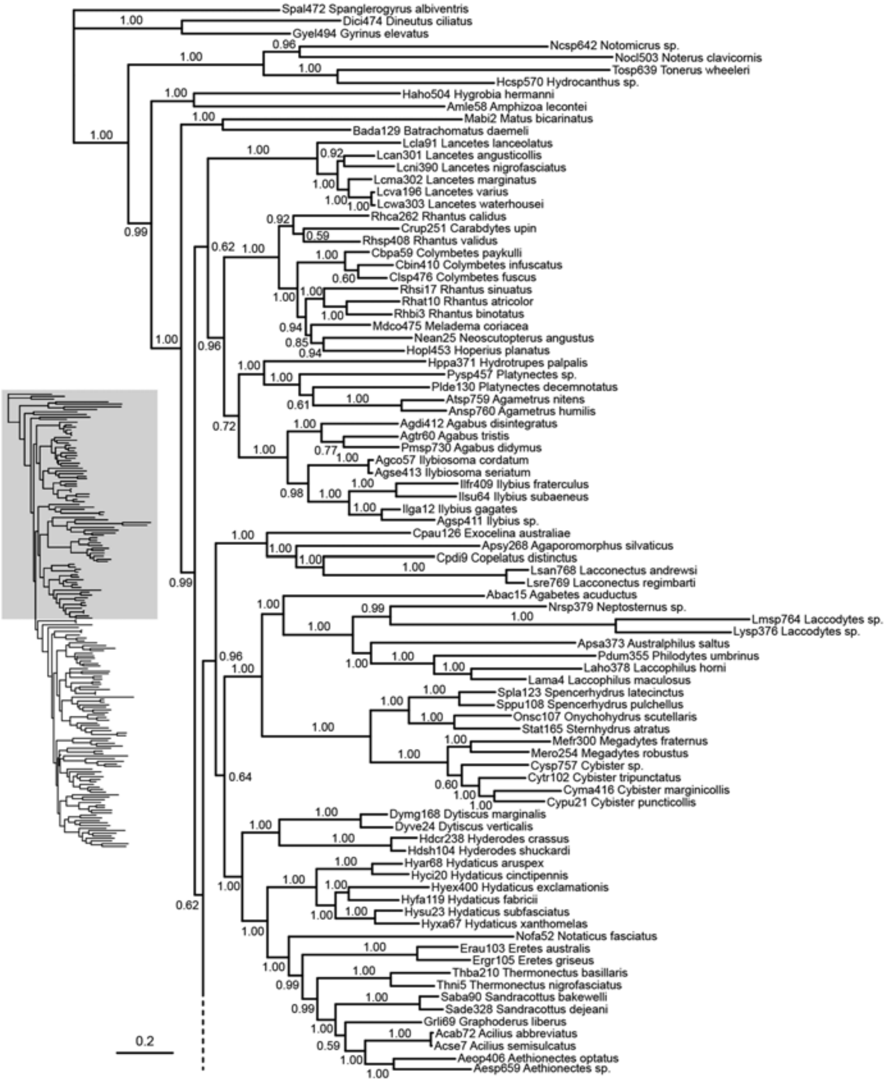

Fig. 3.3 Majority-rule consensus tree derived from the combined Bayesian MCMC analysis with a partitioned model for morphology and DNA sequence data. Numbers at branches are posterior probability clade support values

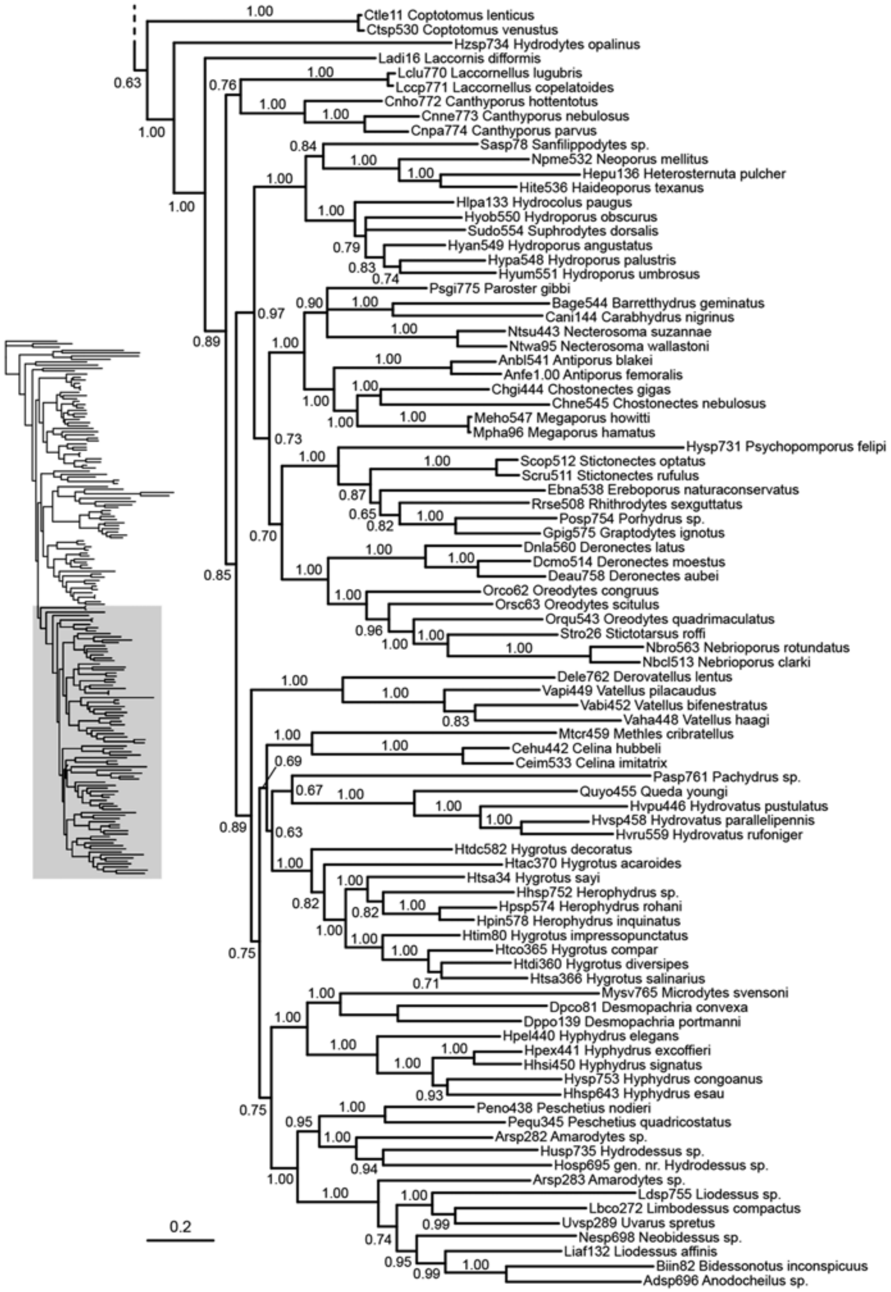

Fig. 3.3 (continued)

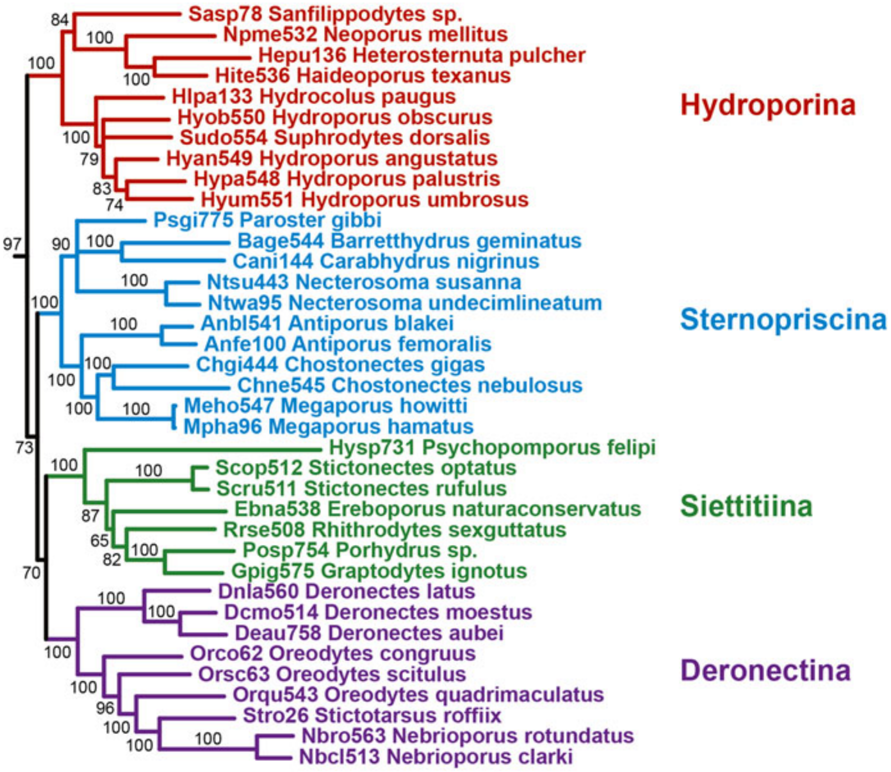

Fig. 3.4 Internal topology of Hydroporini derived from combined (model-partitioned) Bayesian analysis of morphology and DNA sequence data showing relationships among subtribes. Numbers at branches are posterior probability clade support values (x100)

3.4 Discussion

Diving beetle classification has moved from higher taxa based on authoritative schemes emphasizing few characters (e.g., Régimbart 1879; Sharp 1882), to a post-Hennigian reclassification emphasizing monophyletic groups based in large part on morphology (e.g., Burmeister 1976, 1990; Miller 2001; Wolfe 1985, 1988), to recent sophisticated phylogenetic approaches developing evidence from both morphology and DNA sequence data (Miller 2003; Miller et al. 2007b, 2009a; Ribera et al. 2002, 2008). This history has resulted in considerable phylogenetic progress by developing a much better understanding of diving beetle phylogenetic history, improving the classification, and illuminating areas in need of further study. This analysis similarly develops greater clarity in diving beetle phylogenetic history and updates the classification yet points out areas of weakness in our knowledge. Each of the following treatments discusses the history of phylogenetic ideas about each group as well as conclusions based on this analysis.

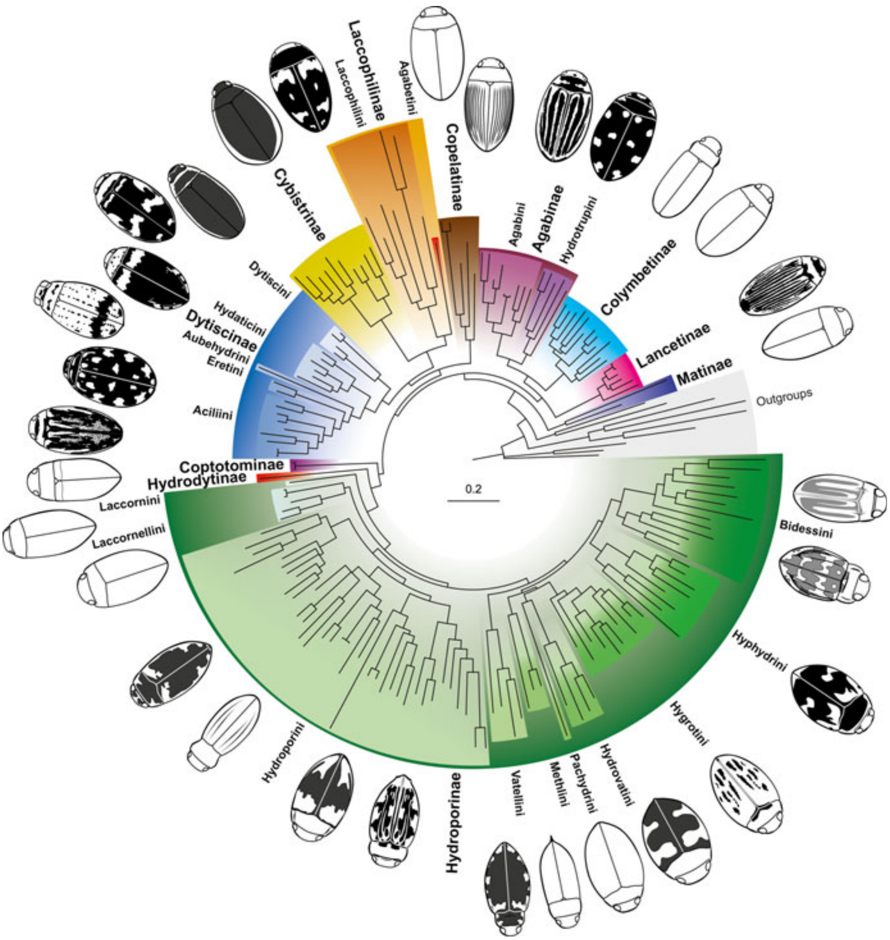

Fig. 3.5 Summary tree derived from combined (model-partitioned) Bayesian analysis of morphology and DNA sequence data for diving beetles (Dytiscidae) showing revised classification of subfamilies and tribes

3.5 Diving Beetle Phylogeny and Classification

3.5.1 Matinae Branden, 1885

3.5.1.1 Type Genus

Matus Aubé, 1836.

3.5.1.2 Diagnosis

These are dytiscidae with: (1) the medial portion of the prosternum and prosternal process distinctly longitudinally sulcate, (2) the head with a distinct longitudinal postocular carina, (3) the anterodorsal margins of metatarsomeres I-IV distinctly lobed, and (4) the female genitalia with "amphizoid-type" of configuration (Miller 2001), and with a large accessory gland reservoir attached to the fertilization duct.

3.5.1.3 Discussion

This group has usually been placed as a tribe in Colymbetinae until Miller (2001) elevated it to subfamily rank. Miller (2001) found the group to be sister to all other diving beetles. Ribera et al. (2008) found Matines placed near Hydrodytinae and these two groups, together with Lancetinae and Dytiscini, weakly placed as sister group to the rest of Dytiscidae. Relationships among the genera (based on larvae) were investigated by Alarie et al. (2001b). A recent revision (Hendrich and Balke 2013) synonymized *Allomatus* Mouchamps with *Batrachomatus* Clark and keyed and diagnosed all the Australian species.

In this analysis, Matinae was found to be monophyletic (Fig. 3.3, pp = 1.00) and sister to all other known diving beetles, with good support (Fig. 3.3, pp = 1.00). This corroborates the relationship first proposed by Miller (2001) based on morphology alone. This relationship is interesting in part because of the dramatically disjunct distribution of members of Matinae with *Matus* in eastern North America *Batrachomatus* in Australia suggesting a possible ancient vicariance.

3.5.1.4 Taxon Content

Matinae comprises two genera: *Matus* Aubé, 1836 from eastern North America, and *Batrachomatus* Clark, 1863 from Australia.

3.5.2 Lancetinae Branden, 1885

3.5.2.1 Type Genus

Lancetes Sharp, 1882.

3.5.2.2 Diagnosis

Lancetinae are Dytiscidae with: (1) the elytral apices sinuate or subtruncate, (2) the female reproductive tract with two genital openings and a distinctive bursa, and with the spermathecal duct extending from the anterior apex of the bursa, (3) the female gonocoxae weakly, but distinctly fused dorsally, (4) the median lobe asymmetrical with a distinct, elongate ventral sclerite, and (5) the metatarsal claws unequal in length in both sexes.

3.5.2.3 Discussion

Recognized as monophyletic and placed as a tribe in Colymbetinae *sensu lato* for much of its history, Lancetinae was regarded as potentially closely related to Dytiscinae by Ruhnau and Brancucci (1984) and *Coptotomus* (as a tribe Coptotomini of Colymbetinae) by Brinck (1948). Nilsson (1989) suggested *Lancetes* and Laccophilinae (including *Agabetes*) may be closely related based on larval features. Miller (2001), based on adult characters, and Alarie et al. (2002a), based on larvae, found the group resolved as sister to Dytiscinae. Ribera et al. (2008) found Lancetinae together with Dytiscini, Hydrodytinae and Matinae as sister to the rest of Dytiscidae, though these relationships were not strongly supported in their analysis.

In this analysis, Lancetinae is monophyletic with strong support (Fig. 3.3, pp = 1.00) and is resolved as sister to Colymbetinae + Agabinae, although support for this is not strong (Fig. 3.3, pp = 0.62). The single Australian species is resolved as sister to the South American species in the analysis (Fig. 3.3, pp = 1.00). This is one of the few Australian + South American biogeographic relationships among Dytiscidae.

3.5.2.4 Taxon Content

Lancetinae includes a single genus, *Lancetes* Sharp, 1882, with numerous species in temperate and high-elevation areas of South America and one species, *L. lanceolatus* (Clark) in Australia.

3.5.3 Agabinae Thomson, 1867

3.5.3.1 Type Genus

Agabus Leach, 1817.

3.5.3.2 Diagnosis

This fairly homogeneous subfamily is characterized by adults with a series of closely-spaced setae at the anteroventral angle of the metafemur. This is absent in some specimens of *Hydrotrupes*, *Hydronebrius* and some *Platambus*, but secondarily (Nilsson 2000; Ribera et al. 2004).

3.5.3.3 Discussion

This subfamily has usually been recognized as a monophyletic tribe within Colymbetinae until Miller (2001) elevated it to subfamily rank since, in that analysis, it was not found to be related to Colymbetini or other members traditionally placed in that subfamily. This was further confirmed by Ribera et al. (2002) and Ribera et al. (2008) who found Agabinae to be paraphyletic with the *Platynectes-group* of genera not related to the *Agabus*-group. Roughley (2000) placed the anomolous genus, *Hydrotrupes*, in its own subfamily based on larval features presented by Beutel (1994) that suggested the genus is sister to all Dytiscidae except Copelatinae. This was not supported by Miller's (2001) analysis of adult morphological features or Alarie's (1998) analysis of larval characters, each of which found *Hydrotrupes* related to Agabinae. Ribera et al. (2008) found *Hydrotrupes* resolved together with the *Platynectes*-group of genera. A more focused analysis on the subfamily by Ribera et al. (2004) also supported a distinction between the *Agabus-group* of genera and the *Platynectes*-group. The *Agabus*-group includes a number of primarily Holarctic taxa whereas the *Platynectes*-group includes several genera from northern and high-elevation South America, Central America, southeast Asia and Australia, and, possibly, the North American and east Asian genus *Hydrotrupes* (Ribera et al. 2004, 2008).

This analysis found a monophyletic Agabinae as historically defined, including *Hydrotrupes*, though support for the clade is moderate (Fig. 3.3, pp = 0.72). Agabinae is sister to Colymbetinae with high support (Fig. 3.3, pp = 0.96), and together this clade is sister to Lancetinae, although this last relationship is not strongly supported (Fig. 3.3, pp = 0.62). Within Agabinae, two larger clades are strongly resolved, one including the *Platynectes*-group of genera (including *Hydrotrupes*) (Fig. 3.3, pp = 1.00) and the second including the *Agabus*-group of genera (Fig. 3.3, pp = 1.00). Based on these results, we recognized two separate tribes within Agabinae, Hydrotrupini Roughley (**new status**), to include *Hydrotrupes* and the *Platynectes-group* of genera and Agabini, to include the remaining, primarily Holarctic genera. Details of their diagnoses and taxon content are described below under each tribe.

3.5.3.4 Taxon Content

Two tribes are included in Agabinae, Hydrotrupini Roughley, 2000 and Agabini Thomson, 1867.

3.5.4 Agabini Thomson, 1867

3.5.4.1 Type Genus

Agabus Leach, 1817.

3.5.4.2 Diagnosis

These are Agabinae characterized by having: (1) linear, marginal foveae present either at the anterolateral angles of the clypeus or extending entirely across the clypeus, and (2) females without natatory setae along the ventral margins of the metatibia and metafemur (except in the species, *Ilybius discedens* Sharp, which is clearly derived within Agabini (Larson 1987; Nilsson 1996, 2000).

3.5.4.3 Discussion

The bulk of the species of Agabinae are in this group, and collectively they have generally been regarded as a natural group and near Colymbetini. One exception to this is *Hydronebrius* Jakovlev that has been placed in its own tribe, Hydronebriini Guignot (and Hydronebriini Brinck), based on the absence of a metafemoral series of setae. Nilsson (2000) found this character unconvincing for tribal status suggesting lack of this series to be simply the result of increased punctation. He synonymized the tribe with Agabini *sensu lato*. Ribera et al. (2004) investigated relationships among the many species in this group and Bergsten et al. (2012) explored the degree to which species could be diagnosed based on a mitochondrial marker.

Here Agabini is monophyletic with good support (Fig. 3.3, pp = 1.00) and sister to Hydrotrupini (Fig. 3.3, pp = 0.72). The unusual genus *Hydronebrius* was not included, but based on descriptions of the genus (Brancucci 1980; Nilsson 2000; Toledo 1993) it seems clear the genus is related to the other genera in this group.

3.5.4.4 Taxon Content

Based on Nilsson's (2000) work and confirmation of generic limits by Ribera et al. (2004) there are six genera in this tribe. *Platambus* and *Agabinus* were not included, but these are clearly members of this tribe (Nilsson 2000; Ribera et al. 2008).

Agabus Leach, 1817
Agabinus Crotch, 1873
Hydronebrius Jakovlev, 1897
Ilybiosoma Crotch, 1873
Ilybius Erichson, 1832
Platambus Thomson, 1859

3.5.5 Hydrotrupini Roughley, 2000

3.5.5.1 Type Genus

Hydrotrupes Sharp, 1882.

3.5.5.2 Diagnosis

Members of this group are Agabinae characterized by (1) sublateral elliptical foveae on the clypeus (somewhat ambiguous in *Hydrotrupes*), and (2) females with natatory setae along the ventral margins of the metatibia and metafemur (natatory setae entirely absent in *Hydrotrupes*). Predaceous diving beetle males generally have ventral natatory setae on the metatibia and metafemur, but females of many groups do not. Within Agabinae, only hydrotrupines have ventral setae in both males and females with the exception of the species, *Ilybius discedens* Sharp, which is clearly derived within Agabini (Larson 1987; Nilsson 1996, 2000).

3.5.5.3 Discussion

The *Platynectes*-group of agabine genera was recognized as a unique component of the Agabinae by Brinck (Brinck 1948), Guéorguiev (1971, 1972), Nilsson (2000) and Ribera et al. (2004) (see above under Agabinae for a discussion of this group and *Hydrotrupes*). To date, there has been no hypothesis of the internal phylogenetic history of genera in the *Platynectes*-group. Hydrotrupini Roughley (at the subfamily rank) was originally erected to include only the genus *Hydrotrupes*, but here it is expanded to include several other agabine genera.

Hydrotrupes and members of the *Platynectes*-group of genera were here found to be monophyletic with strong support (Fig. 3.3, pp = 1.00). *Hydrotrupes* is resolved as sister to the rest of the group, also with high support (Fig. 3.3, pp = 1.00).

3.5.5.4 Taxon Content

Five genera are included in the tribe. *Andonectes* and *Leuronectes* were not included in this analysis, but, based on morphology and the analysis by Ribera et al. (2008), which included *Leuronectes*, there is little doubt the genera belong with others in this group.

Agametrus Sharp, 1882
Andonectes Guéorguiev, 1971
Hydrotrupes Sharp, 1882
Leuronectes Sharp, 1882
Platynectes Régimbart, 1879

3.5.6 Colymbetinae Erichson, 1837

3.5.6.1 Type Genus

Colymbetes Clairville, 1806

3.5.6.2 Diagnosis

These are Dytiscidae characterized by adults with: (1) the eyes anteriorly emarginate, (2) the male median lobe asymmetrical, but not generally strongly so, (3) the lateral lobes bilaterally symmetrical, (4) the female gonocoxae flattened and apically rounded, (5) the prosternum and prosternal process together in the same plane, and (6) the apices of the elytra evenly rounded and except Rhantus tristanicola (Brinck) and Rhantus selkirki Jäch, Balke & Michat (7) abdominal pleurite II with transverse rugae (not visible with elytra closed, and (8) metatarsal claws unequal in length.

3.5.6.3 Discussion

This subfamily included for many years taxa now placed in Lancetinae, Matinae, Agabinae, Coptotominae, Copelatinae, and even Laccophilinae (*Agabetes*) (e.g., Sharp 1882). The taxon content of Colymbetinae changed considerably as these taxa were removed over several years based on recognition of the large-scale paraphyly of the traditional concept (Beutel 1994; Burmeister 1976, 1990; Miller 2001; Ruhnau 1986; Ruhnau and Brancucci 1984). The current definition is considerably restricted (Miller 2001). An unusual species, *Carabdytes upin* Balke, Hendrich and Wewalka, was described from New Guinea and placed in its own tribe, Carabdytini Balke, Hendrich and Wewalka, 1992. Miller (2001) retained the tribal classification, but a molecular analysis by both Ribera et al. (2008) and Balke et al. (2009) resolved *Carabdytes* within Colymbetini, though no formal change was made to the classification until Morinière et al. (2014) synonymized Carabdytini with Colymbetini. Morinière et al. (2014) also tested the position of the two monotypic genera Senilites Brinck (from Tristan da Cunha) and Anisomeria Brinck (from Juan Fernández) that made up the poorly understood tribe Anisomeriini erected by Brinck (1948). They found both genera nested inside a group of Rhantus species and formally synonymized Anisomeriini with Colymbetinae. The internal relationships of Colymbetinae have been investigated especially using larvae (Alarie 1995, 1998; Alarie and Balke 1999; Alarie and Larson 1998; Michat 2005; Michat and Archangelsky 2009), but, in general, taxon sampling has not been adequate to determine the relationships among colymbetine taxa given the extreme diversity of the genus *Rhantus* and its evident paraphyly (Ribera et al. 2008).

Here, Colymbetinae is monophyletic with high support (Fig. 3.3, pp = 1.00) and is sister to Agabinae with high support (Fig. 3.3, pp = 0.96). *Carabdytes* is nested within Colymbetini (Fig. 3.3), corroborating Ribera et al. (2008) and Balke et al. (2009).

3.5.6.4 Taxon Content

Colymbetinae includes eight genera (including *Carabdytes*) though with greater study, it seems likely that the paraphyletic *Rhantus* will require subdivision into additional genera out of which Carabdytes will be part of one. *Bunites* and *Melanodytes* were not included in the analysis, but there is little doubt the two genera are closely related to other Colymbetini included here (Bachmann and Tremouilles 1982; de Marzo 1974; Franciscolo 1979; Michat 2005; Spangler 1972; Trémouilles and Bachmann 1989).

Bunites Spangler, 1972
Carabdytes Balke, Hendrich and Wewalka, 1992
Colymbetes Clairville, 1806
Hoperius Fall, 1927
Meladema Laporte, 1835
Melanodytes Seidlitz, 1887
Neoscutopterus J. Balfour-Browne, 1943
Rhantus Dejean, 1833

3.5.7 Copelatinae Branden, 1885

3.5.7.1 Type Genus

Copelatus Erichson, 1832.

3.5.7.2 Diagnosis

Copelatinae are Dytiscidae with: (1) the metacoxal lines closely approximated medially (lines absent in *Lacconectus* Motschulsky, *Aglymbus* Sharp and *Madaglymbus* Shaverdo and Balke, but corresponding medial regions of metacoxae narrow), (2) the scutellum externally visible with the elytra closed, and (3) the metatarsal claws subequal in length in both sexes.

3.5.7.3 Discussion

Members of this group have a long history of placement within Colymbetinae. More recently the group has been recognized as a subfamily sister to the rest of the Dytiscidae based on the presence of a foregut with a crop and serrated mandibles (and presumed ingestion of solid food particles) in larvae of some *Copelatus* (Beutel 1994, 1998; de Marzo 1976; Larson et al. 2000; Ruhnau 1986; Ruhnau and Brancucci 1984), though larvae of most *Copelatus* and several other copelatine genera are unknown and the generality of this feature remains unclear. Recent analyses have contradicted this sister-group relationship (Miller 2001; Ribera et al. 2002, 2008), but there has been no consensus regarding copelatine relationships with other dytiscids. In fact, Ribera et al. (2008) found Copelatinae not monophyletic with the Neotropical *Agaporomorphus* related to the Nearctic Coptotominae, instead. Within Copelatinae Balke et al. (2004a, b) and Shaverdo et al. (2008) used mitochondrial data to test the relationships among the several genera, a couple of which, *Copelatus* and *Exocelina*, are extremely diverse at the species level.

This analysis supports a monophyletic Copelatinae, including *Agaporomorphus*, with good support (Fig. 3.3, pp = 1.00). Also supported strongly is a sister group relationships between Copelatinae and Dytiscinae + (Laccophilinae + Cybistrinae) (Fig. 3.3, pp = 0.96). This relationship is by no means obvious based on any morphological features, but neither is any other relationship of Copelatinae with other predaceous diving beetle groups. Interestingly, Ribera et al. (2002) found copelatines nested within this same clade (with the anomalous addition of Paelobiidae), though a later analysis by Ribera et al. (2008) did not resolve a similar configuration. What is suggested by each of these results, however, including ours, is that the unique larval ingestion of particulate food (Beutel 1994, 1998; de Marzo 1976; Larson et al. 2000; Ruhnau 1986; Ruhnau and Brancucci 1984) is derived in this taxon (at least the known species).

3.5.7.4 Taxon Content

Copelatinae has no tribal subdivisions and currently includes eight genera but a new genus has been discovered in South Africa and is about to be described (D. Bilton, personal communication). The genus *Rugosus* García was described in Colymbetinae (García 2001), but the holotype specimen of *Rugosus emarginatus* García (in Universidad del Zulia, Maracaibo, Venezuela, J. Camacho, curator; examined by KBM) clearly belongs in Copelatinae based on close approximation of the margins of the medial portion of the metacoxae (metacoxal lines absent), subequal metatarsal claws, and other general features. *Rugosus* García is here moved to Copelatinae (**new placement**). The very diverse genus *Copelatus* has been divided into multiple genera recently (Balke et al. 2004a, 2004b) and will likely continue to be subdivided with continued study. Members of *Aglymbus*, *Liopterus*, *Madaglymbus,* and *Rugosus* were not included in the analysis, but all except *Rugosus* have been included in previous analyses (Balke et al. 2004a, b; Ribera et al. 2008; Shaverdo et al. 2008).

Agaporomorphus Zimmermann, 1921
Aglymbus Sharp, 1880
Copelatus Erichson, 1832
Exocelina Broun, 1886
Lacconectus Motschulsky, 1855
Liopterus Dejean, 1833
Madaglymbus Shaverdo and Balke, 2008
Rugosus García, 2001

3.5.8 Laccophilinae Gistel, 1848

3.5.8.1 Type Genus

Laccophilus Leach, 1815.

3.5.8.2 Diagnosis

These are Dytiscidae with: (1) the female gonocoxae strongly fused along the dorsal margin with the apex pointed, or bi-pointed with a narrow apical emargination, and the rami fused medially with anteriorly projecting processes and ventrally with distinct teeth, (2) two distinct female genital openings, and (3) both males and females with natatory setae along the posteroventral margin of the metatarsomeres but the metatibia without posteroventral natatory setae.

3.5.8.3 Discussion

There are two groups associated with Laccophilinae *sensu lato*, Agabetini van den Branden, with a single genus *Agabetes* Crotch and two species, and Laccophilini Gistel, which includes the bulk of the diversity in the subfamily. Without the inclusion of *Agabetes*, Laccophilinae has been a consistently recognized group for much of the history of dytiscid classification. Although placed in its own family-group by Branden (1885), *Agabetes* had usually been placed in Colymbetinae until Burmeister (1976) pointed out the unusual female genitalia that linked the genus more closely with Laccophilinae, a result corroborated by Ruhnau and Brancucci (1984). He later (Burmeister 1990) elevated the tribe to subfamily rank within Dytiscidae based on attributes of the female genitalia, though he recognized a close affinity between Agabetinae and Laccophilinae. Many subsequent authors (with some exceptions, see Larson et al. 2000) have instead recognized Laccophilinae with two tribes, Agabetini and Laccophilini while adding additional evidence from adult and larval morphology (Alarie et al. 2002b; Miller 2001). Ribera et al. (2008) did not, however, find a close association between *Agabetes* and Laccophilinae. There has been no general consensus of relationships of Laccophilinae with other dytiscid groups, though they were historically often placed with Noterinae before that group was removed from Dytiscidae (e.g.,, Sharp 1882). Larval evidence (Ruhnau and Brancucci 1984) and female reproductive musculature (de Marzo 1997) has suggested some affinities with Hydroporinae, and Nilsson (1989) raised the possibility of close relationship between Laccophilinae and Lancetinae.

In this analysis, *Agabetes* is resolved as the sister to Laccophilini with strong support (Fig. 3.3, pp = 1.00) corroborating Burmeister (1990), Miller (2001), and Alarie et al. (2002b). Here we recognize Laccophilinae with two tribes, Agabetini and Laccophilini. The sister relationship between Laccophilinae and cybistrines and sister-group relationship between this clade and Dytiscinae (*sensu stricto*, i.e. without Cybistrini) is unexpected and perplexing because there is little obviously supporting this from morphology, and there appears to be considerable morphological support for Dytiscinae as historically recognized (i.e., with Cybistrini as a part of it). Dytiscinae *sensu lato* is supported by several features from adult and larval morphology including: (1) large size in general (compared with small to very small size in Laccophilinae), (2) adults with rounded eyes anteriorly, (3) the median lobe bilaterally symmetrical with a distinct, elongate ventral sclerite, (4) a single genital opening in the female reproductive tract (RT) with the opening for sperm reception into the RT the same opening used for oviposition (laccophilines with two genital openings as with most other Dytiscidae), (5) larval abdominal segments VII-VIII with distinct lateral fringe of setae presumably used during a “shrimping” type of swimming behavior (lateral setae absent in laccophilines), and (6) the larval antennomeres and maxillary and labial palpomeres subdivided into additional sub-segments (not subdivided in laccophilines). Taken together, this has made Dytiscinae among the best-defined predaceous diving beetle groups in analyses based entirely or mainly on morphology (Alarie et al. 2011; Miller 2000, 2001, 2003). Analyses based entirely or mainly on molecular data, however, have not supported this grouping at all with Cybistrini resolved elsewhere (Fig. 3.3, Ribera et al. 2002) or with Dytiscinae in three separate clades (Ribera et al. 2008). Support for Laccophilinae + Cybistrini is strong in our analysis (Fig. 3.3, pp = 1.00) as is support for Dytiscinae *sensu stricto* (Fig. 3.3, pp = 1.00), though the clade Dytiscinae *sensu stricto* + (Laccophilinae + Cybistrini) is not so strongly supported (Fig. 3.3, pp = 0.64). Based on this support and the overall robustness of our results and this analysis in general, it would seem the most prudent thing to do is to change the classification to reflect this best evidence for the phylogeny. Therefore Cybistrini is elevated from tribe to subfamily rank here, Cybistrinae (**new status**) and Dytiscinae is restricted to the remaining tribes, Dytiscini (=Hyderodini, see below), Hydaticini, Aubehydrini, Eretini and Aciliini. What these relationships imply is that either the several rather unusually distinctive characteristics shared by Cybistrinae and Dytiscinae are independently derived in those groups or lost (reversed) in Laccophilinae. Possibly, some of these features are closely associated with size that is large in Cybistrinae and most Dytiscinae, but is relatively much smaller in Laccophilinae. The considerable length of many branches within Laccophilinae as over against other nearby taxa suggests this group may have undergone more rapid evolution than have other dytiscid taxa.

Laccophilinae, Cybistrinae, and Dytiscinae do share very similar configurations of the external female genitalia. All have the gonocoxae fused and apically somewhat knifelike and the rami well-developed and fused (modified in Eretini and Aciliini and some Hydatcini to be little or much less knifelike) (Miller 2000, 2001, 2003). In some cases, the rami of Cybistrinae are additionally similar to laccophilines in having the rami ventrally at least somewhat denticulate (Miller 2000, 2001, 2003). Also Cybistrinae and Laccophilinae have asymmetrical male suction cups on protarsus (symmetrical in Dytiscinae *sensu stricto*), though this is the plesiomorphic condition in Dytiscidae.

3.5.8.4 Taxon Content

Two tribes, Agabetini Branden, 1885 with one genus and two species, and Laccophilini Gistel, 1848 with several genera and many species.

3.5.9 Agabetini Branden, 1885

3.5.9.1 Type Genus

Agabetes Crotch, 1873

3.5.9.2 Diagnosis

These are Laccophilinae with: (1) the scutellum visible with the elytra closed, (2) two subequal metatarsal claws, and (3) less strongly lobed metatarsomeres than in Laccophilini. These are medium-sized, darkly colored, oval beetles which are superficially similar to certain agabines and copelatines, but lack a series of closely-placed setae at the apical angle of the metafemur and have the distinct metacoxal lines broadly separated, among other things. In addition, the dorsal surface is covered with short, fine grooves and males have a distinctive pair of longitudinal grooves on abdominal sternum VI (males of *A. svetlanae* Nilsson not known).

3.5.9.3 Discussion

Agabetini is sister to Laccophilini (all other known Laccophilinae) with good support (Fig. 3.3, pp = 1.00) (see above under Laccophilinae for further discussion).

3.5.9.4 Taxon Content

Agabetini includes one genus, *Agabetes* Crotch, 1873, with two species *A. acuductus* (Harris) in eastern North America and *A. svetlanae* Nilsson, from the Caspian coast of Iran.

3.5.10 Laccophilini Gistel, 1848

3.5.10.1 Type Genus

Laccophilus Leach, 1815.

3.5.10.2 Diagnosis

These are Laccophilinae with: (1) the scutellum not visible with the elytra closed, (2) a single metatarsal claw, and (3) prominent lobes at the anteroapical apices of the metatarsomeres.

3.5.10.3 Discussion

This tribe comprises the bulk of Laccophilinae diversity and is sister to Agabetini with good support (Fig. 3.3, pp = 1.00). Relationships among the numerous genera in the group have not been adequately investigated, though Alarie et al. (2000) presented some phylogenetic work based on larval features in four genera (see above under Laccophilinae for further discussion).

3.5.10.4 Taxon Content

There are 12 genera in Laccophilini with members of several of them very rarely collected and obscure (e.g., *Napodytes*, *Laccosternus*) and others extremely common, abundant and species-rich (e.g., *Laccophilus*, *Neptosternus*). There may be at least one undescribed genus from South America which appears to include the two species of "*Laccodytes*" included in this analysis (Fig. 3.3, Toledo et al. 2011).

Africophilus Guignot, 1948
Australphilus Watts, 1978
Japanolaccophilus Satô, 1972
Laccodytes Régimbart, 1895
Laccophilus Leach, 1815
Laccoporus J.Balfour-Browne, 1939
Laccosternus Brancucci, 1983
Napodytes Steiner, 1981
Neptosternus Sharp, 1882
Philaccolilus Guignot, 1937
Philaccolus Guignot, 1937
Philodytes J.Balfour-Browne, 1939

3.5.11 Cybistrinae Sharp, 1880, New Status

3.5.11.1 Type Genus

Cybister Curtis, 1827.

3.5.11.2 Diagnosis

This is one of the most well defined groups in all of Dytiscidae. Members of the clade exhibit numerous unambiguous adult and larval synapomorphies including adults with: (1) the metafemur and metatibia very broad and short; (2) the metatibial spurs different in size and shape, with the anterior spur acuminate and broader than the posterior one; (3) a posteroapical cluster of bifid setae on the metatibia; (4) a cluster of stiff setae on the apicoventral surface of the elytron; (5) females with two glands near the base of the common oviduct; (6) females with extensive muscles surrounding the vagina; (7) males with the adhesive setae on the mesotarsomeres apically simple (when present); (8) natatory setae present along the dorsal margin of metafemur, and larvae with; (9) the anterior margin of the clypeus prominently dentate; (10) the abdominal tergites reduced; (11) egg bursters absent in instar I; (12) the anterior margin of the prementum with a distinct lobe lacking spinous setae; (13) the antennae, maxillary palpi and labial palpi subdivided in all instars, and (14) the cerci very short or absent (Alarie et al. 2011; Miller et al. 2007b).

3.5.11.3 Discussion

This group has traditionally been recognized as a tribe within Dytiscinae. The group has generally been considered strongly supported as monophyletic (Alarie et al. 2011; Miller 2000, 2001, 2003; Ribera et al. 2002, 2008). The internal phylogeny of Cybistrinae was investigated by Miller et al. (2007b). Within Dytiscidae, the group has been found to be a member of the Dytiscinae and sister to the rest of the subfamily (Miller 2000, 2001, 2003). Results from other analyses of molecular data, however, suggest the group is not related to other Dytiscinae (Ribera et al. 2002, 2008).

This analysis recovered a monophyletic Cybistrinae (Fig. 3.3, pp = 1.00) sister to Laccophilinae with strong support (Fig. 3.3, pp = 1.00). Elevation of the clade here from tribe to subfamily rank represents a change to Cybistrinae Sharp, 1880 (**new status**) (see above under Laccophilinae for further discussion of the unexpected relationship of Cybistrinae + Laccophilinae).

3.5.11.4 Taxon Content

This tribe currently includes seven genera with *Cybister* and *Megadytes* each with several subgenera (Miller et al. 2007b).

Austrodytes Watts, 1978
Cybister Curtis, 1827
Megadytes Sharp, 1882
Onychohydrus Schaum and White, 1847
Regimbartina Chatanay, 1911
Spencerhydrus Sharp, 1882
Sternhydrus Brinck, 1945

3.5.12 Dytiscinae Leach, 1815

3.5.12.1 Type Genus

Dytiscus Linnaeus, 1758.

3.5.12.2 Diagnosis

These are Dytiscidae with: (1) the eyes not emarginate along the anterolateral margin, (2) the aedeagus (both the median lobe and lateral lobes) bilaterally symmetrical, (3) a single genital opening in the female, (4) the gonocoxae fused dorsally, (5) the prosternum and prosternal process together in the same plane, (6) the pro- and mesotarsi distinctly pentamerous, (7) males with the protarsal adhesive setae apically with a circular sucker-disc, (8) larval abdominal segments VII-VIII with a distinct lateral fringe of setae, and (9) the larval antennomeres and palpomeres secondarily divided into additional segments. Cybistrinae, until now, has been a part of this subfamily and shares many of the aforementioned characteristics. Major differences between Cybistrinae and Dytiscinae as here defined include the presence in cybistrines of elongate-oval apices of the male protarsal adhesive setae and the anterior metatibial spur broad and apically acuminate. Dytiscines have the anterior spur slender and similar to the posterior spur.

3.5.12.3 Discussion

This group has maintained its composition of taxa for a long time with a couple of exceptions. One of these is the genus *Notaticus* Zimmermann, with one species, which was originally described in Hydaticini. Guignot (1949), however, subsequently erected the junior synonym *Aubehydrus* Guignot and placed it in its own subfamily Aubehydrinae based on the absence of an externally visible scutellum. Miller (2000) found evidence for placement of the genus within Dytiscinae, a result that was subsequently corroborated using both adult morphology and molecular data (Miller 2001, 2003; Ribera et al. 2002, 2008) and larval features (Miller et al. 2007a). The subfamily (along with Cybistrinae) has been thought to be closely related to Colymbetinae (or the narrower Colymbetini) and, possibly, Lancetinae (Alarie et al. 2002a; Miller 2000, 2001; Ruhnau 1986; Ruhnau and Brancucci 1984) though there has not been a general consensus at this point.

In this analysis, Dytiscinae, as traditionally defined, that is, including Cybistrinae, is not monophyletic (Fig. 3.3). Dytiscinae without Cybistrinae is, though, with the latter group sister to Laccophilinae and that clade sister to the rest of Dytiscinae (Fig. 3.3, see further discussion under Cybistrinae and Laccophilinae above). Dytiscinae as restricted here is monophyletic with strong support (Fig. 3.3, pp = 1.00). Within Dytiscinae a clade comprised of Aubehydrini, Hydaticini, Aciliini and Eretini is well-supported, as well (Fig. 3.3, pp = 1.00). This group includes members with series of short, appressed setae along the apical margins of meso- and metatarsomeres I-IV and larvae with characteristic swimming behavior and various morphological features (Alarie et al. 2011; Miller 2000, 2001, 2003; Miller et al. 2007a). Dytiscini + Hyderodini (here regarded as one tribe, Dytiscini, see below) is also well-supported (Fig. 3.3, pp = 1.00).

3.5.12.4 Taxon Content

Dytiscinae currently includes five tribes:

Aciliini Thomson, 1867
Aubehydrini Guignot, 1942
Dytiscini Leach, 1815
Eretini Crotch, 1873
Hydaticini Sharp, 1880

3.5.13 Dytiscini Leach, 1815

3.5.13.1 Type Genus

Dytiscus Linnaeus, 1758.

3.5.13.2 Diagnosis

This group is characterized within Dytiscinae by: (1) absence of short, adpressed setae along the apical margins of the meso- and metatarsomeres and (2) metatarsal claws equal in length.

3.5.13.3 Discussion

Dytiscus and *Hyderodes* were placed in a single tribe by Sharp (1882). Roughley (1990) also regarded them as sister groups. Miller (2000), however, found evidence from morphology that *Hyderodes* is sister to a clade including Aubehydrini, Hydaticini, Eretini and Aciliini and placed the genus in its own tribe, Hyderodini Miller. This was corroborated by subsequent analyses, as well (Miller 2001, 2003). Ribera et al. (2002) found *Hyderodes* nested in a clade of Aubehydrini and Hydaticini, and Ribera et al. (2008) found *Hyderodes* sister to Hydaticini.

In this analysis the genera *Dytiscus* and *Hyderodes* are together monophyletic with strong support (Fig. 3.3, pp = 1.00) suggesting a more traditional interpretation of the classification of the group. Because of clear support for doing so, we here synonymize Hyderodini Miller with Dytiscini Leach (**new synonymy**). Dytiscini is sister to the rest of Dytiscinae, as defined here (without Cybistrinae).

3.5.13.4 Taxon Content

Two genera, the Holarctic *Dytiscus* Linnaeus, 1758 and the Australian *Hyderodes* Hope, 1838.

3.5.14 Hydaticini Sharp, 1880

3.5.14.1 Type Genus

Hydaticus Leach, 1817.

3.5.14.2 Diagnosis

These are Dytiscinae with: (1) the oblique anterolateral margin of the metasternum (the anterior margin of the metasternal wing) straight or slightly concave, and (2) males with a stridulatory apparatus formed by a reticulate file on the dorsal surface of the male protarsomere II and short spines on the dorsoproximal margin of the protibia (absent in a few taxa) (Larson and Pritchard 1974; Miller 2003).

3.5.14.3 Discussion

Hydaticini has usually be recognized as monophyletic, though one analysis, by Miller (2003), found Aciliini + Eretini nested within Hydaticini, albeit with low support. *Notaticus* (Aubehydrini) was originally included in Hydaticini. However, the distinctively straight anterolateral margin of the metacoxa, the uniquely irregular grooves on the female pronotum and elytron and the male protarsal/protibial stridulatory device are convincing morphological synapomorphies of the group (Miller et al. 2009a). Historically this group has had two genera, *Prodaticus* and *Hydaticus*, the latter with several subgenera including *Hydaticus sensu stricto*, *H.* (*Guignotities*), *H.* (*Hydaticinus*) and *H.* (*Pleurodytes*). A recent cladistic analysis by Miller et al. (2009a) resulted in a revised classification that recognized the same two genera, but with considerable content rearrangement. *Prodaticus*, which previously included only two species, was synonymized with each of the *Hydaticus* subgenera except *Hydaticus sensu stricto*. Thus, the content of the genus *Hydaticus* was reduced to only seven species, whereas *Prodaticus* included about 130, but with each genus demonstrably monophyletic. Nilsson (2010, 2014) preferred to avoid considerable reassignment of species names and placed *Prodaticus sensu* Miller et al. (2009a) as a subgenus of *Hydaticus sensu lato*. Miller (2001) and Miller et al. (2009a) found Hydaticini resolved as sister to Aubehydrini + (Eretini + (Aciliini)) morphologically supported by the presence of short, appressed setae along the apical margins of meso- and metatarsomeres I-IV.

This analysis resulted in a monophyletic Hydaticini with strong support (Fig. 3.3, pp = 1.00). The tribe is resolved as sister to the clade Aubehydrini + (Eretini + Aciliini), also with strong support (Fig. 3.3, pp = 1.00), corroborating Miller (2001).

3.5.14.4 Taxon Content

One genus, *Hydaticus*, with two subgenera, *H.* (*Prodaticus*) Sharp, 1882 and *Hydaticus sensu stricto* Leach, 1817.

3.5.15 Aubehydrini Guignot, 1942

3.5.15.1 Type Genus

Aubehydrus Guignot, 1942 (=*Notaticus* Zimmermann, 1928).

3.5.15.2 Diagnosis

Within Dytiscinae, members of this tribe are unique in having a concealed scutellum with the elytra closed.

3.5.15.3 Discussion

Notaticus was originally described in Hydaticini by Zimmermann (1928). Guignot (1942) erected a new subfamily, Aubehydrinae, for his new genus, *Aubehydrus* Guignot, which was later synonymized with *Notaticus* by Spangler (1973). *Notaticus* remained in its own subfamily until Miller (2000) placed it back within Dytiscinae based on a phylogenetic analysis of morphology. This was further confirmed by several independent studies (Alarie et al. 2011; Miller 2001, 2003; Miller et al. 2007a; Ribera et al. 2002, 2008). It has been resolved as sister to Hydaticini + Eretini + Aciliini (Miller 2000, 2001), sister to Aciliiini (Miller 2003), within Hydaticini (Ribera et al. 2002) or as sister to (Aciliini + Eretini) + (Hyderodini + Hydaticini) (Ribera et al. 2008).

In this analysis, Aubehydrini was resolved as sister to Eretini + Aciliini with strong support (Fig. 3.3, pp = 1.00).

3.5.15.4 Taxon Content

Aubehydrini includes a single genus, *Notaticus* Zimmermann, 1928.

3.5.16 Eretini Crotch, 1873

3.5.16.1 Type Genus

Eretes Laporte, 1833.

3.5.16.2 Diagnosis

Eretini are Dytiscinae with: (1) the prosternal process apically narrow and sharply pointed, (2) the pronotum with a narrow lateral marginal bead, (3) the surfaces of the meso- and metatarsomeres with adpressed, flattened setae, (4) the posterolateral margin of the elytron with a linear series of short, curved, black spines, (5) the elytra very thin and flattened and relatively lightly sclerotized overall; (6) the elytra punctate with each puncture bearing a black spot, and (7) general pale color on all surfaces with small to extensive black markings on the dorsum of the head, pronotum, and elytra.

3.5.16.3 Discussion

Eretes has been recognized in its own tribe for many years, and the species in the group are relatively homogeneous, though they are quite distinctive from other Dytiscidae. Four species are currently recognized after the revision by Miller (2002a), though there is some disagreement about species limits (Larson et al. 2000). The tribe has long been associated with Aciliini, and this has been confirmed with recent phylogenetic analyses (Alarie et al. 2011; Bukontaite et al. 2014; Miller 2000, 2001, 2003; Ribera et al. 2002) with *Eretes* nested within Aciliini, in some cases (e.g., Ribera et al. 2008).

In this analysis, Eretini is monophyletic (Fig. 3.3, pp = 1.00) and resolved as sister to Aciliini with strong support (Fig. 3.3, pp = 0.99). Eretini and Aciliini are very similar in larval features (Alarie et al. 2011; Miller 2002a), and many adult morphological characters, as well (Miller 2000, 2001, 2002a, 2003).

3.5.16.4 Taxon Content

The tribe has one genus, *Eretes* Laporte, 1833.

3.5.17 Aciliini Thomson, 1867

3.5.17.1 Type Genus

Acilius Leach, 1817.

3.5.17.2 Diagnosis

This tribe includes dytiscines with both metatibial spurs apically bifid.

3.5.17.3 Discussion

Aciliini includes some of the more common large predaceous diving beetles from throughout the world and have attracted considerable attention from biologists. The group has a long history of close association with Hydaticini and Eretini (e.g., Sharp 1882) and its monophyly has not been generally questioned, though the analysis by Ribera et al. (2008) placed *Eretes* within Aciliini. A recent comprehensive analysis of the genera within Aciliini supported the tribe as monophyletic, Eretini as the sister clade and each of the seven included genera as monophyletic (Bukontaite et al. 2014). Neotropical Thermonectus occupied the basalmost position in the tribe followed by Afrotropical Aethionectes and Tikoloshanes (Bukontaite et al. 2014).

Here Aciliini is resolved as monophyletic with high support (Fig. 3.3, pp = 0.99). The clade is sister to Eretini, also with high support (Fig. 3.3, pp = 0.99), and these are together in a clade with Hydaticini and Aubehydrini corroborating numerous previous analyses (Miller 2000, 2001, 2003).

3.5.17.4 Taxon Content

There are currently seven genera assigned to Aciliini. *Rhantaticus* and *Tikoloshanes* were not included in this analysis, but was included in the analysis by Bukontaite et al. (2014).

Acilius Leach, 1817
Aethionectes Sharp, 1882
Graphoderus Dejean, 1833
Rhantaticus Sharp, 1880
Sandracottus Sharp, 1882
Thermonectus Dejean, 1833
Tikoloshanes Omer-Cooper, 1956

3.5.18 Coptotominae Branden, 1885

3.5.18.1 Type Genus

Coptotomus Say, 1830.

3.5.18.2 Diagnosis

These are Dytiscidae with: (1) a characteristic habitus being medium size (5.5–8.8 mm), elongate and relatively narrow and streamlined, (2) the pronotum with a well-developed lateral bead, (3) the metacoxal lobes large and rounded with the metacoxal lines not closely approximated medially, (4) the prosternum and prosternal process in the same plane, (5) the pro- and mesotarsi distinctly tetramerous, (6) the scutellum externally visible with the elytra closed, (7) the metafemur without an anteroapical series of setae, (8) metatarsomeres I-IV with anteroapical angles lobed, and (9) the metatarsal claws subequal in length in both sexes. In addition, larvae are characterized by having lateral tracheal gills on the abdomen, segment VIII with a lateral fringe of natatory setae (in instars II and III), and the clypeus with a distinct frontal "horn" (Larson et al. 2000).

3.5.18.3 Discussion

Historically, this family group was recognized mainly at the tribe rank within Colymbetinae, although it has been occasionally recognized as a subfamily (e.g., Bacon et al. 2000). Miller (2001) also placed it at subfamily rank. Recent analyses resolve it in either an isolated position with respect to other subfamilies (Miller 2001) or closely associated with Copelatinae (Ribera et al. 2008).

This analysis resolved a monophyletic Coptotominae (Fig. 3.3, pp = 1.00) as sister to Hydrodytinae + Hydroporinae, though only with modest support (Fig. 3.3, pp = 0.63).

3.5.18.4 Taxon Content

Coptotominae includes a single North American genus, *Coptotomus* Say, 1830.

3.5.19 Hydrodytinae Miller, 2001

3.5.19.1 Type Genus

Hydrodytes Miller, 2001.

3.5.19.2 Diagnosis

These are Dytiscidae with: (1) the scutellum visible with the elytra closed, (2) the pro- and mesotarsi distinctly pentamerous in both sexes, (3) the prosternum and prosternal process in the same plane and without a median tubercle, (4) the female gonocoxa with a prolonged anterior apodeme, and (5) the metathoracic wing broad with vein M4 reaching oblongum cell and with distinct subcubital binding patch. The rami of the female genitalia are sinuate and the male genitalia are bilaterally asymmetrical in the single species known to have males.

3.5.19.3 Discussion

Members of this Neotropical group were placed in the copelatine genus *Agaporomorphus* until that genus was subdivided by Miller (2001) who erected a new genus, *Hydrodytes*, and subfamily for the included species. The entire subfamily was revised by Miller (2002b), including description of a new genus, *Microhydrodytes* Miller. Miller (2001) found Hydrodytinae to be sister to Hydroporinae based on the anterior apodeme of the female gonocoxae and characters of the metafurca. Ribera et al. (2008) found Hydrodytinae resolved as sister to Matinae.

Here, Hydrodytinae is resolved as sister to Hydroporinae with strong support (Fig. 3.3, pp = 1.00), corroborating Miller (2001).

3.5.19.4 Taxon Content

Hydrodytinae includes two Neotropical genera, *Hydrodytes* Miller, 2001 and *Microhydrodytes* Miller, 2002.

3.5.20 Hydroporinae Aubé, 1836

3.5.20.1 Type Genus

Hydroporus Clairville, 1806.

3.5.20.2 Diagnosis

These are Dytiscidae with: (1) the anteromedial portion of the prosternum in a distinctly different plane than the prosternal process (i.e., the prosternal process is declivous with respect to the prosternum, though this is somewhat less dramatic in some taxa such as Methlini), (2) the pro- and mesotarsi pseudotetramerous with tarsomere IV small and hidden within the lobes of tarsomere III (some taxa, such as *Bidessonotus*, *Necterosoma*, and *Sternopriscus* with the pro- and mesotarsi more distinctly pentamerous), and (3) the scutellum concealed with the elytra closed (*Celina* with a distinctively visible scutellum and some *Hydrocolus* with the scutellum partially visible).

3.5.20.3 Discussion

Hydroporinae has been recognized as a natural group for most of the history of dytiscid classification (e.g., Sharp 1882) with a few exceptions. The main one of these is *Celina* (or Methlini inclusive), which has a visible scutellum with the elytra closed and a less strongly declivous prosternal process (though *Methles* has a concealed scutellum). Numerous investigators have recognized this group at the subfamily rank (Bilardo and Rocchi 1990; Franciscolo 1966; Omer-Cooper 1958; Pederzani 1995; Trémouilles 1995). Other groups of hydroporine have been occasionally elevated to subfamily rank during their history (such as Vatellinae *sensu* Omer-Cooper 1958), but not as commonly. The group has usually been recovered as monophyletic (Burmeister 1976; Miller 2001; Miller et al. 2006) though Ribera et al. (2002) found Hydroporinae paraphyletic with respect to a large portion of dytiscid diversity and Ribera et al. (2008) found Laccophilini nested within Hydroporinae. Miller (2001) found a sister group relationship between Hydroporinae and Hydrodytinae based on similarities in the female genitalia and metafurca. This relationship was not confirmed in subsequent molecular analyses (Ribera et al. 2002, 2008). The internal tribal phylogeny has been investigated several times within a more modern, cladistic context (Miller et al. 2006; Ribera et al. 2002, 2008; Wolfe 1985, 1988). Because of these efforts, a phylogenetic tribal classification has developed in the past 30 years with clarification of several relationships (see under each tribe below).

In this analysis, Hydroporinae is monophyletic with strong support (Fig. 3.3, pp = 1.00). It is resolved here sister to *Hydrodytes* (Hydrodytinae), as originally suggested by Miller (2001), also with strong support (Fig. 3.3, pp = 1.00). Within the group, most traditionally recognized tribes are monophyletic with a few exceptions (see under each tribe below). However, relationships among the tribes are subtended by relatively shorter branches and lower support values than within the tribes (Fig. 3.3). See below under each tribe treatment for further discussion about relationships among the tribes more specifically.

3.5.20.4 Taxon Content

There are more genera and species in this group than in any other diving beetle subfamily, about 2,000 species or 50 % of the total species diversity of predaceous diving beetles (Nilsson 2001). There are currently ten tribes recognized in

Hydroporinae with one new tribe and one synonymy (of a tribe with a subtribe of Hydroporini, see below). Several genera of Hydroporinae are currently *incertae sedis* with respect to tribe.

Bidessini Sharp, 1880
Hygrotini Portevin, 1929
Hydroporini Aubé, 1836
Hydrovatini Sharp, 1880
Hyphydrini Gistel, 1848
Laccornini Wolfe and Roughley, 1990
Laccornellini **new tribe**
Methlini Branden, 1885
Pachydrini Biström, Nilsson and Wewalka, 1997
Vatellini Sharp, 1880
Genera *incertae sedis* with respect to tribe
  Kuschelydrus Ordish, 1976
  Morimotoa Uéno, 1957
  Phreatodessus Ordish, 1976
  Terradessus Watts, 1982
  Typhlodessus Brancucci, 1985

3.5.21 Laccornini Wolfe and Roughley, 1990

3.5.21.1 Type Genus

Laccornis Gozis, 1914.

3.5.21.2 Diagnosis

Laccornini are Hydroporinae with: (1) the metacoxal lobes large and apically rounded, (2) the metafemur extending to metacoxal lobe along the anterior margin (not separated from it by the metatrochanter), and (3) the female external genitalia with laterotergites.

3.5.21.3 Discussion

Members of this group were included in Hydroporini *sensu lato* until Wolfe (1985, 1988) investigated more carefully the phylogenetic relationships of *Laccornis* and proposed the genus as sister to the rest of Hydroporinae. *Laccornis* was formally placed in its own tribe by Wolfe and Roughley (1990). Miller (2001) corroborated this relationship, though subsequent molecular analyses have not (Ribera et al. 2008).

In this analysis, *Laccornis* (Laccornini) is resolved as sister to all other Hydroporinae with good support (Fig. 3.3, pp = 0.89) corroborating Miller (2001), Wolfe (1985, 1988), and Wolfe and Roughley (1990). Only a single species of the single genus, *Laccornis*, was included in the analysis, so monophyly of the tribe was not examined, though others have established the probable monophyly of the group (Alarie 1989; Roughley and Wolfe 1987; Wolfe 1985; Wolfe and Roughley 1990; Wolfe and Spangler 1985).

3.5.21.4 Taxon Content

Laccornini includes one genus, *Laccornis* Gozis, 1914.

3.5.22 Laccornellini, New Tribe

3.5.22.1 Type Genus

Laccornellus Roughley and Wolfe, 1987.

3.5.22.2 Diagnosis

This taxon includes Hydroporinae species with the following features: (1) the metafemora extend to the metacoxal process, (2) the prosternal pore absent at the anterolateral angle of the prosternum, (3) without an oblique carina across the epipleuron at the humeral angle, (4) abdominal terga VII and VIII apically evenly rounded, and (5) female genitalia without laterotergites. Two other characters were proposed by Roughley and Wolfe (1987): (1) the metacoxal process medially incised and (2) the sublateral row of the mesotibial spines relatively sparse. These are more difficult to adequately homologize across Hydroporinae but help to characterize Laccornellini, as well.

3.5.22.3 Discussion

Members of *Laccornellus* and *Canthyporus* have been historically placed in Hydroporini, but near *Laccornis* (Sharp 1882; Zimmermann 1919, 1920). Wolfe (1985, 1988) and Roughley and Wolfe (1987) suggested that *Laccornellus* and *Canthyporus* may be closely related to each other and together may be phylogenetically near Laccornini, Methlini and Hydrovatini. Ribera's et al. (2008) analysis reinforced the relationship between the two genera as well as their isolated position phylogenetically. The seemingly plesiomorphic character states combined with their unique biogeography as austral disjuncts makes *Laccornellus*, from southern

South America, and *Canthyporus*, from southern Africa particularly interesting with respect to the evolutionary history of the subfamily Hydroporinae.

In this analysis, the two genera *Canthyporus* and *Laccornellus* are together monophyletic with modest support (Fig. 3.3, pp = 0.76) corroborating Roughley and Wolfe (1987) and Ribera et al. (2008). This clade is sister to all other Hydroporinae except Laccornini, also with good support (Fig. 3.3, pp = 0.89). Because of the monophyly of the group and its unique phylogenetic position with respect to other members of the subfamily the clade is recognized as a new tribe, Laccornellini (**new tribe**).

3.5.22.4 Taxon Content

The tribe includes two genera, *Laccornellus* Roughley and Wolfe, 1987 and *Canthyporus* Zimmermann, 1919.

3.5.23 Hydroporini Aubé, 1836

3.5.23.1 Type Genus

Hydroporus Clairville, 1806.

3.5.23.2 Diagnosis

This tribe includes Hydroporinae with: (1) the metepisternum extending to the metacoxal cavities, (2) the prosternal process extending to the metasternum between the mesocoxae (except in a few taxa including the North American *Stictotarsus minipi* Larson and several subterranean taxa which have been variously classified), (3) the metatarsal claws subequal in length, (4) the male lateral lobes of the aedeagus with a single segment, (5) the transverse tooth on the proventriculus without five elongate, finger-like lobes, (6) the medial portion of the metacoxa in a different plane from the base of the abdomen, (7) the metacoxal lobes prominent, (8) the female genitalia with the laterotergites absent, (9) the apex of the elytra and the last abdominal segment not acutely pointed, and (10) the metafemur along the dorsal margin broadly separated from the metacoxal lobes by the metatrochanter.

3.5.23.3 Discussion

Hydroporini historically included a great many Hydroporinae now classified in other tribes including Laccornini, Hygrotini, and even many Bidessini. Removal of several groups into separate tribes has improved the definition of Hydroporini, but it has seemingly remained a “dumping-ground” for taxa left over after other, more easily diagnosible groups have been recognized, and the character combination above includes no unambiguous synapomorphy for the group. This has been generally recognized, though several apparently monophyletic groups within the tribe have been recognized including the *Deronectes*-group (Angus and Tatton 2011; Balfour-Browne 1944; Nilsson and Angus 1992), the *Graptodytes*-group (Ribera and Faille 2010; Ribera et al. 2002, 2008; Seidlitz 1887), the *Necterosoma*-group (Ribera et al. 2002, 2008) and the *Hydroporus*-group (Ribera et al. 2002, 2008). *Laccornellus* and *Canthyporus* have also been historically placed in this group, though they are here removed and placed in their own tribe (see above). Each of these genus groups was found to be monophyletic by Ribera et al. (2008), but they were not together monophyletic.

In this analysis, Hydroporini, with the exception of *Laccornellus* + *Canthyporus* (Fig. 3.3, see above), is, somewhat surprisingly monophyletic with strong support (Fig. 3.3, pp = 0.97). Within Hydroporini, four well-supported clades are resolved corresponding to the four genus-groups mentioned above. Given the strength of these clades, and the existence of corresponding family-group names, we here recognize four subtribes within Hydroporini.

3.5.23.4 Taxon Content

As defined here, Hydroporini includes four subtribes. One genus, *Siamoporus* Spangler, a subterranean genus, is listed here as subtribe incertae sedis

Hydroporina Aubé, 1836
Deronectina Galewski, 1994
Siettitiina Smrž, 1982
Sternopriscina Branden, 1885
Genera *incertae sedis* with respect to subtribe
  Siamoporus Spangler, 1996

3.5.24 Hydroporina Aubé, 1836

3.5.24.1 Type Genus

Hydroporus Clairville, 1806.

3.5.24.2 Diagnosis

These are Hydroporini with: (1) the elytral epipleuron abruptly narrowed medially and narrow throughout the apical half, (2) the transverse tooth of the proventriculus not apically shallowly multilobed, (3) the rami of the female genitalia variously shaped, but not elongate curved nor apically fused together, (4) the mesosternal fork and the anteromedial process of the metasternum not connected, (5) male pro- and mesotarsomeres I-III with ventral adhesive discs, and (6) no ring-shaped sclerite (receptacle) on the female bursa.

3.5.24.3 Discussion

This group is monophyletic in the analyses by Ribera et al. (2002, 2008) who recognized the clade as the "*Hydroporus*-group".

In this analysis, the genera included in this group are monophyletic with strong support (Figs. 3.3, 3.4, pp = 1.00) and these genera are placed in the subtribe Hydroporina (**new status**). Hydroporina is resolved as the sister to a clade with the remaining Hydroporini, though support for this other clade is not particularly strong (Figs. 3.3, 3.4, pp = 0.73).

3.5.24.4 Taxon Content

As defined here, Hydroporina includes eight genera after *Suphrodytes* was synonymized with *Hydroporus* by Bergsten et al. (2013). The genera *Lioporeus* and *Stygoporus* were not included in our analysis. These genera are placed here, though only provisionally. *Lioporeus* has the morphological character combination for this subtribe. *Stygoporus* is a subterranean genus from Oregon, USA that is ambiguously placed here.

Haideoporus Young and Longley, 1976
Heterosternuta Strand, 1935
Hydrocolus Roughley and Larson, 2000
Hydroporus Clairville, 1806
Lioporeus Guignot, 1950
Neoporus Guignot, 1931
Sanfilippodytes Franciscolo, 1979
Stygoporus Larson and LaBonte, 1994

3.5.25 Deronectina Galewski, 1994

3.5.25.1 Type Genus

Deronectes Sharp, 1882.

3.5.25.2 Diagnosis

This group differs from other Hydroporini in at least four diagnostic characteristics: (1) the transverse tooth of the proventriculus is apically shallowly multilobed, (2) the rami of the female genitalia are characteristically shaped, elongate curved, apically fused and together apically rounded (Miller 2001; Miller et al. 2006), (3) the mesosternal fork and anteromedial process of the metasternum is not connected (Nilsson and Angus 1992), and (4) male pro- and mesotarsomeres I-III lack ventral adhesive discs (though at least some members of Sternopriscina, below, have a similar condition, Nilsson and Angus, 1992).

3.5.25.3 Discussion

This group has a history of recognition as a cluster of closely related taxa (Angus and Tatton 2011; Balfour-Browne 1944; Nilsson and Angus 1992). Ribera et al. (2008) found the group to be monophyletic and in a clade together with the *Graptodytes*-group (Siettitiina, see below) and Hygrotini.

In this analysis the genera of the *Deronectes*-group are together monophyletic with strong support (Figs. 3.3, 3.4, pp = 1.00). This clade is sister to Siettitiina (the *Graptodytes*-group), though this is not strongly supported (Figs. 3.3, 3.4, pp = 0.70). Deronectina is here resurrected to include members of this clade (**new status**).

3.5.25.4 Taxon Content

Currently this group includes seven genera. Three of these were not included in this analysis, *Boreonectes*, *Scarodytes*, and *Trichonectes*, but each of these has been traditionally placed with other members of the group and were resolved together with them in Ribera's et al. (2008) analysis.

Boreonectes Angus, 2010
Deronectes Sharp, 1882
Nebrioporus Régimbart, 1906
Oreodytes Seidlitz, 1887
Scarodytes des Gozis, 1914
Stictotarsus Zimmermann, 1919
Trichonectes Guignot, 1941

3.5.26 Siettitiina Smrž, 1982

3.5.26.1 Type Genus

Siettitia Abeille de Perrin, 1904.

3.5.26.2 Diagnosis

This subtribe has one potential synapomorphy: the female genitalia has a ring-shaped sclerite on the bursa, possibly homologous with the receptacle in other Hydroporinae (Miller 2001; Miller et al. 2009b, 2006).

3.5.26.3 Discussion

This family group was originally conceived to include multiple unrelated subterranean Hydroporinae (Smrž 1982). Others have noted similarities between certain subterranean Palaearctic species and the epigean *Graptodytes* and related genera (Abeille de Perrin 1904; Castro and Delgado 2001). Ribera and Faille (2010) found these genera to be monophyletic.

In this analysis, several genera are resolved as monophyletic with strong support (Figs. 3.3, 3.4, pp = 1.00) corresponding to the *Graptodytes*-group of Ribera and Faille (2010). This includes several Palaearctic taxa as well as the Nearctic subterranean taxa *Ereboporus* (Miller et al. 2009b) and *Psychopomporus* (Jean et al. 2012) (Figs. 3.3, 3.4). These genera are here placed in the subtribe Siettitiina (**new status**). This group is sister to Deronectina, though support for this is low (Figs. 3.3, 3.4, pp = 0.70).

3.5.26.4 Taxon Content

This tribe currently includes ten genera. The genera *Iberoporus*, *Metaporus*, *Etruscodytes* and *Siettitia* were not included in the analysis, but are placed in this tribe based on data presented by Ribera and Faille (2010) and Mazza et al. (2013) that they belong to this group.

Ereboporus Miller, Gibson and Alarie, 2009b
Etruscodytes Mazza, Cianferoni and Rocchi, 2013
Graptodytes Seidlitz, 1887
Iberoporus Castro and Delgado, 2001
Metaporus Guignot, 1945
Porhydrus Guignot, 1945
Psychopomporus Jean, Telles and Miller, 2012
Rhithrodytes Bameul, 1989
Siettitia Abeille de Perrin, 1904
Stictonectes Brinck, 1943

3.5.27 Sternopriscina Branden, 1885

3.5.27.1 Type Genus

Sternopriscus Sharp, 1880.

3.5.27.2 Diagnosis

From the other Hydroporini this subtribe has few discrete distinguishing features though all have the elytral epipleuron relatively broad in the apical half with only gradual narrowing posteriorly. A few other Hydroporini have the elytral epipleuron relatively broad throughout (e.g., *Deronectes*), and members of one genus in this clade, *Paroster*, have the epipleuron more narrow apically than others members of the tribe.

3.5.27.3 Discussion

This group of genera has been historically regarded as monophyletic, and has been called the *Necterosoma* group of genera (Balke and Ribera 2004; Ribera et al. 2002, 2008).

In this analysis, the clade that includes the Australian Hydroporini is strongly supported as monophyletic (Figs. 3.3 and 3.4, pp = 1.00), and is here placed in the subtribe Sternopriscina (**new status**). Sternopriscina is sister to the clade Deronectina + Siettitiina, though support for this is low (Figs. 3.3 and 3.4, pp = 0.73).

3.5.27.4 Taxon Content

This group comprises ten genera. *Carabhydrus* was previously placed in its own tribe, Carabhydrini Watts, based in large part on fusion of the metacoxa with visible abdominal sternite I, the weakly deflexed prosternum, and a characteristic habitus (Watts 1978), each potentially derived within other tribes. Although strongly supported as nested well within the *Necterosoma* group of genera here (Figs. 3.3 and 3.4) and in other analyses (Balke and Ribera 2004; Ribera et al. 2008), it was not formally synonymized with Hydroporini other than in the updated electronic version of the world catalogue distributed by the author (Nilsson 2014). Carabhydrini is placed here as a junior synonym of Sternopriscina, **new synonymy**.

Antiporus Sharp, 1882
Barretthydrus Lea, 1927
Carabhydrus Watts, 1978
Chostonectes Sharp, 1880
Megaporus Brinck, 1943
Necterosoma Macleay, 1871

Paroster Sharp, 1882
Sekaliporus Watts, 1997
Sternopriscus Sharp, 1880
Tiporus Watts, 1985

3.5.28 Vatellini Sharp, 1880

3.5.28.1 Type Genus

Vatellus Aubé, 1837

3.5.28.2 Diagnosis

These are Hydroporinae with: (1) the prosternal process not reaching the metasternum (the mesocoxae are contiguous), (2) abdominal sternite VI with an invaginated, heavily sclerotized gland system (“speleum”, Miller 2005), (3) the metepisternum separated from the mesocoxae by the mesepisternum (in extant taxa), and (4) females with an apically expanded and broadly truncate process at the apex of the spermatheca. Members of this tribe are among the most apomorphic and distinctive within the subfamily. They have long legs and an elongate, often somewhat cylindrical body which is slightly to strongly discontinuous laterally. An extinct member of the group, *Calicovatellus petrodytes* Miller and Lubkin, has the metepisternum extending to the mesocoxal cavities (Miller and Lubkin 2001).

3.5.28.3 Discussion

Relationships of this tribe with other members of Hydroporinae have been among the most unresolved of any in the subfamily (Miller 2001; Ribera et al. 2002, 2008) and there has not been any particular consensus.

In this analysis, Vatellini is monophyletic (Fig. 3.3, pp = 1.00). It is resolved as sister to a large clade of Hydroporinae with the tribes Methlini, Pachydrini, Hydrovatini, Hygrotini, Hyphydrini and Bidessini, with moderately good support (Fig. 3.3, pp = 0.89).

3.5.28.4 Taxon Content

The group historically included four genera, *Vatellus* Aubé, *Macrovatellus* Sharp, *Derovatellus* Sharp, and *Mesovatellus* Trémouilles. A revision of the classification by Miller (2005) resulted in synonymy of *Macrovatellus* with *Vatellus* and *Mesovatellus* with *Derovatellus*, so that now only two genera are recognized within the tribe, *Vatellus* Aubé, 1837 and *Derovatellus* Sharp, 1882.

3.5.29 Methlini Branden, 1885

3.5.29.1 Type Genus

Methles Sharp, 1882

3.5.29.2 Diagnosis

This tribe includes Hydroporinae characterized by: (1) the metafemur extending to the metacoxal lobe and (2) terga VII and VIII modified, tergum VIII posteriorly acute and with dorsal and ventral lobes, the dorsal lobe posteriorly modified into a trifid structure with a pair of long apodemes extending anteriorly, and tergum VII also with shorter anterior apodemes. In general, the posterior apex of the abdomen and elytra in methlines is acuminate, though more pronounced in *Celina* than *Methles*. Members of the New World *Celina* are characterized additionally by an externally visible and large scutellum (with the elytra closed), which is unique among Hydroporinae genera.

3.5.29.3 Discussion

Sharp (1882) recognized close similarity between the two included genera, *Methles* and *Celina*. Wolfe (1985, 1988) proposed potential synapomorphies for Methlini and suggested that the group exhibited a number of plesiomorphies within Hydroporinae that made them close to *Laccornis*, *Laccornellus* and *Canthyporus*. He also thought Methlini and *Hydrovatus* are sister groups based on a number of similar features associated with the abdominal apex. Ribera et al. (2008) found a monophyletic Methlini sister to *Peschetius*.

In our results, Methlini is strongly supported as monophyletic (Fig. 3.3, pp = 1.00) and is sister to a clade including Pachydrini, Hydrovatini and Hygrotini, though this relationship is only weekly supported (Fig. 3.3, pp = 0.69).

3.5.29.4 Taxon Content

Methlini includes two genera, *Methles* Sharp, 1882 and *Celina* Aubé, 1837.

3.5.30 Hydrovatini Sharp, 1880

3.5.30.1 Type Genus

Hydrovatus Motschulsky, 1853.

3.5.30.2 Diagnosis

This tribe is characterized by: (1) the elytral epipleuron with an oblique carina at the humeral angle, (2) the apex of the prosternal process broad and triangular and laterally distinctly margined, (3) the metatarsal claws equal in length, and (4) the metacoxal apices distinctly incised on each side of midline subtending a narrowly or broadly rounded metacoxal lobe. The great majority of the species in this group belong to the genus *Hydrovatus*, which is distinct in having (1) the elytral and abdominal apices acuminate, (2) the metacoxal lobes elongate and slender and marginal incision mediad of lobe deep and narrow, and (3) the female gonocoxae together fused into a knife-like structure with elongate lateral flanges extending from the anterior base. The other species in the group are in the Neotropical genus *Queda* Sharp and are characterized by (1) the elytral and abdominal apicies obtusely pointed, (2) shorter and more broadly rounded metacoxal lobes with shorter margin incisions mediad of lobes, and (3) the female gonocoxae not fused, with each gonocoxa apically tri-lobed.

3.5.30.3 Discussion

Sharp (1882) placed *Queda* and *Hydrovatus* together in his tribe Hydrovatini and they were classified this way until Wolfe (1985, 1988) argued that *Hydrovatus*, *Celina* and *Methles* (the last two in the tribe Methlini) share many similarities that he considered plesiomorphic within the Hydroporinae (though without making formal classfication changes). Biström (1990, 1996) reviewed the morphological evidence and concluded that *Queda* and *Hydrovatus* do together form a monophyletic group and that Methlini may be sister to Hydrovatini. Monophyly of Hydrovatini was corroborated also by Miller (2001, 2006) who found the tribe to be phylogenetically near Hygrotini and Hyphydrini. Ribera et al. (2008) did not include *Queda*, but found a monophyletic *Hydrovatus* sister to Vatellini.

In this analysis, *Hydrovatus* and *Queda* are together monophyletic with strong support (Fig. 3.3, pp = 1.00). Hydrovatini is sister to Pachydrini, though this relationship is poorly supported (Fig. 3.3, pp = 0.67). Also in a clade with Pachydrini + Hydrovatini are Hygrotini and Methlini, though branches subtending these relationships are very short and poorly supported (Fig. 3.3). The sister group relationship between Pachydrini + Hydrovatini and Methlini (Fig. 3.3) may support some of the initial observations by Wolfe (1985, 1988) of morphological similarities between *Hydrovatus* and Methlini.

3.5.30.4 Taxon Content

Hydrovatini includes two genera, *Hydrovatus* Motschulsky, 1853 and *Queda* Sharp, 1882.

3.5.31 Pachydrini Biström, Nilsson and Wewalka, 1997

3.5.31.1 Type Genus

Pachydrus Sharp, 1882.

3.5.31.2 Diagnosis

Pachydrini are Hydroporinae with: (1) the elytral epipleuron with an oblique carina at the humeral angle, (2) the metacoxal lobes absent and the metacoxae medially at the same level as the abdominal sterna, (3) the apex of the prosternal process very broad, laterally unmargined, and broadly in contact with the metasternum, (4) the metasternal wing broad medially, (5) the anterior metatarsal claw shorter than the posterior, and (6) female genitalia with laterotergites. Members of this group also have the metacoxae fused with the abdomen (shared with Bidessini and *Desmopachria* of the Hyphydrini) and the ventrolateral carina of the elytron thick and undulating among a few other more obscure characters (see Biström et al. 1997).

3.5.31.3 Discussion

Historically, members of this group were placed in Hyphydrini, but Biström et al. (1997) placed the two included genera in their own tribe, Pachydrini. Pachydrini was synonymized with Hyphydrini by Miller (2001), a result corroborated by Miller et al. (2006) based on morphological data. However, Ribera and Balke (2007) and Ribera et al. (2008) resurrected the tribe based on analysis of molecular data that indicate the genera are not closely related to Hyphydrini.

Monophyly of the tribe was not tested here because only a single representative of *Pachydrus* was included. It is resolved as sister to Hydrovatini, though this is not well-supported (Fig. 3.3, pp = 0.67). Despite its somewhat uncertain placement, given its phylogenetic position in the subfamily here and other evidence

(Biström et al. 1997; Ribera and Balke 2007; Ribera et al. 2008) Pachydrini is here recognized as a tribe.

3.5.31.4 Taxon Content

Pachydrini includes two genera, *Pachydrus* Sharp, 1882 and *Heterhydrus* Fairmaire, 1869.

3.5.32 Hygrotini Portevin, 1929

3.5.32.1 Type Genus

Hygrotus Stephens, 1828.

3.5.32.2 Diagnosis

These are Hydroporinae with the following character combination: (1) the elytral epipleuron with an oblique carina at the humeral angle, (2) the metacoxae with broadly rounded lobes covering the bases of the metatrochanters, (3) the metatarsal claws equal in length, and (4) the apices of the abdomen and elytra not acuminate.

3.5.32.3 Discussion

Members of this tribe were placed in Hydroporini by most authors until Nilsson and Holmen (1995) more formally recognized and diagnosed the tribe (following Portevin (1929) and Houlbert (1934)). There has been relatively little work done to resolve relationships among the genera within Hygrotini, though Alarie et al. (2001a) presented some evidence for relationships based on the few groups known from larvae. Several of the genera are not well collected and are poorly known in general.

Hygrotini is monophyletic in our analysis with strong support (Fig. 3.3, pp = 1.00). It is resolved as sister to Pachydrini + Hydrovatini, though relationships among these groups are not well-supported (Fig. 3.3, pp = 0.69).

3.5.32.4 Taxon Content

The tribe Hygrotini currently includes four genera. The genus *Hygrotus* has historically included two subgenera, *Hygrotus s. str.* and *H.* (*Coelambus*). Evidence is mounting that these two subgenera are not closely related, and *Hygrotus s. str.* may be paraphyletic (Fig. 3.3). There are several species that are not well placed in either of these two genera, and until a broader analysis can be conducted, we continue to recognize *Coelambus* as a subgenus of *Hygrotus*. *Heroceras* and *Hyphoporus* are not included in this analysis, nor included by Ribera et al. (2008), and so their placement here is somewhat provisional.

Heroceras Guignot, 1949
Herophydrus Sharp, 1880
Hygrotus Stephens, 1828
Hyphoporus Sharp, 1880

3.5.33 Hyphydrini Gistel, 1848

3.5.33.1 Type Genus

Hyphydrus Illiger, 1802.

3.5.33.2 Diagnosis

These diving beetles are Hydroporinae with: (1) the elytral epipleuron with an oblique carina at the humeral angle, (2) the metacoxal lobes absent or extremely small and subtriangular and the metacoxae medially at the same level as the abdominal sterna, (3) the apex of the prosternal process narrow and pointed, (4) the metasternal wing narrow medially, and (5) the anterior metatarsal claw shorter than the posterior.

3.5.33.3 Discussion

Some members of Hyphydrini have been variously classified historically, though the numerous genera have been usually grouped together with a few exceptions (see Biström et al. 1997). Prominently, *Pachydrus* and *Heterhydrus* were placed in a separate tribe, Pachydrini, by Biström et al. (1997). This was disputed by Miller (2001) and Miller et al. (2006) who placed these genera back in Hyphydrini based on evidence from morphology. Ribera et al. (2008) argued against this as their analysis placed Pachydrini phylogenetically distant from Hyphydrini and sister to Bidessini similar to Ribera and Balke (2007), and they resurrected the tribe.

In this analysis, Hyphydrini (excluding Pachydrini) is monophyletic with strong support (Fig. 3.3, pp = 1.00). *Pachydrus* is resolved as sister to Hydrovatini with weak support (pp = 0.67) and is here excluded from Hyphydrini following Biström et al. (1997) and Ribera et al. (2008) (see Pachydrini above). Hyphydrini is here resolved as sister to Bidessini though this is a weekly supported relationship (Fig. 3.3, pp = 0.75).

3.5.33.4 Taxon Content

This tribe includes 14 genera. *Pachydrus* Sharp and *Heterhydrus* Sharp are excluded from the tribe and placed back in Pachydrini Biström, Nilsson and Wewalka (see above). Several genera were not included in this analysis, though Biström et al. (1997) argued convincingly for the monophyly of all the genera. Several Afrotropical genera not included in this analysis were included in analyses by Ribera and Balke (2007) and Ribera et al. (2008) finding a monophyletic Hyphydrini as defined here.

Agnoshydrus Biström, Nilsson and Wewalka, 1997
Allopachria Zimmermann, 1924
Andex Sharp, 1882
Anginopachria Wewalka, Balke and Hendrich, 2001
Coelhydrus Sharp, 1882
Darwinhydrus Sharp, 1882
Desmopachria Babington, 1841
Dimitshydrus Uéno, 1996
Hovahydrus Biström, 1982
Hydropeplus Sharp, 1882
Hyphovatus Wewalka and Biström, 1994
Hyphydrus Illiger, 1802
Microdytes J.Balfour-Browne, 1946
Primospes Sharp, 1882

3.5.34 Bidessini Sharp, 1880

3.5.34.1 Type Genus

Bidessus Sharp, 1882.

3.5.34.2 Diagnosis

Current diagnostics of this tribe within Hydroporinae are based on characters that are not readily accessible without dissection of internal tissues. The two primary synapomorphies defining the tribe are: (1) presence of a spermathecal spine, and (2) presence of five-lobed teeth on the proventriculus. Additional features include (1) most genera with the metacoxae fused to the first visible abdominal sternum, (2) most genera with two- or three-segmented male lateral lobes (parameres) of the aedeagus, and (3) most genera with metatibia basally slender and apically gradually expanded.

3.5.34.3 Discussion

The classification of this large and important group of dytiscids has been addressed by a number of influential authors. The historical definition of this group began with Sharp (1882) who placed several taxa, mainly previously placed in *Hydroporus*, in a new tribe based on the fusion of the metacoxae with the first visible abdominal sternum. He believed this to be unique among Coleoptera, and, with this definition, placed in Bidessini the genera *Pachydrus, Heterhydrus*, and *Desmopachria,* currently placed in Pachydrini and Hyphydrini. The next main diagnostic effort was by Zimmermann (1919) who defined the group based on the equal-length metatarsal claws and an approximately club-shaped metatibia which resulted in removal of *Pachydrus*, *Heterhydrus*, and *Desmopachria* to Hyphydrini. Later influential authors (e.g., Young 1967) used a similar character definition for the group. However, in the most comprehensive modern treatment of the group by Biström (1988), the group was thoroughly reviewed and defined based on the presence of two- or three-segmented male parameres. This resulted in the exclusion of two genera historically placed in the Bidessini, *Amarodytes* Régimbart and *Hydrodessus* J. Balfour-Browne, which, based on his examined specimens, lack segmented lateral lobes. He placed these as Hydroporinae *incertae sedis*. During a phylogenetic analysis of the family by Miller (2001), a new compelling synapomorphy for the tribe was discovered, a heavily sclerotized spine inside the female spermatheca. Members of *Amarodytes* were found to have such a spine and the genus was placed by Miller (2001) back into Bidessini. It was also discovered that at least some species currently attributed to *Amarodytes*, and specifically *A. duponti* (Aubé), have bisegmented male lateral lobes (Benetti and Régil Cueto 2004), though others do not (suggesting *Amarodytes* itself may not be monophyletic). Most recently, another synapomorphy for Bidessini was discovered by Miller et al. (2006), a five-lobed transverse tooth of the proventriculus. This feature is present in *Amarodytes* and also the genus *Peschetius* Guignot, a genus previously placed in the Hydroporini. *Peschetius* also has a distinctive spermathecal spine. *Amarodytes* was, therefore, reconfirmed as a genus of Bidessini and *Peschetius* was formally moved into Bidessini. In contrast to that, Ribera et al. (2008) found *Peschetius* separate from Bidessini and sister to Methlini.

Based on our results, Bidessini is monophyletic including the genera *Peschetius*, *Amarodytes* and, new to this analysis, *Hydrodessus*, which is placed back into this tribe here (**new classification**) (Fig. 3.3, pp = 1.00). Numerous *Hydrodessus* specimens were examined as part of an ongoing revision of the genus by the first author and many of the species have a prominent spermathecal spine, though not all do (Miller, unpublished). Interestingly, the genera historically disputed as bidessines, *Peschetius*, *Amarodytes,* and *Hydrodessus* (along with an anomolous *Hypodessus* that may belong to a new genus of Bidessini) are all part of one clade except for a species of *Amarodytes* that is sister to the other Bidessini (Fig. 3.3, pp = 0.95). Bidessini is an exceptionally large taxon with many small members in numerous genera. The internal phylogeny of the clade needs considerable phylogenetic revisionary work because of the difficulty of many morphological character combinations defining the various genera and many uncomfortably placed taxa and potentially paraphyletic groups.

3.5.34.4 Taxon Content

This is one of the largest groups in Dytiscidae with about 650 currently recognized species, and probably many more unknown species. There are 45 genera with new genera described (and others synonymized) on a regular basis. Many of these are not included here, though sampling included much of the evident phylogenetic diversity of the tribe. Nevertheless, work remains to be done to clarify placement of the genera and relationships among them.

Africodytes Biström, 1988
Allodessus Guignot, 1953
Amarodytes Régimbart, 1900
Anodocheilus Babington, 1841
Bidessodes Régimbart, 1900
Bidessonotus Régimbart, 1895
Bidessus Sharp, 1882
Borneodessus Balke, Hendrich, Mazzoldi and Biström, 2002
Brachyvatus Zimmermann, 1919
Clypeodytes Régimbart, 1894
Comaldessus Spangler and Barr, 1995
Crinodessus Miller, 1997
Fontidessus Miller and Spangler, 2008
Geodessus Brancucci, 1979
Gibbidessus Watts, 1978
Glareadessus Wewalka and Biström, 1998
Hemibidessus Zimmermann, 1921
Huxelhydrus Sharp, 1882
Hydrodessus J.Balfour-Browne, 1953
Hydroglyphus Motschulsky, 1853
Hypodessus Guignot, 1939
Incomptodessus Miller and García, 2011
Kakadudessus Hendrich and Balke, 2009
Leiodytes Guignot, 1936
Limbodessus Guignot, 1939
Liodessus Guignot, 1939
Microdessus Young, 1967
Neobidessodes Hendrich and Balke, 2009
Neobidessus Young, 1967
Neoclypeodytes Young, 1967
Pachynectes Régimbart, 1903
Papuadessus Balke, 2001
Peschetius Guignot, 1942

Petrodessus Miller, 2012
Platydytes Biström, 1988
Pseuduvarus Biström, 1988
Sharphydrus Omer-Cooper, 1958
Sinodytes Spangler, 1996
Spanglerodessus Miller and García, 2011
Tepuidessus Spangler, 1981
Trogloguignotus Sanfilippo, 1958
Tyndallhydrus Sharp, 1882
Uvarus Guignot, 1939
Yola Gozis, 1886
Yolina Guignot, 1936

3.6 Family-Group Classification of Dytiscidae Leach, 1815

Subfamily **Matinae** Branden, 1885
  Tribe **Matini** Branden, 1885

Subfamily **Lancetinae** Branden, 1885
  Tribe **Lancetini** Branden, 1885

Subfamily **Colymbetinae** Erichson, 1837
  Tribe **Colymbetini** Erichson, 1837

Subfamily **Agabinae** Thomson, 1867
  Tribe **Agabini** Thomson, 1867
  Tribe **Hydrotrupini** Roughley, 2000, **new status**

Subfamily **Copelatinae** Branden, 1885
  Tribe **Copelatini** Branden, 1885

Subfamily **Laccophilinae** Gistel, 1848
  Tribe **Agabetini** Branden, 1885
  Tribe **Laccophilini** Gistel, 1848

Subfamily **Cybistrinae** Sharp, 1880, **new status**
  Tribe **Cybistrini** Sharp, 1880

Subfamily **Dytiscinae** Leach, 1815
  Tribe **Dytiscini** Leach, 1815
  Tribe **Hydaticini** Sharp, 1880
  Tribe **Aubehydrini** Guignot, 1942
  Tribe **Aciliini** Thomson, 1867
  Tribe **Eretini** Crotch, 1873

Subfamily **Coptotominae** Branden, 1885
  Tribe **Coptotomini** Branden, 1885

Subfamily **Hydrodytinae** Miller, 2001
  Tribe **Hydrodytini** Miller, 2001

Subfamily **Hydroporinae** Aubé, 1836
  Tribe **Laccornini** Wolfe and Roughley, 1990
  Tribe **Laccornellini, new tribe**
  Tribe **Hydroporini** Aubé, 1836
    Subtribe **Hydroporina** Aubé, 1836, **new status**
    Subtribe **Sternopriscina** Branden, 1885, **new status**
    Subtribe **Deronectina** Galewski, 1994, **new status**
    Subtribe **Siettitiina** Smrž, 1982, **new status**
  Tribe **Vatellini** Sharp, 1880
  Tribe **Methlini** Branden, 1885
  Tribe **Pachydrini** Biström, Nilsson and Wewalka, 1997
  Tribe **Hydrovatini** Sharp, 1880
  Tribe **Hygrotini** Portevin, 1929
  Tribe **Hyphydrini** Gistel, 1848
  Tribe **Bidessini** Sharp, 1880

3.7 Future Directions

This dytiscid phylogeny is far from dispositive. It seems, however, that several conclusions are becoming increasingly well supported, including the monophyly of the subfamilies and tribes as classified here. Within subfamilies, the relationships among the tribes of Dytiscinae are moderately well understood and well supported (Miller 2000, 2001, 2003). What is considerably less clear are the relationships among the subfamilies and relationships among the tribes of Hydroporinae. These relationships are critical for understanding the evolutionary history and current biogeographic patterns of dytiscids and will be major topics for future phylogenetic analyses. Phylogenetic relationships among genera within some of the very large groups such as Laccophilinae, Copelatinae, Agabinae, Hydroporini, and Bidessini, are also very poorly known, and there is likely to be considerable paraphyly within some of these. Finally, large numbers of new taxa remain undiscovered (as many as half of all extant taxa), and these may be of considerable help in clarifying the phylogeny of the group. Some of these, such as the great many subterranean taxa remaining undescribed, are difficult to place morphologically, and DNA sequence data, or other data, may be critical for understanding their relationships (Miller et al. 2009b). Certain biogeographic regions are likely to yield large numbers of new species once they have been more thoroughly surveyed including southeast Asia south through the many islands of the Pacific, much of South America, and central Africa.

To date, no dytiscid has had its genome sequenced, but the transcriptome (the entirety of expressed genes) of Cybister lateralimarginalis (De Geer) is available from the 1KITE project (www.1kite.org), opening up for the development of new markers for phylogenetic analysis."Next generation" sequencing methods allow for vast numbers of sequence data that may soon be available for use in dytiscid phylogenetics. That said, there remain numerous morphological systems that remain unexamined but may also prove useful in clarifying relationships. Female reproductive structures were only poorly known until recently, but have proven to have considerable phylogenetic, and evolutionary, significance in the group (Miller 2001, 2003, Chap. 5 this book). It might be expected that other morphological systems could prove equally rewarding.

Appendix

Morphological characters and states used in combined phylogenetic analysis of Dytiscidae. Characters used in this analysis are derived from several other recent analyses which should be consulted for additional description and illustration (Miller 2000, 2001, 2009; Miller and Bergsten 2012; Miller et al. 2007b, 2009a, 2006).

Head

1. Anterolateral margin of eye: (0) Not emarginate, (1) Emarginate.
2. Mandibles: (0) Apically acute, (1) Apically broad.
3. Postocular carina: (0) Absent, (1) Present.
4. Transverse occipital line: (0) Absent, (1) Present.
5. Anterior clypeal groove: (0) Broadly interrupted, (1) Continuous.
6. Anterior clypeal margin: (0) Unmodified, (1) Margin produced or beaded.
7. Fronto clypeal suture: (0) Medially effaced, (1) Entire.
8. Anterior prothoracic glands: (0) Absent, (1) Present.
9. Eyes: (0) Not divided, (1) Divided but contiguous (as in *Spanglerogyrus*), (2) Completely divided (as in most Gyrinidae).
10. Antennae: (0) Simple, (1) With enlarged scape and pedicel and short, compact flagellum (as in Gyrinidae).
11. Scape: (0) Simple, (1) Medially distinctly constricted (as in Noteridae).

Thorax

12. Scutellum: (0) Not externally visible with elytra closed, (1) Externally visible with elytra closed.
13. Lateral pronotal margin: (0) Unbeaded, (1) Beaded.
14. Longitudinal sublateral basal striae on pronotum: (0) Absent, (1) Present.

15. Prosternum, prosternal process: (0) In same plane as prosternum, (1) Declivous, in different plane from prosternum.
16. Prosternal process: (0) Not reaching metasternum, (1) Reaching metasternum.
17. Prosternal process: (0) Flat to carinate, (1) With distinct, medial, longitudinal sulcus.
18. Prosternal process apex: (0) Pointed or narrowly rounded, (1) Broad, apically truncate.
19. Metepisternum: (0) Not reaching mesocoxal cavities, separated by mesepimeron (1) Reaching mesocoxal cavities.
20. Transverse metasternal suture: (0) Absent, (1) Present.
21. Small lateral lobe on medial portion of metacoxa: (0) Absent, (1) Present.
22. Metacoxa anterior expansion: (0) Not anteriorly expanded, (1) Anteriorly expanded.
23. Metacoxa and abdominal sternite II: (0) Not fused, (1) Fused.
24. Medial cleft of metendosternite: (0) Narrow, (1) Broad and rounded.
25. Noterid platform: (0) Absent, (1) Present.
26. Retractoris mesothoracis muscle insertion on metendosternite: (0) Deeply concave, distinct from margins, (1) Shallow, flattened.
27. Furcodorsalis metathoracis muscle insertions on anterior rami of metendosternite: (0) Medially, (1) Apically.
28. Basal portion of metendosternite: (0) Broad, lateral margin divergent anteriorly, (1) Narrow, lateral margins parallel.

Abdomen

29. Transverse rugae on dorsum of abdominal segment II: (0) Absent, (1) Present.
30. Speleum: (0) Absent, (1) Present (in Vatellini).
31. Apex of female sternum six: (0) Evenly curved, (1) Medially emarginate.
32. Abdominal tergum VIII: (0) Not modified, (1) Apically acute or acuminate with anteriorly directed processes.

Elytron

33. Anterior oblique epipleural carina: (0) Absent, (1) Present.
34. A field of short impressed striae at base of female elytron: (0) Absent, (1) Present.
35. Elytral apices: (0) Not acuminate, (1) Distinctly acuminate.
36. Elytral apices: (0) Not truncate or sinuate, (1) Truncate and slightly sinuate.
37. Apicoventral elytral setae: (0) Absent, (1) Present.
38. Apicoventral elytral setae: (0) A large region of fine setae, (1) A small region of stiff setae, (2) A linear submarginal series.

Legs

39. Pro- and mesotarsi: (0) Clearly pentamerous, (1) Pseudotetramerous.
40. Apices of male protarsal adhesive setae: (0) Oval to elongate, (1) Round, sucker shaped.
41. Anterior protibal spur in male: (0) Absent, (1) Present.
42. Posterior protibial spur in male: (0) Absent, (1) Present.
43. Protibial hooked spur: (0) Absent, (1) Present (as in Noteridae).
44. Ventral series of setae on mesofemur: (0) Shorter than width of mesofemur, (1) Longer than width of mesofemur.
45. Oblique line of setae on mesotarsomeres: (0) Absent, (1) Present.
46. Posterodorsal series of setae on mesotibia: (0) Simple, (1) Bifid.
47. Posterodorsal series of setae on metatibia: (0) Simple, (1) Bifid.
48. Posterodorsal setae on metatibia: (0) A linear series, slightly curved, (1) A large cluster, (2) A strongly oblique series.
49. Posteroapical setae on meso- and metatibia: (0) Simple, (1) Bifid.
50. Appressed striae on metacoxa: (0) Absent, (1) Present.
51. Metacoxal lines: (0) Not closely approximated medially, (1) Closely approximated.
52. Posteromedial metacoxal lobes: (0) Absent, (1) Present small, (2) Present large rounded.
53. Posteromedial metacoxal rim: (0) Discontinuous medially, (1) Continuous medially.
54. Metacoxal cavities: (0) Separated broadly, (1) Contiguous or closely approximated.
55. Metacoxa: (0) Medial portion not concave, (1) Medial portion concave laterally.
56. Deep, oblique groove on metatrochanter: (0) Absent, (1) Present.
57. Linear series of setae in groove near anteroapical angle of metafemur: (0) Absent, (1) Present.
58. Dorsal series of natatory setae on metafemur: (0) Absent, (1) Present.
59. Apices of metatibial spurs: (0) Simple, (1) Bifid.
60. Anterior metatibial spur: (0) Similar to posterior, (1) Acuminate, broad (Cybistrini).
61. Posteroventral series of setae on metatarsomere I: (0) Absent, (1) Present.
62. Posterodorsal series of setae on metatarsomere I: (0) Absent, (1) Present.
63. Adpressed setae along apicodorsal and apicoventral margins of metatarsomeres I-IV: (0) Absent, (1) Present.
64. Natatory setae along posteroventral margin of metatarsi: (0) Absent on males and females, (1) Present on males, absent on females, (2) Present on males and females.
65. Natatory setae along posteroventral margin of metatibia and tarsomeres: (0) Present or absent on both, (1) Present on metatarsomeres but absent on metatibia in both sexes.
66. Anterodorsal margin of metatarsomeres I-IV: (0) Unlobed, (1) Lobed.

67. Metatarsal claws: (0) Male and female unequal, posterior shorter than anterior, (1) Male and female with claws equal, (2) Male equal, female unequal, anterior shorter than posterior, (3) Male and female unequal, anterior shorter than posterior, (4) Male single, female unequal, anterior shorter than posterior, (5) Male and female each with a single claw.
68. Legs: (0) Not expanded, (1) Meso- and metatibia broad, elongate, apically with elongate extension (as in Spanglerogyrus), (2) Meso- and metatibia short and broad, meso- and metataromeres I-IV very broad, subtriangular (as in most Gyrinidae).

Internal

69. Proventriculus: (0) Without five finger-like lobes on crusher teeth, (1) With five finger-like lobes on crusher teeth.

Male Genitalia

70. Median lobe: (0) Asymmetrical, (1) Bilaterally symmetrical.
71. Ventral sclerite on median lobe: (0) Absent, (1) Present.
72. Lateral lobes: (0) With one segment, (1) With two segments, (2) With three segments.
73. Lateral lobes: (0) Symmetrical, (1) Asymmetrical.

Female Gentalia

74. Genital configuration: (0) carabid-type, (1) noterid-type, (2) amphizoid-type, (3) hydroporine-type, (4) *Agaporomorphus*-type, (5) dytiscine-type (Miller 2001).
75. Gonocoxal fusion: (0) Not fused, (1) Weakly fused, (2) Completely fused.
76. Anterior apodeme on gonocoxae: (0) absent, (1) present.
77. Gonocoxal shape: (0) Not short and broad, (1) Short and broad.
78. Gonocoxal shape: (0) Not extremely elongate, (1) Extremely elongate.
79. Dorsolateral carina on gonocoxa: (0) Absent, (1) Present.
80. Dorsolateral carina on gonocoxa: (0) Not dentate, (1) Dentate.
81. Gonocoxae: (0) Rounded or not flattened, (1) Strongly laterally flattened.
82. Articulation of laterotergite and gonocoxa: (0) Strongly angled, laterotergite extending posteriorly, (1) Not angled.
83. Laterotergites: (0) Absent, (1) Present.
84. Series of short spinous setae along medial margin gonocoxosternite: (0) Absent, (1) Present.
85. Rami dentation: (0) Not dentate, (1) Weakly dentate, (2) Strongly dentate.
86. Rami configuration: (0) Not modified, (1) Strongly sclerotized, apically fused, anteriorly divergent.

87. Bursa size: (0) Short, (1) Long, slender, slightly twisted.
88. Bursal shape: (0) Various, (1) Flattened, with thick-walled, parallel margins.
89. Bursal gland reservoir: (0) Absent, (1) Present.
90. Bursal sclerotization: (0) Not heavily sclerotized, (1) Heavily sclerotized.
91. Bursal attachment to gonocoxal apparatus: (0) Anteriorly near bases of gonocoxae, (1) Posteriorly near apices of gonocoxae.
92. Receptacle: (0) Absent, (1) Present.
93. Receptacle shape: (0) Not cone shaped, (1) Cone shaped with basal sclerotized ring.
94. Spermathecal and fertilization ducts: (0) Not coiled, (1) Coiled.
95. Spermatheca: (0) Not reduced, (1) Reduced.
96. Spermathecal spine: (0) Absent, (1) Present.
97. Triangular spermathecal process: (0) Absent, (1) Present.
98. Large accessory gland reservoir near base of fertilization duct: (0) Absent, (1) Present.
99. Large accessory gland reservoir on spermatheca: (0) Absent, (1) Present.
100. Spermathecal disc: (0) Absent, (1) Present.
101. Base of fertilization duct: (0) Without modifications, (1) A heavily sclerotized, irregular ring.
102. Gland reservoirs laterally at base of oviduct: (0) Absent, (1) Present.
103. Thick musculature on vagina: (0) Absent, (1) Present.

Habitat

104. Habitat: (0) Not on water surface, (1) On water surface.

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Chapter 4
Morphology, Anatomy, and Physiological Aspects of Dytiscids

Siegfried Kehl

> *The dytiscus and the hydrophilus…both frequent the water of deep ponds, ditches or pools. With their legs flattened like oars and their very smooth bodies arched on the top, and shaped underneath like the keel of a ship, they are first class swimmers and divers. It is a pleasure to the eye to follow the graceful agility of their oars as they row quietly on the surface, or float under water*
>
> (Jean-Henri Fabre 2002)

Abstract Although the morphology of dytiscids is generally distinct from other aquatic insects, there is considerable variation within this highly diverse family. In the first part of this chapter I discuss the external morphology of adult and larval Dytiscidae, as well as highlight the morphological adaptations to the aquatic environment. In the second part of this chapter the internal anatomy and some physiological aspects, e.g., respiration and digestion, are discussed. The morphology of adult and larval Dytiscidae is very well documented, whereas pupae and the internal anatomy of all stages are neglected. Almost all taxonomic keys (e.g., Epler, The water beetles of Florida – an identification manual for the families Chrysomelidae, Curculionidae, Dryopidae, Dytiscidae, Elmidae, Gyrinidae, Haliplidae, Helophoridae, Hydraenidae, Hydrochidae, Hydrophilidae, Noteridae, Psephenidae, Ptilodactylidae and Scirtidae. Florida Department of Environmental Protection, Tallahassee, 2010; Arnett and Thomas, American beetles. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia, vol 1. CRC Press, Boca Raton, 2000; Larson et al., Predaceous diving beetles (Coleoptera: Dytiscidae) of the Nearctic region, with emphasis on

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D.A. Yee (ed.), *Ecology, Systematics, and the Natural History of Predaceous Diving Beetles (Coleoptera: Dytiscidae)*, DOI 10.1007/978-94-017-9109-0_4,

the fauna of Canada and Alaska. NRC Research Press, Ottawa, 2000; Nilsson and Holmen, The aquatic Adephaga (Coleoptera) of Fennoscandia and Denmark. II. Dytiscidae. Brill, Leiden, 1995; Franciscolo, Coleoptera-Haliplidae, Hygrobiidae, Gyrinidae, Dytiscidae. Fauna d'Italia, vol. XIV. Edizioni Calderini, Bologna, 1979) give descriptions of the morphology of larvae and adults. Detailed information is also given in some textbooks (e.g., Balke 2005, 7.6. Dytiscidae Leach, 1915. In: Beutel RG, Leschen RAB (eds) Handbook of zoology. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, Beetles. Volume 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim.). Walter de Gruyter, Berlin/New York, 2005, Wesenberg-Lund, Biologie der Süsswasserinsekten. Springer, Berlin, p 682, 1943). Internal anatomy and physiological aspects are best documented in larger species (e.g., *Dytiscus marginalis*). Particularly, Korschelt (1923, 1924) (Bearbeitung einheimischer Tiere. Erste Monographie: Der Gelbrand *Dytiscus marginalis* L., vol 2, Engelmann, Leipzig, p 863, 1923, Bearbeitung einheimischer Tiere. Erste Monographie: Der Gelbrand *Dytiscus marginalis* L., vol 2, Engelmann, Leipzig, p 964, 1924) and his academic staff, as well as Blunck (1923) (Z Wiss Zool 100:459–492, 1912a; Z Wiss Zool 102:169–248, 1912b, Z Wiss Zool Leipzig 111:76–151, 1914, Z Wiss Zool Leipzig: 117(1):1–129, 1917, Z Wiss Zool Leipzig 121(2): 172–392, 1923) provide detailed documentation of their observations, experiments, and dissections that occurred almost 100 years ago. These documents still represent some of the best work on these subjects, however new techniques using advanced microscopic and laboratory methods could provide even great insights into the anatomy and physiology of this group of insects.

Keywords Anatomy • Digestion • Morphology • Physiology • Respiration

4.1 External Morphology

The overall shape and size of adults and larval predaceous diving beetles is highly varied, but there are several features that helps to make them distinct from other aquatic beetles. Here, morphology includes aspects of the outward appearance, such as shape, structure, and color, as well as the form and structure of the internal parts (anatomy).

4.1.1 External Morphology of Adults

Adults show considerable range in size (e.g., Fig. 4.2a) and span 1–45 mm in length. The largest dytiscid adults are found in the *Dytiscinae* (e.g., *Dytiscus latissimus* grows to 45 mm), whereas very small adults are found in Hydroporines

(Bidessini) (e.g., *Liodessus flavicollis* 1.5 mm, *Uvarus subtilis* 1.5 mm), and in several stygobiont species that are about 1.0 mm in length. The largest dytiscid in the world is *Megadytes ducalis* (Sharp 1882) and reaches 48 mm in length. The type species found in Brazil in the nineteenth century is the only known specimen, hence it is listed in the IUCN red List of threatened species as extinct. The oval outlined and frequently dorsoventrally flattened body of adults give them a streamlined shape, which is, in combination with the natatorial setal fringes on the hind legs of most species, a perfect adaptation to the aquatic environment (Figs. 4.1a–f and 4.2b). Adults are commonly dark in color (i.e., brown, black), sometimes with yellowish margins or spots, but other colors exist including reddish, testaceous, or pale with a dark patterned dorsal side; subterranean forms are translucent often appearing testaceous or reddish brown. Coloration patterns can be an effective antipredator defense (Larson 1996; Wohlfahrt and Vamosi 2009), especially in waters with sparse vegetation and sand, silt, or gravel bottoms (Galewski 1971). Extant species of Laccophilinae often have a greenish tinge from internal organic pigments (i.e., a mixture of carotenoids with the blue bile pigment) (Dettner and Hopstätter 1980; Chap. 6 in this book). Their elytra cuticle is usually smooth and glabrous or finely setose or strongly punctate (Fig. 4.2c–e). Many species possess large polygonal impressed meshes (reticulation) that sometimes occur in combination with a smaller, fine reticulation (microreticulation), that are often modified in various ways (Fig. 4.2c–e). Wolfe and Zimmerman (1984) provide detailed Scanning Electron Microscopic examinations of elytral surface of Hydroporinae.

The head of dytiscids is inserted up to the level of the eye into the large pronotum. Ocelli are absent and compound eyes are generally large, but absent or reduced in stygobiont or subterranean species. Adults usually have filliform antenna with 11 cylindrical segments. The maxillary palpus have four segments whereas the labial palpus have three. The pro- and mesotarsomeres of the five segmented tarsus in males is usually dilated laterally and sometimes are modified into adhesive setae or discs (Figs. 4.1e and 5.3), which enable the males to adhere to the smooth dorsal surface of females (generally on the pronotum, Fig. 4.2b) prior to mating (see also Chap. 5 in this book). In *Dytiscus alaskanus* the adhesive strength is four times the mass of a female (Aiken and Khan 1992). In most species this distinctive character on the front- and midlegs helps to determine the sexes. Hind legs are often modified for swimming, and are lined with natatorial setae and are sometimes broadened like paddles. Unlike Hydrophilidae and Haliplidae, adult predaceous diving beetles move both hind legs simultaneously for swimming. The midlegs are sometimes additionally used for swimming in small or medium-sized species, but are often restricted to maneuvering (Nachtigall 1977; Ribera et al. 1997). The abdomen has six visible abdominal segments (sternites), with the first true segment not visible and the last three segments, which bear the sclerotized genitalia, are invaginated (Larson et al. 2000).

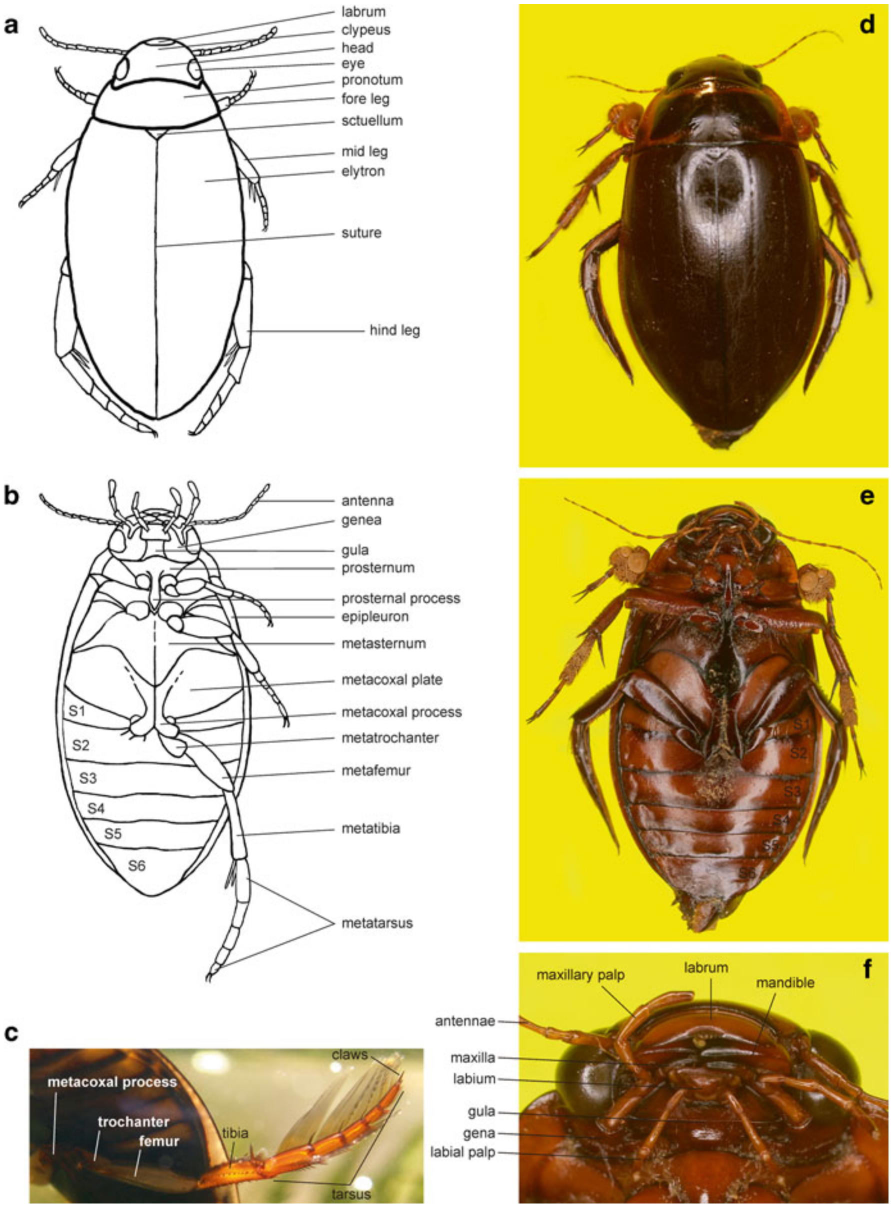

Fig. 4.1 External morphology of adult Dytiscidae. (**a**) Schematic dorsal view of Dytiscidae, (**b**) schematic ventral view of Dytiscidae, (**c**) natatorial hind-leg of *Acilius canaliculatus*, (**d**) dorsal view of male *Dytiscus marginalis*, (**e**) ventral view of male *Dytiscus marginalis*, (**f**) head with view on mouthparts of *Dytiscus marginalis*. *S1–S6* visible abdominal segments 1–6

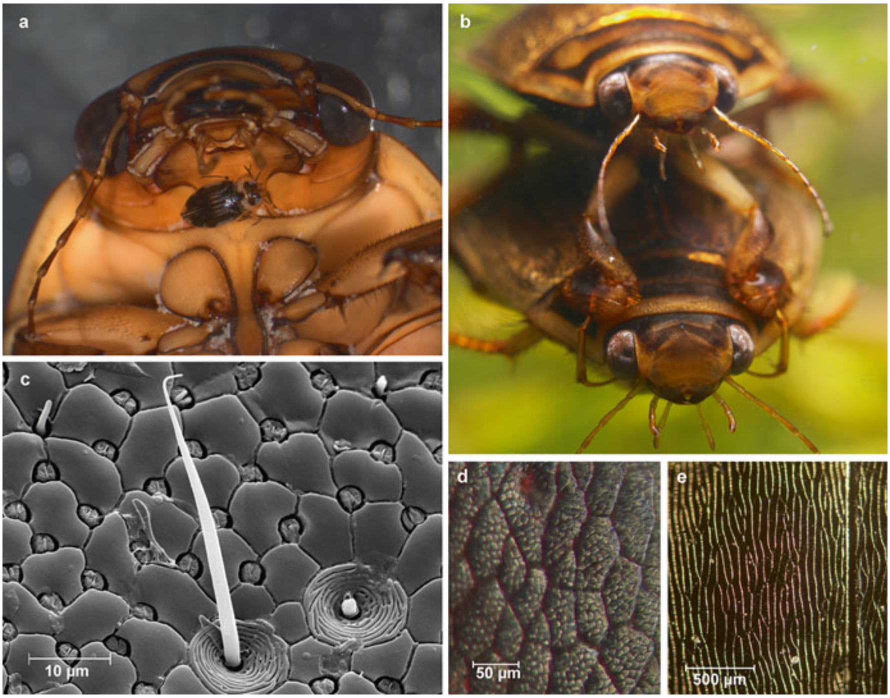

Fig. 4.2 External morphology of adult Dytiscidae (**a**) Different size classes; Adult *Liodessus obscurellus* sitting below the head of an adult *Dytiscus* sp. (**b**) *Acilius canaliculatus* in copula. Male (above) attached with the suckers of the forelegs to the pronotum of female. (**c**) Cuticular surface of elytra of *Oreodytes sanmarkii* (SEM picture) with microreticulation and different sensilla. (**d**) Elytral sculpture of *Agabus melanarius* with large polygonal meshes. (**e**) Strongly elongated meshes on the elytra of *Agabus bipustulatus* (Fig. 4.2a Photo by Donald A. Yee, rest by S. Kehl)

4.1.2 External Morphology of Larvae

Like adults, larvae vary in size among species. Individuals range from 1 up to 70 mm long. Larvae are elongated, campodeiform, and more or less parallel-sided, or oblong to ovate, typically broadest near the middle (Fig. 4.3b, d, e). Larvae possess well developed five segmented legs and a short and inconspicuous pretarsus with claws (Fig. 4.3h). The last abdominal segment has a pair of urogomphi (Fig. 4.3b, d). Individuals are often heavy sclerotized on the dorsal side (i.e., head, thoracic, and abdominal tergites), whereas the sclerotization on ventral side varies among species and instars (Balke 2005; Larson et al. 2000). Larvae show color variation, with testaceous, pale yellow to dark grey, or dark brown to black or greenish found on the dorsal side. Moreover, they frequently possess a characteristic color pattern, including stripes. Besides their ferocity, this color pattern helps us to understand the use of "water tiger" as a common term for larvae. The ventral side has unsclerotized parts that are typically yellowish-white or transparent. The integument of most larvae is

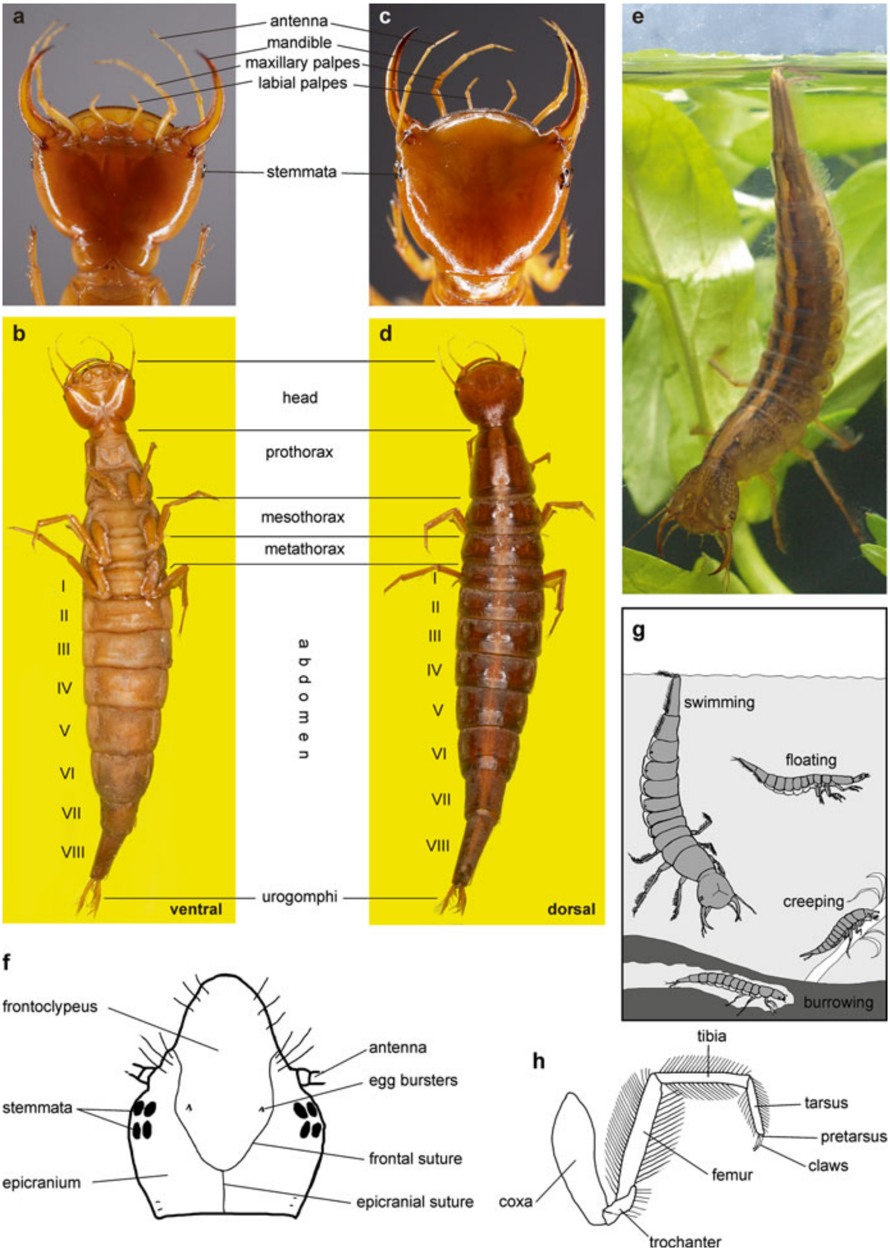

Fig. 4.3 Morphology of predaceous diving beetles larvae. (**a**–**d**) *Dytiscus marginalis* (**a**) ventral side of head; (**b**) ventral side of larvae (**c**) dorsal side of head (**d**) dorsal side of larvae; (**e**) *Dytiscus marginalis* in typical posture at the water surface for gas exchange. (**f**) head of a hydroporine larvae (**g**) The four main larval life styles of dytiscidae larvae. Actively swimming (e.g., *Dytiscus*), creeping (e.g., *Hyphydrus*), burrowing (e.g., *Matus*) and floating (e.g., *Graphoderus* and *Acilius*). (**h**) typical leg of dytiscidae larvae (here foreleg of *Dytiscus*)

normally smooth with scattered setae that varies among instars and is useful for taxonomic purposes.

The shape of the head varies strongly from triangular, rectangular, or rounded, with most deviation occurring in Hydroporinae that possess a frontoclypeus with a well developed frontal projection (nasale or "nose") (Fig. 4.3f). A Y-shaped epicranial suture divides the head dorsally into the frontoclypeal region and two lateral epcranial plates (Fig. 4.3f; Larson et al. 2000). In most species the first of the three instars posses egg-bursters on the frontoclypeus (Fig. 4.3f). Most larvae have a closed mouth opening and prognathous mouthparts with well developed sucking mandibles (Figs. 4.3a, c and 4.7). The mandibles of Hydroporinae are typically curved inwards and upwards.

The slender antenna of larvae are typically four segmented, but subdivided in Dytiscinae (Larson et al. 2000). The maxillary palpus typically contain three segments, the labial palpus typically has two segments, and in some dytiscids the palpes are secondary subdivided. The head has six stemmata on each side of the epicranium, which are reduced in stygobiont species. Unlike adults the pronotum is elongated and longer than mesothorax and metathorax (Fig. 4.3c). The abdomen has eight visible segments and the apex of the last segment is often elongated.

Within the larvae different life styles, varying in behavior, shape, and morphology, can be distinguished (Fig. 4.3g) (Wesenberg-Lund 1943; Galewski 1971; Wichard et al. 2002). Creeping or crawling larvae move along the bottom of the water close to the substrate or on aquatic plants. These rather bulky small to medium sized species (many Hydroporines and also *Agabus* and *Ilybius*) have comparatively small eyes and reduced swimming hairs on the legs. Others are able to swim very fast by moving their well-developed legs alternately. These ambush or active predators have moderately large eyes and most of the larger species (e.g., *Dytiscus*) belongs to this group. The nectonic or pelagic larvae of some species (e.g., *Acilius*, *Graphoderus*) are able to float, move, and skillfully swim in open water. Their legs and last two abdominal segments have well developed fringes of swimming hairs. Their body is similar to a shrimp with an elongated prothorax, and are specialized for feeding on large zooplankton or small aquatic insect larvae. Larvae are able to bend down their abdomens rapidly when they are attacked or disturbed, so that they propel themselves backwards through the water with great speed. Some species have larvae that are able to burrow in the substrate, most distinctively developed in the larvae of some *Matus*, which have broad pro- and mesotibae (pseudochelate) (Alarie et al. 2001). Finally, many species found in running waters will burrow in the streambed or are found between the roots of aquatic plants.

4.1.3 External Morphology of Pupae

Morphology of predaceous diving beetle pupae are understudied, likely because of difficulties in physically locating them for many species and in difficulties with rearing them under laboratory conditions. Commonly, mature larvae leave the water

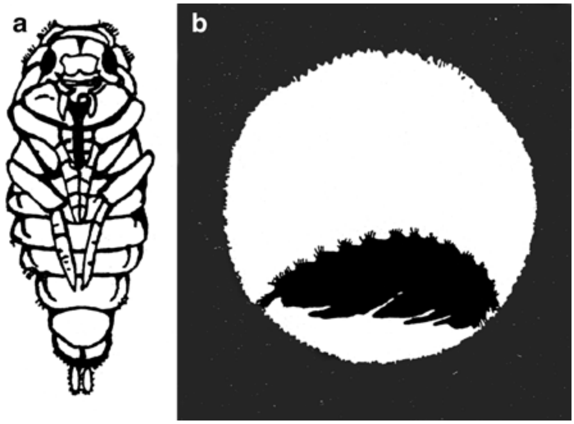

Fig. 4.4 (**a**) Habitus of pupae of *Dytiscus marginalis*. (**b**) Pupa (in black) in pupal chamber (in grey) in its typical position on the back; seen from the side (Redrawn from Naumann 1955)

and pupate in a self-constructed pupal chamber of mud or particles (Fig. 4.4). Within this cell the pupae lies on its back in an suspended position, held up from the floor only at the anterior and posterior ends (head and urogomphi) by setae. The pupa of exarata type have a nine segmented abdomen, with the last one rather small and urogomphi present on segment 8. The color of the relatively soft cuticle is whitish with a slight addition of yellow, orange, or brown. Pupation times varied widely from a few weeks to several months, although such information is lacking for the majority of species. Further information on pupae can be found in Formanowicz and Brodie (1981), Bertrand (1972), Ruhnau (1986), and Korschelt (1924).

4.2 Internal Anatomy and Physiology

Compared to some aspects of their natural history or ecology, the anatomy of adult Dytiscidae is well studied, which is due to the large size of many species, especially in the Dytiscinae. Nevertheless, knowledge of the physiology and function of their internal structures is still incomplete.

4.2.1 Digestive System and Digestion

Like other insects, the digestive system of Dytiscidae can be divided into three sections: the foregut, midgut, and hindgut. Although the foregut and hindgut are ectodermal invaginations and are lined with cuticle, the midgut is of endodermal origin. Generally the foregut of adults consist of the oral cavity, the pharynx, esophagus, crop, and proventriculus, whereas the midgut often has diverticles, and the hindgut can be separated into the ileum and rectum with a large rectal ampulla (Fig. 4.5). The crop, as a dilatation of the hind esophagus, functions mainly as food storage area, but it also is the site of the initiation of digestion with digestion fluids from the midgut

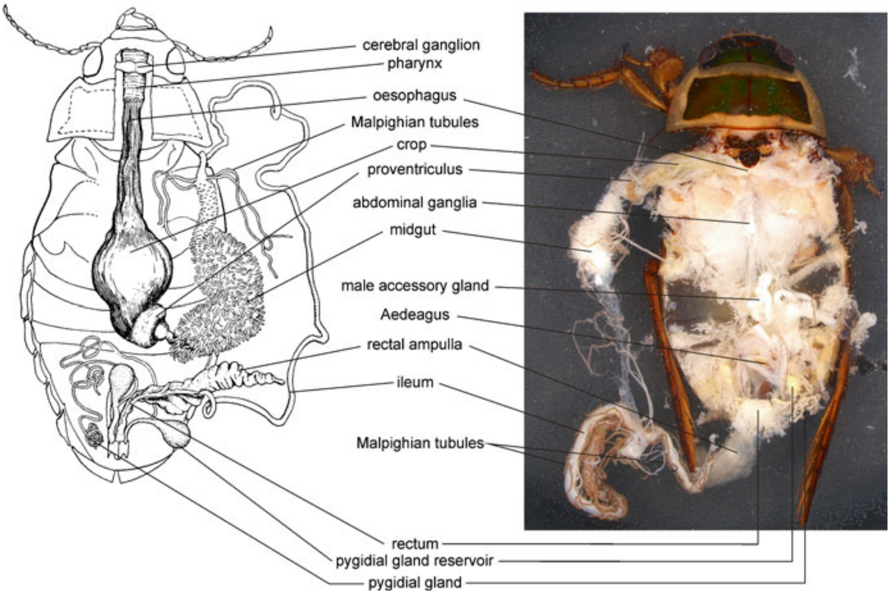

Fig. 4.5 Internal anatomy of *Dytiscus marginalis. Left side*: overview of the digestive system (Modified after Rungius 1911). Muscles, fat body, and sexual organs not shown. *Right side*: Photograph of dissected male for comparison

passing the proventriculus (i.e., filter function). The proventriculus of adult Dytiscidae is armored with four main lobes and four intermediate lobes, and in some species it is tubular and strongly muscular. The variety of different proventriculi in Dytiscidae are described by Balfour-Browne (1934), who used this part of the anatomy as a taxonomic character. The proventiculus controls the passage of the food to the midgut, but it may also be used to crush larger food items. Indigestible food particles may be arrested by the proventriculus in the crop and expelled by vomiting. The passage time of all food from crop to midgut vary among species and activity. For instance, passage time was measured at approximately 14 h in the 4 mm sized *Scarodytes halen*sis (Kehl and Dettner 2003). In general, the foregut can be easily removed from adult beetles and the contents observed under the microscope for diet analysis (Kehl and Dettner 2003; Deding 1988; Dettner et al. 1986; see also Chap. 8 in this book).

The midgut of predaceous diving beetles consist of a section with many crypts, and is the main region of secretion of enzymes and absorption of digestive products. The hindgut is separated in the very long ileum and rectum (Fig. 4.5). Here, absorption of water, salts, and other beneficial substances take place. Food residues can be stored in the rectal ampulla and if the beetle is disturbed this strongly smelling material may be released as a form of protection. The rectal ampulla also functions as a hydrostatic organ (Hicks and Larson 1991): the buoyancy of the beetle can be controlled by ingesting and expelling water. Residing between the hind- and midgut is the pyloric valve, which prevents back-flow of material from the hindgut. The

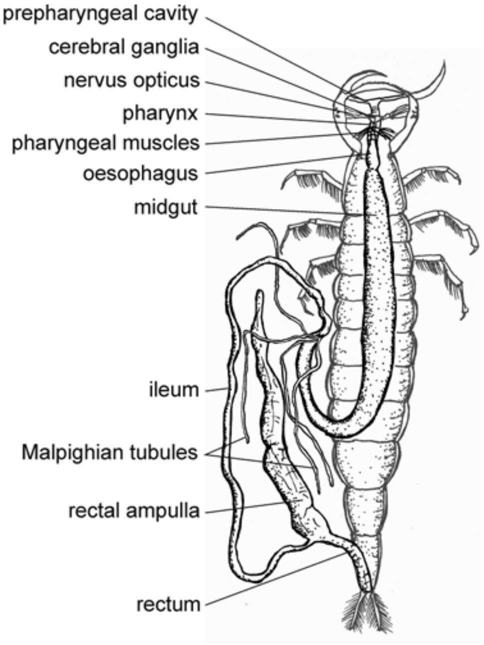

Fig. 4.6 Internal structure of *Dytiscus marginalis* larva. Muscles, tracheal trunks, fat body removed (After Rungius 1911)

products of excretion are emptied from the four Malpighian tubules into the alimentary canal at the passage from mid- to hindgut. In terms of osmoregulation, dytiscids cannot achieve sodium balance in fresh water without dietary sodium input, although they are able to regulate sodium loss (Frisbie and Dunson 1988). Dytiscid larvae take up ions into the hemolymph almost exclusively through the intestine. The ileum, which is lined by a highly differentiated transporting epithelium throughout its entire length, is the main site of ion absorption (Schmitz and Komnick 1976).

Larvae have extra-oral digestion and their digestive anatomy differs from that of adults. In larvae, the crop and proventriculus are missing whereas the midgut is well developed (although a crop is present in Copelatinae, Balke 2005). The rectal ampulla is large and sometimes extends forward into the head (Fig. 4.6). The rectal ampulla in larvae also function as a hydrostatic organ, but there is some evidence that it may also play an important role during molting. For instance, expanding of the rectal ampulla may help to split the outer shell and also may help to form the new cuticle (Naumann 1955). Most remarkably are the modification of the mandibles and internal head structures (Fig. 4.7). Most larvae have a closed mouth opening and use the well-developed, falcate modified suctorial mandibles for piercing the prey, injecting digestive enzymes from the midgut, and ingesting the liquefied food by means of a cibarial-pharyngeal sucking pump. The suctorial mandibles have a narrow, almost closed in canal or channel extending from near the tip to the base on the inner margin (Fig. 4.7d). In closed position, the mandibles have basal openings that are connected with a transverse prepharyngeal chamber (Fig. 4.7b), which is

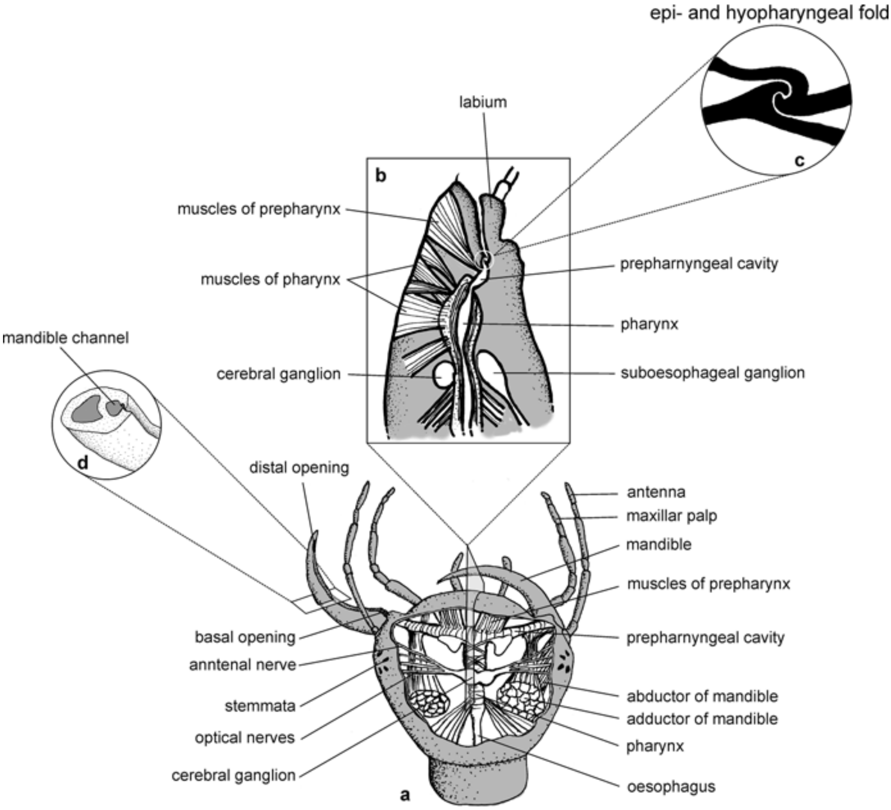

Fig. 4.7 Internal structure of head of *Dytiscus marginalis* larvae. (**a**) Opened head capsule with view on the transverse prepharyngeal chamber and muscles of the sucking pump. (**b**) Sagital section of anterior head. (**c**) Magnification of the epi- and hypopharnygeal tegmentary folds. (**d**) Cross section of sucking mandible (Modified and combined after Weber 1933; Naumann 1955; Korschelt 1924)

formed by tightly locked epi- and hypopharnygeal tegmentary folds (Fig. 4.7c) (Wesenberg-Lund 1943; De Marzo 1979; De Marzo and Nilsson 1986; Gorb and Beutel 2000; Korschelt 1924). Thus, most taxa are dependent on liquefied food ingested with their sucking mandibles, but some (e.g., *Graphoderus*, *Acilius*) can still open the mouth and can consume particulate material (Wesenberg-Lund 1943). The sucking channel is absent in Copelatini, Hydrotrupes, and Agabetes (Balke 2005). Mandible geometry has been linked to variation in hunting tactics and prey selectivity behavior (Wall et al. 2006). The mouthparts, especially mandibles and pharyngeal sucking pump are equipped with well developed muscles (Fig. 4.7a, b). Salivary glands are missing in adults and larvae. In the past it was assumed that a paralyzing venom was injected into the prey via the sucking mandibles, but so far no venom glands or toxin has been found. The paralyzing effect that larval feeding appears to have on captured prey is solely caused by the midgut digestion enzymes.

4.2.2 Reproductive System

Due to the phylogenetic importance of the male and female genitalia, the sclerotized structures are well documented in many identification keys (Franciscolo 1979; Larson et al. 2000; Nilsson and Holmen 1995). The internal reproductive organs (ovaries and testis) were often of minor interest, but they can be also helpful, for example, in age structure analysis (Dettner et al. 1986). More recently, the internal genetalia have provided insight into potential post-copulation sexual conflict in many species of dytiscids, especially in the Hydroporinae (see Chap. 5 in this book).

A number of authors have described the scleotized male genitalia (e.g., Balfour-Browne 1950; Franciscolo 1979; Balke 2005). The male reproductive organs (Fig. 4.8b) consist of paired testes with vas deferentia leading to the seminal vesicles (in Hydroporinae seminal vesicles and testes are closely connected and rolled up). Large paired accessory glands are also present, and in most species they typically are recurved at approximately half the length in mature adults.

Female reproductive organs (Fig. 4.8a) consist of a pair of ovaries made up of numerous ovarioles, each ovary with a short oviduct, leading to a single common oviduct. A vagina, spermatheca (receptacelum seminis) and in some taxa a bursa copulatrix is present. Bursa copulatrix and the vagina generally have separate openings. Different configurations of the female genitalia are summarized by Miller (2001) and in Chap. 5 in this book. Several glands and gland reservoirs can be present. The ovaries are, like in all Adephaga, polytrophic-meroistic (nurse cells present, grouped together and alternating with oocytes). The structure of ovipositors can be found elsewhere (Burmeister 1976). Note that the appearance of unsclerotized male and female reproductive organs can vary depending on the age of the beetles. Glands can be of very different sizes (male accessory gland sometimes extending up in the prothorax) and also the ovaries exhibit great variation in size and shape according to the age class (Dettner et al. 1986; Classen and Dettner 1983). The paired or grouped spermatozoa of Dytiscidae have been thoroughly studied by many authors (Dallai and Afzelius 1985, 1987; Werner 1982; Jamieson et al. 1999) and the sperm evolution in diving beetles is discussed by Higginson et al. (2012a, b) as well as in Chap. 5 in this book. Oogenesis in Dytiscidae was studied by Urbani and Russo-Caia (1969, 1972).

4.2.3 Muscles of Thorax

In most Dytiscidae locomotory musculature (flight and leg musculature) are well developed. A good overview of the locomotory muscles of Dytiscidae is given by Larsen (1966) and Balfour-Browne (1967) with a more physiological approach provided by Kallapur (1970).

Dytiscids adults in general are not considered to be strong flyers, and in several species or specimens the flight muscles are degenerated or reduced, but it remains unclear if the reduction is age dependant (“oogenesis flight syndrome”) or if these

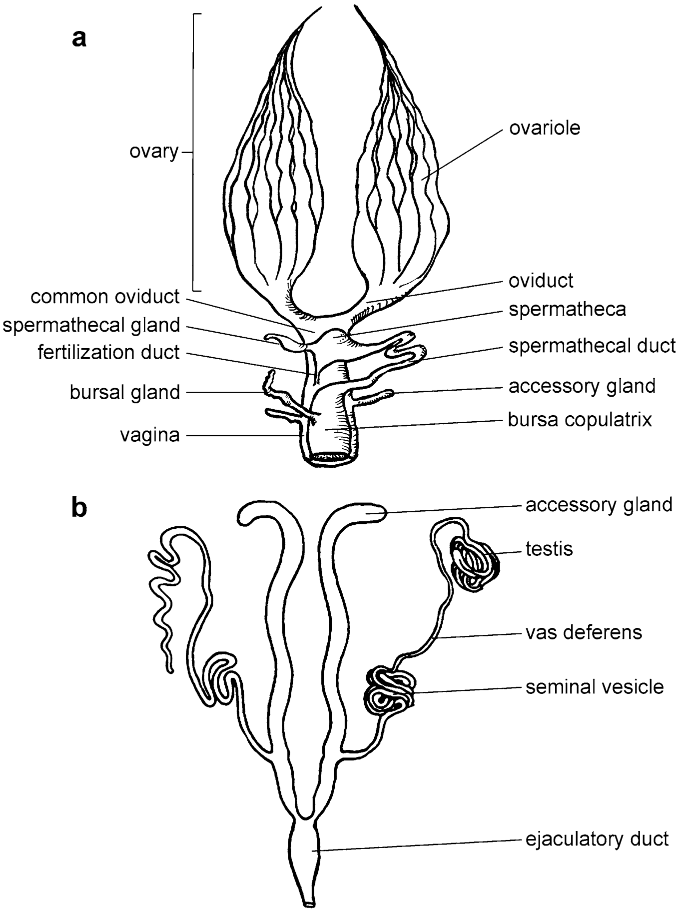

Fig. 4.8 Reproductive systems of Dytiscidae (schematic). Note that, depending on species, glands (gland reservoirs) and ducts could be reduced, shortened or enlarged. Also different parts could be enlarged or reduced depending on age class (See Dettner et al. 1986 and Chap. 5 in this book). (**a**) Female reproductive organs; (**b**) male reproductive organs

individuals have lost the ability to fly. Flight capacity and flight muscles analysis can be found in the comprehensive works of Jackson (1952, 1956a, b, 1973). The indirect flight musculature of Dytiscidae (Fig. 4.9) are attached to the thorax and not to the wing base. The longitudinal muscles (e.g., M60) are the depressors, forcing the wings down by arching up the tergite. The dorso-ventral muscles (e.g., M64 and M75) are the antagonistic muscles and raise the wings (Jackson 1956a). Several other muscles help to position the wings. For details of the muscles of *Dytiscus marginalis* adults see Bauer (1910) and Korschelt (1923). More on dispersal and movement via flight in dytiscids can be found in Chap. 9 in this book.

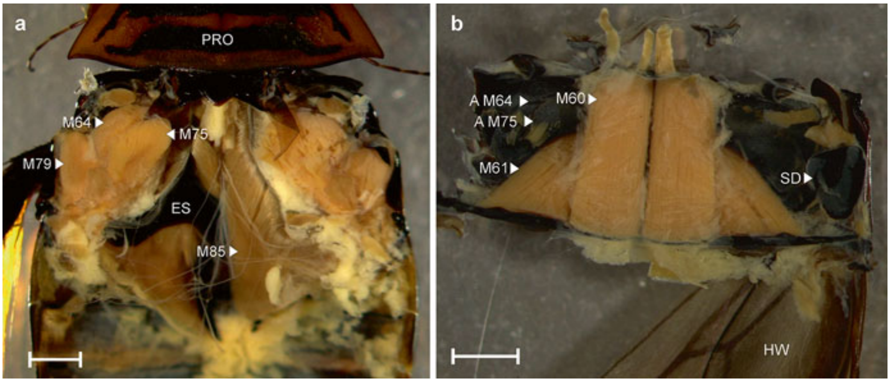

Fig. 4.9 Metathoracic muscles of *Acilius sulcatus*. (**a**) Dorsal view of the opened metathorax, with foregut and left side of M85 removed. (**b**) Dissected metatergum (*ventral view*) with the dorsal muscles M60 and M61. *PRO* pronotum, *ES* endosternite, *HW* hind wing, *SD* subalar plate, *M60* musculus metanoti primus, *M61* musculus metanoti secundus, *M64* musculus dorsoventralis primus, *M75* musculus noto coxalis anterior, *M79* musculus coxa-subalaris, *M85* musculus furca-trochanteralis, *A M64* insertion of M64, *A M75* insertion of M75. Nomenclature of muscles according to Larsen (1966). Scale bars: 1 mm (From Kehl and Dettner 2007)

4.2.4 Nervous System

Dytiscidae are similar to other insects in having a relatively simple central nervous system with a dorsal brain linked to a ventral nerve cord. The brain is a complex of three pairs of ganglia located dorsally within the head capsule above the esophagus. The first pair of the fused ganglia of the brain (protocerebrum) is associated with vision and innervate the compound eyes in adults or the six stemmata on each side in larvae. The second pair (deutocerebrum) process sensory information from the antennae, and the third pair (tritocereprum) innervate the labrum and link the brain with the subesophageal ganglion (and the rest of the ventral nerve cord) and with the stomodaeal nervous system via the frontal nerve and the frontal ganglion (Fig. 4.10a). The subesophageal ganglion, located below the brain and esophagus, innervates the mouthparts and is linked to the thoracal ganglia. The three thoracal ganglia are connected with short connections followed by the nearly fused abdominal ganglia. The main function of the thoracal ganglia is to control locomotion by innervating the legs and wings (Fig. 4.10b). The prothoracal ganglia innervates the forelegs and the prothoracal glands, the mesothoracal ganglia the midlegs and the elytra, and the metathoracal ganglia the hind legs and the wings. The first abdominal ganglia is more or less fused with the metathoracal ganglia and also the remaining abdominal ganglia fused into a short column. Holste (1910) supposed that the first abdominal ganglion is a fused ganglion from abdominal segment 1 and 2, and that the last abdominal ganglion (abdominal ganglion 6 in Fig. 4.10) is a fused ganglion of the seventh and last abdominal segment.

The stomodaeal nervous system innervates and controls the internal organs. The paired frontal nerves connect the unpaired frontal ganglion with the tritocerebrum.

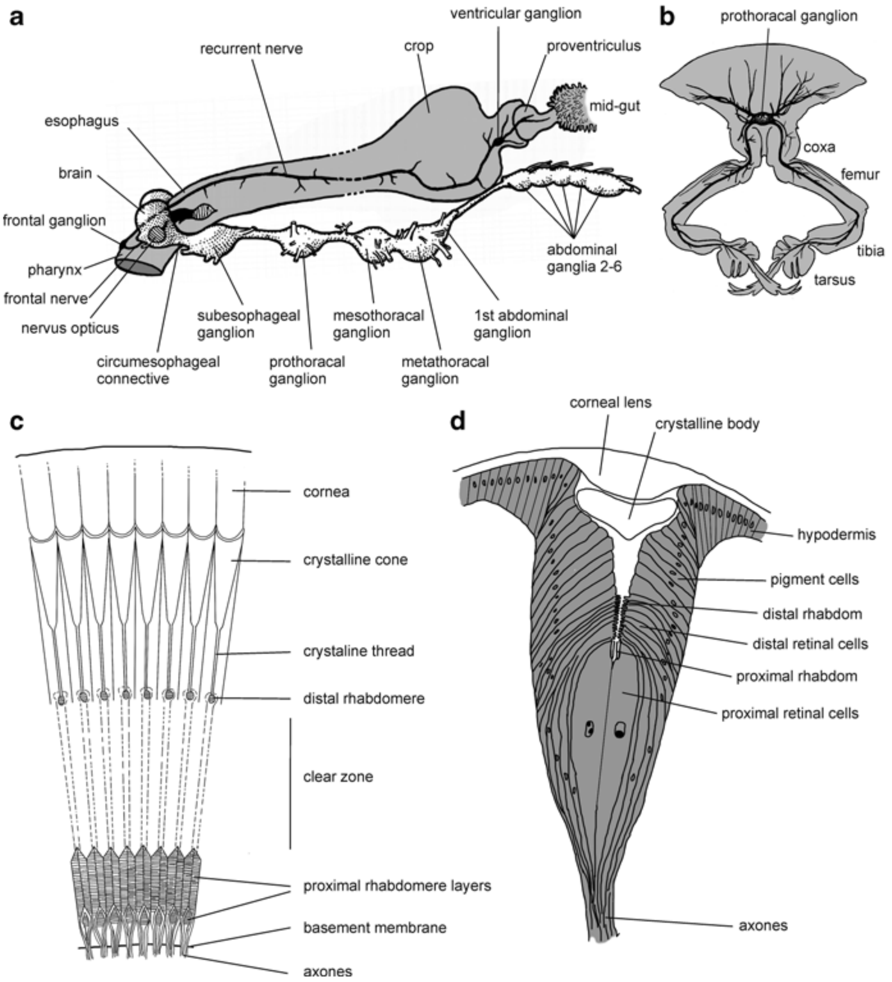

Fig. 4.10 Nervous system and eyes of Dytiscidae. (**a**) Central nervous system (*white dotted*) and stomatogastric nervous system (*black*) of adult *Dytiscus marginalis*. (**b**) cross section prothorax in the region of the prothoracal ganglion of adult *Dytiscus marginalis*. Only central nervous system shown. (**c**) Schematic section through the compound eye of *Dytiscus marginalis*. (**d**) Section through the stemmata of *Dytiscus marginalis* (**a** and **b** modified after Holste (1910) and Wesenberg-Lund (1943), **c** combined from Günther (1912) and Horridge (1969), **d** modified from Günther (1912))

The frontal ganglion innervates the pharynx and is connected with a long single nerve (recurrent nerve), which runs under the brain on the esophagus to the ventricular ganglion at the end of the crop.

Dytiscids possess a variety of sensilla that allow them to effectively interact with the environment. In addition to several different types of mechanorecptors (Wolfe and Zimmerman 1984; Hochreuther 1912; Lehr 1914) and chemical receptors (Jensen and Zacharuk 1991, 1992; Baker 2001), Dytiscidae have well developed visual systems. The compound eyes of adults (Horridge et al. 1970; Meyer-Rochow

1973) (Fig. 4.1f) and the stemmata of larvae (Sbita et al. 2007; Maksimovic et al. 2011; Mandapaka et al. 2006; Buschbeck et al. 2007; Schöne 1951) (Fig. 4.2a) are well studied. The compound eyes (Fig. 4.10c), made up of 9,000 single ommatidia in *Dytiscus marginalis* (Günther 1912), are adapted to work in aquatic and terrestrial environments. Unlike air, the refractive index of water is more similar to that of the cornea, so the simple curved corneal lens that is present in many terrestrial insects is unable to focus an image underwater (Lancaster and Downes 2013). The cornea of dytiscids is flat on the external surface and composed of layers of unequal refractive index, with horizontal layers in the distal part and concentrically formed layers around a region of highest refractive index on the axis (Meyer-Rochow 1973). The retina of *Dytiscus* has a tiered structure, with rhabdomeres at three different levels. Crystalline threads stretch from the crystalline cones to the distal layer of rhabdomeres. Between the distal rhabdomere and the proximal rhabdomeres layers is a wide clear zone (Fig. 4.10c), where light reaching the proximal rhabdomeres of a single ommatidium will have been refracted from several facets of different ommatidia. The proximal rhabdomeres layers therefore seems to be concerned with light perception, while the distal rhabdomere for perception of form or movement (Horridge et al. 1970). The compound eyes could be light- and dark-adapted, showing a thousand times stronger sensitivity during night. But the diurnal variations in visual function seems to be independent of retinal pigment migration (Jahn and Wulff 1941, 1943). Several Dytiscidae are known to be sensitive to polarized light, which helps them to find water bodies during flight (Schwind 1995).

Larvae of most dytiscid species have six stemmata located on each side of their head posterior to the origin of each antenna (Fig. 4.1a, c, f). Some species have an additional pair of eye spots. The spatial arrangement of the stemmata on the head capsule varies greatly in dytiscid larvae, which may result from the different hunting strategies. Usually the stemmata are covered by a corneal (cuticular) lens and a crystalline body focus the light to the retina. In *Dytiscus marginalis*, Günther (1912) described two rhabdomer layers (Fig. 4.10d) and in *Thermonectes* at least two retinas are present (Mandapaka et al. 2006). The proximal retina consists of unusual horizontal rows of long rhabdoms parallel to the light path.

In most insects, stemmata are generally described as simple eyes, with perception involving either bright and dark vision or a rough mosaic vision. This is not so in dytiscid larvae. For example, *Thermonectes marmoratus* is a highly efficient visually-guided predator with highly specialized eye structures and morphologically and functionally different stemmata. The two forward-looking dorsal pairs are tubular and may be primarily used for prey capture, but they have an extremely narrow visual field. The visual field is enlarged through a scanning behaviour of the larvae by performing a dorso-ventral head and thorax movement, prior to prey capture (Buschbeck et al. 2007). The distal retina is green sensitive, whereas the proximal retina is UV sensitive (Maksimovic 2011). Furthermore, the proximal retina can support polarization vision, which may allows them to better detect prey. Two sharp images are focused on the distal and proximal retina by a real bifocal lens and there is evidence that larvae are able to determine prey distance.

Besides vision, other senses seem to be well developed in the Dytiscidae. These include hearing via chordotonal organs of the antennae (Lehr 1914) or by abdominal mechanoreceptors (Hughes 1952). The olfactory receptors of the antenna appear to work both in water and in air (Behrend 1971). To detect the presence of predators, adult beetles seem to rely on visual stimuli when visibility is good, while in darkness they seem to use chemical stimuli (Åbjörnsson et al. 1997). There is also some evidence for chemical reception of pheromones in adults (Herbst et al. 2011).

4.2.5 Respiration and Tracheal System

The basic physical (Alt 1912; Wesenberg-Lund 1943) and physiological details (Ege 1915; Wolvekamp 1955; Gilbert 1986) of respiration in Dytiscidae are well established (except for stygobiont species), which makes it all the more remarkable that several new findings relating to respiration in Dytiscidae have recently been published (e.g., Calosi et al. 2007, 2012; Kehl and Dettner 2009; Madsen 2012).

All aquatic insects, including Dytiscidae, need oxygen for respiration, which can be obtained from the atmosphere (aeropneustic) or directly from the water (dissolved oxygen, hydropneustic). In general, adult dytiscids have an air store under the elytra in the subelytral cavity, where the eight pairs of abdominal spiracles open (Heberdey 1938; Alt 1912). This air store must be renewed regularly at the water surface, and the beetles accomplish this by breaking the water surface with the tip of the abdomen (Fig. 4.11a). A hydrofuge portion of the apical abdominal tergites guarantee the gas exchange will occur with the subelytral cavity. There are some hints for a controlled air circulation and specialized spiracles for exhalation and inhalation during gas exchange at the water surface (Gilbert 1986). The duration of diving varies depending on species, temperature, and activity (Calosi et al. 2007), but can be prolonged by a small air bubble (Fig 4.11b, c) pressed out from the subelytral cavity and held by the hydrofuge hairs at the tip of the abdomen (Larson et al. 2000). This air bubble acts as a physical gill (compressible gas gill, Rahn and Paganelli 1968; Ege 1915), where dissolved oxygen from the water diffuses in, but the same time nitrogen diffuses slowly out of the bubble and the size of the bubble shrinks over time. With the decreasing bubble surface, the rate of gas exchange decreases and the beetles must surface again. During inactivity the physical gill allows the beetle to dive for a long period of time, and may be used for survival under ice during winter. The carbon dioxide from the beetles metabolism diffuses out in the water, due to the high solubility of CO_2. Dive duration varies from a few minutes up to 24 h (Madsen 1967; Calosi et al. 2007; Kehl and Dettner 2009). However, some species remain submerged for very long periods. For example, *Hydroglyphus hamulatus* remained submerged for 10 weeks (Meuche 1937), whereas *Deronectes aubei* can stay submerged for an unlimited time (at 13 °C water temperature) and have specialized setae on the elytra, pronotum, and ventral side that act as tracheal gills (Kehl and Dettner 2009, but see also Madsen 2012) (Fig. 4.12a). These tracheated setae (Figs. 4.2c and 4.13) also occur in many other small Hydroporinae, enabling them to stay submerged, but they also can use the conventional mode of respiration by surfacing and the subelytral air store. Already Smrž (1981) assumed, on the basis of the diameters and branching of the intraelytral tracheae

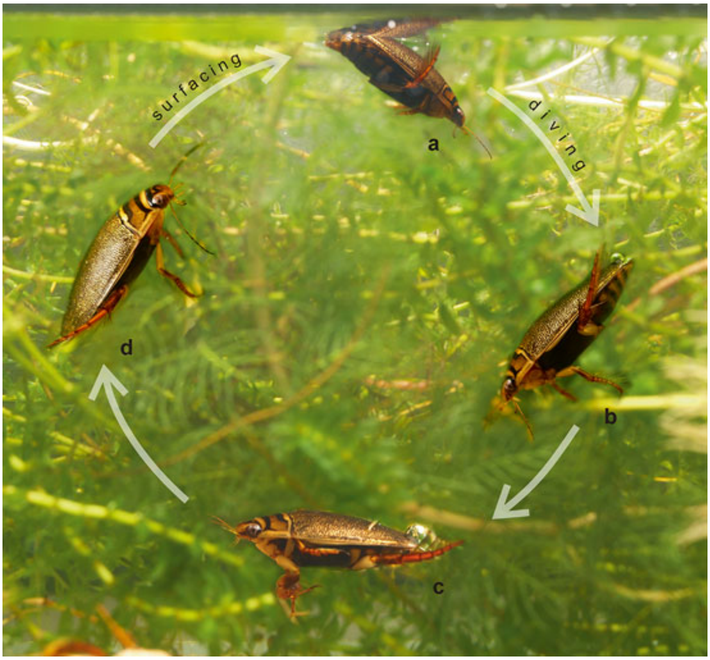

Fig. 4.11 Respiration of adult *Acilius canaliculatus*. (**a**) Gas exchange on the water surface. (**b**) and (**c**) Diving, note the air bubble on the tip of the abdomen, acting as physical gill. (**d**) surfacing

(Fig. 4.13a, b), that cuticular gas exchange exists via the elytra in stygobiont species. However, the gas exchange of stygobiont species remains unclear, while *Siettitia*, *Phreatodessus*, and *Kuschelhydrus* possess these setae for cuticular gas exchange (Kehl and Dettner 2009 and personal observations). It is noteworthy that *Paroster* and other Australian stygobiont species do not have this type of cuticular surface (Bradford 2010, personal observations).

Adults posses two pairs of thoracic spiracles (mesothoracic spiracle situated between the pro- and mesothorax), eight pairs of abdominal spiracles (Fig. 4.12a–d) and large thoracic air-sacs (Fig. 4.12e) that can be filled with air in preparation for flight, to reduce weight, and to supply the large muscles with sufficient oxygen during flight. Some time is often required before adults can return to water after flight, as they must deflate these air-sacs before diving and engaging in aquatic respiration. Detailed information of spiracles and the tracheal system of adults can be found in Alt (1912) and Gilbert (1986).

The tracheal system in larvae (Fig. 4.12f) mainly consists of two strong, longitudinal tracheae, starting at the last abdominal spiracles and proceeding up to the prothorax. In the prothorax, the main tracheae split in an upper and lower tracheae that lead into the head. More detailed information of tracheation of larvae can be found in Alt (1912). The two longitudinal trunks are connected by dorsal commissures in each segment. The two main tracheal trunks can often be seen in live specimens through the cuticle. The taenidum (chitinous fiber forming the spiral thread) is well developed in larvae, and often has a dark appearance, so that the tracheal system is

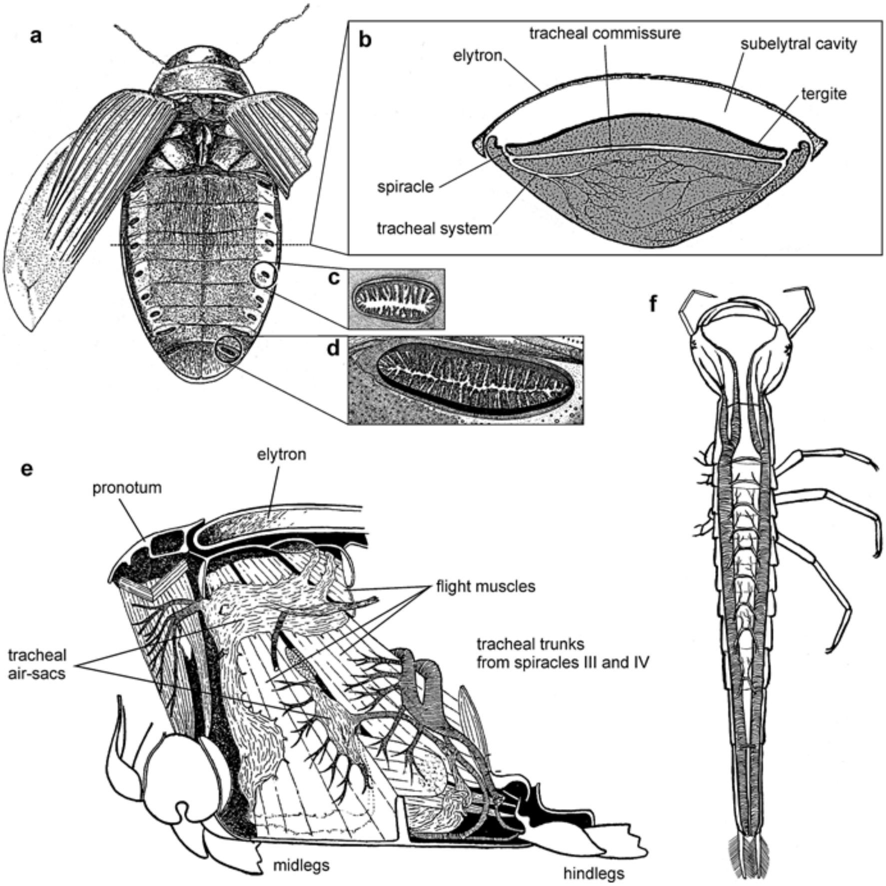

Fig. 4.12 Tracheal system and respiration in Dytiscidae. (**a**) Abdominal spiracles of female *Dytiscus marginalis*. Dorsal view, with elytra folded sideward and hindwings removed. (**b**) Cross section of *Dytiscus marginalis* in the region of the 3rd spiracle showing the subelytral cavity and tracheal system (hind wings removed). (**c**) Abdominal spiracle. (**d**) Last abdominal spiracle. (**e**) Longitudinal cut of thorax of *Dytiscus marginalis* showing the thoracal air-sacs supplying the strong musculature with enough oxygen. (**f**) Tracheal system of *Dytiscus* larvae (1st instar). The two strong longitudinal trunks are the only air store of larvae (All figures modified after Alt (1912), except **b** after Naumann (1955))

not as shiny and silvery as in other insects. The number of functional spiracles in larvae depends on the larval instar. In the first instars only the last pair of spiracles are present (segment VIII), the lateral abdominal and thoracic spiracles absent, but internal structures are already present. The spiracles on the thorax of second instars are already visible but closed and not functional (except the last pair). In the last instars two thoracic and eight abdominal spiracles are present, but remain generally closed by a mechanism except in the last pair (Larson et al. 2000; Blunck 1923; Lawrence 1991). Last instars of *Heterosternuta* and *Neoporus* do not have functional lateral spiracles (Larson et al. 2000; Balke 2005).

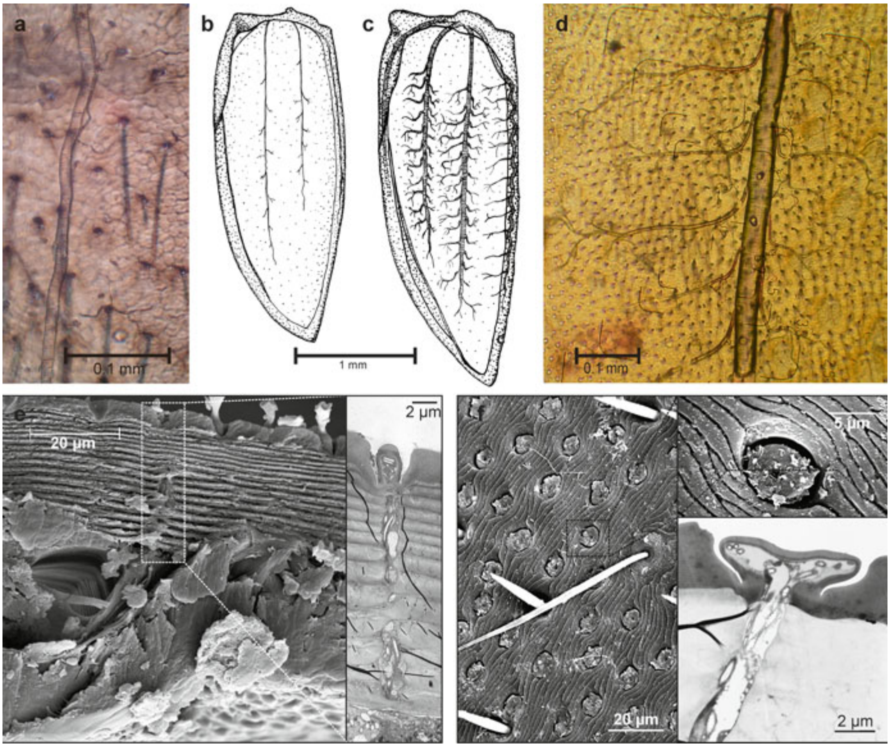

Fig. 4.13 Cuticular gas exchange in adult Dytiscidae with the help of tracheated setae. (**a** and **b**) elytra of *Hydroporus palustris* (no tracheated setae present) with small intraelytral tracheae with only few branchings. (**c** and **d**) Elytra of *Deronectes aubei* (with tracheated setae) with a strong, richly branched, longitudinal intraelytral trachea. The diameter of the intraelytral tracheae can give evidence for the capability of cuticular gas exchange via the elytra. (**e**) Cross section of elytra of *Deronects aubei* with longitudinal trachea cut (*left side*), from which smaller tracheae and tracheoles goes upwards through the "hairchannel" into the base of the setae. (**f**) Tracheated setae in *Stictotrarsus duodecimpustulatus*. The tiny modified setae (sensilla placoidea type 1 according to Wolfe and Zimmerman 1984) are richly tracheated

Cuticular gas exchange may occur in all larvae, but is only sufficient in smaller species or early instars. Larvae of larger species obtain oxygen at the water surface by functional posterior spiracles and store this air in the strong longitudinal tracheal trunks. Unique in Dytiscidae are the larvae of *Coptotomus*, which have elongated lateral gills, a pair on each of the first six abdominal segments (Fig. 4.14). These larvae are able to remain continuously beneath the surface and may go deeper than other dytiscid larvae (Usinger 1956). In *Celina* the apical elytral spines and the spinose ends of the abdomen in adults are supposed to gain oxygen by piercing plants roots (e.g., *Typha*). It is also possible that the peculiar posteriorly extended lateral tracheal trunks of the abdominal apex in larvae may be used to obtain intracellular air from plants (Hilsenhoff 1993; Spangler 1973).

Fig. 4.14 Larva of *Coptotomus loticus* with unusual elongated lateral gills on the first six abdominal segments (Photo courtesy of Donald Chandler 2013)

4.3 Future Directions

There are a number of questions remaining to be answered for dytiscids, especially those that link ecology and physiology. For instance, in relation to their distribution and habitat selection, Why do certain species only occur in certain waters or have a restricted distribution? A step in that direction is given by Calosi et al. (2010) who suggest that the latitudinal range extent and position of *Deronectes* species could be best explained by their absolute thermal tolerance. Specifically, species' northern and southern range limits are related to their tolerance of low and high temperatures, respectively. Further work in this direction should include examinations of larvae, as they are surely more sensitive to environmental conditions than the more mobile adults. Moreover, understanding the larval ecophysiology is a key function to understand habitat requirements. The ecology of dytiscid eggs is also an interesting area in need of more data, considering that for most species egg deposition sites are and female egg-laying behavior are unknown.

Most morphological and physiological studies are many decades old, and it would be interesting to use new scientific tools (e.g., molecular, electrophysiological, and optical) established and refined over the last few years to understand the fascinating world of predaceous diving beetles. Understanding the microorganism relationships (e.g., gut bacteria and intracellular bacteria e.g., *Rickettsia* and *Wollbachia*) may give new insights into the biology of the beetles, as well as their physiological functions (see also Chap. 6 in this book). In terms of respiration, there are many unresolved questions, including, How do the tracheated setae function in detail?, What is the evolution of the tracheated setae?, and How do subterranean species respire? We are just beginning to understand the visual system in some species (e.g., *Thermonectes*), but the knowledge of other species is poor. The function and mechanisms of other sensilla and setae on antenna, mouthparts, and body surface is almost entirely unknown. More work on internal structures (e.g., reproductive organs, nervous system including sense organs, gut system, tracheal system) and the comparison in different species may also help support systematics and taxonomic investigations.

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Chapter 5
Predaceous Diving Beetle Sexual Systems

Kelly B. Miller and Johannes Bergsten

> *The evolution of sex is the hardest problem in evolutionary biology.* John Maynard Smith
> *Ein der saugnäpfe berauptes männchen wäre zur ausfürung der Copula nicht imstande*
> [Translation: *A male deprived of his suction cups would not be able to copulate*]. (Blunck 1912c)

Abstract Predaceous diving beetles have an impressively diverse array of morphological and behavioral attributes associated with sexual systems. These include anatomical dimorphisms with males and females exhibiting many secondary sexual features, behavioral dimorphisms in precopulatory and copulatory activities, extensive variation in male and female genitalia, and sperm complexity that includes sperm conjugation and heteromorphism. Many of these attributes appear to be correlated, suggesting emphasis by certain clades on particular sexual systems. For example, members of Dytiscinae appear to emphasize pre-insemination sexual selection with female resistance behavior possibly associated with the male ability to threaten suffocation of females during copulatory activities, which take place over many hours of mate guarding. In this case, males have large adhesive discs on their protarsi used to better subdue a resistant female, whereas females have modified pronotal and elytral cuticle that interfere with male adhesive discs. This group also has among the simplest male sperm and female reproductive tract

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morphology, suggesting more limited post-insemination selection, but strong pre-insemination sexual antagonism. In contrast, members of Hydroporinae have no obvious pre-insemination mating behaviors and only short mating durations. This group also has dramatically complex female reproductive tracts and male sperm morphology including conjugation and heteromorphism suggesting intensity in post-insemination sperm choice, sperm cooperation, and sperm competition. Here, dytiscid sexual attributes are reviewed along with discussion of dytiscid sexual system evolution.

Keywords Sexual selection • Evolution • Sexual antagonism • Reproduction • Insemination • Genitalia

5.1 Introduction

Sexual selection is a type of natural selection in which an individual's fitness directly depends on reproductive activities and selective consequences of these activities within a particular species. As such, it involves a range of components from mate finding to copulation to insemination and fertilization to even parental investment in care of offspring, especially when this influences earlier mating decisions. Sexual selection may include competitive interactions between members of the same sex (intrasexual competition) including such things as male-male combat, male dominance hierarchies, resource guarding, mate guarding, parental care, and sperm competition. Other competitive interactions may represent a conflict of interest between males and females over the decision to mate (intersexual competition) because, in general, the sexes have different mating frequency optima because of differential investment in gametes and offspring. These interactions include such things as mate choice (generally by females on males, but not always), cryptic female choice (sperm selection), and sexual antagonism (forced mating). Individuals, populations, species and even groups of species generally exhibit particular manifestations of sexual selection, with multiple, complex strategies often evident in the same species. These "sexual systems" are expected, like any other phenotypic attributes of organisms, to have a macroevolutionary pattern that may be discovered through phylogenetic investigation. Sexual selection has been invoked to explain many unusual phenotypes including genitalia and "exaggerated" phenotypes such as antlers, bright colors, singing, and courtship behaviors, among many others. In particular, it has been used to explain features that seem to be especially maladaptive when considered from other, more typical natural selection perspectives (Darwin 1871).

Predaceous diving beetles (Coleoptera: Dytiscidae) exhibit some of the richest diversity of sexual systems and related morphology and behavior of any arthropod group. Knowledge of this diversity and its evolutionary patterns and processes is only just beginning, but what is known is tantalizingly suggestive of an excellent system for the study of complex evolution of sexual systems.

All predaceous diving beetles, as far as known, are dioecious, promiscuous, and polygamous. The only known possible exception to this are certain species of *Hydrodytes* (Hydrodytinae), for which only females are known, and which may be parthenogenetic (Young 1989; Miller 2002b), though this is unconfirmed. All other known species have direct sperm transfer and internal fertilization, and, as such, are expected to be subject to the same fitness influences based in sexual selection that are other animals. That is, predaceous diving beetles should be influenced by overall differential interests in mating and mate choice between males and females, associated fitness benefits and costs of mating and mate choice, and the inter- and intrasexual competition that manifests from these effects. Here, emphasis is placed on a review of the diversity of mating-related morphology, behavior, and mating systems in dytiscids.

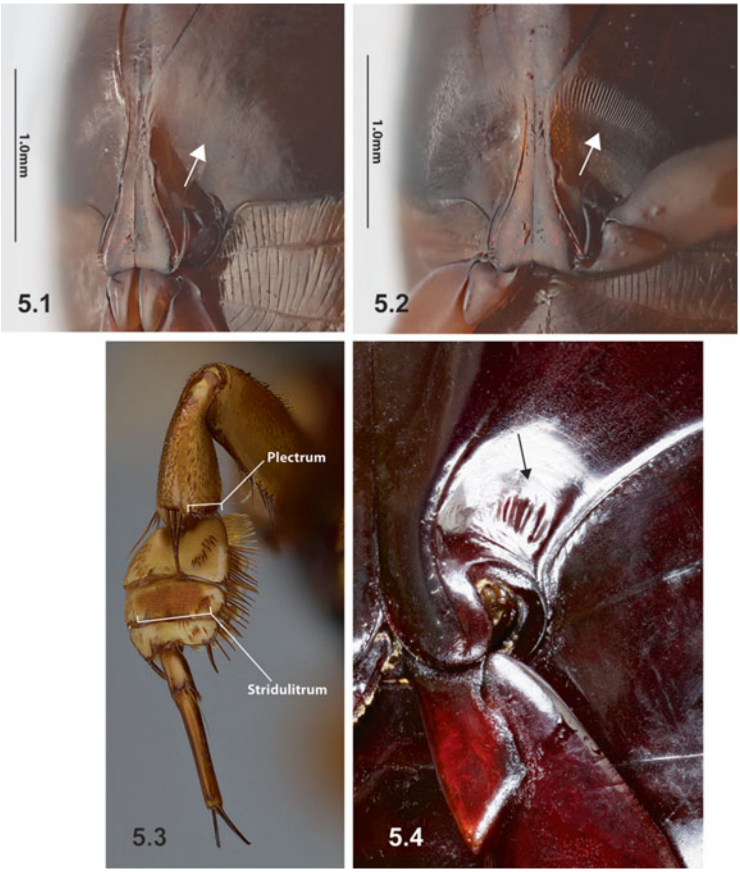
5.2 Sexual Variation

5.2.1 Secondary Sexual Dimorphisms

Diving beetles exhibit numerous and diverse secondary sexual phenotypic dimorphisms, with the “unusual” or “exaggerated” state most often, though not always, exhibited by males. Dimorphic features include chemical, behavioral (including sound production), and morphological attributes.

5.2.1.1 Chemical

Among the least known dimorphic systems in diving beetles are pheromones, and the first example of male detection of female release of sexually attractive pheromones (in *Rhantus suturalis* MacLeay) was discovered only recently (Herbst et al. 2011). In this case, males were significantly attracted to females using chemical cues (Herbst et al. 2011). Diving beetles are exceptional chemical producers for defense and other purposes (Dettner and Schwinger 1980; Dettner 1985, see Chap. 6 in this book), and it might be expected that they would use this ability in sexual systems, but little is known about the use of chemical sexual signaling in aquatic insects in general, and certainly this is true of Dytiscidae. This may prove to be a fruitful avenue for study in diving beetles. Expanded male antennomeres in numerous groups of diving beetles may be related to this type of signaling (see 5.2.1.3 below), but this is also unknown.



Figs. 5.1–5.4 Dytiscid stridulatory devices. 5.1 and 5.2, *Laccophilus maculosus* Say; 1, female; 2, male, arrow indicated stridulitrum. 5.3, *Hydaticus flavolineatus* Boheman, male left protibia and tarsus. 5.4, *Cybister fimbriolatus* (Say), male left metacoxa

5.2.1.2 Acoustic

In contrast, acoustic signaling in dytiscids appears to be produced by males to attract potentially receptive females. Apparent stridulatory devices occur throughout Dytiscidae, but usually only on males, (present in both males and females in some species such as *Laccophilus hyalinus (DeGeer)*) and are seemingly unrelated to defensive sound production, though, to date, no sound production or behavior associated with these devices has been directly observed (Larson and Pritchard 1974). It is possible that male members of Hydaticini seek instead to attract predators during pre-mating activities (see below). Groups with suspected male stridulatory devices on many or, at least, some species include *Laccophilus* (Figs. 5.1 and 5.2), *Hydrovatus*, Hydaticini (Fig. 5.3), *Agabus*, *Cybister* (Fig. 5.4), *Colymbetes* (Larson and Pritchard 1974) and *Agaporomorphus* (Miller 2001b).

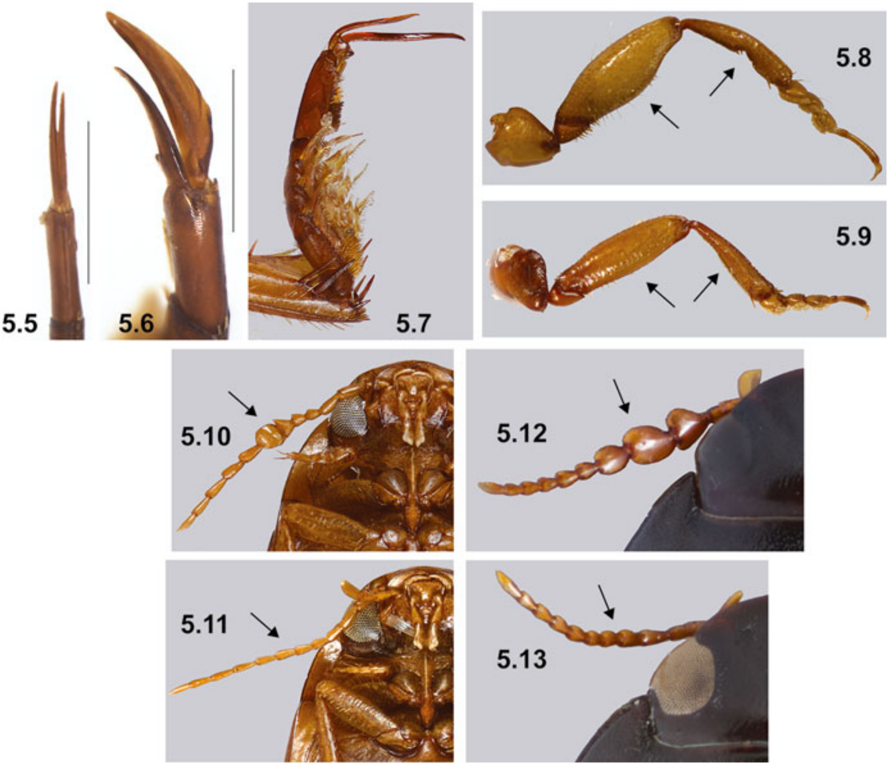
5.2.1.3 Morphology

In addition to stridulatory devices, morphological dimorphisms are common and often obvious in dytiscids, but are certainly better known than chemical or behavioral dimorphisms. For example, sexual size dimorphism is common in predaceous diving beetles. Size may be biased either toward females or males (Zimmerman 1970; Aiken and Wilkinson 1985; Ribera 1994; Schulte-Hostedde and Alarie 2006; Fairn et al. 2007). Selection pressure for or against large relative size in males or females is complex, and in predaceous diving beetles poorly known, as is general knowledge of the degree of size dimorphism in groups across the family (Fairn et al. 2007). Also, body shape can differ between the sexes like in a *Suphrodytes* species in which females are relatively shorter and broader than males, independent of isometric size differences (Bergsten et al. 2012).

Male diving beetles of many species throughout several subfamilies are characterized by secondary morphological features that are often species specific. One common manifestation of this is protarsal or (less commonly) mesotarsal claws that may be asymmetrically more or less strongly curved, hooked, toothed, unequal in length, or otherwise modified (Figs. 5.5–5.7). These features are commonly used as species diagnostic character states in many groups of diving beetles (e.g., see Nilsson and Holmen 1995; Larson et al. 2000). Within the context of mating systems, presumably these function in these beetles as species-specific grasping devices during mating encounters, but their behavioral correlates remain largely undocumented. Other apparent grasping devices may include conspicuous modifications to protibial shape such as in *Necterosoma* (Figs. 5.8 and 5.9, Watts 1978) or some *Coelambus* (Leech 1966) and the antennae found in several groups including *Agaporomorphus* (Figs. 5.10 and 5.11, Miller 2001b), *Lioporeus* (Wolfe and Matta 1981), *Allopachria* (Wewalka 2000), *Laccornis* (Wolfe and Roughley 1990), *Queda* (Figs. 5.12 and 5.13, Biström 1990), and others. Some of these may represent expansions of the male antennae for increased chemoreception, though some seem more evidently useful as grasping devices.

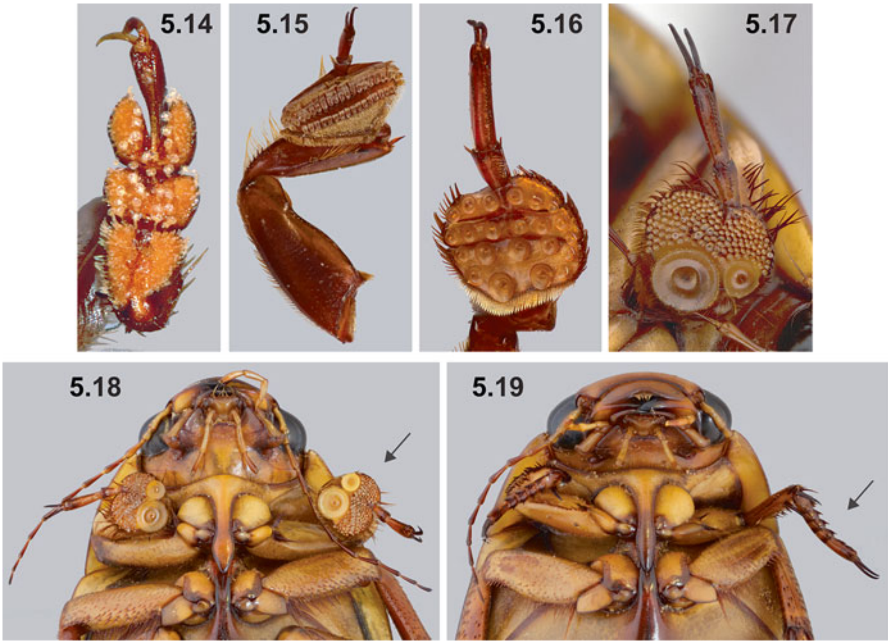
One of the most common male sexual dimorphisms across diving beetles is greater lateral expansion of the pro- and/or mesotarsomeres (generally tarsomeres I-III), often with adhesive setae or a greater density, number, or size of adhesive setae ventrally than in females (Figs. 5.14–5.19). These adhesive setae come in a variety of forms, and their presence and variation is not particularly unusual for male beetles in general (Stork 1980). These structures are seemingly used for increased adhesion to the female during mating activities, though this is not known for certain for most species. An exception is the sucker-shaped adhesive setae on pro- and (sometimes) mesotarsomeres I-III in Dytiscinae (Figs. 5.16–5.19). These setae have been interpreted as an improved grasping device for adherence to female surfaces prior to and during the mating event within a sexual conflict context (see below, Bergsten et al. 2001; Miller 2003; Bergsten 2005; Bergsten and Miller 2007).

There are many other examples of secondary sexual characters exhibited by dytiscid males. Some males of *Queda* have dramatically modified metatibiae (Fig. 5.20, Biström 1990). Male members of *Graptodytes* (Balfour-Browne 1934; Fery 1995;

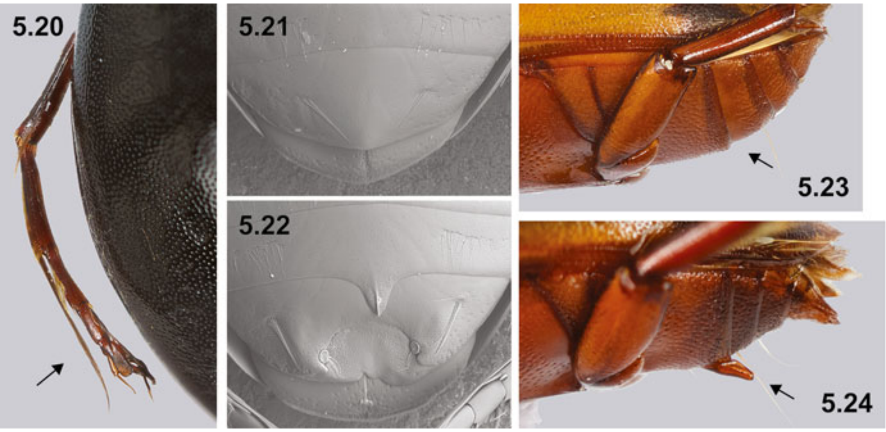


Figs. 5.5–5.13 Dytiscid sexually dimorphic features. 5.5 and 5.6, *Agabus bipustulatus* (Linnaeus), protarsal claws; 5.5, female; 5.6, male. 5.7, *Rhantus notatus* (Fabricius), male protarsus. 5.8 and 5.9, *Necterosoma penicillatum* (Clark), left proleg, anterior aspect; 5.8, male; 5.9, female. 5.10 and 5.11, *Agaporomorphus knischi* Zimmermann, right side of head, ventral aspect; 5.10, male; 5.11, female. 5.12 and 5.13, *Queda youngi* Biström, left side of head, dorsal aspect; 5.12, male; 5.13, female

Ribera and Faille 2010), *Hygrotus* (Anderson 1971), and many Laccophilinae (Zimmerman 1970; Brancucci 1983) have the last visible abdominal sternite variously modified in a species-specific way. Male *Africophilus* have the last two abdominal sternites modified (Figs. 5.21 and 5.22, Omer-Cooper 1969). Some *Hyphydrus* have males with a large abdominal spine (Figs. 5.23 and 5.24), a modified metatibial spur, or modified protrochanter (Biström 1982). Some *Desmopachria* have males with the prosternal process apically forked with a deep pit between the two branches (Young 1995; Miller 2001a). Some *Hygrotus* have the profemur unusually modified (Leech 1966). Members of *Bidessonotus* have the ventral surface more strongly concave than that of females or most other predaceous diving beetles (Balfour-Browne 1947; Young 1990). Just from these examples, one can appreciate the great number of male-specific modifications affecting many structures across Dytiscidae.



Figs. 5.14–5.19 Dytiscid sexually dimorphic features. 5.14, *Coelambus impressopunctatus* (Schaeller), male left protarsus, ventral aspect. 5.15, *Cybister fimbriolatus* (Say), male left proleg, ventral aspect. 5.16, *Hydaticus flavolineatus* Boheman, male left protarsus, ventral aspect. 5.17, *Dytiscus marginalis* Linnaeus, male left protarsus, ventral aspect 5.18 and 5.19, *Dytiscus marginalis*, ventral surface; 5.18, male; 5.19, female



Figs. 5.20–5.24 Dytiscid sexually dimorphic features. 5.20, *Quedea youngi* Biström, male left leg, dorsal aspect. 5.21 and 5.22, *Africophilus nesiotes* Guignot, apical abdominal sternites, ventral aspect; 5.21, female; 5.22, male. 5.23 and 5.24, *Hyphydrus lyratus* Swartz, abdominal sternites, left lateral aspect; 5.23, female; 5.24, male

Figs. 5.25–5.30 Dytiscid sexually dimorphic dorsal surfaces. 5.25–5.27, *Dytiscus dauricus* Gebler, habitus; 5.25, male; 5.26 and 5.27, female. 5.28–5.30, Hyderodes shuckardi Hope, habitus; 5.28, male; 5.29 and 5.30, female

Female-specific modifications are not as common, but there are several conspicuous examples. Many predaceous diving beetle females have the surface of the cuticle, particularly the pronotum and all or portions of the elytron, more heavily microsculptured than in males. In many taxa this is intrasexually dimorphic with some females more extensively microsculptured than others (e.g., Miller 1998; Bilton et al. 2008; Drotz et al. 2010). The most dramatic examples of this are in Cybistrinae and Dytiscinae (Figs. 5.25–5.42, Miller 2003). Many cybistrine females have the elytron with conspicuous striations or "scratches" or reticulate patterns (Brinck 1945; Miller 2003; Miller et al. 2007). Within Dytiscinae, many species of *Dytiscus* have females with deep, elongate grooves or striae in the elytra and densely punctate pronota (Figs. 5.25–5.27, Roughley 1990; Bergsten et al. 2001; Miller 2003; Härdling and Bergsten 2006). The two species of *Hyderodes* have some females with

Figs. 5.31–5.36 Dytiscid sexually dimorphic dorsal surfaces. 5.31–5.33, *Hydaticus continentalis* Balfour-Browne, habitus; 5.31, male; 5.32 and 5.33, female. 5.34–5.36, *Thermonectus nobilis* Zimmermann, habitus; 5.34, male; 5.35 and 5.36, female

densely granulose pronota and elytra (Figs. 5.28–5.30, Watts 1978; Miller 2003). In *Hyderodes* and *Dytiscus*, many populations have females variable with some individuals modified and others smooth and similar to males (Watts 1978; Roughley 1990; Bergsten et al. 2001; Miller 2003; Härdling and Bergsten 2006). Many females of Hydaticini have deep, irregular grooves laterally on the pronotum and elytron with relatively continuous variation across species from nearly unmodified females to more strongly modified females (Figs. 5.31–5.33, Roughley and Pengelly 1981; Miller 2003). Females of *Eretes* have an elongate sulcus laterally on the elytron (Miller 2002a). Within Aciliini, *Thermonectus* females have conspicuous scratches on the pronotum and elytron (Figs. 5.34–5.36), some females of *Graphoderus zonatus* have dense granulations (Figs. 5.37–5.39) and irregular sculpturing on the

Figs. 5.37–5.42 Dytiscid sexually dimorphic dorsal surfaces. 5.37–5.39, *Graphoderus zonatus* (Hoppe), habitus; 5.37, male; 5.38 and 5.39, female. 5.40–5.42, *Acilius sulcatus* (Linnaeus), habitus; 5.40, male; 5.41 and 5.42, female

pronotum and elytron (Bergsten et al. 2001; Härdling and Bergsten 2006), and females of many *Acilius* have broad, deep grooves on the elytron and hairs on the pronotum and in the elytral grooves (Figs. 5.40–5.42, Bergsten and Miller 2005; Bergsten and Miller 2007). Dytiscinae female cuticular modifications have been interpreted within a sexual antagonism scenario (see below for details, Bergsten et al. 2001; Miller 2003; Bergsten and Miller 2007).

Females of a few dytiscid groups have the elytron with a subapical denticle, including some *Bidessonotus*, *Oreodytes* (Figs. 5.43 and 5.44), *Neobidessodes*, and *Hembidessus* (Balfour-Browne 1947; Young 1990; Nilsson and Holmen 1995; Miller 2001d). The function of this structure is unknown, though it may provide a place for males to grasp using the metatarsal claws. It is present in both males and females of some species in groups like *Nebrioporus* (Toledo 2009) and *Neobidessodes* (Hendrich et al. 2009).

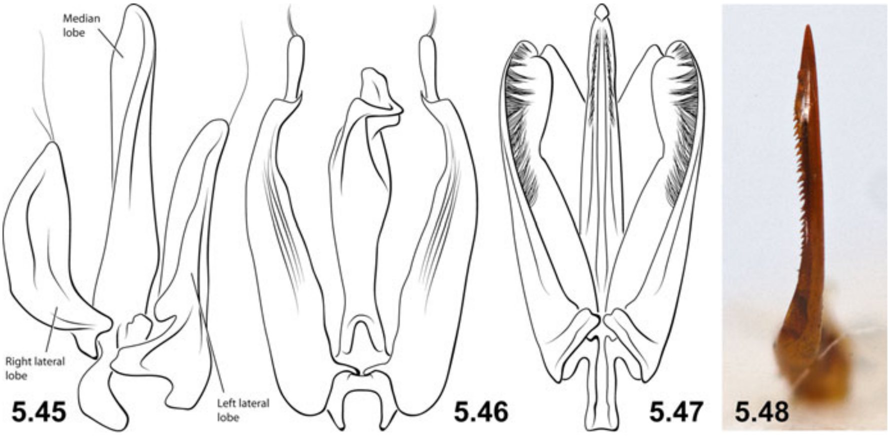
Figs. 5.43 and 5.44 *Oreodytes alpinus* (Paykull), habitus; 5.43, male; 5.44, female

Behavioral dimorphisms (in addition to sound production) are much more poorly known because behavioral observations of predaceous diving beetles are extremely sporadic. It seems clear that there are few or no courtship behaviors in diving beetles (e.g., see video supplement to Bergsten and Miller 2007), though some groups do have conspicuous precopulatory or copulatory behaviors that are often species-specific (Aiken 1992; Miller 2003; Cleavall 2009). Many of the morphological dimorphisms discussed above are likely correlated with behaviors, though most of these are not well known.

5.2.2 Genitalia

5.2.2.1 Male Genitalia

Male animal genitalia are thought to be under considerable female choice selection pressure and, in many animals, exhibit rapid, divergent evolution (Eberhard 1985). Male external genitalia are often highly characteristic of species of Dytiscidae, and are frequently either the only or the main character system used in species diagnostics. The morphology of this system was discussed by Sharp and Muir (1912) and within a taxonomic context by many other authors (detailed in Chap. 4 in this book). The major structures associated with the male external genitalia (aedeagus) are an elongate median lobe that has a variably expanded area at its base where a pair of elongate lateral lobes (parameres) articulate (Figs. 5.45–5.47). The median lobe has a ventral groove with a weakly developed membranous structure (possibly the remnants of the endophallus) that bears the gonopore through which passes the spermatophore. Other structures appear to be used primarily to facilitate extrusion of the aedeagus. For example, there is a variously sclerotized ring around this tri-lobed structure that may represent components of abdominal sternite VIII and



Figs. 5.45–5.48 Dytiscidae, male genitalia. 5.45, *Laccophilus maculosus* Say, dorsal aspect. 5.46, *Copelatus* sp., dorsal aspect. 5.47, *Dytiscus thianschanicus* (Gschwendtner), dorsal aspect. 5.48, *Copelatus* sp., ventral aspect

tergite IX, but precise homology of these with other insect abdominal sclerites is difficult. There is also a ventral "strut" comprised typically of an elongate sclerotized structure ventrad to the genital capsule. Finally, abdominal sternite VII is typically longitudinally divided medially into two lateral plates connected anteriorly by a sclerotized ring. There is no large, membranous endophallus or "internal sac". There is exceptional variation in male genitalic shape across diving beetles, and often structures can be somewhat challenging to homologize across many taxa. At least some species exhibit dramatic spines or saw-like structures that may have an antagonistic evolutionary component (see 5.3.1 below).

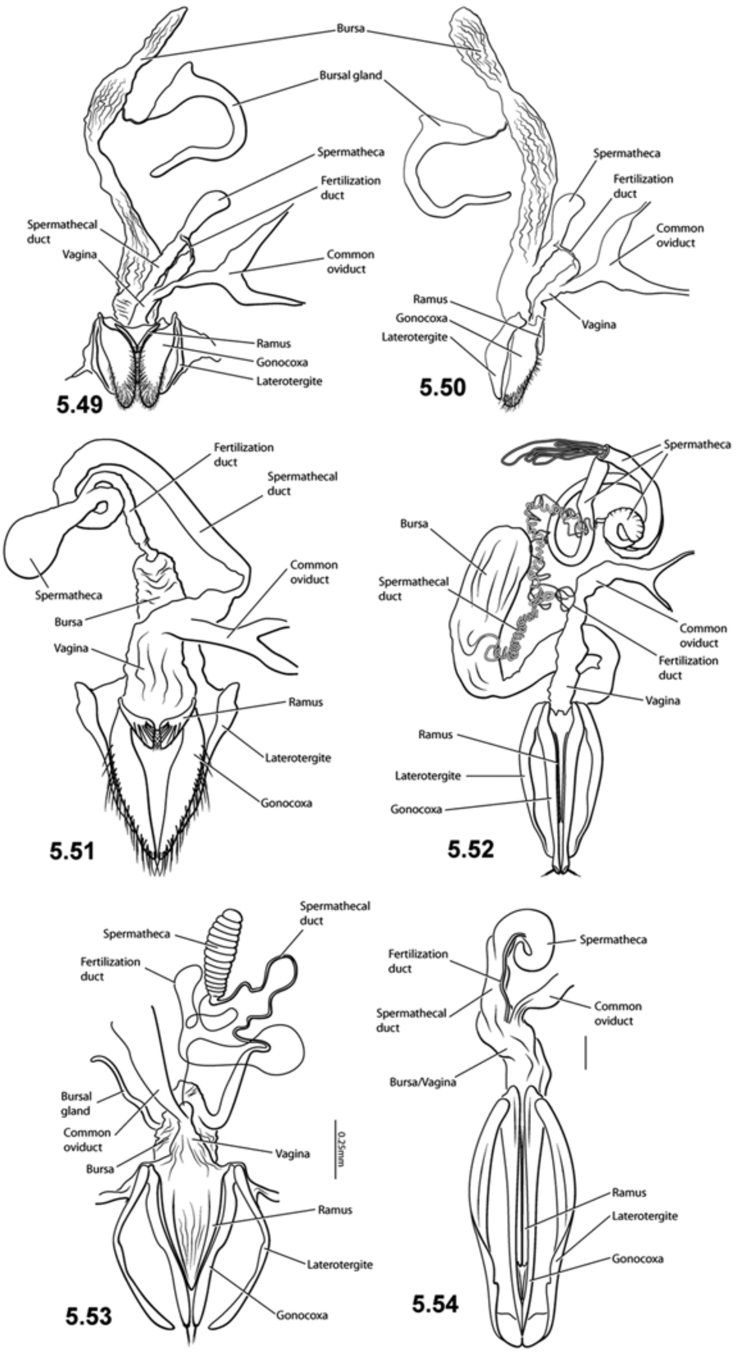
A major theme in the morphology of the external male genitalia is "retournement" or rotation of the genitalia at repose (Sharp and Muir 1912; Jeannel and Paulian 1944; Jeannel 1955). Usually, the diving beetle aedeagus (i.e., median lobe and lateral lobes, or parameres) are rotated 90° in repose and subsequently rotated another 90° during copulation (Blunck 1912a; Sharp and Muir 1912; Miller and Nilsson 2003). This configuration may have resulted from conservation of aedeagal position during mating as the "male on top" mating position evolved from an "end to end" position (Jeannel 1955). Additional widespread morphological variation includes degree of symmetry of the median lobe and lateral lobes (Figs. 5.46 and 5.47). The lateral lobes are bilaterally asymmetrical, as is the median lobe, in members of Laccophilini (Laccophilinae, Fig. 5.45) and in a few, isolated groups of Hydroporinae (e.g., some *Bidessonotus* and *Neobidessus* within Bidessini (Young 1977; Young 1981; Young 1990)). The median lobe is moderately to strongly asymmetrical with symmetrical median lobes in many dytiscids (Fig. 5.46) except the subfamilies Cybistrinae, Dytiscinae, and Hydroporinae, which have distinctly symmetrical genitalia (Fig. 5.47), at least plesiomorphically, with a few other taxa, such as some *Ilybius*, having nearly symmetrical male median lobes. Within Hydroporinae, there are certain groups that have secondarily asymmetrical median lobes including *Graptodytes* (Siettitiini) and several Bidessini genera.

The internal male genitalia has not been carefully investigated in dytiscids, but known species have paired, elongate, tubular testes and associated glands (Blunck 1912a; Jamieson et al. 1999). It is not known whether male morphology varies significantly with variation in sperm morphology (see below).

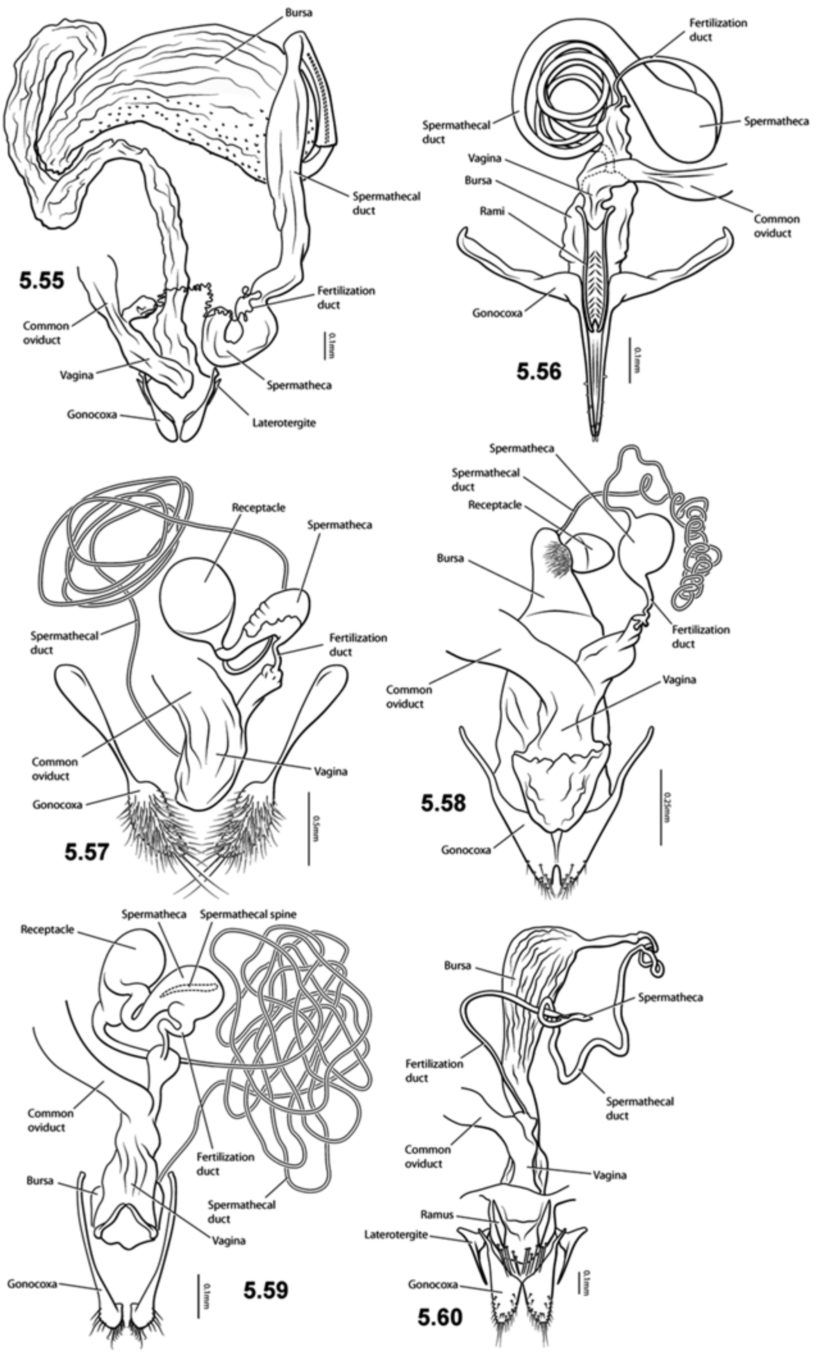
5.2.2.2 Female Genitalia

Female genitalia are not expected to be as strongly divergent as male genitalia because they are not under the same types of mate choice selection pressure (Eberhard 1985). Dytiscid female genitalic morphology (external and internal) has been reviewed especially by Deuve (1988, 1993), Burmeister (1976, 1980, 1990b), and Miller (2001c) with less comprehensive work by others (e.g., Böving 1912; Galewski 1974; Angus 1985; de Marzo 1997). Female external genitalia are developed primarily for various activities associated with oviposition. Several groups have specific modifications for endophytic oviposition such as medial fusion of the gonocoxae into a strengthened, knife-like structure, or development of denticles on the rami or gonocoxae. Modifications like these are present in *Hydrovatus* (Hydrovatini), *Ilybius* (Agabini), Laccophilinae, Cybistrinae, and many Dytiscinae (Blunck 1912b; Jackson 1960; Miller 2001c; Inoda 2011). Others have a great many different shapes and configurations, but little is known about most egg laying and how the external genitalia function to do so.

Female internal genitalia in predaceous diving beetles (Figs. 5.49–5.60) is particularly unusual among arthropods in one important aspect, the organization of the reproductive tract (RT) into a "loop" with two genital openings (e.g., Fig. 5.50, Heberdey 1931; Jackson 1960; Burmeister 1976; Miller 2001c). One opening is to the bursa copulatrix ("bursa") and is for sperm (or spermatophore) reception. The bursa may or may not have an associated gland (or glands and gland reservoir), though the function of the gland is unknown. From the bursa, a variously modified spermathecal duct leads to the spermatheca. From the spermatheca, a fertilization duct leads to the vagina near the base of the common oviduct, and the vagina leads out the apex of the abdomen for oviposition of eggs. Effectively, this decouples the evolution of sperm reception from fertilization and oviposition, thereby releasing constraints on the morphology of the RT that happen when these structures must perform multiple functions. The result of this is dramatic variation in RT morphology across the Dytiscidae, with particular diversity within the Hydroporinae (Figs. 5.55–5.60), which are characterized by extra chambers, exceptionally long ducts, setae, large spines, sculpturing, and other dramatic modifications. In contrast, members of Dytiscinae have the female genitalia reduced, and have, secondarily, a single genital opening (Fig. 5.54). These marked differences between Hydroporinae and Dytiscinae may be associated with the evolution of two dramatically different mating systems (see below). Members of Amphizoidae and Paelobiidae also have two genital openings, homologous with the condition in Dytiscidae (Burmeister 1976; Burmeister 1990a; Miller 2001c). An analogous condition exists in ditrysian Lepidoptera (Scoble 1995).



Figs. 5.49–5.54 Dytiscidae female reproductive tract, ventral aspect except 5.50 right lateral aspect. 5.49 and 5.50, *Rhantus atricolor* (Aubé). 5.51, *Lancetes lanceolatus* (Clark). 5.52, *Exocelina australis* (Clark). 5.53, *Hydrotrupes palpalis* Sharp. 5.54, *Dytiscus verticalis* Say



Figs. 5.55–5.60 Dytiscidae female reproductive tract, ventral aspect. 5.55, *Pachydrus* sp. 5.56, *Hydrovatus* sp. 5.57, *Megaporus howitti* (Clark). 5.58, *Porhydrus nigroadumbratus* (Clark). 5.59, *Hemibidessus celinoides* (Zimmermann). 5.60, *Laccornis oblongus* (Stephens)

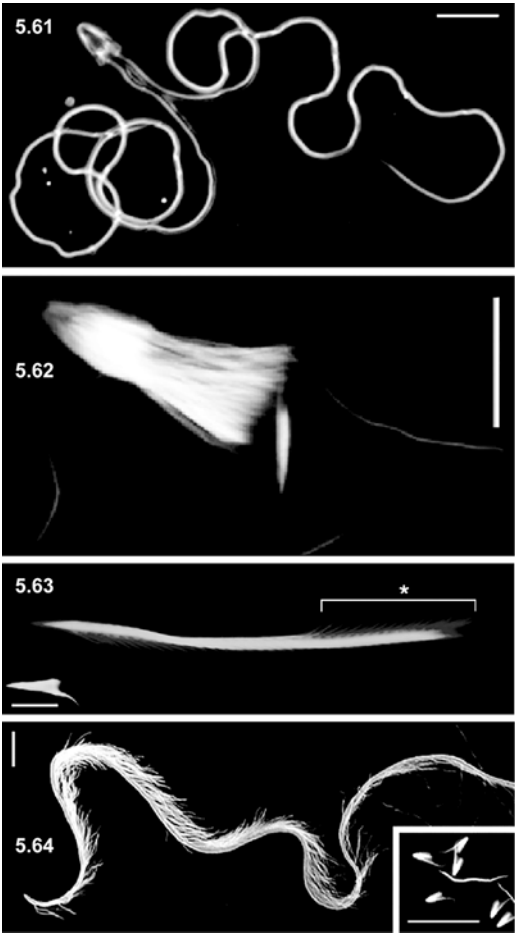
Miller (2001c) described four basic configurations of internal genitalic morphologies in Dytiscidae. The first is the "Amphizoid-type" with two genital openings, and with the spermathecal duct extending from the posterior base of the bursa (Figs. 5.49 and 5.50). This type characterizes Amphizoidae, Paelobiidae, Matinae, and many Colymbetinae and Agabinae. The second is the "Hydroporine-type" with the spermathecal duct attached at the anterior apex of the bursa (Figs. 5.52 and 5.53, 5.55–5.60). This configuration characterizes Hydroporinae, Lancetinae, Copelatinae, Coptotominae, Laccophilinae, and some Colymbetinae and Agabinae. The third type, the "Dytiscine-type," has a single genital opening with both the fertilization duct and spermathecal duct extending from the vagina/bursa to the spermatheca (Fig. 5.54). This condition is secondarily derived in Cybistrinae and Dytiscinae (Miller 2001c) and represents a reversal to the type of genitalia present in, for example, Noteridae and Gyrinidae. In Cybistrinae and Dytiscinae, the spermatophore is transferred to a separate area ventrad of the main female genitalia (Aiken 1992). The final type is the "*Agaporomorphus*-type" wherein the bursa appears to be completely reduced, which occurs only in the copelatine genus *Agaporomorphus*.

Miller (2001c) investigated the evolution of female genitalia in a phylogenetic context. He found that two genitalic openings is plesiomorphic for Dytiscidae (the condition is present also in Palaeobiidae and Amphizoidae) and secondarily reduced to a single opening in Dytiscinae. He also found that adaptations for apparent endophytic oviposition was derived multiple times within Dytiscidae, in Laccophilinae, *Ilybius* (Agabinae), Dytiscinae, and *Hydrovatus* (Hydroporinae). Other larger transitions in dytiscids include loss of the laterotergite in Hydroporinae (except Laccornini) and loss of the bursal gland in numerous lineages, among much other more taxon-specific variation (Miller 2001c).

5.2.3 *Sperm*

The dramatic variation in female RT morphology in dytiscids suggests that sperm morphology could vary just as dramatically as sperm and RT coevolve. Sperm fitness is heavily influenced both by interactions with the female RT (cryptic female choice) and other male sperm within the RT (sperm competition) (Parker 1970). Sperm fitness may also be influenced by cooperative effects between sperm from the same ejaculate (Higginson and Pitnick 2011). All of these affects appear to be operating on predaceous diving beetle sperm.

Although certain aspects of diving beetle sperm have been known for many years (Auerbach 1893; Ballowitz 1905), this is a relatively poorly studied area of dytiscid sexual biology. Much of the state of knowledge was reviewed by Jamieson et al. (1999). Sperm and sperm selection are clearly major components of dytiscid sexual evolution because in some cases sperm can account for up to 13 % of the total male body mass (e.g., *Dytiscus sharpi*, Inoda et al. 2007). Recent studies have begun to shed light on the dramatic and considerable diversity in dytiscid sperm morphology and have attempted to correlate that diversity with female reproductive tract variation within a phylogenetic context (Higginson et al. 2012b; Higginson et al. 2012a).



Figs. 5.61–5.64 Dytiscid sperm. 5.61, simple conjugate of two sperm, *Graphoderus liberus* (Say). 5.62, aggregation of multiple sperm, *Ilybius oblitus* Sharp. 5.63, Rouleaux conjugate, *Neoporus undulatus* (Say). 5.64, Rouleaux conjugate, *Hygrotus sayi* Balfour-Browne (Pictures from Higginson et al. 2012b)

Within the wealth of variation in diving beetle sperm, certain patterns can be discerned. Some diving beetles have singleton sperm of a single type, like many animals, and there is much variation in dytiscid sperm length and head shape (Higginson et al. 2012b; Higginson et al. 2012a). However, dytiscid sperm is of particular interest because of two notable syndromes: (1) conjugation and (2) heteromorphism, with co-occurrence of each in certain species.

Conjugation refers to a phenotype where two or more sperm that unite at the head to form a cooperative unit (Higginson and Pitnick 2011). In some diving beetles, a simple form of conjugation occurs wherein two sperm heads unite to form a pair (Fig. 5.61). This is found in Cybistrinae, Dytiscinae, and the colymbetine genus *Melanodytes* (Ballowitz 1905; Mackie and Walker 1974; Werner 1976; Jamieson et al. 1999; Higginson and Pitnick 2011; Higginson et al. 2012a). A second type of conjugation is aggregation of multiple sperm heads together (Fig. 5.62). This is found in many Agabinae, Colymbetinae, *Batrachomatus* (Matinae), some *Pachydrus* (Hydroporinae), *Hygrotus* (Hydroporinae), and possibly *Lioporeus* (Hydroporinae) and *Agabetes* (Laccophilinae) (Ballowitz 1905; Mackie and Walker 1974; Werner 1982; Dallai and Afzelius 1988; Higginson and Pitnick 2011; Higginson et al. 2012a). Finally, a complex type of conjugates in diving beetles are called "rouleaux" (Fawcett and Hollenberg 1963; Shepherd and Martan 1979; Heath et al. 1987) and comprise sperm conjugates with cone-shaped heads that form ordered stacks by nesting together (Figs. 5.63 and 5.64, Higginson and Pitnick 2011; Higginson et al. 2012a). This type of conjugation is found across many Hydroporinae and in *Matus* (Matinae) (Higginson et al. 2012b). Not all diving beetles exhibit conjugation. Singleton sperm are known to be characteristic of Copelatinae, Coptotominae, *Desmopachria*, some *Pachydrus* (Hydroporinae), *Porhydrus* (Hydroporinae), and some *Thermonectus* (Dytiscinae) (Higginson et al. 2012a).

Another unusual phenotype in dytiscid sperm is the presence in certain taxa of heteromorphism, or more than one sperm morphology in the same ejaculate. This occurs in *Agabetes* (Laccophilinae), Coptotominae, *Derovatellus* (Hydroporinae), *Hygrotus* (*Coelambus*) (Hydroporinae), *Ilybius* (Agabinae), *Platambus* (Agabinae) (Higginson et al. 2012a), and, possibly, *Cybister* (Cybistrinae) (Voïnov 1902). Of these, several have both conjugation and heteromorphism including *Agabetes*, *Derovatellus*, *Hygrotus*, *Ilybius* and *Platambus*. Interestingly, there appears also to be some evidence of eupyrene and apyrene spermatozoa in the same ejaculate in *Cybister tripunctatus* (Mukherjee et al. 1989).

The evolution of sperm in diving beetles was studied by Higginson et al. (2012a, b). Their studies investigated primarily head shape, sperm length, type of conjugation and heteromorphism in a phylogenetic context. They found aggregation sperm to be the plesiomorphic condition within Dytiscidae with multiple independent transitions to singleton sperm, paired sperm, and rouleaux, and some reversals. Head shape and conjugation were closely correlated, but length and heteromorphism were not. There are within Dytiscidae both long and short conjugated sperm, and heteromorphic sperm in singleton or conjugated systems.

5.3 Dytiscid Sexual Systems

Mating behavior and mating system evolution in dytiscids is just beginning to be investigated, and it is somewhat difficult to generalize, though several lines of evidence are beginning to accumulate based in part on many of the behaviors and morphology described above. A better picture of these systems in Dytiscidae is emerging and revealing a deeply complex range of evolution of syndromes.

Presumably both sexes of most predaceous diving beetle species mate multiple times. Males and females of observed species do so (Blunck 1912a; Aiken 1992; Miller 2003; Cleavall 2009). Also, females are often observed with multiple sper-

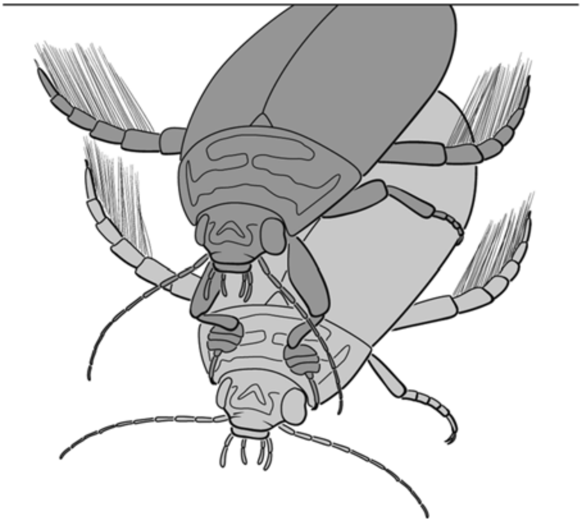


Fig. 5.65 Dytiscidae mating position, *Acilius sulcatus* (Linnaeus), male dorsal, female ventral

matophores in the RT (Miller 2001c). The sexual systems evidently operating in dytiscids based on morphology and behavior (sexually antagonistic selection, sperm selection, and competition, see below) are predicated on multiple matings. Mate finding appears to be either a scramble competition with males actively seeking females, or potentially associated with either male (acoustic) (Larson and Pritchard 1974) or female (chemical) (Herbst et al. 2011) signaling and response. Any signaling would, therefore, represent the traditionally understood combination of competition among males for better signal production or female signal sensing, and female choice on male sound production or ability to sense female signals (Thornhill and Alcock 1983). Other selection effects may be operating to influence signaling as well, such as signal interception by potential predators (Thornhill and Alcock 1983). Other than seemingly limited signal production in predaceous diving beetles, though uninvestigated, there appears to be little or no courtship mating behavioral displays. Copulatory and postcopulatory behaviors, in contrast, are considerably more complex in certain groups of predaceous diving beetles.

Mating takes place in a "male above" position (Fig. 5.65) with the male aedeagus extruded and the median lobe or both the median lobe and lateral lobes placed inside the female RT (Blunck 1912a; Aiken 1992; Cleavall 2009). There is no eversible internal sac, and the mechanism of sperm movement from the male into the female is not known. Most, if not all, predaceous diving beetle males pass a spermatophore to females during copulation. These spermatophores can often be observed within the female bursa upon female RT dissection. Little to nothing is known of spermatophore morphology, production, constituents, or metabolism within the female. Some limited descriptive work has been done with *Dytiscus marginalis* spermatophores (Blunck 1912a).

The many different grasping devices (e.g., modified antennae, claws, legs) in males, and the often dramatically complex and variable male external genitalia probably represent either species specific variation selected for during female choice of particular stimulations, morphologies, or mechanical fit (Eberhard 1985) or antagonistic selection driven by conflicting interests and reduction of associated costs rather than active choice for better genes (Arnqvist and Rowe 2005). Male predaceous diving beetles seem to routinely attempt mating with other beetles they encounter, even if they are the wrong species or the wrong sex (Cleavall 2009). Signals exchanged during these encounters probably preclude "mating errors," which may help reinforce species isolation as well.

There are no known examples of parental care of fertilized eggs or larvae in predaceous diving beetles beyond female placement of eggs, so contribution of this potential fitness component to sexual evolution in the group is not apparently significant. Given the unusual complexity of female genitalia, it is possible that females differentially invest in eggs internally, but this is completely unknown in predaceous diving beetles.

5.3.1 Pre-insemination Sexual Systems

Among the most dramatic of the sexual systems exhibited by predaceous diving beetles is an apparent sexually antagonistic coevolution scenario exhibited among members of the subfamily Dytiscinae. Sexual conflict involves evolutionary conflicts of interest between males and females that may produce characteristic coevolutionary patterns as each sex seeks greater control over the decision to mate (Parker 2006). Although females, in particular, may derive benefits from mating multiple times (Eberhard and Cordero 1995; Yasui 1998; Arnqvist and Nilsson 2000), there are potentially large costs associated with mating as well (Daly 1978; Wing 1988; Martens and Rehfeldt 1989; Le Boeuf and Mesnick 1991; Magnehagen 1991; Fairbairn 1993; Rowe 1994; Watson and Lighton 1994; Watson et al. 1998). Certain male phenotypes may increase costs to females to the point of intense trauma or even death (e.g., Morrow and Arnqvist 2003; Reinhardt et al. 2003; Rönn et al. 2007). Unlike traditional ideas about sexual selection, wherein choice of a sexual partner increases both male and female average fitness, sexual conflict predicts that males and females may diverge with development of a strategy that increases fitness in one sex (e.g., manipulative strategies in males) that simultaneously decreases fitness in the other sex (e.g., females) (Pizzari and Snook 2003). The effect of reduced overall lifetime fitness in females can cause them to evolve resistance behaviors and morphologies. Males are then expected to respond by evolving features that are able to overcome the female resistance (e.g., grasping devices), and this adaptation-counteradaptation is expected to develop further into an escalating "arms-race" as each sex seeks to manipulate control of the decision to mate (Parker 1979; Alexander et al. 1997; Pizzari and Snook 2003; Arnqvist and Rowe 2005; Härdling and Smith 2005; Parker 2006). It is this type of mating system that appears to be operating in members of Colymbetinae, Dytiscinae, and Cybistrinae, at least, among dytiscids (Bergsten et al. 2001; Miller 2003; Bergsten and Miller 2005; Bergsten and Miller 2007).

Although mating behavior is known for only a few taxa, males of *Dytiscus*, *Thermonectus, Acilius*, and *Rhantus* (Smith 1973; Aiken 1992; Miller 2003; Cleavall 2009) have males that abruptly grasp females in an attempt to mate, whereupon females engage in erratic and swift swimming that sometimes successfully dislodges the male (Aiken 1992; Bergsten and Miller 2007; Cleavall 2009). Aggressive behavior by itself is not sufficient evidence for sexual antagonism over against mutualistic sexual selection since the behavior may simply be seductive or stimulative to females or may represent female assessment without incurring a cost to them (Pizzari and Snook 2003; Parker 2006). However, mate guarding is extremely long in these species, with some mating events lasting hours (Aiken 1992; Miller 2003; Cleavall 2009) as males possibly attempt to ensure paternity through sperm selection or competition. This prolonged mating event duration may explain some of the direct costs inherent to females. Mating pairs may be more susceptible to predation, for example, a situation that occurs in other insects (Magnehagen 1991; Rowe 1994).

A means by which males can control females is critical to any sexual antagonism system. The ability by males to threaten suffocation may represent a strong coercive force ultimately giving males a strong advantage over females. Although predaceous diving beetles are aquatic, they breathe atmospheric oxygen that they carry with them under their elytra and they have to frequently return to the surface to replenish the oxygen. During mating, males are above females and are able to hold females under water thereby restricting their ability to breathe (Fig. 5.65). In some cases, after intromission, males have been observed tilting females upward so they can access air during the mate guarding phase (Aiken 1992; Cleavall 2009).

Whatever the possible costs to females and coercive abilities of males, compelling evidence that a sexually antagonistic arms race is operating in Dytiscinae also comes from morphology. Males in this subfamily have the protarsi extremely broad with large, sucker-shaped adhesive setae (Figs. 5.16–5.18, see above). Some groups have sucker setae on the mesotarsomeres, as well. These are used to adhere to the smooth dorsal surface of the female prior to and during mating (Aiken 1992; Bergsten et al. 2001; Miller 2003; Bergsten 2005; Bergsten and Miller 2007; Cleavall 2009). These setae are quite strong, with some able to lift 4× the weight of a female (Aiken and Khan 1992), and are presumably an improved grasping device in evolutionary response to the female behavioral resistance (Bergsten et al. 2001; Miller 2003), though it cannot be discounted, based on current evidence, that the expanded protarsi represent a handicap of some kind used by females to determine mate quality.

As further evidence of sexual antagonism, however, females in several groups within Dytiscinae also have unusual morphology with the dorsal surface of the pronotum and elytra irregularly modified with dramatic modifications to the cuticle (Figs. 5.25–5.42, see above). These modifications interfere with the adhesive ability of the male sucker setae (Bergsten and Miller 2007), and they appear to be an evolutionary response to the male improved grasping device (sucker-setae) (Miller 2003). Recently, Karlsson Green et al. (2013) measured mechanically the adhesion force of male suction cups on male versus modified female elytra in two species. The adhesion (pull-off force measured in Newtons) of male protarsal setae was two to five times weaker on the modified female elytra compared to the smooth male elytra, confirming the antagonistic effect of the modification. Female morphological "anti-grasping" devices are rare in animals, which has been thought to do considerable violence to the sexual antagonism argument (Eberhard 1985, 2004, 2005, 2006; Arnqvist and Rowe 2002, but see Rönn et al. 2007). Predaceous diving beetles may, therefore, be relatively unique among animals in exhibiting just such devices.

Thus, it would appear that dytiscines are operating under an escalating sexual antagonism scenario precipitated by (1) male mate guarding, prolonged mating event duration, and coercive male behaviors (such as holding females underwater) that may result in increased costs of matings (and reduced direct fitness) in females, leading to (2) female resistance to male mating attempts, leading to (3) male development of an improved grasping device in the form of circular sucker-shaped setae, and, finally, development of (4) multiple origins of modifications to female dorsal cuticle in response to the male grasping device (Miller 2003). It should be stressed, though, that specific tests of direct and indirect fitness in females of dytiscines, and, therefore, sexual antagonism, have not been done. The behavioral and morphological evidence, while compelling, has not been definitively correlated with differential fitness between males and females, though tests of this may be particularly rewarding in this taxon.

There are several more detailed components to this scenario in predaceous diving beetles that have been investigated. For example, in certain groups, such as *Acilius*, it has been shown that sexual antagonism is driving speciation and the coevolution of changes in male and female secondary sexual characters including curved setae along the margin of the male protarsi, setal tufts on male mesotarsi, setae on the dorsal surface of the female pronotum and elytron, and the presence of longitudinal grooves on the female elytron (Fig. 5.66, Bergsten and Miller 2007). Also, populations of certain species in *Dytiscus*, *Hyderodes*, and *Graphoderus* have female intrasexual dimorphism with some individuals modified and others smooth, like males (Bergsten et al. 2001; Miller 2003; Härdling and Bergsten 2006). In *Dytiscus sharpi*, this is controlled genetically with the modified condition dominant (Inoda et al. 2012). The presence of two distinct morphs in a population raises questions about what balancing selection or dynamic enables them to coexist. Theoretical work has indicated that such polymorphism can be maintained through sexual conflict and non-random mating (Härdling and Bergsten 2006; Härdling and Karlsson 2009). Non-random mating leads to genetic correlation between male and female morphs. With negative frequency dependent selection the common female morph has a disadvantage, and as the frequency declines the genetic correlation also drags along the associated male morph. Hence, both direct selection on the female morph and indirect selection on the male morph leads to an increase in the more rare morphs until the frequencies and selection forces are reversed. Eventually such a system can maintain equilibrium with polymorphism in both sexes (Härdling and Bergsten 2006). Whereas dimorphism in dytiscids has mostly been documented in females, Bilton et al. (2008) showed that the two female morphs of *Hydroporus memnonius* also have two distinct associated male morphs differing in tarsal characteristics. However, the degree to which mating is non-random in polymorphic populations remains to be studied in

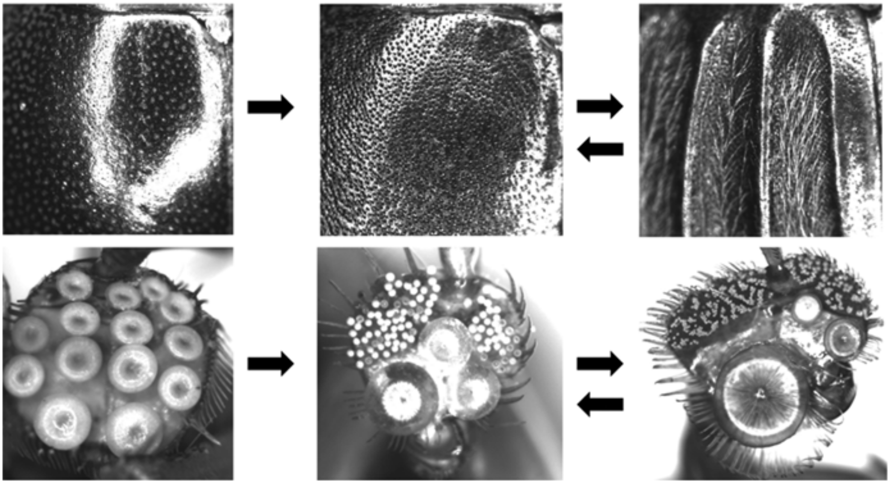


Fig. 5.66 Major coevolutionary transitions in intersexual arms race across phylogeny of *Acilius* species. *Top*: close-up of female elytra showing transition to dense punctures, to setaceous sulci and back to dense punctures; *bottom*: male protarsi with adhesive setae showing change in size disparity of sucker setae, to extreme size disparity, and back to a simple size disparity. Picture from Bergsten and Miller (2007)

dytiscids. Also, in some species the frequency of different morphs show geographic patterns, which also remain to be fully understood, and it cannot be excluded that environmental factors or genetic drift are involved as well (Karlsson Green et al. 2014).

Male adhesive setal disks have dramatically disparate size in *Dytiscus*, *Eretes*, *Acilius* and certain other species, such as *Graphoderus zonatus* (Figs. 5.17 and 5.66). These taxa have male protarsi with one or more very large setal disks, and a great many very small ones (Roughley 1990; Bergsten et al. 2001; Bergsten and Miller 2005). Other groups, such as Hydaticini, have these disks more uniform in size within and between species (Fig. 5.16, Bergsten et al. 2001). Variability in size may be correlated with female modifications, as greater variability in setal disk size may increase ability to adhere to irregular surfaces, whereas a smooth surface may instead have an associated optimal size. Indirect evidence of this was presented for *Graphoderus zonatus* in which populations with a high proportion of modified females have males with more divergent setal size, and in populations with a low proportion of modified females (more smooth females) males have more similar-sized setae (Bergsten et al. 2001). A close phylogenetic correlation between interspecific variability in male adhesive setal size and modification to females was found in *Acilius* (Fig. 5.66, Bergsten and Miller 2007).

Interestingly, once the male has “subdued” the female, many species have species-specific stereotypical male copulatory behaviors, as well. These include rocking or bobbing by the male in *Dytiscus* and *Thermonectus* (Aiken 1992; Cleavall 2009), and "fluttering" or rubbing of the legs during attempted intromission by *Thermonectus* and *Acilius* (Miller 2003; Cleavall 2009). So it would seem that even though females resist mating and males seek to force them to mate, once mating ensues, males still must "entice" a female through copulatory behaviors. In flour beetles it has been shown that the intensity of male rubbing of the female with his legs during copulation is correlated with his fertilization success in multiply mated females, apparently through female choice (Edvardsson and Arnqvist 2000). It is possible that the behavior in dytiscids can have a similar function.

In at least some species of *Dytiscus*, a mating plug is produced by males comprised of an unknown substance smeared around and in the apex of the abdomen of the female (Balduf in Blunck 1912a; Sivinski 1980; Aiken 1992), presumably as a attribute of post-insemination male-male competition for paternity (Alcock 1994). This behaviour was observed during matings in the autumn, but spring matings, closer to oviposition time, did not result in a plug (Aiken 1992).

There are a great many unanswered and perplexing questions regarding predaceous diving beetles and this mating system. For example, members of Hydaticini are nested within this group, and females have distinct modifications to the cuticle of the pronotum or pronotum and elytron that would seem to inhibit the sucker setae present in males (Roughley and Pengelly 1981; Miller 2003). It seems reasonable, therefore, to expect this group also exhibits sexual antagonism with females resisting male mating attempts, though mating behavior has never been documented in hydaticines. Unexpectedly, however, males have an apparent stridulatory device on the male protibia and protarsus (Larson and Pritchard 1974; Miller 2003; Miller et al. 2009). If males are signaling to females, and females are responding, then there seems little reason for females to resist male mating attempts because by responding they have already made the decision to mate. If mating was not desired, they could simply not respond to the signal. Possibly the sucker setae and female cuticular modifications interact in the decision to end the mating encounter, or perhaps this group displays alternative mating systems depending on circumstances, or possibly the male sound production is associated with copulatory stimulation. Male sound production may also serve to attract predators to induce females to copulate more quickly (a form of male coercion) as occurs in some water striders (Han and Jablonski 2010).

It seems also possible that the considerable disparity in size between members of Cybistrinae and Dytiscinae and other predaceous diving beetles (some dytiscines and cybistrines reach up to 50 mm in length) may reflect this sexual system. As males get larger in order to better "subdue" a reluctant female, females may respond with larger size to better resist their mating attempts. Not all members of this group are unusually large, and variation in size in related taxa within the group may be related to the intensity of evolutionary operation of this system. Considerable variation in size within some groups (e.g., *Thermonectus* species, Miller, unpublished) may also be related to intrasexual competition among males interacting with intersexual antagonism. Large size in this group may also reflect a higher demand for atmospheric oxygen allowing for the possibility of male coercion. Smaller predaceous diving beetles, in at least some cases, are able to breathe directly from the water (Madsen

2012) perhaps removing the opportunity for males to use asphyxiation as a coercive strategy and disallowing sexual antagonism as a sexual system.

Finally, another important aspect of this mating system is the observation that Dytiscinae and Cybistrinae have among the simplest configuration of female RT morphology in dytiscids. In these groups there is a secondary reduction to a single genital opening and a simple bursa, fertilization and spermathecal ducts and spermatheca (Miller 2001c). Remarkably, they also have among the simplest dytiscid sperm morphology, with simple conjugation of sperm pairs (Higginson et al. 2012a). It would seem that among Dytiscinae, and related groups, most of the complexity of sexuality is concentrated in precopulatory and copulatory (pre-insemination) mating behaviors and morphology, with considerably less complexity in the post-insemination environment of the female RT and sperm. The extent to which sperm selection and competition is happening in this group is not known, but observations of their mating behavior and morphology would suggest that they play a much smaller role in these dytiscids than do the pre-inseminatory activities. Even so, in at least some species of *Dytiscus*, sperm production can account for up to 13 % of total male body mass (Inoda et al. 2007), suggesting there may be more to post-insemination cryptic selection and sperm competition than may be currently evident.

Other predaceous diving beetle groups besides dytiscines and cybistrines may exhibit sexual antagonism as well. For example, several predaceous diving beetle males have unusually modified male intromittent organs with spines (e.g., some *Hyphydrus* Biström 1982) or slender saw-like or needlelike structures (e.g., some *Copelatus*, Fig. 5.48). In other arthropods (e.g., bruchine seed beetles (Rönn et al. 2007)) spinous median lobes are associated with severe damage to internal female genitalia and sexual antagonism. Needlelike median lobes are associated with "traumatic" or "hypodermic" insemination in other arthropods (e.g., bedbugs (Morrow and Arnqvist 2003)). Mating behavior has not been investigated in *Hyphydrus* or *Copelatus*.

5.3.2 Post-insemination Sexual Systems

In marked contrast, the subfamily Hydroporinae has, overall, the most dramatic diversity of both female RT (Miller 2001c) and sperm morphology (Higginson et al. 2012b; Higginson et al. 2012a) within Dytiscidae, and among the most complex in all insects. Hydroporines have female RTs with extra ducts, chambers, internal setae, sculpturing, extremely long and slender spermathecal and fertilization ducts, and other remarkable variation. Complex female reproductive tract morphology is expected to be associated with post-insemination female choice (Hellriegel and Ward 1998; Presgraves et al. 1999). At least some of this complexity may have to do with differential sperm storage strategies and enhanced female control over paternity (Snow and Andrade 2005).

One of the most conspicuous modifications to the female RT in many groups of Hydroporines is the presence of a large, second chamber, often as large as or larger than the spermatheca, called the “receptacle” by Miller (2001c). This structure is either on the bursa, the spermathecal duct, or the spermatheca itself (Miller 2001c). Spermathecal shape is often complex, as well (Miller 2001c), which may also represent differential sperm storage strategies. Secondary chambers and complex sperm storage structures suggest the possibility of extensive female post-insemination mate choice through sperm selection (Hellriegel and Ward 1998; Snow and Andrade 2005), but sperm storage has not been comprehensively investigated in these dytiscids.

Another characteristic of many Hydroporinae (and certain other dytiscids, such as some Agabinae, Coptotominae, and Copelatinae) is long and slender to exceptionally long and slender spermathecal and/or fertilization ducts, or other portions of the female RT (Miller 2001c). Female RT tract length is often closely correlated with sperm selection or other reproductive benefits to females (Birkhead et al. 1993; Miller and Pitnick 2002; Miller and Pitnick 2003), a possibility in predaceous diving beetles.

Finally, other hydroporine RT features include fields of setae, irregular surface structures, or possible glands in different areas of the RT (Miller 2001c). Presumably, these have something to do with sperm selection by the female, but nothing is known about possible correlates with sperm behavior or morphology. One of the most dramatic of these modifications is the large, internal spermathecal spine characteristic of Bidessini (Miller 2001c). Spermathecal spines in other arthropods are known to puncture the spermatophore (Gack and Peschke 1994), but the bidessine spermathecal spine is not apically sharp, and it is not clear what it might be used for.

Consistent with post-insemination sexual selection and sperm competition, Hydroporinae also have dramatically modified sperm with most members of the group having “rouleaux” sperm, or complex conjugations, in some cases with sperm heteromorphism, as well (Higginson et al. 2012b; Higginson et al. 2012a). Sperm complexity in the group is certainly interesting and dramatically unusual for animals, but perhaps not entirely unexpected given the phenomenally complex sperm selection environment involved, the hydroporine female RT (see above). Sperm and the female RT are expected to evolve in complex ways because sperm are coevolving with both the female reproductive tract (sperm selection) and other male sperm (sperm competition) (Parker 1970; Birkhead 1996; Presgraves et al. 1999; Miller and Pitnick 2002). Predaceous diving beetles in the Hydroporinae may be particularly suitable for the study of complex post-insemination sexual selection.

Relatively fewer hydroporines have had their mating behavior documented, but the information known suggests that the mating event is short and relatively free of behavior (Miller 2001c). Thus, it would seem that within Hydroporinae, most of the complexity of sexual evolution is post-inseminatory with the pre-insemination sexual activities much simpler and less important in the sexual evolution of the group.

5.4 Summary

Predaceous diving beetles show an extraordinary range of sex-specific internal and external morphological modifications, and recent studies are starting to shed light on their role in pre-, intra-, and postcopulatory phases of the mating system. It appears that within predaceous diving beetles there has been the evolution of two extreme mating system strategies, one (Cybistrinae and Dytiscinae) that focuses on pre-insemination and copulatory behaviors and morphology, including sexual antagonism, and a second (Hydroporinae) that focuses on post-insemination sperm selection and sperm competition (Fig. 5.67). Other subfamilies are seemingly somewhat intermediate between these extremes or have yet to be studied in detail.

5.5 Future Directions

Although a picture of the evolution of sexual systems is developing in dytiscids, knowledge is extremely fragmentary. Nearly every aspect of dytiscid sexual systems requires further investigations. Perhaps the best known components are morphologies of male and female external genitalia and female internal genitalia (e.g., Miller 2001c, 2003). Female internal RT structures are exceptionally diverse, and there is likely to be considerable new information forthcoming as investigators survey more completely the diversity across the group. However, internal male genitalia (testes and associated ducts and glands) are only poorly known. Sperm morphology is known for numerous dytiscids, and sperm evolutionary history has been investigated (Higginson et al. 2012a, b), but functional characteristics correlating with sperm morphology as well as sperm activity, location, and storage within the complex female RT is virtually unknown, but likely incredibly interesting for study of sperm cooperation, competition, and selection in animals in general. Mating behavior data is the least known among the various aspects of dytiscid sexual systems. Because of its ephemeral nature and difficulty in acquisition, knowledge of dytiscid mating behavior has lagged along with related aspects such as sexual signaling (visual, chemical, etc.). This knowledge will be critical for understanding the evolution of sexual antagonism, especially, but also for other dytiscid groups that could have complex variation in stereotypical behaviors. Finally, beyond the basic characterization of these various components of sexual systems, their evolutionary interactions, transitions, correlations, and contributions to diversification of dytiscids remains unexplored. Dytiscids have some of the greatest complexity of sexual system evolution in animals, and are likely to become a model for the study of such systems in the future.

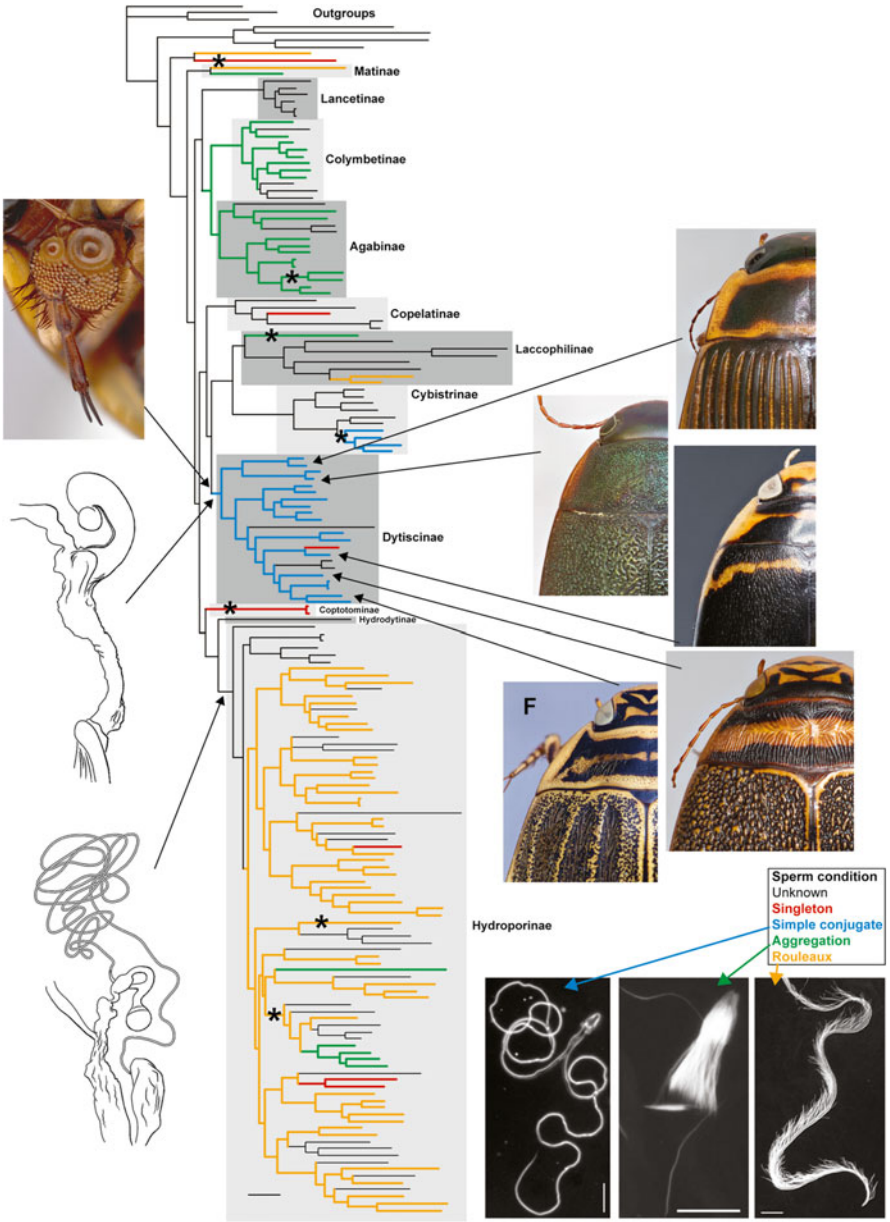


Fig. 5.67 Phylogeny of Dytiscidae from Miller and Bergsten (Chap. 3 in this book) with sexual system characters mapped. * = sperm heteromorphism

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Chapter 6
Chemical Ecology and Biochemistry of Dytiscidae

Konrad Dettner

> *Wenn man einen solchen Kefer* [Cybister lateralimarginalis] *fängt, so lässt er insgemein zwischen dem Hals-Schild eine blaulichte Materie hervor fliessen, welche einen widerwärtigen Geruch von sich giebt und vielleicht Ursache ist, dass diese Kefer alle Zeit einen eckelhaften Gestank haben. [If such a beetle* Cybister lateralimarginalis *is caught, between the pronotum a bluish fluid appears which is characterized by a disagreeable odor that is probably responsible for the nauseous stench of the whole beetle.],*
>
> Rösel von Rosenhof

> *I must tell you what happened … in my early entomological days. Under a piece of bark I found two carabi (I forget which) and caught one in each hand, when … I saw a sacred* Panagæus crux major. *I could not bear to give up either of my Carabi, and to lose* Panagæus *was out of the question, so that in despair I gently sized one of the carabi between my teeth, when to my unspeakable disgust and pain the little inconsiderate beast squirted his acid down my throat and I lost both Carabi and Panagus!,*
>
> Charles Darwin

Abstract The chapter deals with chemical mechanisms that help to control intra- and interspecific interactions with respect to predaceous diving beetles. Apart from chemical receptors and senses within Dytiscidae there are described intraspecific (pheromones) and especially interspecific interactions with respect to this water beetle family. The last group of behavioral modifying compounds includes kairomones and allomones. Allomone constituents from pygidial glands, prothoracic defensive glands, and pupal glands are completely compiled for a large group of predaceous

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diving beetles. With respect to the natural compounds, their chemistry, distribution within Hydradephaga, biological activities, and especially their significance for dytiscids are discussed. In addition, further secondary compounds from these beetles are presented, including epicuticular lipids or pigments that may be responsible for the coloration of the adult beetles and their larvae. Finally, the microorganisms and their secondary metabolites that are associated with predaceous diving beetles are presented. The described microorganisms range from culturable to non-culturable taxa.

Keywords Dytiscidae • Chemical ecology • Allomones • Glands • Secondary compounds

6.1 Chemical Ecology of Freshwater Organisms

Since 1970, after the publication of the book entitled "Chemical Ecology", edited by E. Sondheimer & J. B. Simeone, the field of chemical ecology has been recognized as a distinct interdisciplinary research area. Chemical signals are perhaps the oldest form of communication among organisms, and this discipline investigates how naturally occurring chemicals mediate ecological interactions. In most cases, chemoecological studies focus on ecological mini-systems that include few species or individuals, whereas complex biocenosis are not analyzed. Moreover, chemical ecology often starts with an observation – e.g., chemical defense of a bombardier beetle or attraction of one sex of a moth species to the other sex through sexual pheromones. Chemical ecology is concerned with the identification and synthesis of those substances (semiochemicals = ectohormones) that convey information and interact between different individuals of organisms (allelochemicals as allomones, kairomones, or pheromones). Moreover, this discipline also elucidates the exocrine gland systems, receptors, and the transduction systems that recognize and pass on these semiochemicals. In addition, the developmental, behavioral, and ecological consequences of these chemical signals also are investigated. All of these areas rely upon bioassays in the laboratory and in the field. The results of chemoecological studies may be important in plant protection, in the development of highly selective techniques for pest control, and even in integrated plant protection. Dependent on the research areas of the scientists working on chemical ecology, classification and investigation of these phenomena varies considerably. Natural product chemists and biochemists are interested in biosynthesis and chemical structures of the secondary compounds involved. In contrast, ecologists may favor research that focuses on the interactions among trophic levels. As chemical ecology studies the interactions among different individuals of the same or different species other scientists potentially are interested in knowing the senders and receivers of chemical signals, and in knowing if an ectohormone is of advantage or disadvantage for these individuals. Finally, entomologists interested in chemical ecology may focus on exocrine glands or chemical signals on the body surface or want to learn if the compounds are biosynthesized by the insects, sequestered from plants, or produced by endosymbiontic microorganisms.

As compared with chemoecological studies in terrestrial ecosystems, which has been intensively studied the 1970s, chemical ecology of aquatic systems was initially neglected, but now there are considerable data available concerning the chemoecology of aquatic systems (e.g., Brönmark and Hansson 2012; Burks and Lodge 2002; Ferrari et al. 2010; Gross 2011). However, marine systems were often studied with the priority in identifying new biologically active natural products. In spite of the fact that freshwater chemical ecology lags behind terrestrial and marine chemical ecology, a constant increase of publications in this interesting field is recognizable (Burks and Lodge 2002). It was found that among allelochemicals kairomones mediate the majority of species interactions in freshwater systems. Fish and predaceous insects act largely as senders, zooplankton on the contrary comprise the most studied receivers. Other organisms such as predaceous insects may be both receivers of cues from larger predators as well as senders of their own cues to lower trophic levels, such as zooplankton (Burks and Lodge 2002). In freshwater systems, chemoecological investigations have especially targeted the study of predator–prey, plant-plant, and plant-herbivore interactions (including microorganisms) and the role of allelochemicals (Ferrari et al. 2010; Gross 2011).

The chapters in recent compilations on chemical ecology in aquatic systems (e.g., Brönmark and Hansson 2012) are of different significance for those who are interested in freshwater systems. Whereas information conveyed by chemical cues (Elert 2012) are highly informative, other chapters such as chemical defense (Kicklighter 2012) are only partially valuable, because marine systems are over represented and data from freshwater systems are nearly completely lacking. However taxonomically simple freshwater organisms such as Alveolata, Porifera, Cnidaria, or flatworms (Dettner 2010) are as important as chemically defended Hydrachnidia, water beetles and water bugs (Coleoptera: e.g., Dytiscidae, Noteridae, Hygrobiidae, Haliplidae; Heteroptera: Corixidae, Notonectidae, Naucoridae, Belostomatidae) or even chemically defended trichopteran larvae.

In this chapter I focus on all aspects of chemical ecology for adults and to a certain extent pupae of dytiscids. Data on glands or semiochemicals of dytiscid eggs and larvae are, unfortunately, not available, although such information would no doubt be interesting and valuable for our understanding of this family of beetles. For adult dytiscids, there exist only a few data on pheromones (Sect. 6.3) and kairomones (Sect. 6.4.1). In contrast, the Dytiscidae possess various complex glands and much is known for allomones (defensive compounds, Sect. 6.4.2). Moreover, behavior modifying chemicals may not be volatile or water soluble, but instead may cover the entire body surface as a kind of distinguishing mark, and the nature of such epicuticular lipids are examined here (Sect. 6.5.2; Dettner and Liepert 1994). Because animal coloration represent secondary compounds, natural pigments of predaceous diving beetles also are reviewed (Sect. 6.5.3). Finally, various aspects of microorganisms associated with predaceous diving beetles are presented (Sect. 6.6) and future directions in research (Sect. 6.7) are offered.

6.2 Chemical Senses

Aquatic insects evolved secondarily in aquatic environments and therefore are capable of sensing odors from a diverse range of sources (Crespo 2011). The recent review by Crespo (2011) on chemosensation and related behavior in aquatic insects is mainly focused on hemimetabolous aquatic orders including Ephemeroptera, Odonata, and Plecoptera, and the holometabolous Trichoptera and Diptera. In contrast, aquatic Coleoptera are completely omitted, however specific investigations on dytiscid beetles do exist elsewhere.

Nikolaas Tinbergen (1907–1988), a Dutch born British zoologist (Fig. 6.1a) shared the Nobel prize in 1973 with Karl von Frisch and Konrad Lorenz for research on the social behavior of animals. As early as 1936 he reported on his investigations with adults and larvae of *Dytiscus marginalis*. Although adults possess very large complex eyes (Fig. 6.1b) they do not react to living tadpoles within water filled test tubes. In contrast, adult beetles will quickly move their antennae and swim strongly within an odor plume of meat extract (Fig. 6.1c, d). Tinbergen also discusses the chemosensation of *Dytiscus* larvae. Further results concerning chemical senses of *Dytiscus* larvae are presented by Korschelt (1924).

During the next several decades the chemical senses of dytiscids were investigated by physiologists and zoologists. Schaller (1926) reported that dytiscids have very good chemical senses (odor, taste) that are especially important for detecting potential food. The receptors for these senses are located on different parts of their body. Dytiscids can taste sweet, sour, salty, and bitter with their taste receptors that are concentrated on their maxillary and labial palpi. Odor receptors (but not taste receptors) are found on the antennal surface.

Bauer (1938) showed during trainings experiments (mainly with adult *Dytiscus marginalis*) that beetles can differentiate between a variety of specific chemicals, including saccharose and hydrochloric acid. Furthermore, they can select saccharose when it is offered together with hydrochloric acid, sodium chloride, and the bitter quinine hydrochloride (bitter tasting alkaloid). Finally, they can select hydrochloric acid when it is offered together with glucose, quinine hydrochloride, and sodium chloride. However, beetles cannot differentiate between saccharose and glucose, hydrochloric and tartaric acid, quinine hydrochloride and salicin (bitter tasting alcoholic β-glucoside), or quinine hydrochloride and aloin (anthraquinone glucoside). It was found that these beetles can detect 18 different sugars and may perceive different compounds at different thresholds (e.g., saccharose 0.01 mol; sodium chloride 0.001 mol, salicin 0.0000625 mol, quinine hydrochloride 0.0000012 mol) (Bauer 1938).

Besides large species such as *Dytiscus,* chemoreception in aqueous and gas phases were studied in the a smaller species *Laccophilus maculosus* (Hodgson 1953). In this species the sensilla basiconica are located on the tips of antennae and represent chemoreceptors for gaseous and liquid stimuli. Due to inherent specialization these receptors have the lowest threshold of antennal receptors. Hodgson (1953) also reported that those sensilla basiconica that are located on the tips of the maxillary

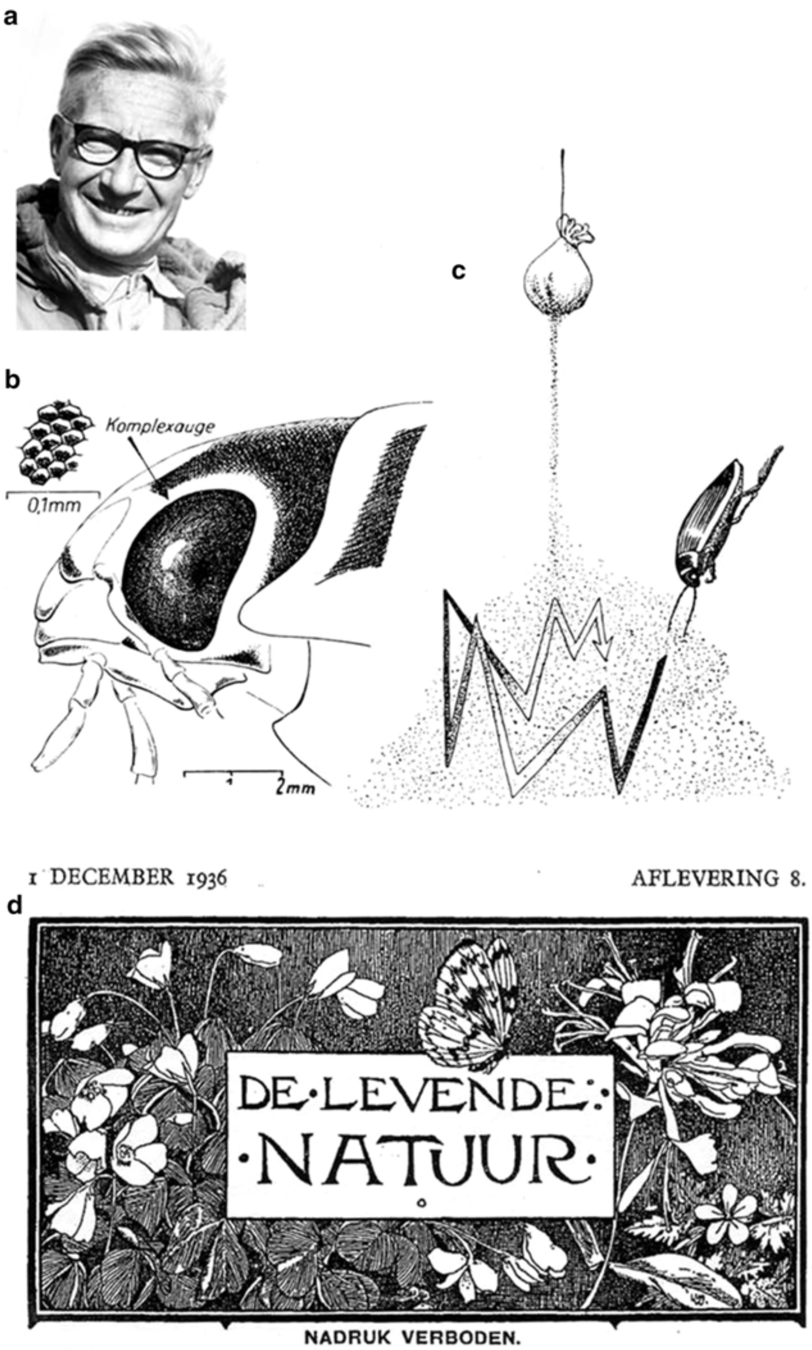


Fig. 6.1 Nobel laureate Nikolaas Tinbergen (1907–1988; **a**) and his investigations on orientation of *Dytiscus marginalis* (Tinbergen 1936). In spite of the large complex eyes of adults (**b**) during detection of prey the beetle strongly reacts to a meat broth by swimming behavior within an odor plume of a meat extract (**c** according to Tinbergen 1951). The title page of the journal "De levende Natuur" from 1936 is shown (**d**)

and labial palpi also represent chemoreceptors, although with higher thresholds. Hydrochloric acid, 1-pentanol, and sodium chloride all stimulated receptor areas on the tips of antennae and palpi. In addition, Hodgson (1951) showed that cations in uniform anion combination stimulated in the following odor of effectiveness according to the order of their ionic motilities: hydronium (=hydroxonium) >> ammonium > potassium > sodium > lithium. In contrast, anions in uniform cation combinations stimulated in the following order of effectiveness: hydroxide >> iodine$^-$ > bromine > sulfate$^-$, acetate, chloride > phosphate. With respect to low molecular organic compounds, thresholds to primary to alcohols decreased with increasing in CH_2-groups (e.g., methyl alcohol 3.6 mol, ethyl alcohol 4.3 mol, propyl alcohol 3.2 mol, butyl alcohol 0.046 mol, amyl alcohol 0.0073 mol, hexyl alcohol 0.0011 mol). This trend is apparently directly related to lipid solubility of the alcohols. Behrend (1971) analyzed the responses of single pore plate olfactory cells on odorous compounds in either air or water. The olfactory cells responded either to various organic acids and amino acids (class 1) or to nitrogenic compounds (class 2). Identical stimuli resulted in the same response in air and in water, which does not depend on the physicochemical state of the stimulating molecules within their carriers (air or water).

There exist various light microscopic and electron microscopic studies concerning the sensillae of Dytiscidae. Light microscopic details and a survey was produced by Korschelt (1923). Electron microscopic studies were performed on the fine structure of the sensilla on the distal antennal segment of *Graphoderus occidentalis* (Jensen and Zacharuk 1991), the digitiform from sensilla on the distal segment of maxillar palps of *Agabus bipustulatus* (Guse and Honomichl 1980), and antennal sensillae of *Acilius sulcatus* (Ivanov 1966). However, little recent work has been conducted on the specific microstructure of dytiscid chemical sensory structures.

6.3 Intraspecific Interactions: Sex-Pheromones

Sex pheromones are well known from Lepidoptera and other terrestrial insects, as well as a few examples from marine systems (Wyatt 2003). However observations on sex pheromones in freshwater systems are very rare in both invertebrates (e.g., *Gammarus*; Borowsky and Borowsky 1987) and vertebrates (Sorensen and Hoye 2010).

As far back as 1912 Blunck (1912b) reported that female *Dytiscus marginalis* produce a certain “Geschlechtsduft” (sexual odor) that leads males to females within an area of 20–30 cm. He also mentioned that males, excited by females, would quickly move their antennae and palpi during an increase in their swimming movements. Blunck (1912b) also found that secretions of female pygidial glands did not arouse males. Smith (1973) reported on sound production in both sexes of different species within genus *Rhantus*, which was observed in a behavioral context of emigration. During his experiments he reported that intra- and interspecific recognition is achieved through an olfactory clue, and in the laboratory interspecific location even functioned in total darkness.

Recently Herbst et al. (2011) demonstrated the presence of sex pheromones in the predaceous diving beetle *Rhantus suturalis*. Within non-permeable glass flasks,

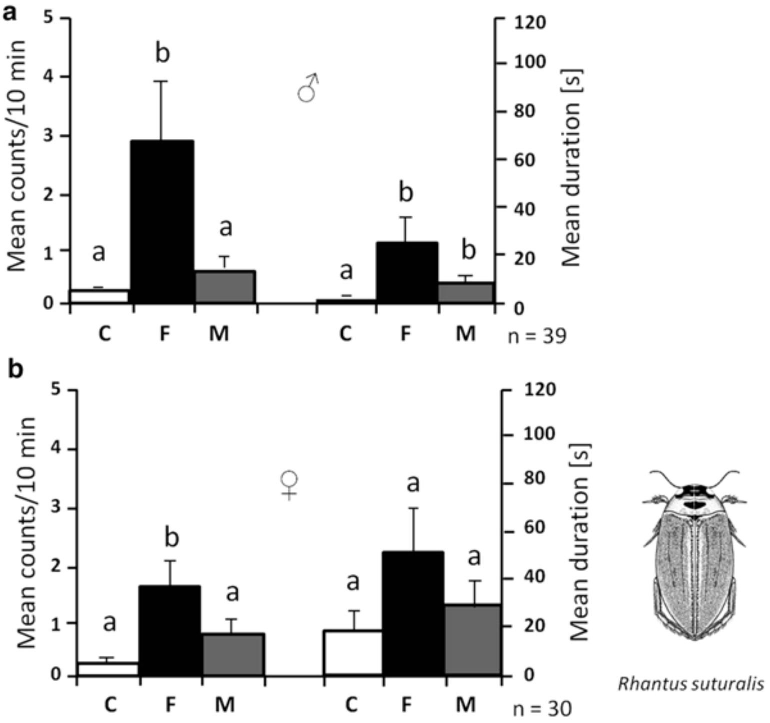


Fig. 6.2 Reaction of male (**a**, above) and female (**b**, below) *Rhantus suturalis* beetles to a vessel made of finely woven steel, containing one female (F) or one male conspecific (M) or to an empty control vessel (C). *Left*: mean counts of beetle contacts with the vessels. *Right*: mean sitting duration of beetles on the vessels. Error bars indicate standard errors. Bars with different letters are significantly different at $P \leq 0.05$. *n* number of replicates (After Herbst et al. 2011)

which did not allow the diffusion of chemicals, males and females did not stimulate any reaction by conspecifics of either sex. However in permeable vessels (e.g., made of finely woven steel) male predaceous diving beetles were significantly attracted to females. In addition, female *R. suturalis* were attracted to other females when they perceived chemical and optical cues simultaneously. Specifically, Fig. 6.2 illustrates the numbers of contacts with (left axis) and the sitting contacts with the vessel in male (a) and female (b) *R. suturalis* to a permeable steel vessel containing one female (F), one male conspecific (M) or an empty control vessel (C). Both with respect to contacts with the vessel and sitting durations on the vessels, males significantly selected females over males of controls. In addition, female *R. suturalis* had significantly more contacts with conspecifics than with males (Fig. 6.2).

With these results in mind, it would be interesting to now elucidate the chemical structure of the substances that modify female behavior in dytiscids. Some aquatic vertebrates (e.g., fishes, amphibians) unlike terrestrial insects use unusual polar compounds that serve as sex pheromones (Sorensen and Hoye 2010) such as l-kynurenine (Masu salmon of genus *Oncorhynchus*), prostaglandin $F_1\alpha$, $F_2\alpha$ (*Salmo*), a dihydroxypregnan-20-one-3-glucuronide (African catfish *Claria*), dihydroxy-4-pregnen-3-one and prostaglandins (*Carassius auratus*), newts in the genus *Cynops* (decapeptides as sodefrin, silefrin) or the tree frog *Litoria splendida* (25-amino acid peptide splendiferin). Further data which characterize pheromones of aquatic organisms are presented by Breithaupt and Thiel (2011) and Brönmark and Hansson (2012). Remarkably both kynurenin and steroids represent important metabolites of Dytiscidae. An intriguing question for the findings of Blunck (1912b) is if the prothoracic defensive glands are important for sexual pheromone activities.

6.4 Interspecific Interactions

During evolution, predators, parasitoids, and prey have developed various methods in order to detect, to defend, or generally to interact with each other (see Peckarsky 1984; Williams and Feltmate 1992). Apart from visual communication in aquatic ecosystems with low visibility and effective superposition eyes, predaceous diving beetles seem to especially use non-visual stimuli for their interactions and rely on chemoreception, which is very efficient in both adult and larval dytiscids. Interspecific chemical interactions are generally mediated by allelochemicals, which may be further subdivided depending on whether these chemicals are advantageous for the sending (allomone, see Sect. 6.4.2) or for the receiving (kairomone, see Sect. 6.4.1) organisms.

6.4.1 Kairomones and Other Allelochemicals

Kairomones represent interspecific behavioral modifying chemicals that are of advantage for the receiver and in contrast are negative or disadvantageous for the producing organisms. They are important in most predator/prey or host/parasite-systems.

With respect to dytiscids, our knowledge of chemical ecology varies depending on if the dytiscids represent prey (Sect. 6.4.1.1) or predators (Sect. 6.4.1.2). In addition, dytiscids may perceive kairomones (Sects. 6.4.1.1 and 6.4.1.2) or may function as kairomone emitters (Sect. 6.4.1.3). In all cases, there exist many laboratory and field observations, however the mechanisms for these behavior modifying kairomones is unknown.

There is growing evidence both from laboratory and mesocosm studies that insect predators that orientate towards the water surface are often absent in the presence of fishes. However, these insects may have effects on potential prey (e.g., zooplankton) that are analogous to fish predators (Herwig and Schindler 1996). As an example, larval *Acilius semisulcatus* significantly affect the vertical distribution of *Daphnia pulex* prey (especially large specimens; Arts et al. 1981). If dytiscid predators are present, a greater percentage of *Daphnia*-prey was found near the bottom of the experimental cages. Thus it seems highly probable that chemical signals, such as kairomones produced by dytiscid beetles, are involved in this response.

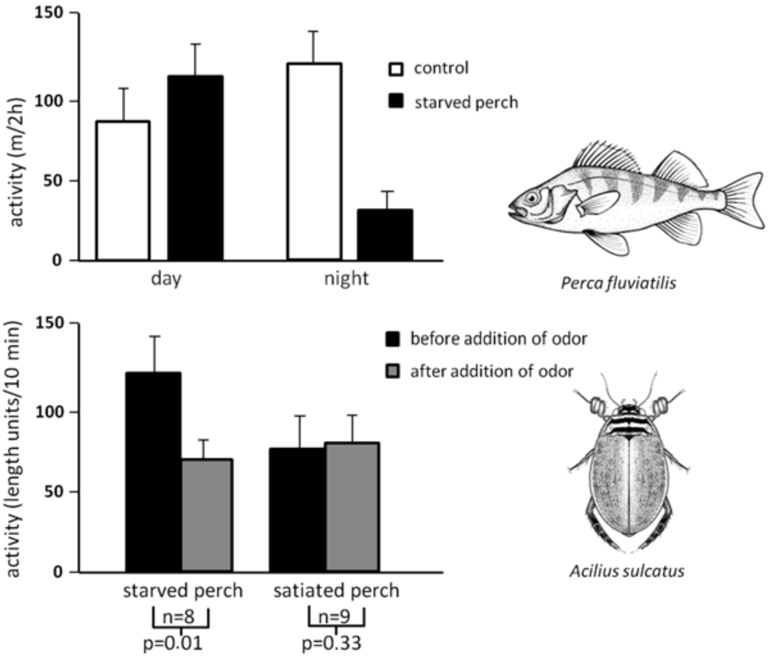


Fig. 6.3 Responses of dytiscid beetles (*Acilius sulcatus*) to chemical cues from perch *Perca fluviatilis*. *Above*: Activity (m moved within 2 h) for *Acilius sulcatus* in the different treatments in the fluviarium experiment (mean + SE). *Below*: Activity (mean + SE) of *Acilius sulcatus* counted as the number of quadrats past during 10 min before and after adding "fish-water" in the aquarium experiment. The *P*-value shows the result of the Wilcoxon-signed-rank test of the difference in activity before and after adding "fish-water". Changed according to Åbjörnsson et al. (1997)

6.4.1.1 Dytiscid Prey and Fish Predators

The importance of fish predation on aquatic insects, including some species of predaceous diving beetles, were reviewed by Healey (1984) and Sih (1987). Fish can exert strong and negative effects on dytiscid communities (Chap. 10 in this book) and may be important for food web dynamics as dytiscids can be both fish prey and predator (Chap. 8 in this book). In one example (Åbjörnsson et al. 1997) it was determined that *Acilius sulcatus* responded to chemical cues from perch (*Perca fluviatilis*). Whereas odor or visibility alone did not affect the activity of *A. sulcatus*, a significant interaction occurred when the two factors were combined (Fig. 6.3). The lowest activity of the beetles was found when *A. sulcatus* was exposed to water scented by starved perch at night (Fig. 6.3). When the activity was counted as the number of quadrats passed during 10 minutes before and after adding "fish-water", activity decreased after the addition of odor from starved perch (Åbjörnsson et al. 1997). This finding strongly suggests that beetles may alter their behavior in the presence of fish predators.

6.4.1.2 Dytiscids Predators and Vertebrate Prey

Larval dytiscids are often predators of vertebrates and may use kairomones emitted by their prey. There exist various examples where such interactions are described. In 1995, Mathis et al. reported that alarm pheromones of fathead minnows (*Pimephales promelas*) function as attractants for both predatory fish like pike (Esocidae) and adult predaceous diving beetles. When traps were supplied with skin extracts of alarm substance cells of non-breeding fishes (that had alarm pheromone cells) significantly more beetles were caught in the traps bated with alarm substances as compared with the controls (lacking alarm pheromone cells). These traps recorded seven species including *Acilius semisulcatus, Colymbetes sculptilis, Dytiscus alaskanus, D. circumcinctus, D. cordieri, Graphoderus occidentalis*, and *G. perplexus*, although only *C. sculptilis* were present in the sufficient numbers for statistical analysis. The evolutionary significance of such alarm signals that attract predators and are useful for alarm signal emitters was summarized by Chivers and Smith (1998) and Chivers et al. (1996).

Recently larvae of *Dytiscus sharpi* were recognized as being capable of detect not only prey motion but also prey scent (Inoda 2012). When larvae were exposed only to prey odors in the form of chemical signals from tadpoles they were more likely to be attracted to traps with tadpoles than to empty control traps. In contrast, *D. sharpi* larvae were not attracted to a trap containing conspecific larvae. The author suggested that the larvae are capable of recognizing prey scent (but not prey size), which may increase foraging success but decrease cannibalism.

Manteifel and Reshetnikov (2002) conducted laboratory experiments and allowed different predators to prey on noxious versus non-noxious tadpoles. Whereas predatory fishes and *Aeshna* nymphs actively consumed *Rana* tadpoles, *Bufo* tadpoles were rejected. On the contrary, larvae of *Dytiscus marginalis* attacked both tadpoles. These results are interesting from a chemically perspective, however the degrees of noxiousness of skins and interior bodies of *Bufo* and *Rana* tadpoles were not analyzed in this study. Therefore, interpretation of these results is difficult especially with respect to strategies of nutrition by different predators (i.e., sucking vs. chewing).

6.4.1.3 Dytiscid Predators and Egg-Laying Prey

In temporary pools, larvae of the mosquito *Culiseta longiareolata* are highly vulnerable to the common predatory backswimmer *Notonecta maculata* (Silberbush et al. 2010). It was recently found that adult female mosquitoes use kairomones that are released by these predators to detect the risk of predation. Specifically, oviposition of female mosquito is effectively repelled by n-heneicosane and n-tricosane, two hydrocarbon kairomones produced by *Notonecta* (Silberbush et al. 2010). The same effect was observed recently in females of the wetland mosquito *Culex tritaeniorhynchus* that strongly avoided laying eggs at oviposition sites in the presence of the predaceous diving beetle *Eretes griseus* (Ohba et al. 2012). In contrast, female

Aedes albopictus mosquitoes laid eggs in both the absence and presence of predator cues, probably because they could not detect the hitherto chemically unknown *Eretes* cues or are not sensitive to them. This was the first report to show that mosquitoes can detect the chemical cues of coleopteran beetles. In addition, Ohba et al. (2012) found that mosquito larvae near the water surface were eaten less frequently by *Eretes griseus* than those at the bottom of the containers. Therefore, filtering at the water surface appears to be an appropriate adaptive response in the presence of this predator.

Beyond the effect of dytiscids on invertebrates, Urban (2008) studied interactions between salamander larvae (*Ambystoma maculatum*) and *Dytiscus* larvae due to kairomones. It was evident that *Dytiscus* kairomones strongly reduced the daytime activity of *A. maculatum* larvae but presence of beetle larvae did not induce lower larval amphibian body masses, suggesting that perhaps feeding activity was not modified by predator presence.

6.4.2 Allomones

Allomones represent substances that are produced and released by an individual of one species that affects the behavior of an individual of another species. In contrast to kairomones (Sect. 6.4.1), allomones such as defensive compounds or antibiotics are advantageous for the sender and disadvantageous for the receiver. For both types of interactions allomones and kairomones there exist many detailed observations and bioassays in the field and the laboratory. However, compared to allomones, detailed data on the chemical character of behavior modifying kairomones are completely lacking. In contrast, hydradephagan beetles produce huge amounts of chemically identified natural products and allomones in their complex pygidial and prothoracic defensive glands. Therefore, Dytiscidae are well known to harbor elaborate biosynthetic apparatuses for manufacturing either steroids or aromatics (Blum 1981; Morgan 2004). Before reporting on the two gland systems where these natural products are produced, it is important to mention another internal structure, the rectal ampullae.

Both larvae and adult dytiscids possess rectal ampullae. If adults of larger Dytiscidae (Dytiscinae) are handled they often immediately react by depleting their rectal ampulla. This is evident by an unpleasant odor resembling hydrogen sulfide (H_2S) or ammonia (NH_3). Eisner (1970) named these defensive reflexes enteric discharges and discerns between regurgitation and defecation. After uptake of water the rectal ampulla may primarily serve as hydrostatic organ to increase the specific weight of the beetle, for example when it lands on a shining water surface (Naumann 1955; Wesenberg-Lund 1943; Hicks and Larson 1991). Moreover, a lot of valuable compounds such as ions and sugars are reabsorbed from the rectal epithelium into the hemolymph (Cochran 1975; Dettner and Peters 2010). In addition, this organ represents the first defecation-defense of adult dytiscids, before prothoracic defensive glands are depleted. Usually the rectal ampulla, which extends through the whole abdomen (Fig. 6.4a), is filled with water and very often with excrements

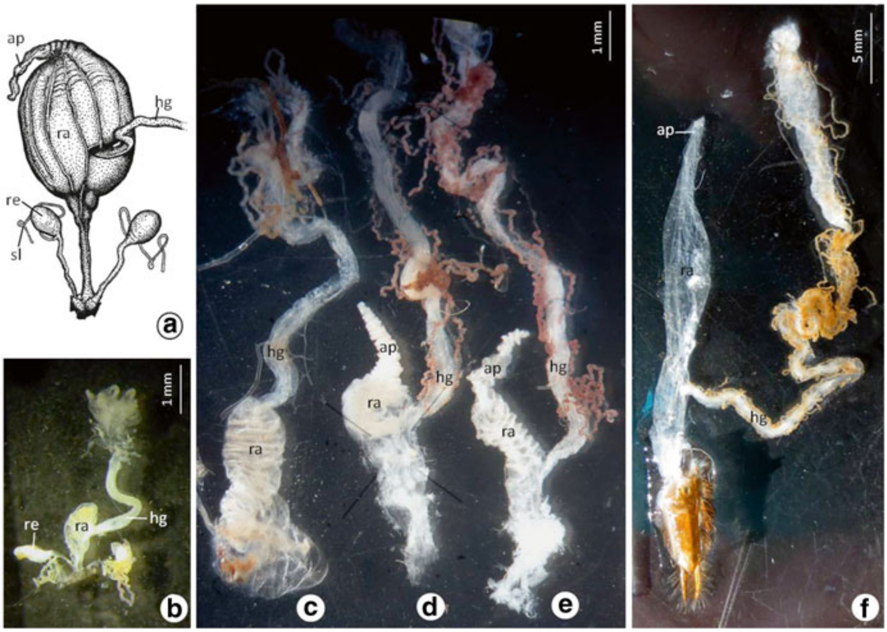


Fig. 6.4 (**a**) Filled rectal ampulla of *Dytiscus marginalis* with appendix, hind gut and paired pygidial glands. (**b**–**d**) Mid- and hind gut, rectum and rectal ampulla of *Hyphydrus ovatus* (**b**), *Ilybius crassus* (**c**), *Acilius sulcatus* (**d**), *Hydaticus seminiger* (**e**). Mid- and hind gut, rectum and rectal ampulla together with last abdominal segment and cerci of a *Dytiscus marginalis* larva (L III, **f**). (**a**) According to Naumann (1955). Abbreviations: *re* reservoir of pygidial gland, *sl* secretory lobe, *ra* rectal ampulla, *ap* appendix, *hg* hind gut

(Wesenberg-Lund 1943). Taxonomically a rectal ampulla is found in representatives of adult Dytiscinae (Fig. 6.4d, e) and Hydroporinae (Fig. 6.4b). Here the hind gut laterally meets the ampulla at its midway point (Fig. 6.4b). The same configuration was observed in *Agabus bipustulatus*. Within representatives of Colymbetinae the posterior part of the hind gut widens considerably, but otherwise the small hind gut meets the widened hind gut terminally or subapically (Fig. 6.4c). When larger and selected specimens of adult Dytiscinae are molested, odorous irritations are the only threat to humans or other vertebrate predators. It is interesting that large, full-grown larvae, especially of Dytiscinae, possess extremely lengthened rectal papillae (Fig. 6.4f). Sometimes the rectal ampulla, which also serves primarily as hydrostatic organ, is so long and extends into the larval head. It was suggested that this huge larval appendage serves to increase interior pressure in order to burst the last larval skin (Naumann 1955). Korschelt (1924) reports that the rectal ampulla of *Dytiscus*-larvae does not represent a defensive mechanism as observed in adults but is filled with water after molting. In contrast to adults, the defensive mechanisms of *Dytiscus* larvae are mechanical and are due to biting movements of sharp mandibles.

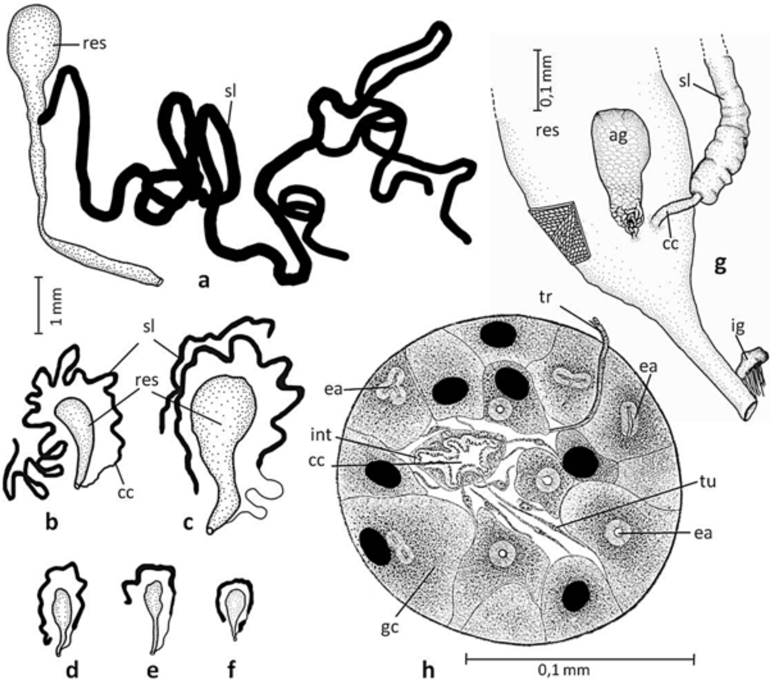


Fig. 6.5 (**a**–**f**) Structure of one pygidial gland system. (**a**) *Dytiscus marginalis*, (**b**) *Acilius sulcatus*, (**c**) *Colymbetes fuscus*, (**d**) *Copelatus (Liopterus) haemorrhoidalis*, (**e**) *Laccophilus minutus*, (**f**) *Nebrioporus depressus*. (**g**) Enlargement of posterior part of the left pygidial gland system of *Hyphydrus ovatus* (Modified after Forsyth 1968). (**h**) Section through secretory lobe of *D. marginalis* (Modified after Korschelt 1923). Abbreviations: *ag* accessory gland, *cc* collecting canal, *ea* end apparatus, *gc* gland cell, *ig* integumental gland, *in* intima, *res* gland reservoir, *sl* secretory lobe, *tr* trachea, *tu* tubule. Nuclei are *black*

6.4.2.1 Pygidial Glands

According to microtome sections, all hydradephagean families (save one) and neighboring taxa possess pygidial glands and their gland constituents (Dettner and Böhner 2009). Pygidial glands were recorded within the recently identified water beetle family Meruidae (Beutel et al. 2006), however, in Aspidytidae the histological data are absent. There exist various data concerning the anatomy and histology of the pygidial defense glands in Dytiscidae, Noteridae, Haliplidae, Gyrinidae (Forsyth 1968), Amphizoidae, and Hygrobiidae (Forsyth 1970; Figs. 6.5 and 6.6). Paired pygidial defensive glands were described for the first time in more detail in the dytiscid genera *Hyphydrus*, *Stictotarsus*, *Laccophilus,* and *Ilybius* (Forsyth 1968). Later abdominal glands from several other dytiscid species were recorded (Dettner 1985). Each gland (Figs. 6.5 and 6.6) comprises an ovoid reservoir that is covered by a muscle coat (Fig. 6.5g inlet figure; 6.6d) and leads into an efferent duct with

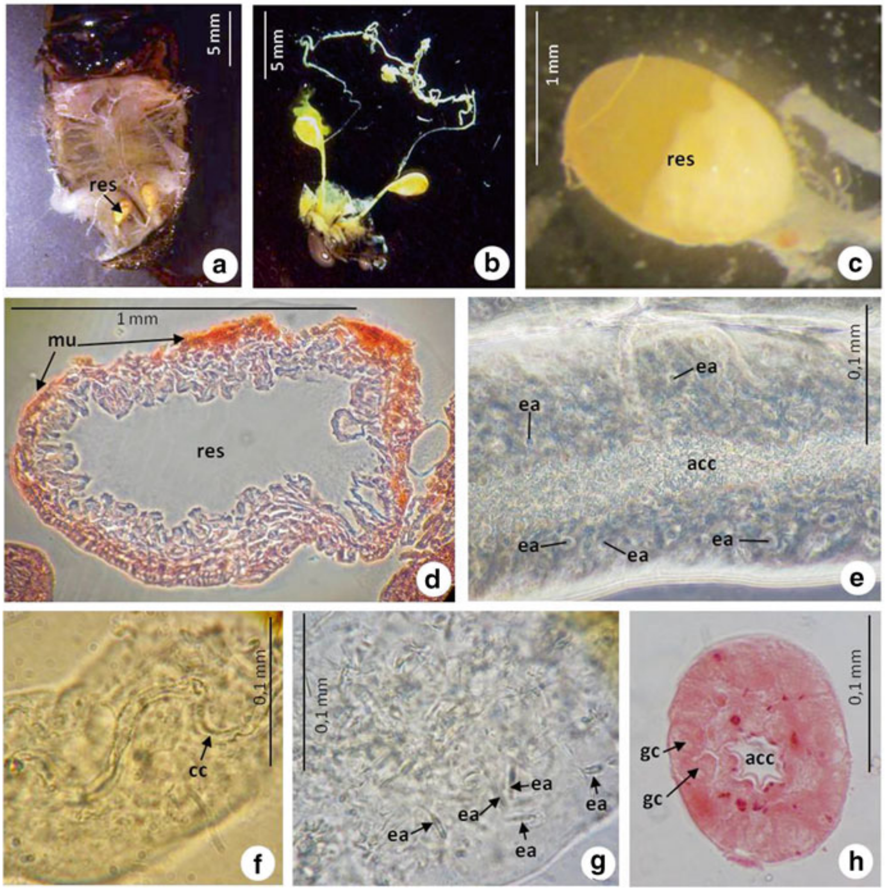


Fig. 6.6 (**a**–**h**) Structure and histology of pygidial glands of *Dytiscus marginalis*. (**a**) Dissected abdomen with paired pygidial glands. (**b**) Enlargement of two prepared pygidial gland systems. (**c**) Pygidial gland reservoir with two organic phases. (**d**) Section through gland reservoir using nuclear fast red-aluminum sulfate solution (**e**) Longitudinal view of squeezed secretory lobe. (**f**) Longitudinal view of squeezed collecting canal. g: Longitudinal view of squeezed secretory lobe with end apparatuses. (**h**) Square section through secretory lobe using nuclear fast read-aluminum sulfate solution

proximal valve. The lobular secretory tissue or secretory lobe (Figs. 6.5a–g and 6.6b, 6.6e, g) is connected to the reservoir by a collecting canal (Figs. 6.5g, h and 6.6f). The openings of the reservoirs are situated on the membranous cuticle behind the eighth abdominal tergite. According to Forsyth (1968, 1970) there exist two types of pygidial gland cells. An organelle of type I is typical for Dytiscidae but absent in Haliplidae, Gyrinidae, and Noteridae. The last three families have organelles of type II, which are also found in Laccophilinae, Hydroporinae, and some Colymbetinae and Dytiscinae. In addition, Laccophilinae and Hydroporinae possess simple unbranched type II organelles, but both simple and branched organelle-forms occur in Dytiscinae and Colymbetinae (Forsyth 1968). Ultrastructural analyses confirmed that two types of eccrine gland cells (racemous and bulbous) exist as reported from pygidial glands of *Dytiscus marginalis* (Kuhn et al. 1972). The central cavity of the gland duct is surrounded by microvilli that are stiffened by microfibrils. Kuhn et al. (1972) reported that the Golgi-apparatus is better developed in racemous cells than in the bulbous cells. In addition, the central cavities contain fine-fluffy substances in racemous cells and osmiophilic materials in the bulbous cells. It is interesting that Forsyth (1968) could also describe accessory glands (Fig. 6.5g) in the genera *Hyphydrus* and *Stictotarsus* that open into the reservoir of the pygidial glands close to the opening of the collecting canal. According to Forsyth (1968), these accessory glands are homologous with the basal combustion chamber in bombardier beetles. Vesicle and organelle of accessory glands are similar to the gland cells of thoracic glands and of the type II cells of the pygidial gland. Moreover an integumental gland (Fig. 6.5g) with about 100 cells opens close to the external reservoir opening in *Hyphydrus* (Forsyth 1968). The secretory lobes are characterized by an axial collecting canal (Fig. 6.5e, h) that is surrounded by gland cells with type I and II organelles (Figs. 6.5h and 6.6e–h).

The secretory lobes may be lengthened (Figs. 6.5a, b and 6.6b) or even branched (Fig. 6.5a, c). The collecting canals may be lengthened as in *Colymbetes, Laccophilus* (Fig. 6.5c, e), or shorter as in *Acilius* (Fig. 6.5b)*,* *Copelatus* (Fig. 6.5d)*, Nebrioporus* (Fig. 6.5f)*,* and *Hyphydrus* (Fig. 6.5g)*,* or are even absent as in *Hydaticus* (not figured) and *Dytiscus* (Fig. 6.5a). In most dytiscid species studied the collecting canals unite near the reservoir opening with the efferent duct of reservoirs (Fig. 6.5b–f), however in *Hyphydrus* (Fig. 6.5g) and especially in *Hydaticus* and *Dytiscus* (Figs. 6.5a and 6.6b) the collecting canal unites more anteriorly with the gland reservoir.

According to Korschelt (1923) the pygidial gland system of *Dytiscus marginalis* is innervated by the paired second nervi that originate from the hind border of the last abdominal ganglion (ganglion VI). Obviously this large nerve (called Nervus proctodaeo-genitalis) innervates all organs from the eighth segment onwards to the abdominal tip.

6.4.2.1.1 Chemistry of the Pygidial Glands and Distribution of Pygidial Gland Constituents Within Dytiscidae and Hydradephaga

Among insects, hydradephagean beetles represent the most prominent taxa producing aromatic exocrines (Dettner and Böhner 2009). Apart from Dytiscidae, aromatic pygidial gland constituents are found in Haliplidae (Dettner and Böhner 2009), Noteridae (Dettner 1997a), Amphizoidae (Dettner and Böhner 2009), and Hygrobiidae (Dettner 1997b), however pygidial gland chemistries of Meruidae, Aspidytidae, and Rhysodidae are unknown. Unusual aromatics that are not present in dytiscid beetles are 3-hydroxyphenylacetic acid and phenyllactic acid in Haliplidae (Dettner and Böhner 2009). In closely related families pygidial glands only contain a few aromatics in usually low amounts. Gyrinidae produce phenylacetaldehyde (Dettner and

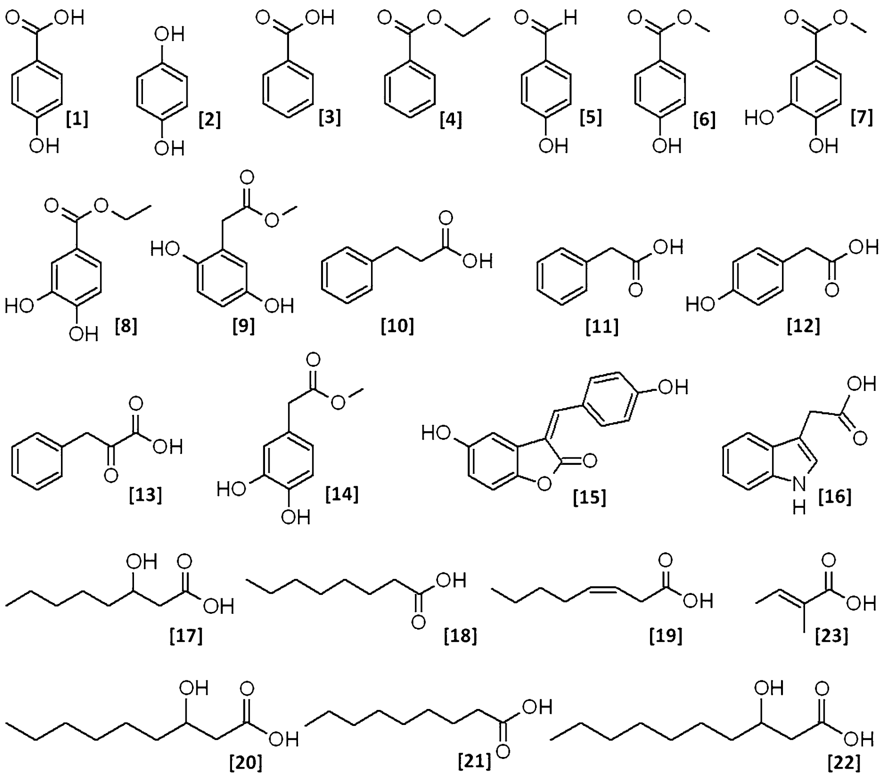


Fig. 6.7 Pygidial gland constituents **1**–**23** of predaceous diving beetles

Böhner 2009), Trachypachidae contain 2-phenylethanole and its esters (Attygalle et al. 2004) and a few carabid and cicindelid taxa contain benzoic acid, phenylacetic acid, and methylsalicylate together with salicylic aldehyde and benzaldehyde (see Francke and Dettner 2005; Dettner and Böhner 2009; Will et al. 2000).

The first results on the chemistry of the pygidial glands of dytiscids were published by Ghidini (1957). He described pygidial gland secretions of Dytiscinae as "disagreeable", whereas representatives of Hydroporinae such as *Hydroporus*, *Potamonectes*, *Deronectes*, *Stictotarsus,* and *Coelambus* were characterized as "sweet" and "agreeable" odors. I have supplied the chemical structure of many of the most common pygidial gland products in Fig. 6.7; hereafter I refer to them by number designations (bold).

Subsequently, Schildknecht et al. (1962) reported the presence of benzoic acid (**3**) (Table. 6.1, Fig. 6.7) and various other aromatics in pygidial glands of different dytiscid species. In the following years, 14 aromatic, 7 aliphatic compounds, a tryptophane-metabolite (**16**) and an unusual pigment (**15**) could be identified from this gland system (Table 6.1, Fig. 6.7; e.g., Dettner 1979, 1985; Schildknecht et al. 1983). Since then, several taxa of dytiscid beetles have been

Table 6.1 Pygidial gland constituents of predaceous diving beetles

Dytiscidae, Hydroporinae	
Hyphydrus ovatus (L.)	11, 12, 16 (Dettner 1979)
Hyphydrus aubei Ganglb.	(2),(3),11,12,13,16 (Dettner 1985)
Hydrovatus cuspidatus (Kunze)	(3)#,(11)#,12#,13#,16#,17#,(18)#,21#,22#
Hydroglyphus geminus (F.)	11,13,16 (Dettner 1979)
Geodessus besucheti Branc.	11 (Dettner 1985)
Hygrotus sanfilippoi (Fery)	11,12,13,16 (Dettner 1985)
Hygrotus inaequalis (F.)	(6)#,7#,11#,12,13,(16),17#,22 (Dettner 1979)
Deronectes aubei (Muls.)	(1)#,(3)#,7#,11#,16#
Deronectes platynotus (Germ.)	11 (Dettner 1985)
Deronectes latus (Steph.)	(3),(5),11 (Dettner 1985)
Deronectes moestus (Fairm.)	11 (Dettner 1985)
Graptodytes pictus (F.)	(3),11,12,13,16 (Dettner 1979, 1985)
Suphrodytes dorsalis (F.)	(3),11,12,(16) (Dettner 1979, 1985)
Hydroporus angustatus Strm.	11,13,16 (Dettner 1979)
Hydroporus tristis (Payk.)	11,12,16 (Dettner 1979)
Hydroporus palustris (L.)	11,12 (Dettner 1979)
Hydroporus obscurus Strm.	11,12,16 (Dettner 1979)
Hydroporus marginatus (Duft.)	11,13,16 (Dettner 1979)
Hydroporus planus (F.)	11,12,13,16 (Dettner 1979)
Hydroporus discretus Fairm. & Bris.	11,13 (Dettner 1979)
Hydroporus ferrugineus Steph.	11,13,16 (Dettner 1979)
Hydroporus obsoletus Aubé	11#,19#
Hydroporus melanarius Strm.	(5),12 (Dettner 1979)
Hydroporus pubescens (Gyll.)	(2),(3),(6),11 (Dettner 1985)
Hydroporus incognitus Shp.	11 (Dettner 1985)
Hydrotarsus lundbladi Falkenström	3#,6#,11#
Oreodytes sanmarkii (C.R.Sahlb.)	(3),(6),11,13 (Dettner 1985)
Nebrioporus depressus (F.)	11,12,(13),16 (Dettner 1979, 1985)
Nebrioporus canaliculatus (Lac.)	(2),(3),11,13,16 (Dettner 1985)
Scarodytes halensis (F.)	(3),(5),11,12,13,16 (Dettner 1979, 1985)
Stictonectes optatus (Seidl.)	(5),(6),11,(16) (Dettner 1985)
Stictotarsus duodecimpustulatus (F.)	11,12,13,16 (Dettner 1979)
Dytiscidae: Colymbetinae	
Liopterus haemorrhoidalis (F.)	(1),2,3,5,6,11,13 (Dettner 1979, 1985)
Liopterus atriceps Shp.	(1),3,(5),11,13 (Dettner 1985)
Ilybiosoma seriatum (Say.)	5,6 (Fescemyer and Mumma 1983)
Agabus binotatus Aubé	1#,3#,5#,6#,7#
Agabus guttatus (Payk.)	2,3,5,6,7,(11),(13) (Dettner 1979, 1985)
Agabus maderensis Wollaston	2#,3#,4#,5#,6#,7#
Agabus biguttatus (Oliv.)	2#,3#,5#,6#,(11) (Dettner 1979, 1985)
Agabus bipustulatus (L.)	1,2,3,5,6,(11) (Dettner 1979, 1985; Schildknecht 1970)
Agabus wollastoni Sharp	2#,3#,5#,6#,7#
Agabus melanarius Aubé	2,3,4,6,7 (Dettner 1979)
Agabus sturmii (Gyll.)	(1),2,3,5,6,(7),(11) (Dettner 1979, 1985)
Agabus nebulosus (Forst.)	2,3,5,6,7# (Dettner 1979)

(continued)

Table 6.1 (continued)

Agabus paludosus (F.)	2,3,5,6,7# (Dettner 1979)
Agabus affinis (Payk.)	2,3,5,6,7,(11) (Dettner 1979, 1985)
Agabus congener (Thunb.)	3,5,6 (Dettner 1979)
Agabus didymus (Ol.)	3,5,6 (Dettner 1979)
Agabus labiatus (Brahm)	(1),2,3,5,6,(7),(11),(13),15 (Dettner 1979, 1985)
Agabus undulatus (Schrank)	(1),2,3,5,6,(7),15 (Dettner 1985)
Agabus serricornis (Payk.)	2,3,5,6,15 (Dettner 1985)
Agabus unguicularis (Thoms.)	2,3,5,6,7,(11) (Dettner 1985)
Agabus brunneus (F.)	2,3,5,6,7 (Dettner 1985)
Platambus maculatus (L.)	(1),2,3,5,6,(7),(11),18,19# (Dettner 1979, 1985)
Platambus obtusatus (Say.)	5,6 (Fescemyer and Mumma 1983)
Colymbetes fuscus (L.)	(1),2,3,5,6,7 (Dettner 1979; Schildknecht 1970)
Colymbetes schildknechti Dett.	2,3,5,6,(11) (Dettner 1985)
Ilybius chalconatus (Panz.)	2,3,5,6,7 (Dettner 1985)
Ilybius wasastjernai (C. R. Sahlb.)	5,6 (Dettner 1979)
Ilybius fuliginosus (F.)	2,3,5,6,(7),(11) (Dettner 1979, 1985)
Ilybius fenestratus (F.)	1,2,3,4#,5,6 (Dettner 1985; Schildknecht 1970)
Ilybius hozgargantae (Burm.)	1#,2#,3#,5#,6#,7# (Schaaf 1998)
Ilybius ater (Deg.)	1,2,3,5,6,(7),(11),23 (Dettner 1979, 1985)
Ilybius crassus Thoms.	2#,3#,4#,5#,6#,7, (Dettner 1979)
Ilybius quadriguttatus (Lac.)	3#,6#
Ilybius guttiger (Gyll.)	1,2,3,5,6,7#,(10)#,(23)# (Dettner 1979)
Ilybius aenescens Thoms.	(1),3,5,6,(7),(11) (Dettner 1985)
Meladema coriacea Laporte	2,3,5,6,(11),(13) (Dettner 1985)
Meladema lanio (F.)	1,2#,3#,4,5#,6#,(7)#
Rhantus suturalis (McLeay)	2,3,5,6,7,(11),(13) (Dettner 1979, 1985)
Rhantus exsoletus (Forst.)	1,2,4,5,6 (Dettner 1985; Schildknecht 1970)
Rhantus suturellus (Harr.)	2,3,5,(6),(7) (Dettner 1985)
Rhantus grapii (Gyll.)	3,5,6 (Dettner 1985)
Dytiscidae, Dytiscinae	
Eretes sticticus (L.)	(2),3,5,6,(7),(11) (Dettner 1985)
Hydaticus seminiger (Deg.)	3,5,6,10,(11)# (Dettner 1979)
Hydaticus leander (Rossi)	2,3,5,(6),10#,(11) (Dettner 1985)
Acilius sulcatus (L.)	2,3,5,6 (Dettner 1979; Schildknecht 1970)
Acilius duvergeri Gob.	1,2,3,5 (Dettner 1985)
Acilius mediatus (Say)	3,5,6 (Newhart and Mumma 1979)
Acilius semisulcatus Aubé	3,5,6 (Newhart and Mumma 1979)
Acilius sylvanus Hilsenh.	3,5,6 (Newhart and Mumma 1979)
Graphoderus cinereus (L.)	1,(2),3,5,6,7 (Dettner 1979, 1985; Schildknecht 1970)
Graphoderus liberus (Say)	3,5,6 (Miller and Mumma 1973)
Dytiscus marginalis L.	3,5,6,7,15 (Dettner 1979; Schildknecht and Weis 1962; Schildknecht et al. 1970)
Dytiscus circumflexus F.	1,2,3,5,6,7,(11) (Dettner 1985)
Dytiscus pisanus Laporte	1,3,5,6,(11),(13) (Dettner 1985)
Dytiscus latissimus L.	3,5,6 (Dettner 1985; Schildknecht 1970)

(continued)

Table 6.1 (continued)

Cybister mesomelas Guignot	3#,6#,10#,11#
Cybister lateralimarginalis (Deg.)	3,5,6,7,8 (Dettner 1985; Schildknecht 1970)
Cybister tripunctatus (Oliv.)	3,5,6 (Dettner 1985; Schildknecht 1970)
Dytiscidae, Laccophilinae	
Laccophilus minutus (L.)	(2),(3),(5),(6),14,17,19,20,22, (Dettner 1985; Schildknecht et al. 1983)
Laccophilus hyalinus (Deg.)	14,17,20,22 (Dettner 1985)

1: 4-hydroxybenzoic acid, **2**: hydroquinone, **3**: benzoic acid, **4**: benzoic acid ethylester, **5**: 4-hydroxybenzaldehyde, **6**: 4-hydroxybenzoic acid methylester, **7**: 3,4-dihydroxybenzoic acid methylester, **8**: 3,4-dihydroxybenzoic acid ethylester, **9**: 2,5-dihydroxyphenylacetic acid methylester, **10**: phenylpropionic acid, **11**: phenylacetic acid, **12**: 4-hydroxyphenylacetic acid, **13**: phenylpyruvic acid, **14**: 3,4-dihydroxyphenylacetic acid methylester, **15**: marginalin (= 4'5-dihydroxybenzalisocumaranone), **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, # new record as compared with Dettner (1985)

checked for their pygidial gland chemistry (Blum 1981; Francke and Dettner 2005) and within insects Dytiscidae represent a valuable source for biosynthesis of various aromatic compounds (Morgan 2004) including 3-indole acetic acid (**16**, Dettner and Schwinger 1977). It is remarkable that a few aromatic main constituents from the pygidial glands (e.g., **5**, **11**) are also present in the thoracic defensive glands of the water bug genera *Ilyocoris* and *Notonecta* or the metapleural glands of various ant genera (see Blum 1981; Staddon and Thorne 1979).

Apart from benzoic acid (**3**) other chemicals (see Fig. 6.7) have been identified including 4-hydroxybenzoic acid (**1**), hydroquinone (**2**), benzoic acid ethylester (**4**), 4-hydroxybenzaldehyde (**5**), 4-hydroxybenzoic acid methylester (**6**), 3,4-dihydroxybenzoic acid methylester (**7**), 3,4-dihydroxybenzoic acid ethylester (**8**), 2,5-dihydroxyphenylacetic acid methylester (**9**), phenylpropionic acid (**10**), phenylacetic acid (**11**), 4-hydroxyphenylacetic acid (**12**), phenylpyruvic acid (**13**) and 3,4-dihydroxyphenylacetic acid methylester (**14**). Remarkably all derivatives of phenylacetic acid (**11**) such as **12** and **13** are typical for the Hydroporinae subfamily (Fig. 6.7) whose representatives share the presence of **11** as a main compound. This strong pleasant odor that is so typical for Hydroporinae is even mentioned in nomenclature. Spangler (1985) described *Hydrodessus fragrans* due to its strong pleasant fragrance during dissection. This odor is typical for **11** but not for inodorous benzoic acid (**3**). Moreover, gentle molestations of certain living Hydroporinae species, as observed in *Hydrotarsus lundbladi*, may result in liberation of small amounts of strongly smelling phenylacetic acid from their pygidial gland reservoirs.

Within Colymbetinae and Dytiscinae, phenylacetic acid (**11**) only occurs as a trace constituent (Table 6.1). However, there is one exception, as both species of *Copelatus* (*Liopterus*) investigated sequester considerable amounts of **11** in their pygidial glands (Figs. 6.7 and 6.8) and are also characterized by the sweetish odor when dissected. In contrast, the ethylester of protocatechuic acid (**8**) was only found in the genus *Cybister* (Table 6.1, Fig. 6.8).

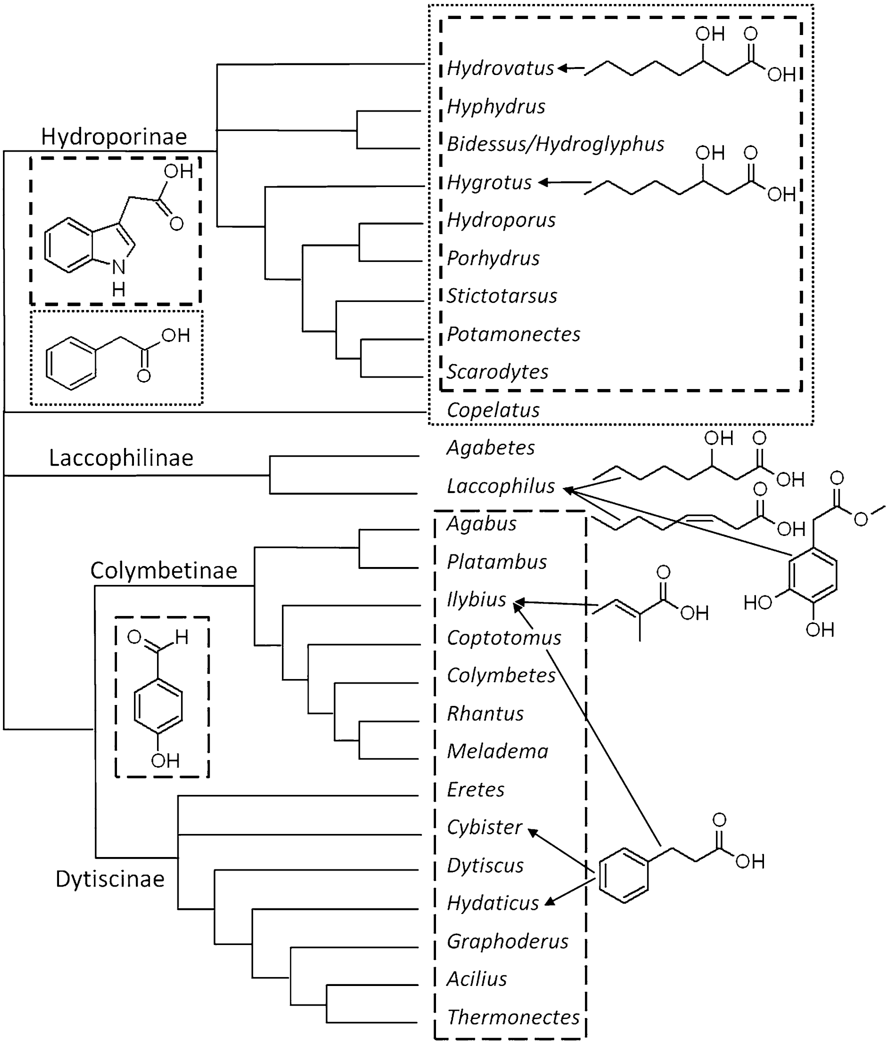


Fig. 6.8 Phylogeny of Dytiscidae genera after Burmeister (1976) and distribution of pygidial gland constituents according to Fig. 6.7. Those compounds which are present in various taxa are figured by *boxes*. Erratically found chemicals are associated with the genera by *arrows*

It was suggested that a further aromatic and extremely yellow colored substance from the pygidial glands of *Dytiscus marginalis* (**15**, marginalin, 4′,5-dihydroxy-benzalisocumaranone; Schildknecht et al. 1970) was biosynthetically produced from precursors such as 2,5-dihydroxyphenylacetic acid methylester (**9**) and 4-hydroxybenzaldehyde (**5**). Principally both of these aromatics (**5** and **9**) might be produced from a precursor such as 4-hydroxyphenylpyruvic acid. Later on this compound was identified from the pygidial glands of three Agabinae (*Agabus labiatus*, *A. undulatus*, *A. serricornis*; Dettner 1985) that are closely related (Ribera et al. 2004). Moreover, it was shown that the natural marginalin from *Dytiscus* represents an

E-isomer (Barbier 1987) and may fix solidly on a variety of supports (Barbier 1990). When this compound is distributed on the beetle surface by cleaning behavior, the yellow compound is likely fixed on microorganisms and algae. Marginalin (**15**) is related to aurone, which represents a plant flavonoid that provides yellow coloration to flowers of various ornamental plants. The *Z*-configuration of most aurones represents the more stable configuration.

In addition, phenylpropionic acid (**10**) is typical for the Dytiscinae genera *Hydaticus* and *Cybister* and for one representative of Colymbetinae genus *Ilybius* (Figs. 6.7 and 6.8). In contrast, 3,4-dihydroxyphenylacetic acid methylester (**14**) are restricted to two Laccophilinae species investigated (*Laccophilus minutus, L. hyalinus;* Figs. 6.7 and 6.8). It is astonishing that most Hydroporinae not only produce the sweetish smelling compound **11** but exclusively contain considerable amounts of the tryptophane-derivative 3-indoleacetic acid (**16**), which is also present in Noteridae (Figs. 6.7 and 6.8).

Aliphatic pygidial gland constituents such as 3-hydroxy acids from octanoic (**17**), nonanoic (**20**), and decanoic (**22**) acids are typical for the Laccophilinae and more basally arranged Hydroporinae genera *Hydrovatus* and *Hygrotus* (Table 6.1, Figs. 6.7 and 6.8). These hydroxyacids are also present in pygidial glands from representatives of Haliplidae (Dettner and Böhner 2009) and in metapleural glands of certain Formicidae (see Blum 1981). Further biosynthetically related acids such as octanic (**18**), 3-octenoic (**19**; Figs. 6.7 and 6.8), and nonanoic (**21**) acids occur in the genera *Hydrovatus*, *Platambus*, and *Laccophilus*. The typical compound of many terrestrial Adephaga (see Blum 1981) that is represented by tiglic acid (**23**) is restricted to two representatives of the genus *Ilybius*.

6.4.2.1.2 Biological Activity of Pygidial Gland Secretions and Their Regeneration

The biological significance of the dytiscid pygidial gland secretions is multifunctional. At first, most compounds (apart from marginalin **15** and probably from 3-indoleacetic acid **16**) hitherto identified represent excellent preservatives that are often used in foodstuff industry. This applies especially for both aromatic compounds (**3**, **6**, and **11**) and aliphatic constituents (e.g., **17**, **19**, **20**, **22**) (Dettner 1985; Dettner and Böhner 2009). These compounds are fungicides and bactericides and show an inhibition on germination and growth of plants. Even Z-3-octenoid acid (**19**) chemically resembles the well-known preservative sorbic acid (E,E-2,4-hexadienoic acid). The role of the plant hormone 3-indoleacetic acid (**16**) in hydroporine pygidial glands remains enigmatic. One specimen of *Stictotarsus duodecimpustulatus* sequesters the same amount of compound **16** which can be isolated from 68,000 *Avena* coleoptiles, representing a rich plant source for this compound (Dettner and Schwinger 1977). This plant hormone is found in various gall-forming insects and from the metathoracic glands of few ant species (together with phyenylacetic acid **11**). However, there are no gall-forming hydroporine species known. Therefore 3-indoleacetic acid in predaceous diving beetles may represent a soft preservative especially if used together with compound **11**.

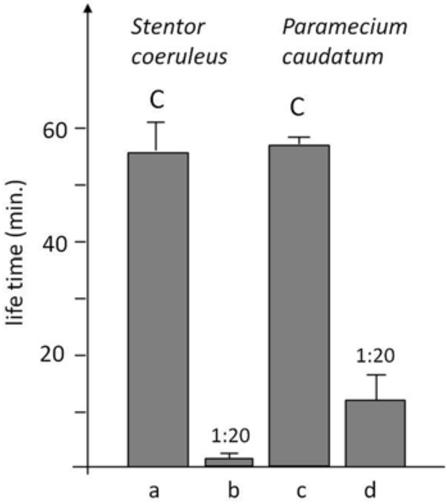


Fig. 6.9 Efficiency of water beetle pygidial gland secretions on protozoans *Stentor coeruleus* (*a–b*) and *Paramecium caudatum* (*c–d*) measured as life time (activity of cilia) at 20 °C. Columns *a*, *c*: water controls; Columns *b*, *d*: secretion of three pygidial gland reservoirs of *Acilius sulcatus* (1:20, v/v)

Finally, derivatives of tryptophan such as 3-indoleacetic acid may represent important excretional products in insects (Cochran 1975).

To distribute their pygidial gland secretions on their body surfaces, dytiscid beetles leave the water. As early as 1967 Maschwitz described this behavior and suggested that these antimicrobial secretions serve to protect the beetles from bacteria and even peritrichic ciliates. This possible protection is illustrated when aqueous dytiscid beetle pygidial gland secretions are tested against the protozoans *Stentor coeruleus* and *Paramecium caudatum* (Fig. 6.9; Cichon et al, in preparation). The behavior of both protozoans was recorded under the microscope as activity of cilia at 20 °C. In both species, diluted aqueous solutions (1:20, v/v) of gland constituents significantly reduced activity of cilia with a stronger effect in *S. coeruleus*, suggesting a negative effect of the beetle secretions on ciliates.

The pygidial gland reservoirs of dytiscids either contain fluids or solid paste-like secretions (Fig. 6.6b). Very often two organic phases, a solid and a fluid, are present within the reservoir (Fig. 6.6c). Depending on their viscosities, the pygidial gland secretions are partly depleted after molestations. Usually only small amounts of the reservoir may be depleted (~13 %,; Classen and Dettner 1983; Dettner 1985) and therefore the pygidial gland secretions of dytiscids likely do not represent defensive secretions against larger predators.

It is remarkable that the above mentioned secretion-grooming is also observed under water while the beetles clasp onto water plants or other structure. Kovac and Maschwitz (1990) described this behavior as secretion-grooming, and suggested that the secretion is used to hydrofuge sensitive body parts such as spiraculi and subelytral tergal respiratory structures. However, when contact angles of definite water droplets on elytral surfaces were carefully measured under a contact angle microscope, all secretions tested from hydradephagan beetles showed a drastic reduction of the contact angle as compared with an untreated elytron of the same beetle specimen when the corresponding second elytron was previously treated with minute amounts of

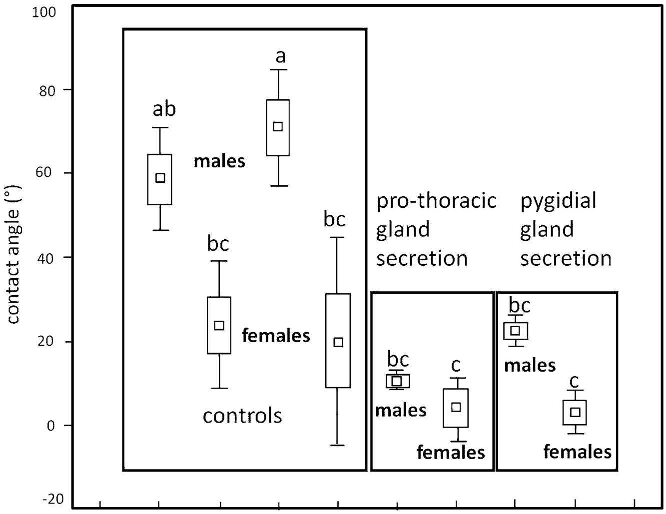


Fig. 6.10 Contact angles of water droplets placed on elytral surfaces of *Acilius sulcatus*. *Left box*: left elytron (first line) and right elytron (third line) of males; left elytron (second line) and right elytron (fourth line) of females, *central box*: effect of prothoracic gland secretion on a contact angles of male and female *Acilius* beetles, *right box*: effect on pygidial gland secretions of male and female (□: mean values; ▯: standard error of mean; and |: standard deviation; Schneider 2008)

pygidial gland secretion (Dettner 1985; Fig. 6.10). The effect of both pygidial and prothoracic gland secretions on contact angles of water droplets are evident (Fig. 6.10) (Schneider 2008). Male *Acilius sulcatus* possess smooth elytra, whereas females are characterized by grooved and hairy elytra. Therefore the contact angles of water droplets on female elytral surfaces are distinctly lower than on male elytra. When treated with prothoracic gland secretions both in males and females results a drastic reduction of contact angles that is more evident in males with their smooth elytra than in females with hairy grooved elytra (Schneider 2008).

Because the contact angle of water on solid surfaces depends both on the surface structure of the elytral epicuticle and from the degree of biofilms on these elytral surfaces, only one freshly collected beetle specimen was used per measurement (Dettner 1985). The wettability after the elytron was treated with gland substance was seen in different species and specimens independently from their pygidial gland chemistries. Even marginalin (**15**), the pigment from the pygidial and preputial glands of *Dytiscus* and few *Agabus* species may significantly lower the contact angle of a water droplet that was placed on a cleaned glass surface (Fig. 6.11). In addition, there was also a significant decrease of the contact angle of 4-hydroxybenzaldehyde (**5**), the main aldehyde of many dytiscid pygidial glands (Fig. 6.11). As many pygidial gland components are amphiphilic (i.e., have a lipophilic and hydrophilous part of the molecule) the increase of wettability of a more or less hydrophilous epicuticle after treatment with benzoic (**3**), phenylacetic (**11**), or aliphatic 3-hydroxy acids (**17**,**20**,**22**) seems plausible.

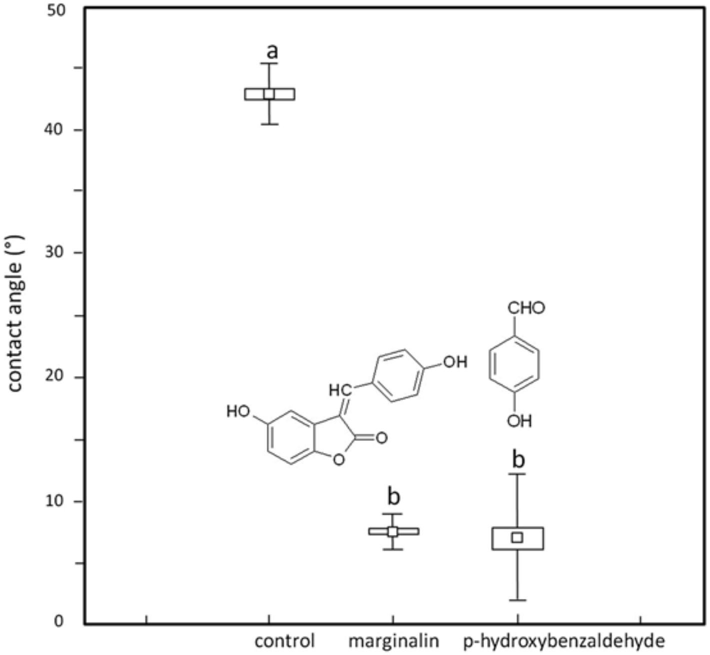


Fig. 6.11 Contact angles of water droplets placed on cleaned glass surfaces (□: mean values; ▭: standard error of mean; and |: standard deviation; Schneider 2008) which were previously treated with aqueous mixtures of marginalin (**15**) and 4-hydroxybenzaldehyde (**5**). Controls represent untreated glass surfaces

In addition to the above mentioned low molecular compounds, pygidial gland secretions of dytiscids also contain marginalin (**15**) and a glycoproteid consisting of 18 amino acids (Schildknecht and Bühner 1968). As described above, marginalin may act as a fixative. In the same way the glycoproteid forms a coherent film (see electron microscopic data in Schildknecht and Bühner 1968), when applied on a glass surface and may fix the low molecular bactericides and fungicides on the beetles surface. In addition, the 3-hydroxy acids **17**, **20**, and **22** may form polyesters that can either fix the metabolites or entangle epizoic microorganisms on the beetles surfaces (Dettner and Böhner 2009).

In general pygidial gland secretion may influence the settlement of external organisms ranging from bacteria to eukaryotic parasites such as Protozoa (Lust 1950; Matthes 1982), fungi (Laboulbeniales, Scheloske 1969), and aquatic mites (Davids et al. 2007). Prothoracic gland secretion was more effective against *Stentor* and *Paramecium* as compared with pygidial gland material (see 4.2.2.2; Fig. 6.9). Scheloske (1969) found that specimens of Hydroporinae (from 416 specimens 13.0 % were parasitized) and Laccophilinae (from 173 specimens 16.8 % were parasitized) showed increased parasitism by Laboulbeniales as compared with Colymbetinae & Dytiscinae (from 815 specimens 10.2 % were parasitized). He suggested that the significantly differing pygidial gland compounds, specifically the missing compounds **3**, **5**, and **6** in Hydroporinae may be responsible for this effect (Scheloske 1969). However, he also mentioned that the role of prothoracic gland secretions against Laboulbeniales remains unknown.

In contrast to organisms that settle on the surface of adult dytiscids or their larvae, internal parasites such as hairworms (e.g., *Gordius* and allied genera; Blunck 1922a), trematodes (e.g., Peters 1957), or gregarines (Geus 1969; Blunck 1923b) are probably not targeted by these glandular secretions. However, it should be investigated if beetles also take up these exocrine secretions orally. In addition, it would be intriguing if maternally derived prothoracic or pygidial gland secretions have any effect on those species of proctrotrupid and chalcid Hymenoptera that parasitize submersed dytiscid eggs.

Seasonal fluctuations of pygidial gland titers were described in the genera *Acilius* (Newhart and Mumma 1979) and *Agabus* (Classen and Dettner 1983). It is unlikely that these fluctuations reflect different degrees of utilization of the gland material, but mainly reflect different age structures of the adult beetles analyzed during a season. It was shown that the secretions of young male and female beetles as determined by analysis of their internal sexual organs quantitatively and qualitatively differ from secretions of older beetle specimens (Classen and Dettner 1983; Dettner 1985), a fact that is probably due to different biosynthetic capacities of beetles of different ages. For example, freshly hatched male and female *Agabus bipustulatus* and *A. paludosus* produce very low amounts of compounds **2**, **3**, **5**, **6**, **7**, whereas older specimens of both species and sexes produce more aromatics per individual with the aldehyde **5** as a main constituent.

Activities of water beetle pygidial gland secretions on other targets are unknown. However, Lousia et al. (2010) reported that pygidial gland secretions resulted in histopathological changes in male accessory glands of *Odontopus varicornis* (Heteroptera, Pyrrhochoridae). These histological changes were described as disintegration of epithelia, disorganized tissues, swollen nuclei, vacuolized cytoplasm, pycnotic and necrotic epithelia, and enlargement of epithelial cells. The effect of these pygidial glands remain one of the largest understudied and potentially most interesting aspect of dytiscid chemical ecology.

6.4.2.2 Prothoracic Defensive Glands

Prothoracic glands (Figs. 6.12, 6.13, and 6.14) are only present within a small fraction of hydradephagean beetles (Dettner 1985). As reported by Beutel et al. (2006) prothoracic defensive glands are absent in Meruidae, Gyrinidae, and Noteridae, the latter representing the sister group of Dytiscidae. In addition, due to the absence of the prothoracic defensive glands, Aspidytidae (Ribera et al. 2002) are excluded from Dytiscidae and Hygrobiidae, which are both characterized by these peculiar thoracic complex glands (Dettner 1987; Forsyth 1968, 1970). According to the phylogeny of aquatic Adephaga (Beutel et al. 2006), Dytiscidae and Hygrobiidae represent sister groups, Amphizoidae, with no prothoracic defensive glands represent the sister group of Dytiscidae + Hygrobiidae, whereas Aspidytidae form a sister of

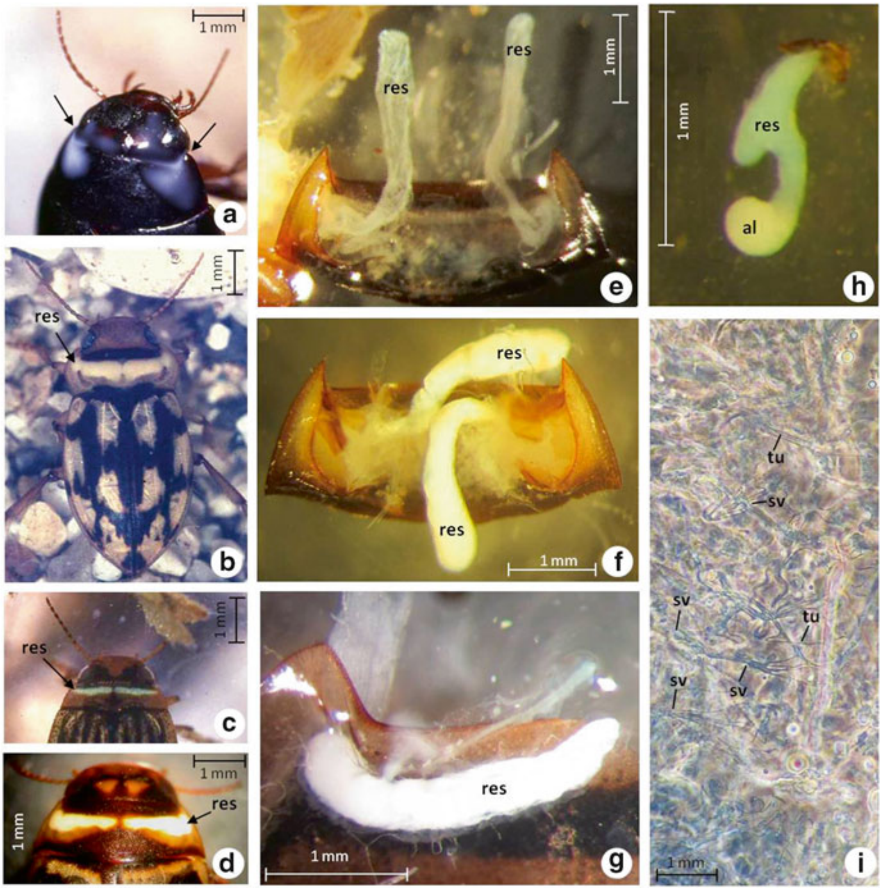


Fig. 6.12 Structure of prothoracic defensive glands of dytiscid beetles. (**a**) Molested specimen of *Ilybius* spec. depleting milky fluid from its paired prothoracic glands. (**b–d**) Prothoracic defensive glands of *Stictotarsus duodecimpustulatus* (**b**), *Hygrotus impressopunctaus* (**c**), *Platambus maculatus* (**d**). Prepared prothoracic defensive glands of *Ilybius fenestratus* (**h**), *Platambus maculatus* (**f**), *Acilius canaliculatus* (**g**), and *Hygrotus inaequalis* (**h**). Abbreviations: *res* reservoir of prothoracic defensive gland, *al* apical limb of reservoir, Squeeze preparation of prothoracic defensive gland tissue of *Hydaticus seminiger* with tubules (*tu*) and sieve plates (*sv*) (**i**)

(Dytiscidae + Hygrobiidae) and Amphizoidae. Forsyth (1970) suggested that the homology of the prothoracic defensive glands between Hygrobiidae and Dytiscidae (Colymbetinae, Hydroporinae, Laccophilinae, Dytiscinae) is uncertain. In Hygrobiidae the prothoracic defensive glands open near the posterolateral angle of pronotum, in contrast gland reservoirs in Dytiscidae open close to the anterolateral angle of the prothorax (Forsyth 1970).

Both the depletion and chemistry of prothoracic glands of Hygrobiidae is unknown. Therefore it is important to observe representatives of the above mentioned Colymbetinae, Hydroporinae, Laccophilinae, and Dytiscinae. When disturbed

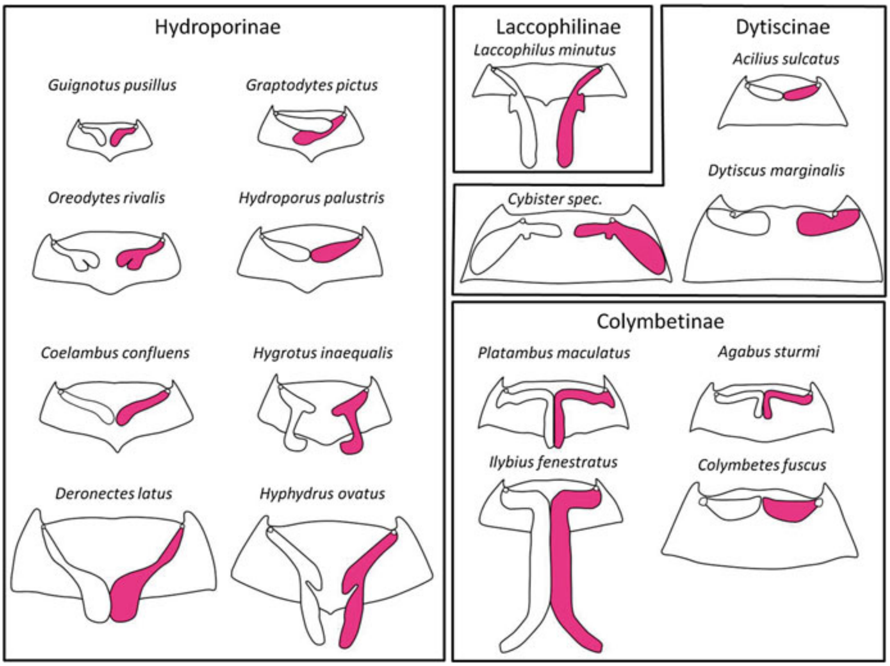


Fig. 6.13 Size and position of prothoracic defensive gland reservoirs in Hydroporinae, Laccophilinae, Dytiscinae and Colymbetinae

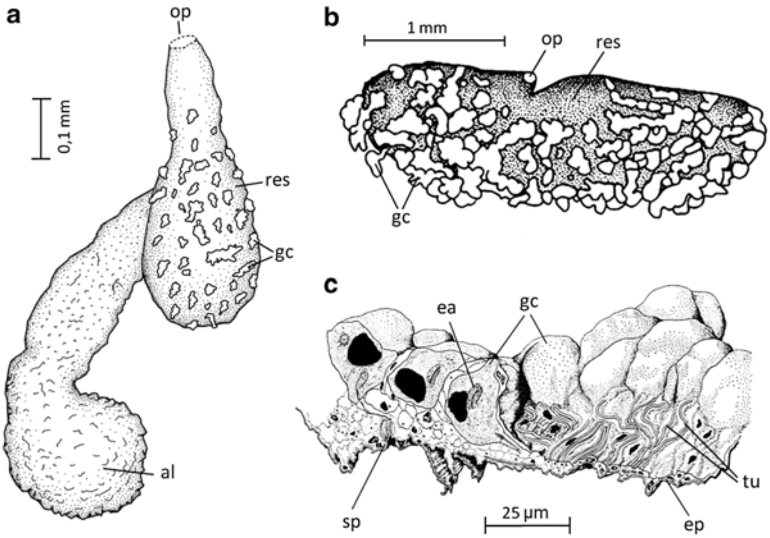


Fig. 6.14 Histology of prothoracic defensive glands. (**a**) *Hygrotus inaequalis*, (**b**) *Dytiscus marginalis* (After Korschelt 1923), (**c**) Section through prothoracic defensive gland of *Hyphydrus ovatus* (Modified after Forsyth 1968). Abbreviations: *al* apical limb, *ea* end apparatus, *ep* epidermis, *gc* gland cell, *op* opening of reservoir, *sp* sieve plate, *tu* tubule. Nuclei are *black*

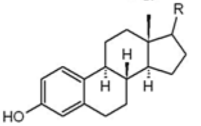
these dytiscids deplete their milky secretions from their prothoracic defensive glands (see *Ilybius* species Fig. 6.12a). Predaceous diving beetles fixated in ethanol usually show adhering droplets of partly denaturated proteinaceous secretions between the posterior border of head and anterior borders of prothorax. The paired prothoracic defensive glands are sac-like structures (Figs. 6.12, 6.13, and 6.14) and are usually restricted to the anterior border of the prothorax as can be observed in *Stictotarsus* (Fig. 6.12b), *Hygrotus* (*Coelambus*) (Fig. 6.12c), *Platambus* (Fig. 6.12d), or *Acilius* (Fig. 6.12g). Openings of the reservoirs are located dorsalaterally on the cervical membrane of pronotum (Figs. 6.12, 6.13, and 6.14). In several genera such as *Oreodytes* (Fig. 6.13), *Hygrotus* s. str. (Figs. 6.12h and 6.13), *Hyphydrus* (Fig. 6.13), and partly *Laccophilus* (Fig. 6.13) reservoirs are branched. In *Cybister* (Fig. 6.13), *Dytiscus* (Fig. 6.13), and *Hydaticus* (not shown) reservoir openings are shifted more centrally and open near a tooth-like posterior projection of the anterior pronotal border. Prothoracic gland reservoirs are not covered by muscle layers as in pygidial glands (Forsyth 1968), however depletion of reservoirs is achieved by increasing of internal turgor pressure and by contraction of tergo-sternal muscles (Forsyth 1968). Discharge of secretions is finally controlled by a single muscle that has its origin on the cervical membrane.

The gland cells cover the surface of the reservoirs partly or completely depending on species. For example in *Hygrotus inaequalis* the prothoracic gland reservoir is covered by clusters of gland cells, however an apical limb of reservoir has no glandular cells (Figs. 6.12h, 6.13, and 6.14a). As already described by Forsyth (1968), secretory cells show tubuli that are connected with a typical end apparatus (Figs. 6.12i and 6.14c). Of note is that every gland cell opens individually into the prothoracic defensive gland reservoir on circular sieve plates (Figs. 6.12i and 6.14c) covering about 5–8 tubules. Sometimes pointed internal projections of the prothoracic defensive gland reservoir are present (e.g., in *Hyphydrus*, Forsyth 1968).

6.4.2.2.1 Chemistry of the Prothoracic Defensive Glands, Emphasizing Those Species with Steroidal Vertebrate Hormones

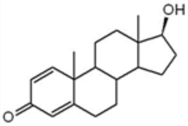
During recent years few insect taxa were shown to produce steroids that are essential for insects. These include several chrysomelid (Chrysomelidae, Laurent et al. 2005), carrion (Silphidae, Staphylinidae, Eisner et al. 2005), and lampyrid beetles (Lampyridae, Laurent et al. 2005; Gronquist et al. 2005), as well as giant water bugs (Belostomatidae, Eisner et al. 2005). In some cases, several steroids have been chemically characterized (e.g., toxic steroidal pyrones (lucibufagins) in lampyrid beetles across their developmental stages (Eisner et al. 2005)). As mentioned above, the prothoracic defensive glands of dytiscids produce an impressive array of known vertebrate steroidal hormones together with many novel steroids and these beetles are unique in manufacturing specific steroids including C_{18}, $C_{19,}$ and C_{21} skeletons (Fig. 6.15, Table 6.2). In both predaceous diving beetles and belostomatid bugs some of these molecules are assumed to be synthesized from cholesterol that is acquired from their prey (Eisner et al. 2005).

estratriene (C_{18})

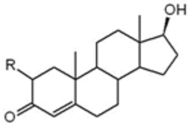


[24]: R: =O: 3-hydroxyestra-1,3,5(10)-trien-17-one; estrone
[25]: R: -OH: 3,17ß-dihydroxyestra-1,3,5(10)-triene; 17ß-estradiol

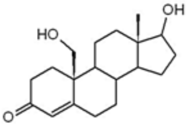
androstene/androstadiene (C_{19})



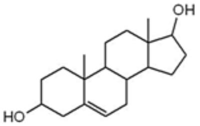
[26]: 17ß-hydroandrost-1,4-dien-3-one; boldenone



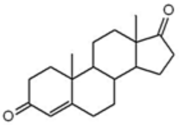
[27]: R: - OH: 2α,17ß-dihydroxyandrost-4-ene-3-one; 2α-hydroxytestosterone
[28]: 2ß,17ß-dihydroxyandrost-4-ene-3-one; 2ß-hydroxytestosterone
[29]: R: -H: 17ß-hydroxyandrost-4-ene-3-one; testosterone



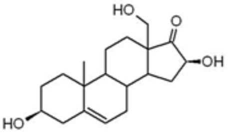
[30]: 17ß,19-dihydroxyandrost-4-ene-3-one; 19-hydroxytestosterone



[31]: 3ß,17ß, dihydroxyandrost-5-ene
[32]: 3α,17ß, dihydroxyandrost-5-ene
[33]: 3ß,17α, dihydroxyandrost-5-ene

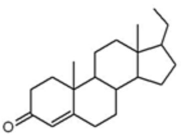


[34]: androst-4-ene-3,17-dione

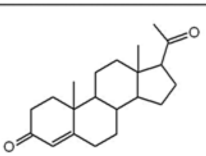


[35]: 3ß,16ß,18-trihydroxyandrost-5-ene-17-one

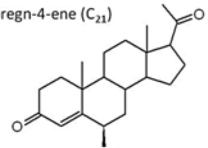
pregn-4-ene (C_{21})



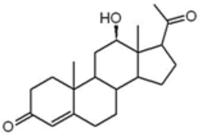
[36]: pregn-4-ene-3-one



[37]: pregn-4-ene-3,20-dione; progesterone

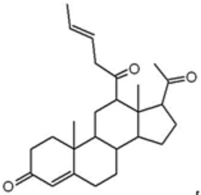


[38]: 6ß-hydroxypregn-4-ene-3,20-dione; 6ß-hydroxyprogesterone

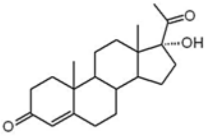


[39]: 12ß-hydroxypregne-4-ene-3,20-dione; 12ß-hydroxyprogesterone

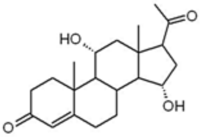
pregn-4-ene (C_{21})



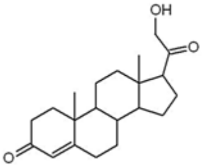
[40]: 12ß-(3'pentenoyl-)pregn-4-ene-3,20-dione



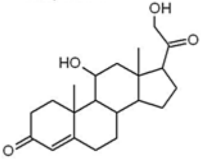
[41]: 17α-hydroxypregn-4-ene-3,20-dione; 17α-hydroxyprogesterone



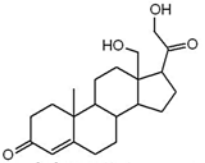
[42]: 11,15-dihydroxypregn-4-ene-3,20-dione; 11,15-dihydroxyprogesterone



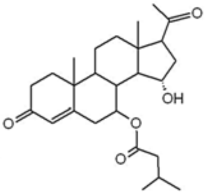
[43]: 21-hydroxypregn-4-ene-3,20-dione; 21-hydroxyprogesterone; cortexone; deoxycorticosterone



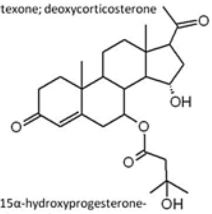
[44]: 11α,21-dihydroxypregn-4-ene-3,20-dione; 11α,21-dihydroxyprogesterone ;
[45]: 11ß,21-dihydroxypregn-4-ene-3,20-dione; 11ß,21-dihydroxyprogesterone; corticosterone



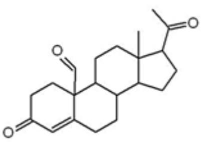
[46]: 18,21-dihydroxypregn-4-ene-3,20-dione; 18,21-dihydroxyprogesterone



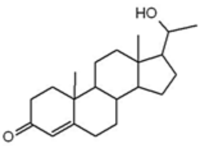
[47]: 15α-hydroxyprogesterone-7α-isobutyrate



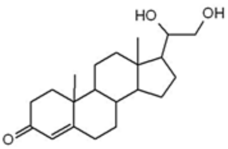
[48]: 15α-hydroxyprogesterone-7α-hydroxyisobutyrate



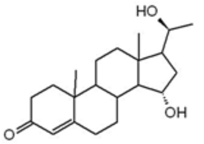
[49]: pregn-4-ene-3,19,20-trione; 19-oxoprogesterone



[50]: 20α-hydroxypregn-4-ene-3-one
[51]: 20ß-hydroxypregn-4-ene-3-one

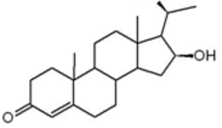


[52]: 20 α,21-dihydroxypregn-4-ene-3-one
[53]: 20ß,21-dihydroxypregn-4-ene-3-one

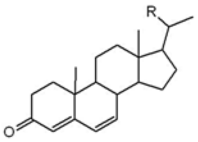


[54]: 15α,20ß-dihydroxypregn-4-ene-3-one

Fig. 6.15 Constituents of Prothoracic defensive glands (**24**–**108**) from dytiscid beetles with continuations pregn-4-ene (C_{21})

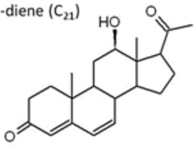


[55]: 16ß,20ß-dihydroxypregn-4-ene-3-one

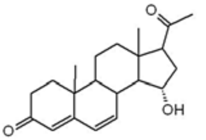


[56]: R = O; pregna-4,6-diene-3,20-dione; 6-dehydroprogesterone
[57]: R = OH; 20α-hydroxypregna-4,6-diene-3-one; cybisterone

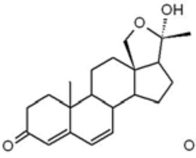
pregna-4,6-diene (C_{21})



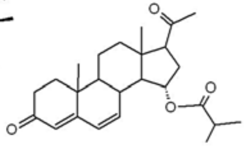
[58]: 12ß-hydroxypregna-4,6-diene-3,20-dione; cybisterol



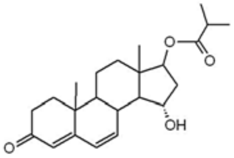
[59]: 15α-hydroxypregna-4,6-diene-3,20-one



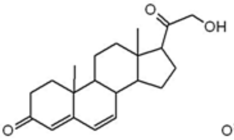
[60]: 18-hydroxypregna-4,6-diene-3-one-18,20-hemiketal; mirasorvone



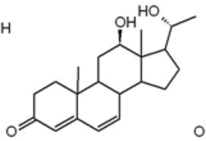
[61]: pregna-4,6-diene-3,20-dione-15α-isobutyrate



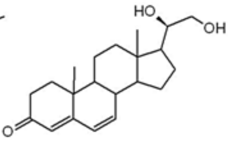
[62]: 15α-hydroxypregna-4,6-diene-3-on-20-isobutyrate



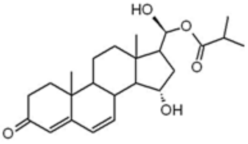
[63]: 21-hydroxypregna-4,6-diene-3,20-dione; 6,7-dehydrocortexone



[64]: 12ß,20α-dihydroxypregna-4,6-diene-3-one

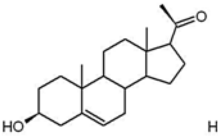


[65]: 20ß,21-dihydroxypregna-4,6-diene-3-one

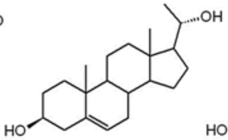


[66]: 15a,20ß-dihydroxypregna-4,6-diene-3-one-20-isobutyrate

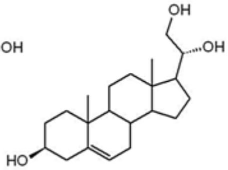
pregn-5-ene (C_{21})



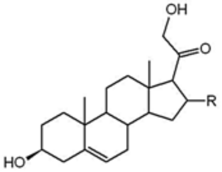
[67]: 3ß-hydroxypregn-5-ene-20-one; pregnenolone



[68]: 3ß,20α-dihydroxypregn-5-ene

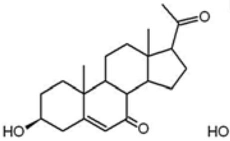


[69]: 3ß,20α, 21-trihydroxypregn-5-ene

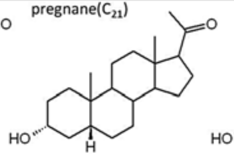


[70]: R = H: 3ß,21-dihydroxypregn-5-ene-20-one; 21-hydroxypregnenolone
[71]: R = OH: 3ß,16α,21-trihydroxypregn-5-ene-20-one; 16α,21-dihydroxypregnenolone

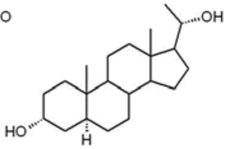
pregnane(C_{21})



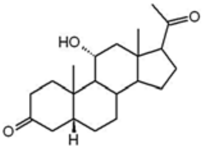
[72]: 3ß-hydroxypregn-5-ene-7,20-dione; 7-oxopregnenolone



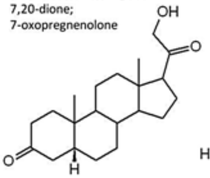
[73]: 3α-hydroxy-5ß-pregnane-20-one



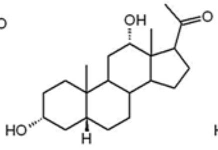
[74]: 3α,20α -dihydroxy-5α-pregnane



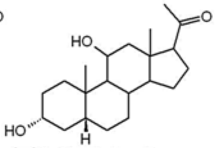
[75]: 11α-hydroxy-5ß-pregnane-3,20-dione



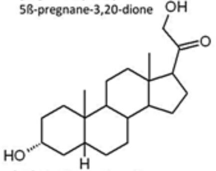
[76]: 21-hydroxy-5ß-pregnane-3,20-dione



[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

Fig. 6.15 (continued)

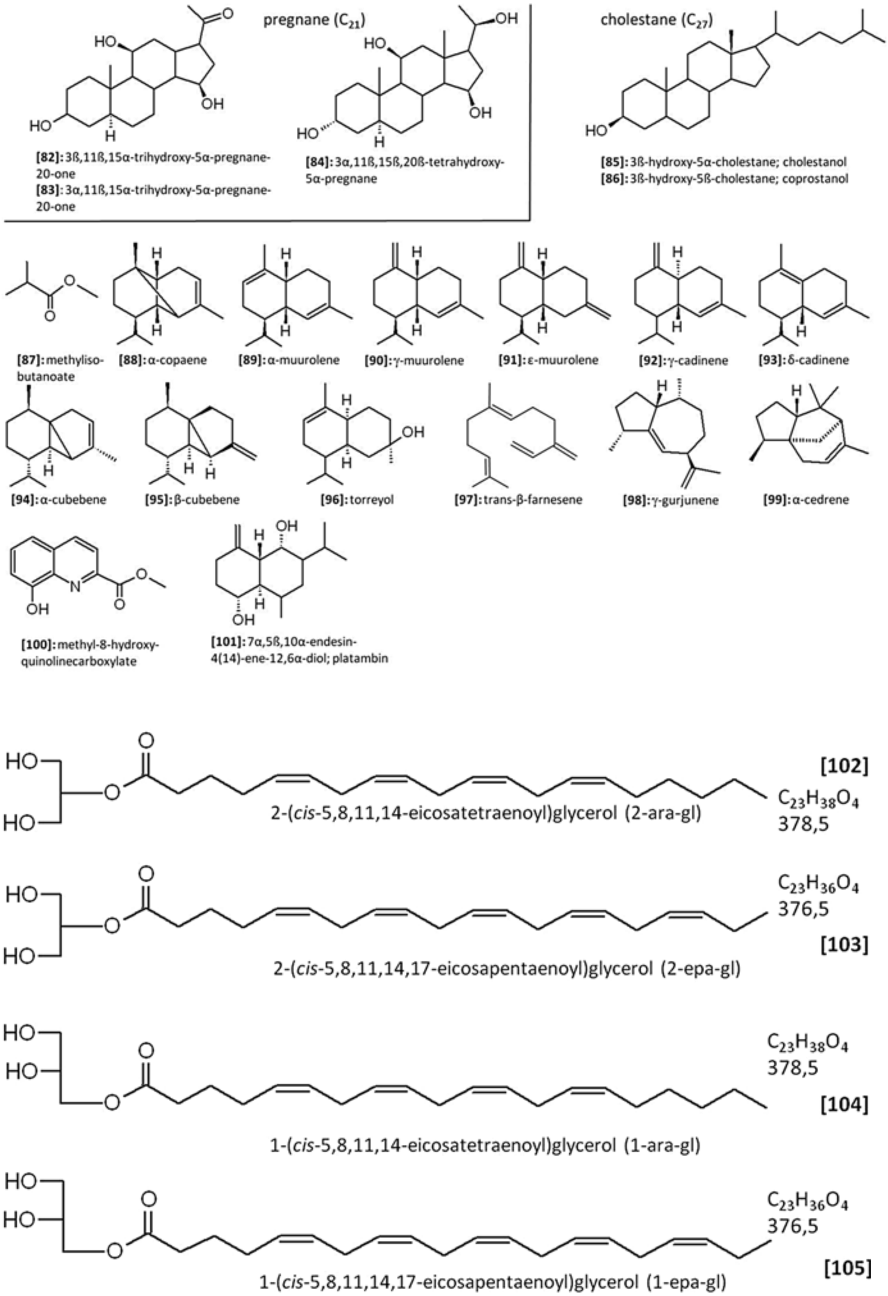


Fig. 6.15 (continued)

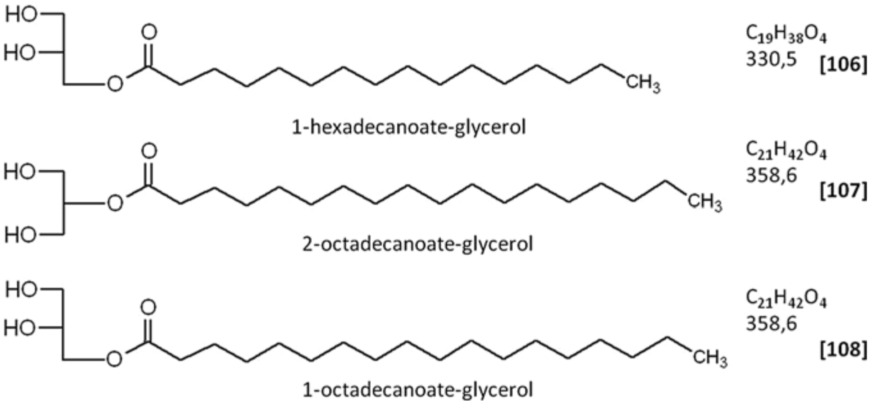


Fig. 6.15 (continued)

Table 6.2 Constituents of prothoracic defensive glands of predaceous diving beetles

Dytiscidae: Colymbetinae	
Ilybiosoma seriatum (Say.)	43 (Fescemyer and Mumma 1983; Miller and Mumma 1973, 1974; Baumgarten 1995)
Agabus guttatus (Payk.)	25,29,38,55,68,73,74,80,82,83,84 (Jungnickel and Dettner 1997)
Agabus bipustulatus (L.)	43,45,50,52,64,80,81 (Schildknecht and Hotz 1970a; Jungnickel 1998; Baumgarten 1995)
Agabus melanarius (Gyll.)	43, 34 (Jungnickel 1998)
Agabus sturmii (Gyll.)	47,48,42,59,61,62, 66 (Baumgarten 1995; Schildknecht and Hotz 1970b)
Agabus nebulosus (Forst.)	41,43,44,46,80 (Jungnickel 1998)
Agabus affinis (Paykull.)	59,102,103,104,105 (Schaaf and Dettner 2000a, b; Baumgarten et al. 1997; Schaaf 1998)
Agabus congener (Thumb.)	59,78,104,105 (Schaaf 1998)
Agabus didymus (Ol.)	70,76,81 (Schaaf 1998)
Agabus unguicularis Thoms.	25,29,43 (Jungnickel 1998)
Agabus brunneus (F.)	70,73,77,85,86 (Schaaf 1998)
Agabus undulatus (Schrank)	25,29 (Jungnickel 1998)
Platambus maculatus (L.)	54,80,101 (Schildknecht et al. 1975, 1969; Schaaf 1998)
Colymbetes fuscus (L.)	Colymbetin, (Schildknecht and Tacheci 1970, 1971)
Ilybius fuliginosus (F.)	29,30,33 (Schildknecht et al. 1967a; Jungnickel 1998)
Ilybius fenestratus (F.)	24,25,29,26,27,28,30,31,32,50,53,54,69,71,87,88,89,90,91,92 ,93,94,95,96,97,98,99,100 (Schildknecht 1977; Schildknecht et al. 1967a, 1971; Schildknecht and Birringer 1969; Jungnickel 1998; Jungnickel 1992)
Ilybius hozgargantae (Burm.)	44,51 (Schaaf 1998)
Ilybius ater (Deg.)	25,29,26,27,28,33 (Jungnickel 1998)
Ilybius crassus (Thoms.)	25,29,26,27,28,30,35,44,53,57,63,65,72,71 (Jungnickel 1998)
Ilybius guttiger (Gyll.)	25,29,26,27 (Jungnickel 1998)

(continued)

Table 6.2 (continued)

Dytiscidae, Dytiscinae	
Acilius mediatus (Say)	Unknown steroid (Newhart and Mumma 1979)
Acilius sulcatus (L.)	43,44,49,50,51,56,57,63 (Schildknecht et al. 1967b; Chapman et al. 1977; Jungnickel 1998; Baumgarten 1995)
Acilius semisulcatus Aubé	43, unknown steroid (Newhart and Mumma 1979; Miller and Mumma 1976a)
Acilius sylvanus (Hilsenhoff)	Unknown steroid (Newhart and Mumma 1979)
Graphoderus cinereus (L.)	67,75,78 (Schaaf et al. 2000)
Graphoderus liberus (Say)	43 (Miller and Mumma 1973; Baumgarten 1995)
Dytiscus marginalis L.	43,50,52,53,57,68 (Schildknecht 1966; Schildknecht et al. 1966; Schildknecht and Hotz 1967; Jungnickel 1998; Baumgarten 1995)
Dytiscus pisanus Cast.	36,37,43,56,57 (Schaaf 1998)
Cybister lateralimarginalis (Deg.)	39,40,43,57,58,63,64 (Schildknecht et al. 1967c; Baumgarten 1995)
Cybister mesomelas Guignot	Benzoic acid, pentadecanoic acid, octadecanoic acid (Dettner unpublished)
Cybister tripunctatus (Cast.)	43,51,58,63 (Chadha et al. 1970; Baumgarten 1995)
Cybister limbatus (F.)	39,43,50,57,58,63 (Chadha et al. 1970; Sipahimalani et al. 1970; Baumgarten 1995)
Cybister confusus Sharp	43 (Chadha et al. 1970; Baumgarten 1995)
Cybister spec. Mexico	58,63 (Schildknecht and Körnig 1968)
Thermonectes marmoratus (Gray)	57,60 (Meinwald et al. 1998)
Dytiscidae, Laccophilinae	
Laccophilus minutus (L.)	73,77 (Schaaf et al. 2000; Baumgarten et al. 1997)
Dytiscidae, Hydroporinae	
Hyphydrus ovatus (L.)	106,107,108, (Baumgarten et al. 1997; Baumgarten 1995)

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-dihydroxyandrost-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-hydroxy-progesterone, **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-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,

(continued)

Table 6.2 (continued)

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-oxo-pregnenolone, **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-trihydroxy-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-octa-decanoate-glycerol, **108**: 1-octa-decanoate-glycerol

What follows is an examination of the chemistry and biological significance of selected prothoracic defensive gland constituents of predaceous diving beetles that especially act as vertebrate hormones. Specifically, I describe estratrienes (**24**–**25**), androstenes/androstadienes (**26**–**35**), pregnanes (**72**–**84**) pregnenes (**36**–**55**, **67**–**71**), pregnadienes (**56**–**66**), and other major groups (Fig. 6.15, Table 6.3). In addition, the utilization of predaceous diving beetles as drugs administered to vertebrates is discussed. The significance of these gland constituents for water beetles is reported in Sect. 6.4.2.2.2. Finally, non-steroidal (**87**–**108**) prothoracic defensive gland constituents are reported.

A considerable fraction of steroids from prothoracic defensive glands in predaceous diving beetles represent well known sexual (estrogens: **24**, **25**, androgens: **26**, **29**, **34**), mineralocorticoid (**43**), or glucocorticoid (**45**) hormones in vertebrates. Table 6.3 summarizes those beetle steroids that occur within vertebrates or act as vertebrates hormones. These vertebrate hormones certainly exhibit no hormonal activities in these beetles. In addition, there exist many steroids in predaceous diving beetles whose hormonal or other activities on both vertebrates and invertebrates are unknown (**27**, **28**, **30**–**33**, **35**, **36**, **38**–**40**, **42**, **44**, **46**–**49**, **52**–**56**, **59**, **60**, **62**–**69**, **72**–**84**, **85**, **86**; see Fig. 6.15). However there exist interesting reports, where predaceous diving beetles are utilized as hormonal drugs for humans and other mammals. Therefore these data are critically discussed with respect to the distribution of prothoracic defensive gland constituents in Dytiscidae (Table 6.2).

In a rather interesting (if not perplexing) use, in East Africa predaceous diving beetles [along with whirligig beetles (Gyrinidae) and larvae of ant lions

Table 6.3 Water beetle steroids which act as vertebrate hormones (for reference numbers see Fig. 6.15)

Type of steroids	Single steroids	Occurrence within vertebrates	Function within vertebrates
C_{18}-steroid Estradienes	Estrone (**24**) 17β–estradiol (**25**)	Produced from cholesterol by mammal ovary and placenta but also by the testes in very low amounts, and possibly by the adrenal cortex (increased biological activity of **25** than **24**). Estrone (**24**) in urine of pregnant woman and mares, follicular liquor, bull-urine, palm kernel oil (Budavari et al. 1989)	Both estrogenes (**24**, **25** mainly bound to proteins), release estrus and are responsible for development and maintenance of secondary female sexual characters (e.g., breast) and further effects. Especially **24** increases proliferation in mammary epithelial cells and altered cell cycle kinetics (Rosen 2008)
C_{19}-steroids Androstenes Androstadienes	Androstenedione (**34**) Testosterone (**29**) Boldenone (**26**)	Androstenes such as **29** and **34** represent most important androgens (mainly bound to proteins) which are produced from cholesterine in interstitial cells of testes. Apart from gonads androstenedione (**34**) is also produced in adrenal glands and represents intermediate of testosterone (**29**). As compared with **34**, testosterone (**29**) is more effective and has a higher daily production in men. The androstadiene boldenone (**26**) naturally occurs in few other species (Brabander et al. 2004)	Both compounds (**29**, **34**) responsible for development and maintenance of secondary male sexual characters. Further effects in vertebrates: male behavior, anabolic activities, growth of bones. Boldenone (**26**) from *Ilybius* species (Table 6.2) represents an anabolic steroid in humans but was originally developed for veterinary use (de Brabander et al. 2004)
C_{21}-steroids Pregn-4-enes	Progesterone (**37**) 17α-hydroxy-progesteron (**41**) 20α-hydroxy-pregn-4-ene-3-one (**50**) 20β-hydroxy-pregn-4-ene-3-one (**51**) Deoxycorticosterone (**43**)	Pregn-4-enes represent active principles of mammal corpus luteum. All human gestagenes such as progesterone (**37**, produced from cholesterol, in corpus luteum during latter half of menstrual cycle), 17α-progesteron (**41**; produced during synthesis of glucocorticoids and sex steroids) and 20α-hydroxy-pregn-4-ene-3-one (**50**; represents an epimer of **51**) are	Gestagenic steroids are responsible for implantation, development, maintenance of embryos within female uteri. In case of pregnancy: continuous secretion of progesterone (**37**), which results in epithelial expansion in mammary gland and there stimulates growth of alveoli. **37** with antiovulatory effect. 17α-Hydroxy-progesteron (**41**) is a natural progestogen and in pregnancy increases in the third trimester primarily due to fetal adrenal production. In ovary,

(continued)

Table 6.3 (continued)

Type of steroids	Single steroids	Occurrence within vertebrates	Function within vertebrates
	Corticosterone (**45**)	present in predaceous diving beetles. 11-Deoxycorticosterone (**43**) is produced by adrenal glands. Corticosterone (**45**) from cortex of adrenal glands is produced in non-human mammals	placenta, adrenals **50** and **51** have properties similar to those of progesterone (**37**) and are in equilibrium with **37**. Deoxycorticosterone (**43**) with mineralocorticoid activity (these steroids such as aldosterone maintain normal blood volume, promote sodium and water retention and increase urinary excretion of potassium and hydrogen ions) and represents precursor to aldosterone. Corticosterone (**45**) represents a glucocorticoid (stimulate gluconeogenesis and increase catabolism of proteins and mobilize free fatty acids) just as cortisol
C_{21}-steroids Pregna-4,6-dienes	6-dehydroprogesterone (**56**) Cybisterone (**57**) Mirasorvone (**60**)	**56** represents a synthetic progestin (=progestogen) which prepares the uterus for implantation and pregnancy. Cybisterone (**57**) and mirasorvone (**60**) represent unique 18-oxygenated pregnan structures described for the first time for insects (Meinwald et al. 1998)	Progestins are used for hormonal contraception, prevent endometrial hypoplasia from unapposed estrogen in hormone replacement therapy. A closely related hormone with mineralocorticoid activity: 18-hydroxydeoxy-corticosterone was isolated from rat adrenals (see corticosterone **45**, Fig. 6.15; Meinwald et al. 1998)
C_{21}-steroids Pregn-5-enes	21-hydroxypregnenolone (**70**) 16α,21-dihydroxy-pregnenolone (**71**)	21-hydroxypregnelone (**70**) was isolated from sulfate fraction of neonatal urine, together with **71**. Shackleton et al. (1987) suggest that **70** is produced in the fetal liver	

(Myrmeleontidae, Neuroptera)] are preferably collected by young girls who use them to stimulate breast development (see Chap. 1 in this book). The girls place the insects on their breasts are at first mechanically stimulated by them using the arthropods mouthparts and surfaces and they subsequently apply the secretions from prothoracic and pygidial glands. This procedure is claimed to be an efficient method to stimulate breast growth in these adolescent girls (Kutalek and Kassa 2005), however the results are anecdotal at best. As this activity is widespread in Africa among many ethnic groups it is worthwhile to search for the possible scientific base of this ethnobiologically important behavior, and I explore some of this background in more detail here.

The link between this human behavior and predaceous diving beetles is perhaps based on the biologically active chemicals produced in the prothoracic defensive glands of these insects (Table 6.2). As a girl approaches adolescence, the first outward signs of breast development begin to appear by an increase of blood gonadotropin-titres that are secreted by adenohypophysis (Rosen 2008). Later on the cyclical estrogen and progesterone secretion, and accumulation of fat in the connective tissue result in enlargement of breasts. Later as the duct systems of the milk glands (i.e., branched tubulo-alveolar modified apocrine sweat glands) grows, acquire a thickened epithelium and secretory glands at the end of the milk ducts are formed, normal female breast developmental stages can be observed. Growth hormone and glucocorticoids, insulin and progesterone contribute to the growth and differentiation of theses glands. The greatest amount of breast glandular differentiation occurs during puberty, however these processes continue for at least a decade and are enhanced by pregnancy (Rosen 2008).

Based on adult dytiscids, gyrinids, and ant lion larvae, biologically active molecules might be of interest. In Gyrinidae, which have no prothoracic glands (see Sects. 6.4.2.1 and 6.4.2.2) the pygidial glands are responsible for both defense and surface hygiene. However the typical gyrinid norsesquiterpenes gyrinidal, isogyrinidal, and gyrinidone, gyrinidione (see Dettner 1985; Meinwald et al. 1972; Schildknecht et al. 1972a) are not known to influence breast development of mammals. The same applies for the antibacterial and smelling low molecular compounds 3-methyl-1-butanol, 3-methyl-1-butanal, 2-methyl-1-propanol and 6-methyl-5-hepten-2-one from gyrinid pygidial glands (Ivarsson et al. 1996; Schildknecht et al. 1972b). On the other hand, by comparison of prothoracic gland steroids from dytiscid beetles with norsesquiterpenes from gyrinid beetles it is evident that norsesquiterpenes from gyrinids are as effective as certain prothoracic gland steroids from Dytiscidae in their penetrating ability trough gill membranes of fishes (Miller and Mumma 1976a, b).

Within predaceous diving beetles there exist a considerable number of species that contain estrone (**24**), 17β-estradiol (**25**) and testosterone (**29**) that can probably influence and stimulate breast growth in females (Table 6.2, 3). Especially various *Agabus*- and *Ilybius*-species contain these compounds (Table 6.2). In addition, progesterone (**37**), which can also influence breast growth is reported from *Dytiscus pisanus* (Table 6.2, 3). Another aspect concerns the steroid amounts per beetle. Sequestration of larger amounts of pregnane derivatives (e.g., deoxycorticosterone, **43**, in *D. marginalis*: 400 µg/beetle; cybisterol, **58**, in *Cybister* spec.: 1,000 µg/beetle) is reported, however estrone (**24**, 2 µg/beetle *I. fenestratus*) and 17-β-estradiol (**25**, 19 µg/beetle *I. fenestratus*, Miller and Mumma 1976a; see Sect. 6.4.2.2) are only found in low quantities. Because there exist natural estrogens, synthetic estrogens (e.g., ethinylestradiol, mestranol, turisteron, moxestrol) and nonsteroid estrogens (e.g., diethylstilbestrol, dimestrol) it would be interesting to look for any of these compounds in these arthropod groups. Moreover, nonsteroid estrogens may be used therapeutically to replace natural estrogenic hormones. It should be also considered that there exist phytoestrogens and mycoestrogens that represent plant- or fungus-derived compounds, which are consumed by animals and might cause estrogenic effects. In some countries, phytoestrogenic plants have been even used in treating menstrual, menopausal, and fertility problems (Müller-Schwarze 2006). Thus, it seems possible that certain arthropod semiochemicals that simultaneously act as vertebrate hormones may bind to estrogen receptors in the mammary glands, or by possibly influencing human hormone regulation or hormone synthesis.

Schildknecht et al. (1967a) report in another paper that water beetles and especially representatives of genus *Gyrinus* were used in European alps as aphrodisiacs against cows and horses (see Ochs 1966). Because *Gyrinus* do not produce steroids, Schildknecht et al. (1967a) suggest that peoples from the alps confused *Gyrinus-specimens* with representatives of *Ilybius*.

The following non-steroid prothoracic gland constituents from adult representatives of Dytiscidae are mainly discussed in Sect. 6.4.2.2.2. Apart from methylisobutanoate (Fig. 6.15, Table 6.2, **87**, Schildknecht 1977) and the preservative benzoic acid (**3**, Fig. 6.7) pentadecanoic and octadecanoic acids have also been identified (Table 6.2). Moreover, several monoglycerides with both saturated (**106–108**, Table 6.2) and unsaturated (**102–105**, Table 6.2, Fig. 6.15) side chains have also been recorded.

Various sesquiterpenes (**88–99**) were identified by Schildknecht (1977) in *Ilybius fenestratus* (Table 6.2, Fig. 6.15). Moreover in *Platambus maculatus*, apart from steroid **55**, an additional sesquiterpene named platambin was recorded (**101**, Table 6.2, Fig. 6.15, Schildknecht 1976, 1977; Weber 1979). Up to now the biological significance of these compounds generally and especially for predacious diving beetles remains obscure.

Even the alkaloid methyl-8-hydroxyquinoline carboxylate (**100**) is abundant in prothoracic defensive gland secretions of *Ilybius fenestratus* (Schildknecht 1976). Due to the yellow color of this compound the *Ilybius* secretion shows a distinct yellow coloration. The free acid could be recently reported from the regurgitate of *Spodoptera* and *Heliothis* larvae (Pesek et al. 2009). The alkaloid derives from the tryptophan metabolism and forms complexes with bivalent metal ions. As an iron-chelator (**100**) it may generally inhibit bacterial infections in the gut. Finally methylesters of leucine and isoleucine were identified from the prothoracic defensive glands of *Ilybius fenestratus*, and in *Dytiscus marginalis*, apart from isoleucine, the valine methylester was also identified (Weber 1979).

Within the Dytiscidae (Fig. 6.16) the Hydroporinae possess well developed prothoracic defensive glands, although it remains a mystery that no constituents of the prothoracic defensive glands have been detectable by gas chromatography–mass

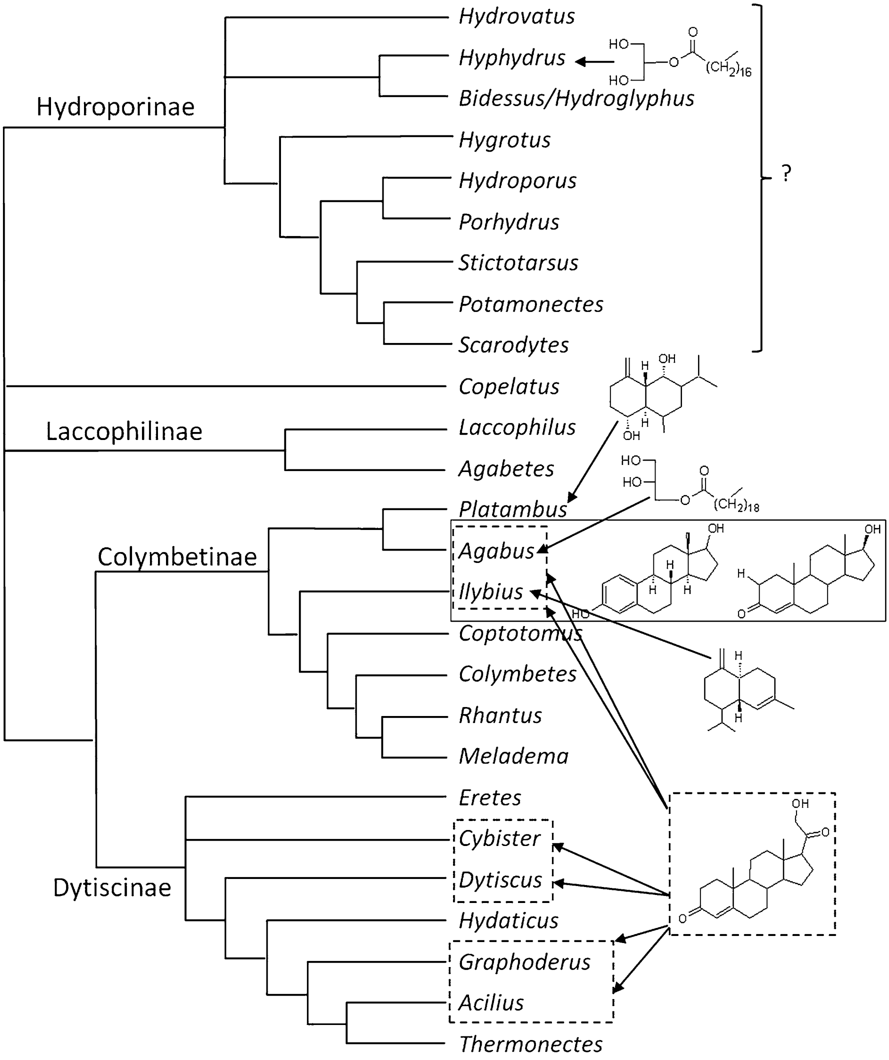


Fig. 6.16 Phylogeny of Dytiscidae genera after Burmeister (1976) and distribution of prothoracic defensive gland constituents according to Fig. 6.15. Those compounds which are present in various taxa are figured by *boxes*. Erratically found chemicals are associated with the genera by *arrows*

spectrometry. Only in *Hyphydrus* (with saturated side-chain; **106–108**) and 2 *Agabus*-species monoglycerides (unsaturated side chains) have been recorded (Figs. 6.15 and 6.16, Schaaf and Dettner 2000b). Within *Agabus* and *Ilybius* two estradienes (C_{18}; e.g., 17ß-estradiol **25**) and ten androstenes (C_{19}; e.g., testosterone **29**) have been exclusively recorded. Other representatives from the Dytiscinae and Colymbetinae subfamily may contain up to 21 different pregn-4-enes (C_{21}; e.g., cortexone **43**), 11 pregna-4,6-dienes (C_{21}), 5 pregn-5-enes (C_{21}), 12 pregnanes (C_{21}) and 2 cholestanes (C_{27}). At the moment, biosynthesis of steroids in dytiscids is only partly understood. Therefore, the polarity of the chemical characters (i.e., the differentiation between plesiomorphic and apomorphic characters) is yet to be defined (see Dettner 1987). It is suggested that C_{27}-steroids might represent rather primitive characters, followed by C_{21}-pregn-5-enes and C_{21}-pregne-4-en-3-ones. If the biogenetic pathway is more advanced, C_{21}-steroids with hydroxyl, pregnanes, or other groups are more advanced. Finally, we would assume that C_{18}- and C_{19}-steroids are highly derived.

Volatile sesquiterpenoids such as platambin (**101**) or γ-cadinene (**92**) seem to be present both in Dytiscinae and Colymbetinae, however careful systematic investigations are absent. The nucleoproteid colymbetin is restricted to the genus *Colymbetes*, whereas methylisobutanol (**87**) was found in the secretion of *Ilybius fenestratus* (Table 6.2). Remarkably, *Colymbetes* does not produce steroids and instead contains the nucleoproteid colymbetin, which lowers blood pressure.

6.4.2.2.2 Biological Activity and Regeneration of Prothoracic Gland Secretions

In the past, Blunck (1911, 1912a, 1917) performed various experiments to investigate the origin, production, and function of the milky secretion that is sequestered in the prothoracic defensive glands named "Schreckdrüsen". The author characterized coloration (milky yellowish fluid), odor (very often aromatic odor) and taste (bitter) of these secretions. More recent work has concerned identification of the biological activities (e.g., feeding deterrents, toxicities, anesthetic activities, membrane absorptions) of steroids and especially defensive steroids of predaceous diving beetles and giant water bugs against both fish (Gerhart et al. 1991; Miller and Mumma 1976a, b; Schaaf et al. 2000; Selye and Heard 1943) and mammals (Selye 1941b; 1942). In addition, preliminary results have characterized pygidial and prothoracic gland secretions against epitrichic ciliates (Schneider 2008). Moreover information on feeding deterrents of polyunsaturated monoglycerides of *Agabus affinis* (Schaaf and Dettner 2000b) and amino acids of *Ilybius fenestratus* (Weber 1979) against fish have been collected. Finally the alkaloid methyl-8-hydroxy-quinolinecarboxylate (**100**) from *Ilybius fenestratus* (Schildknecht 1977) and the nucleoproteid colymbetin from *Colymbetes fuscus* were reported as active against mammal predation (Schildknecht and Tacheci 1971).

Against bluegill sunfishes (*Lepomis macrochirus*) feeding deterrents of three structurally related steroids from prothoracic glands of predaceous diving beetles were determined by using artificial food pellets (Gerhart et al. 1991). It was shown that feeding activities drastically vary depending on specific stereochemistries of the steroids involved. Deoxycorticosterone (=cortexone, **43**) showed the highest activities (94 % inhibition), followed by 20α-hydroxypregn-4-ene-3-one (**50**; 58 % inhibition), whereas its epimer 20β-hydroxypregn-4-ene-3-one (**51**) did not significantly inhibit feeding. Gerhart et al. (1991) stress that these results are in contradiction with earlier data based on toxicities and anesthetic actions by using fish that were immersed with steroid solutions. Therefore, the authors suggest specific receptor-ligand interactions. Feeding deterrents with fully saturated pregnanes (**72–86**) from *Graphoderus cinereus* and *Laccophilus minutus* against the minnow *Phoxinus phoxinus* also showed that these prothoracic defensive steroids act as strong feeding deterrents against fish (Schaaf et al. 2000).

Other work has been accomplished with the effects of these steroids and mammals. Young et al. (1996) studied the behavioral and pharmacological effects of certain steroids in mice. A neurosedative behavior was found in the progesterone (**37**)-metabolite 3α-hydroxy-5α-pregnane-20-one that is chemically similar to compound **73**. An antiaggressive effect was also observed when the brain titer of the deoxycorticosterone (**43**)-metabolite 3α,21-dihydroxy-5α -pregnane-20-one (**80**) was increased. Compound **73** (3α-Hydroxy-5β-pregnane-20-one, = pregnanolon, eltanolon) was also identified as a quickly acting cardiac active hypnotic (Tassani et al. 1996). The metabolites **73** and **80** obviously interact with the γ-aminobutyric acid_A (GABA_A) receptor/chloride canal complex in the central nervous system (Lan and Gee 1994). It is remarkable that the GABA_A receptors are known to contain allosteric modulator sites for therapeutically useful drugs such as benzodiazepines and barbiturates (Lan and Gee 1994).

In detailed investigations, Miller and Mumma (1976a, b) studied toxicities, anesthetic activities. and membrane absorptions of water beetle steroids administered as solutions to immersed minnows (*Pimephales promelas*). Most active steroids in the minnow bioassay were 4-pregnen-3-ones (**36–55**) and related derivatives that are also present in prothoracic defensive glands. The activity of steroids was highly related to the degree of oxygenation. Those steroids oxygenated at the termini of the molecule (C_3 and C_{20} in C_{21}-steroids: **36–55**; C_3 and C_{17} in C_{19}-steroids: **26–35**) were most active; decreased or increased oxygenation of the steroid molecule resulted in a loss of activity. Remarkably, all active steroids were poorly water-soluble and 80 % of steroid absorption occurred via the gills, which are the primary site of steroid-uptake as compared with the skin (20 %).

In comparing bioassays of various structurally different steroids (only a few are also present in dytiscids) against fish (immersed minnows) and mammals (intraperitoneally injected rats), Selye and coworkers showed that those steroids are active in both (Selye 1941a, b, 1942; Selye and Heard 1943) in spite of the fact that both sets of bioassays were completely different. In fishes their activities were even augmented, with lower amounts of tested steroids necessary in fishes (as compared to mammals) to produce deep anesthesia. In mammals, pregnanes with a 3α-OH-5α-H-structure seem to be particularly effective (Purdy et al. 1990), and fast and deep narcosis (intravenous application) in mammals (Gyermek and Soyka 1975) was achieved with 3α-hydroxy-5α-pregnan-20-one and 3α-hydroxy-5β-pregnan-20-one (**73**, *Laccophilus minutus*), with both components being more effective in rats than the barbiturate thiopental (Norberg et al. 1987). Again, stereochemistry plays a central role concerning biological activities of these steroids. The presence of a 3α-OH-group is very important (Phillips 1975; Harrison et al. 1987; Purdy et al. 1990): 3α-OH-5α-H- and 3α-OH-5β-H-Steroids are effective narcotics in mammals, whereas corresponding 3β-OH-steroids are inactive.

It is highly fascinating that four pregnenes (desoxycorticosterone **45**, pregnenolone **67**, progesterone **37**, 3α-hydroxy-pregn-5-ene-20-one) were also recorded from cephalic glands of aquatic belostomatid bugs (Lokensgard et al. 1993). The authors suggest that this remarkable parallel evolution within hemi- and holometabolous fresh water taxa (i.e., belostomatids and dytiscids) may be due to specific predation pressure from fish (Lokensgard et al. 1993).

In a preliminary experiment, epitrichic ciliates in the genus *Opercularia* were isolated from procoxae of *Agabus sturmii* and mixed with droplets of either prothoracic or pygidial gland secretions of the same dytiscid species (Schneider 2008). Under the microscope the movement of the ciliae were registered at the start of the experiment. Cessation of ciliar movement was achieved after 5 min when using pygidial gland secretions, however ciliar activity halted after only 2.5 min when prothoracic gland secretions were used. This may illustrate that prothoracic gland secretions of dytiscids are also active against protozoans, which settle on the surface of many water insects and may be even more efficient as compared with pygidial gland secretion. In contrast, Lust (1950) treated several species of *Orbopercularia* and *Opercularia* with aqueous prothoracic gland secretion of *Ilybius fuliginosus* and observed that most protozoans recovered few minutes after treatment with the solution. Therefore it seems necessary to repeat such experiments by using aequimolar amounts of various prothoracic and pygidial gland constituents.

The sesquiterpene platambin (**101**) from *Platambus maculatus* (Fig. 6.15) was expected to represent a defensive substance against small mammals (Schildknecht 1977), because poikilothermic vertebrates such as amphibians and fishes should be deterred by the co-occurring steroid. Blum (1981) reports that *Cybister fimbriolatus* exudes a prothoracic defensive secretion enriched with potent odorants as sequiterpenes. He suggested either intraspecific activities of these terpenes (e.g., alarm pheromone) or activities of these terpenes as chemical alarm signals for those organisms interacting with these toxic beetles. In the laboratory, juvenile eels (*Anguilla anguilla*) are attracted to the sesquiterpene geosmine (Müller-Schwarze 2006).

The yellow colored alkaloid **100** was suggested to deter especially warm-blooded small vertebrates when the sometimes amphibious species *Ilybius fenestratus* stays on land. In contrast, the complex steroid mixture (Table 6.2) of *I. fenestratus* was expected to act against predatory fish (Schildknecht 1977). The corresponding 8-hydroxyquinoline carboxylic acid represents a strong chelator for Mg^{2+}-ions and moreover has antibiotic activities (Pesek et al. 2009). If *I. fenestratus* was fed with radioactive $^{14}COOH$-marked tryptophane significant amounts were incorporated into alkaloid **100** (Schildknecht et al. 1971).

In a feeding bioassay with the two polyunsaturated monoglycerides (1-ara-gl **104**; 1-epa-gl **105**) of *Agabus affinis*, adult minnows (*Phoxinus phoxinus*) were shown to perceive these monoglycerides, and they acted as a deterrent when compared with controls. Moreover, it was shown that this deterrent effect was only achieved by administering higher amounts of both glycerides compared to those occurring in the glands of the *A. affinis* (Schaaf and Dettner 2000b). Because *A. affinis* prothoracic glands contain both four polyunsaturated monoglycerides and the C_{21} steroid 15α-hydroxy-pregna-4,6-dien-3,20-dione (**59**) it seems probable that the monoglycerides act as emulsifiers for the prothoracic steroid of *A. affinis* that is highly water-insoluble. It is interesting to note that these monoglycerides, such as 2-ara-gl (**102**) have a cannabimimetic potential in mice, which may resemble the anesthetic effects of many steroids in vertebrates.

Amino acids that may be present as free acids or methylesters (Weber 1979) may have various effects on fishes and other predators. Adron and Mackie (1978) found that amino acids such as leucine and isoleucine may represent feeding stimulants for the rainbow trout *Salmo gairdneri*. However other data indicate that leucine and isoleucine, which are present in the secretion of *Ilybius fuliginosus*, may represent both stimulants and deterrents depending on the fish species were tested (Kasumyan and Døving 2003). A compilation from 2006 (Müller-Schwarze) indicates that various freshwater fish species can recognize various prey or plant food odors by using the chemical cues cysteine (earthworm), l-alanine, l-arginine, l-proline (invertebrates, fish, aquatic plants), tyrosine, phenylalanine, lysine (insects, plankton, crustaceans, fish), free amino acids (injured crustaceans), cysteine, asparagine, glutamic acid, threonine, alanine (plants, small animals), cysteine, and arginine (plants).

The whole water-soluble prothoracic gland secretion of *Colymbetes fuscus*, a certain fraction which was assigned as nucleoproteid colymbetin, lowered blood pressure when injected into the veins of urethane-narcotized rats (Schildknecht and Tacheci 1971). For *C. fuscus* six fractions from the prothoracic glands have been found. The two biologically active fractions had molecular masses of about 700. As compared with the alkaloid methyl-8-hydroxy-quinolinecarboxylate (**100**) from the prothoracic defensive glands of *Ilybius fenestratus* that caused clonic spasms in mice (Schildknecht 1977), the biological significance of the various sesquiterpenes from *I. fenestratus* or of platambin from *Platambus maculatus* has yet to be investigated.

Seasonal fluctuations of prothoracic defensive gland titers were described in the species *Agabus seriatus* and *A. obtusatus* (Miller and Mumma 1974; Fescemyer and Mumma 1983). In *A. seriatus* the defensive steroid titer increased from July to September, but low values were obtained during November and December. Further seasonal variations of prothoracic defensive gland constituents were recorded in *Acilius semisulcatus* (Newhardt & Mumma 1979), where the steroid titer increased from July to October, in contrast to the pygidial gland constituents that decreased from July to October. Quantization of deoxycorticosterone (**43**) was performed by means of minnow bioassay in aqueous solutions. The survival time of minnows was correlated to known concentrations of steroids (Miller and Mumma 1974). When the prothoracic gland secretions of *A. seriatus* and *A. obtusatus* were qualitatively and quantitatively analyzed by HPLC both species regenerated about 80 % of their prothoracic gland components within 2 weeks. These defensive gland secretions can be collected simultaneously by electrical shocking with five 20-mA, 90-V DC, 1-s pulses with 5 min within between each pulse (Fescemyer and Mumma 1983).

6.4.3 *Other Exocrine Glands*

Apart from adults, there are few data concerning exocrine glands from other dytiscid developmental stages. Brancucci and Ruhnau (1985) described parastigmatic glands in dytiscid pupae of the genera *Lancetes*, *Copelatus, Agabus*, *Eretes,* and *Dytiscus.* These glands are externally characterized by minute circular openings with a fine peritrema near each spiracle. These unusual pupal glands are described in detail morphologically (as class 3 type according to Quennedey 1998) and chemically in Carabidae (Giglio et al. 2009, 2011). Moreover, when pupal chambers of *Dytiscus* or *Copelatus* were opened special pupal aromatic odors were identified (Blunck 1923a; Naumann 1955). Blunck (1923a) used litmus paper and was successful in detecting an acid secretion near the spiracles. However, he was in doubt if these pupal secretions might deter shrews, moles, or rats that regularly feed on *Dytiscus* pupae. Casper (1913) suggested that the parastigmatic glands secrete fat-like water repellent agents that cover the pupal cuticle. The 31 low molecular weight volatiles (such as linalool, α-terpinene, β-pinene, 4,8-dimethyl-3,7-nonadien-2-ol) and especially ketones, aldehydes, alcohols, esters, and carboxylic acid from the abdominal glands of carabid pupae were suggested to have a deterrent function against predators and a prophylaxis function against pathogens (Giglio et al. 2009). Unpublished data from our lab (Jakob 2008; Dettner unpublished) showed that pupae of *Dytiscus marginalis* are characterized by a coconut-like odor, and 4-hydroxy-methylbenzoate (**6**) (Fig. 6.7) and δ-decalactone (Fig. 6.22, **109**) could be identified from the seven volatiles collected. Through GC-MS analysis of the peristimatic glands of the same species we also recorded indole (Fig. 6.22, **110**) and 1,3-dimethoxy-2-hydroxybenzene (Fig. 6.22, **111**).

Descriptions of preputial glands in males of *Dytiscus marginalis* exist (Korschelt 1923) and these glands are single layer glandular epithelia with tubules and connective tissue that are situated between the ventral borders of the paramers. By thin-layer-chromatography of the intensely yellow colored preputial gland secretion the compounds marginalin (Fig. 6.7, **15**), p-hydroxybenzaldehyde (Fig. 6.7, **5**), and 4-hydroxybenzoic acid methylester (Fig. 6.7, **6**) (Dettner unpublished) were identified.

6.5 Dermal Glands, Epicuticular Lipids, and Body Coloration by Pigments

6.5.1 *Dermal Glands and Epicuticular Lipids*

The cuticle of adult predaceous diving beetles is very often covered in oily materials giving the impression that they have been varnished (Fig. 6.17a, b). This appearance is obviously due to the products of dermal glands. According to Korschelt (1923) single-cell dermal glands with tubules and end-apparatuses first originate in the

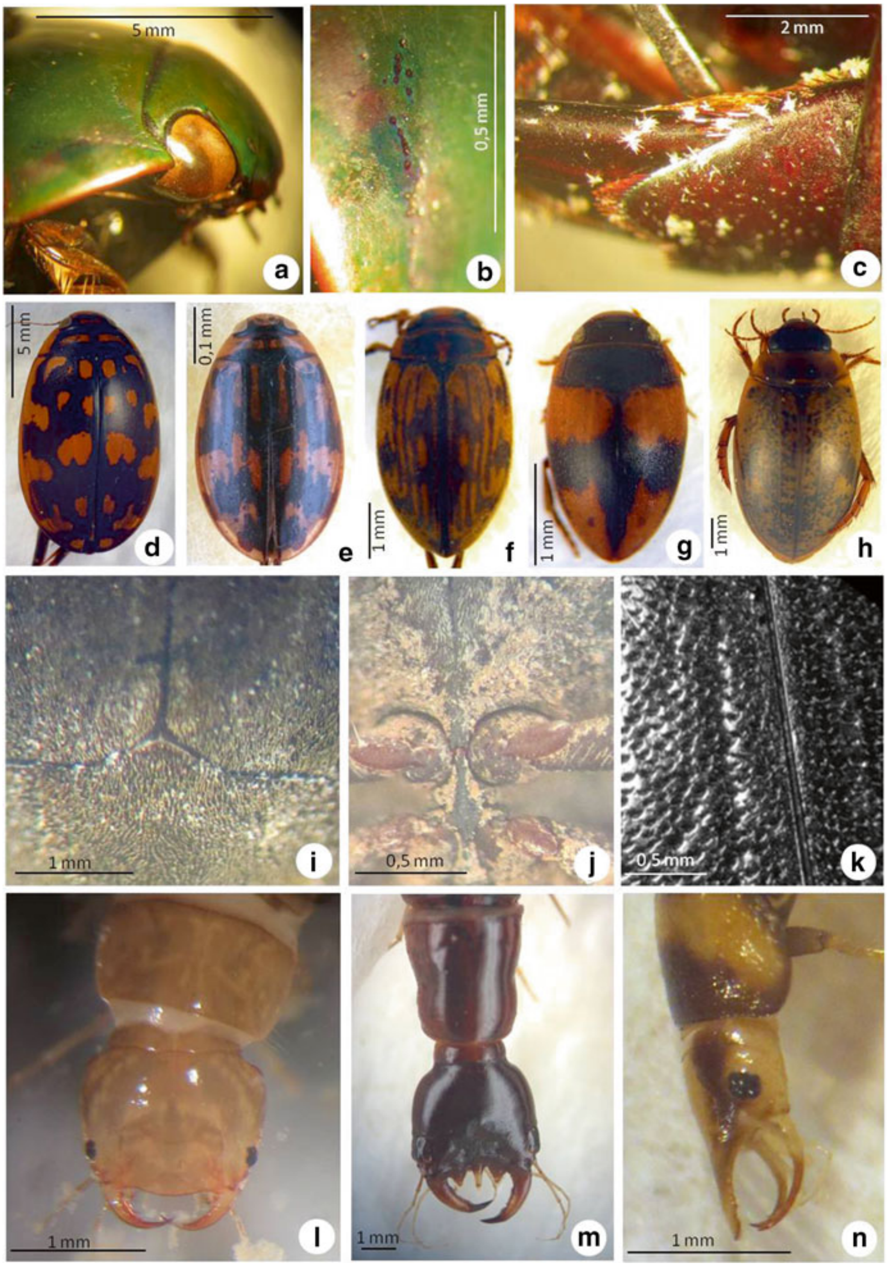


Fig. 6.17 Structural (**a**), secretional (**b**, **c**), and pigmental (**d**–**h**) coloration in Dytiscidae (adults: **a**–**k**, larvae: **l**–**n**). Head and Prothorax of *Cybister vulneratus* (**a**) with structural coloration. Groove on the right pronothal half with fluid epicuticular lipids of *C. vulneratus* (**b**). Tibia and tarsi of *C. vulneratus* with solid crystallized epicuticular lipids (**c**). *Black* and *yellow* coloration patterns in Dytiscidae: *Thermonectus* spec. (**d**), *Sandracottus vestivus* (**e**), *Scarodytes halensis* (**f**), *Graptodytes crux* (**g**) and *Agabus nebulosus* (**h**). Surface structure of *Deronectes moestus* with hairs and dark body coloration (**i**). Underside of *D. moestus* with secretions which obviously serve as adhesives for detritus particles (**j**). Black elytral surface of *Meladema coriacea* (**k**). *Dark* and *yellow* pigments in dytiscid larvae as shown by heads and thoraces of *Copelatus* (*Liopterus*) *haemorrhoidalis* (**l**), *Cybister* spec. (**m**) and *Hyphydrus ovatus* (**n**)

third larval instar, when it has left the water in order to construct a terrestrial pupal chamber; pupae also possess dermal glands. In adult beetles these glandular cells are found on the head and its appendages, the thorax, and the legs. Korschelt (1923) mentions that the density of the dermal glands is significantly larger on the dorsal side of a *Dytiscus* adult as compared with the ventral side. He mentions about 3,000–4,000 per square mm and observed dermal cells within the abdominal tergal structures. Many authors suggest that the dermal glands represent varnish-glands, which produce oils that lower the wettability of the epicuticle. In addition, dermal glands in the area of mouth parts and near articulations of legs serve as a kind of lubricating oil (Korschelt 1923).

As far back as 1922b Blunck states that the wettability of freshly hatched beetles is lower than in older specimens. In addition, the wettability may be significantly modified by hairs (Fig. 6.17i), microsculpture of body surface (Fig. 6.17k), adhering protozoans (Fig. 6.17j), and algae and fungi. However, oily compounds (Fig. 6.17b), which are produced by dermal glands, likely aid in reducing wettability in these beetles.

Various oily materials are known from the surfaces of many dry dytiscid beetles (e.g., *Cybister, Ilybius, Agabus*), and may be recognized when fine surface structures such as microreticulations or colorations are important during determination of the beetles (Roughley 1990). To fully expose morphological features for identification it is often necessary to eliminate these materials by using diethylether, hexane, xylene, ethylacetate, limonene or 1,1,1-trichloroethane as solvents (Warner 2010; Harrison 2012). In addition, both authors generally remark that greasy beetles especially occur in long-lived species which build up considerable fat reserves that degrade and exude from the pinned specimens as an oily or varnish-like covering. Beament (1976) mentions that oily materials on aquatic insects are used for waterproofing. In addition, he found that representatives of *Agabus* and *Ilybius* are found in warm waters because they have higher transition temperatures of about 32 °C. Beament (1976) suggests that the properties of their oily secretions could limit their distribution and would be correlated with their capacity to osmoregulate. In contrast, transition temperatures in *Dytiscus* are at 24 °C, and representatives of this genus would die at 24 °C and congregate in cold water around an ice cube. Although the chemistry of these solid and oily compounds is unknown in Dytiscidae, there exist data from intersegmental glands in Ponerinae ants (Attygalle et al. 1996). These secretions contain linoleic acid, palmitic acid, methyloleate, and several long-chain hydrocarbons, and have no known behavioral-modifying or antibiotic activities but rather seem to function as lubricants.

6.5.2 *Epicuticular Lipids*

Within insects, lipids, and especially hydrocarbons are widespread and serve primarily as a barrier to water efflux, but also as a waterproofing epicuticular layer and may additionally or exclusively function as signals for chemical communication

(Dettner and Peters 2010). According to Blomquist (2010) cuticular hydrocarbons in insects vary from 21 to 60 carbons. As compared with hydrocarbons from plant surfaces, insect hydrocarbons possess various double bonds and methyl branches. It may be that both branching and double bonds may increase informational content of these mixtures in intra- and interspecific chemical interactions, while the waterproofing capabilities remain (Blomquist 2010; Dettner and Liepert 1994).

Concerning freshwater insects and their aquatic developmental stages, there are limited data available with respect to epicuticular hydrocarbons. For several taxa only hydrocarbons from the terrestrial adults are known but aquatic larval stages are unknown (Chrysomelidae: *Donacia*: Jacob and Hanssen 1986; Culicidae: *Anopheles*, *Aedes*, Simuliidae: *Simulium*, Psychodidae: *Phlebotomus*, *Sergentomyia*, *Psychodopygus*, Tabanidae: *Tabanus*, Glossinidae: *Glossina*: Bagnères and Wicker-Thomas 2010). So far, the only work that has identified cuticular hydrocarbons from both aquatic larvae and terrestrial adults is from the stonefly *Pteromarcys californica* (Table 6.4) (Armold et al. 1969). Specifically, adults have more surface lipids and a higher melting surface lipid than larvae, whose surface lipid is an oil at room temperature. Both stages have different surface lipid compositions with adults having a larger percentage of hydrocarbons (adult: 12 %; larva: 3 %), wax esters (adult: 4 %; larva: 1 %), free fatty acids (adult: 49 %; larva: 12 %), and sterols (adult: 18 %; larva: 1 %), while the surface lipids of larvae contain more triglycerides (adult: 7 %; larva: 78 %). With respect to hydrocarbons (Table 6.4) n-alkanes dominate in adults, however more alkenes and 3-methylalkanes are present in larvae, whereas internally branches alkanes occur in comparable titres in both stages. Among free fatty acids, octadecenoic- and octadecatrienoic acids occur in both stages, however hexadecanoic acid dominates in adults, whereas hexadecenoic acid is especially found in females. Because adult *Pteromarcys* specimens do not feed, the differences between adults and larvae cannot be attributed to nutritional effects. Also, if adult stoneflies do not drink, an efficient water conservation mechanism also would be important.

A more recent detailed compilation of epicuticular hydrocarbons from the predaceous diving beetle *Agabus anthracinus* was determined by Alarie et al. (1998). The total ion current chromatogram identified 67 different components, 64 of them could be assigned to n-alkanes (86.4 %), alkenes (27.1 %), terminally (6.1 %) and internally branched monomethylalkanes (15.1 %), or dimethylalkanes (2.7 %). Other branching points in monomethylalkanes are positions 3, 4 or 5. The main components in *A. anthracinus* were n-nonadecane (6 %), n-tricosane (12 %), n-pentacosane (6.5 %), 11-and 13-methylpentacosane (3.4 %), n-heptacosane (7.8 %), 3-methylheptacosane (4 %), 9-C_{27}: 1 (3.3 %), 7-C_{27}: 1 (3.7), 9-C_{29}: 1 (3.7 %), and 9-C_{31}: 1 (4 %).

Other data with respect to hydrocarbon patterns of Dytiscidae where recorded for *Dytiscus marginalis* (both sexes), *Agabus bipustulatus*, and *Ilybius angustior* (Jacob and Hanssen 1986). It is remarkable that several Carabidae possess internally branched monomethylalkanes between 20 and 35 %, whereas monomethylalkanes in Dytiscidae beetles possess between 3.3 and 21.2 %. Also, dimethylbranched alkanes range between 0.4 and 8.0 % in terrestrial Adephaga, whereas they are not present in three Dytiscidae species investigated (apart from *A. anthracinus*: 2.7 %).

Table 6.4 Cuticular Hydrocarbons of Stonefly *Pteronarcys* and Dytiscidae (percentual data)

		Alkanes	Alkenes alkadienes	2-Methyl-alkanes	3-Methyl-alkanes	Internally branched monomethyl alkanes	Dimethyl branched alkanes	Unidentified	
Plecoptera/Pteronartcyidae									
Pteronarcys californica	Adult	63,0	Trace	–	24	12	–	–	Armold et al. (1969)
	Larvae	42,0	12	–	31	13	–	–	“
Coleoptera/Dytiscidae									
Dytiscus marginalis	Male	36,0	59,5	1,8	0,9	1,8	–	–	Jacob and Hanssen (1986)
	Male	58,3	25,1	5,4	3,6	4,2	–	3,4	“
	Female	78,5	8,3	1,8	1,6	5,6	–	4,2	“
Agabus bipustulatus		52,7	47,3	–	–	–	–	–	“
Ilybius angustior		43,0	51,6	1,5	–	1,8	–	2,1	“
Agabus anthracinus		46,8	27,8	–	6,1	15,1	2,7	2,0	Alarie et al. (1998)

In two samples from males of the same species (*D. marginalis*) a significant variability of cuticular hydrocarbons was evident. As compared with males (alkenes 36.0–58.3 %), alkenes in female *D. marginalis* reached 78.5 %.

6.5.3 Coloration of the Integument

Coloration of the integument is important for all developmental stages of aquatic insects, including dytiscids. As predaceous diving beetle larvae and adults serve as prey for many aquatic and terrestrial predators (see Chap. 8 in this book) body coloration, including crypsis or aposematic coloration plays an important role in the aquatic and terrestrial stages of these beetles (Dettner and Peters 2010; Galewski 1971). There exist three mechanisms of coloration within dytiscids that warrant consideration: structural colors, secretion colors, and pigmentary colors.

Structural colors (Fig. 6.17a, b) result from light scattering, interference, or diffractation (Berthier 2007), and many investigations identified these colors based on beetle elytra (Sun and Bhushan 2012). Structural coloration are seldom found within adephagous water beetles but when these colors survive treatments that remove the outer waxy layer of epicuticle this type of coloration seems to be present. In addition these colors tend to vary with the direction of the incident light. In certain representatives of *Ilybius*, *Agabus*, *Cybister* (Fig. 6.17a, b), and *Dytiscus*, structural colors (including blue and green as in *Dytiscus*, Blunck 1909) can be observed. Within hydradephagen beetles diffraction grating has been described in Dytiscidae, Noteridae, and Gyrinidae (Seago et al. 2009; Hinton and Gibbs 1971). Seago et al. (2009) describe diffraction grating as a series of parallel nanoscale ridges that disperses light into ordered spectra.

Secretion colors, which are found in polyphagous water beetles such as within the genus *Helophorus*, are mainly absent in dytiscids. When cuticular surfaces are smooth (Fig. 6.17k) or hairy (Fig. 6.17i) a few species possess epidermal glands that produce a glue that allows for the adhesion of detritus particles on the beetles body surfaces (e.g., *Deronectes moestus*, Fig. 6.17j). These detritus particles may be associated with bacterial biofilms and peritrichic ciliates, which are often associated with aquatic beetles and may aid in crypsis.

The last mechanism for colors in dytiscids are pigmentary colors (Fig. 6.17) that arise from the absorption of light in the visible part of the spectrum by chemical chromophores, also called pigments (Kayser 1985). Adults and most larvae (Fig. 6.17l–n) of dytiscids are commonly dark brown, blackish, or olive in color, and therefore brightly colored (e.g., yellow, red) or marked species are the exception within some genera (Adults: *Thermonectus* Fig. 6.17d, *Sandracottus* Fig. 6.17e, *Scarodytes* Fig. 6.17f, *Graptodytes* Fig. 6.17g, *Agabus* Fig. 6.17h; Larvae: *Hyphydrus* Fig. 6.17n). In some cases, pale spots on the elytra are only visible when the elytra are lifted so that light shines through areas of reduced pigments. Vittae (with longitudinal markings) and fasciae may be either pale or dark depending on the background color. In northern latitudes lightly colored or conspicuously striped, spotted, or mottled specimens are usually associated with streams, the margins of lakes (Young 1960a) or sand-pits (Kehl and Dettner 2003, e.g., *Agabus nebulosus*, Fig. 6.17h; *Nebrioborus canaliculatus*; *Scarodytes halensis*, Fig. 6.17f, *Hygrotus confluens*; *Hydroglyphus geminus*). Specifically, from the Nearctis Young (1960a) mentions the coloration of *Hydroporus lapponum* (edges of tundra lakes) and *Oreodytes* from streams. In contrast, Young (1960a) mentions species from peat pools or vegetated areas that are uniformly black or brown. In addition, brightly colored species of *Hydroporus* or *Nebrioporus* are found in trout ponds and streams (Galewski 1971). In addition, disruptive color patterns of predaceous diving beetles of genera *Thermonectus* (Fig. 6.17d), *Sandracottus* (Fig. 6.17e), *Hydaticus*, and *Prodaticus* in Africa, America, and Australia were reported from exposed habitats with mainly mineral substrates (Larson 1996). Within New Guinea there was found an unusually high portion of dytiscids (e.g., *Laccophilus*) with dark or melanistic forms (Balke et al. 1997). These authors suggested that the shading of the lentic habitats by the luxuriant vegetation may favor the occurrence of dark colored dytiscids.

The aforementioned pigments may be localized in different compartments. Very often all cuticle layers are translucent, and pigments within epidermal cells, within internal organs, compartments, or hemolymph are visible from the outside. In predaceous diving beetles these instances mostly occur in larval and pupal stages. In contrast, adults may possess pigments within different cuticle layers. Larvae of most dytiscid species are rather lightly colored in terms of sclerotized structures and the presence of dark dots are probably due to melanins or represent sclerotin. Some larvae possess dark or black colors (e.g., *Nartus grapei*, several *Hydroporus* species). In other cases, as in larvae of genus *Cybister*, the main total surface of the larvae is membranous and therefore lightly colored.

As in other insects, beetles and especially adephagous predaceous diving beetles may exhibit most chemical classes of biochromes, including carotenoids, chromans, flavonoids, aurones, ternary quinoids, including benzo-, naphtha-, anthra- and polycyclic quinones, tetrapyrroles, including porphyrins and bilins, indolic melanins, ommochromes, papiliochromes, purines, pterines, and isoalloxazines (Needham 1978). These pigments are either synthesized by the beetles themselves or acquired from their food. In many cases the chemical composition on these zoochromes, their distribution among Dytiscidae, and their biosynthesis is unknown.

Carotenoids represent the only tetraterpenoids found in nature that are built up from eight isoprenoid units. Absorbing visible light across 400–500 nm they display yellow to red colors (Figs. 6.17d–h and 6.18b). These pigments are lipophilic and are therefore especially found in insect eggs, and all droplets of fat in hemolymph or fatbodies are thus yellow. Carotenoids are found in most insects from all insect orders (Coleoptera: e.g., Coccinellidae, Chrysomelidae). Generally they cannot be synthesized de novo by dytiscids who may depend on exogene supply from plants, bacteria, and fungi (Kayser 1985).

Most hydradephagean beetles contain lutein, isozeaxanthin, kryptoxanthin, and β-carotene along with 1–2 unknown carotenoids (Table 6.5, Fig. 6.17; Dettner and Hopstätter 1980; Kayser and Dettner 1984). In addition, in *Gyrinus substriatus*

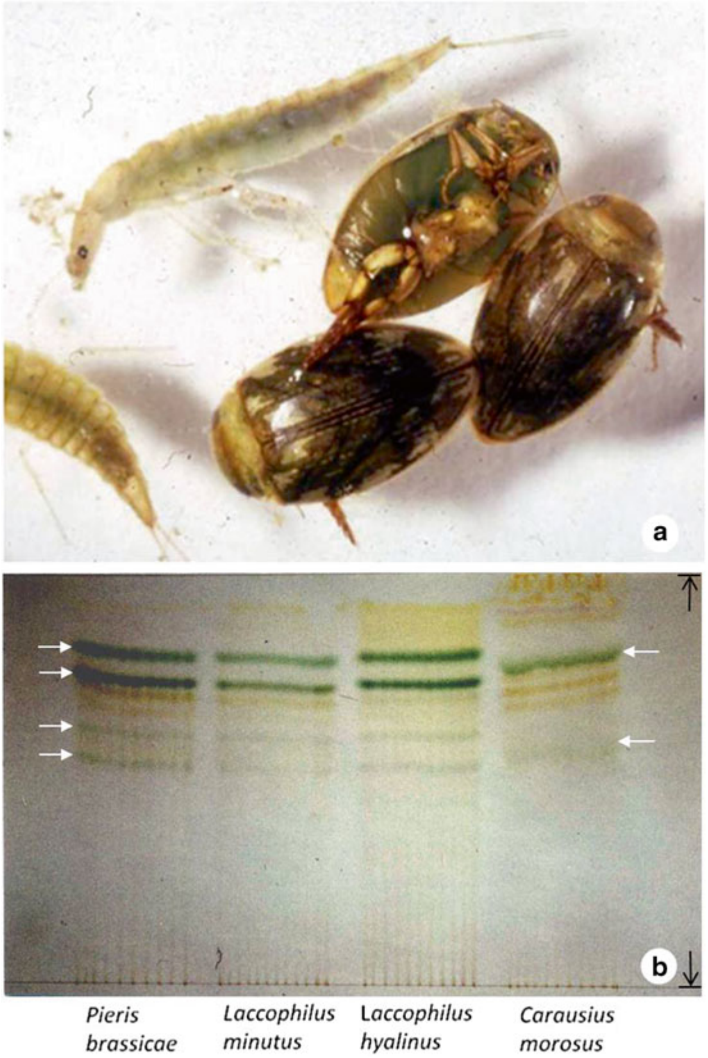


Fig. 6.18 Green coloration of *Laccophilus minutus* beetles and larvae (**a**), and TLC of extracts (**b**) from pierid butterflies *Pieris brassicae*, dytiscid water beetles *Laccophilus minutus*, *L. hyalinus* and stick insects *Carausius morosus*. In *Pieris* and *Laccophilus* there could be shown 4 pterobilin spots respectively (*white arrows*), in *Carausius* biliverdin IXα produces only 2 spots (*white arrows*). Animals were grinded with sodium sulfate and esterified with 8 % HCl/methanol. Chloroform extracts were used for thin-layer chromatography on silica using solvent (benzene/dioxane/glacial acetic acid: 12/2/1; v/v/v). Starting point and solvent front are marked

(Gyrinidae) isokryptoxanthin has been found, whereas *Laccophilus minutus* contains astaxanthin. Analysis of carotenoids in *Haliplus ruficolis* (Haliplidae) and *Hydroporus palustris*, as well as in some Dytiscinae (e.g., *Acilius*, *Dytiscus*) have indicated low concentrations of these yellow pigments.

Table 6.5 Carotenoids in Hydradephaga (see Sect. 6.5.3)

	Lutein (3,3′-diOH-β,ε-carotene)	Isozeaxanthin (4,4′-diOH-β,β-carotene)	Kryptoxanthin (3-OH-β,β-carotene)	Isokryptoxanthin (4-OH-β,β-carotene)	β-carotene (β,β-carotene)	Other carotenoids unidentified	Astaxanthin (3,3′-diOH-*β*,β-carotene-4,4′-dione)
Laccophilus hyalinus (de Geer)	+	+	+	−	+	1	?
Laccophilus minutus (L.)	+	+	+	−	+	1	+
Hydroporus palustris (L.)	−	−	−	−	−	−	?
Rhantus suturalis (McLeay)	+	+	+	−	−	1	?
Agabus bipustulatus (L.)	+	+	+	−	−	−	?
Acilius sulcatus (L.)	+	−	−	−	−	−	?
Dytiscus marginalis L.	+	−	−	−	−	−	?
Noterus clavicornis (de Geer)	+	+	+	−	+	−	?
Gyrinus substriatus Stephens	+	+	+	+	+	2	?
Haliplus ruficollis (de Geer)	+	−	−	−	−	−	?

Whereas chromans and flavonoids are absent in Dytiscidae, the heterocyclic aurones that represent a type of flavonoid are present as gland constituents. The yellow colored marginalin (**15**, Fig. 6.7, Table 6.1) was identified in the pygidial and preputial glands of *Dytiscus* and some *Agabus* species (see Sects. 6.4.2 and 6.4.3) (Dettner 1985).

The green color of certain *Laccophilus* species (*L. minutus*, *L. hyalinus*) is due to the mixture of carotenoids with the blue bile pigment biliverdin IXγ (=pterobiline) (Fig. 6.18). This kind of bile pigment, a tetrapyrrole, was reported for the first time for the order Coleoptera and represents the first identification of biliverdin IXγ outside the lepidopteran order (Kayser and Dettner 1984); biliverdin IXα is present in Odonata, Phasmida (Fig. 6.18b), Orthoptera, Mantodea, Planipennia, and few Lepidoptera (Kayser 1985). The four blue spots in pterobiline and the two spots in biliverdin IXα in Fig. 6.18b probably represent autoxidation products of the pure bile-pigments. Apart from the above mentioned two species, *Laccophilus complicatus* and *L. maculosus* show a green coloration (Bertrand 1928), and this color is also found in pupae of *Laccophilus maculosus*, *L. proximus*, *L. minutus*, and *L. hyalinus*. Both European *Laccophilus* species are found within dense water plants, hence their green coloration seems to provide an excellent adaptation to this environment. It may be possible that the dominant red or brown colors found in tropical Laccophilinae may be due to a morphological color change. In this respect the yellow Mediterranean *Laccophilus testaceus* only seems to represent a subspecies of *Laccophilus hyalinus* [Franciscolo 1979, *Laccophilus hyalinus testaceus* (Deg)].

Ommochromes represent the major part of coloration in insect eyes, but they are also found in the integument of many insect orders and something are responsible for the red color of internal organs (Kayser 1985). They are biosynthetically derived from trypthophan through a degradative pathway via kynurenine and 3-hydroxykynurenine, which is metabolized to xanthurenic acid, 3-hydroxyanthranilic acid, and especially into xanthommatin, acridiommantins, ommins, and ommidins (Kayser 1985). Insects, as well as some fungi and bacteria, can synthesize ommochromes, which are usually bound to protein in intracellular granules. There exist only few records for ommochromes in beetles (Linzen 1974), but dytiscids likely produce these kind of phenoxazine-pigments.

Very often a melanin-type of pigment is used to denote a black pigment without knowledge of its chemical structure. Within dytiscids dark or brown body colorations are likely due to melanins, as melanin-deposition sometimes goes along with the tanning process within the exocuticle and also represents a way of hardening the cuticle. Young (1960b) observed an increase of diffuse melanization in or on the light portions of the color-pattern of water beetles, which are likely driven by the environment in humid regions. In contrast, extension of the dark elements of the color pattern may be genetically controlled.

Dark spots are seen in many adult dytiscids (e.g., Fig. 6.17), the dark surfaces of elytra (Fig. 6.17i, k), and the dark colored sclerites (head, pronotum) in larvae (Fig. 6.17l–n). As a whole, melanins are biosynthesized by oxidation of tyrosine and comprise dark, yellow, brown and even red pigments. Their chemical structures are mostly derived from degradation products of the polymers. Melanins are classified into eumelanins, phaeomelanins, and allomelanins (restricted to plants, fungi, and bacteria), which are based on solubilities, color, elementary composition, and type of degradation products (Kayser 1985). Degradation of eumelanins, which may be deposited in the epidermis or other tissues (about 9 % nitrogen), yields 5,6-dihydroxyindole and 5,6-dihydroxyindole-2-carboxylic acid or pyrrolic acids. In contrast, black allomelanins have lower amounts of nitrogen (1 %). Their degradation results in production of catechol, 1,8-dihydroxynaphtalene and protocatechuic acids.

Sclerotines are generated through sclerotization of insect proteins (arthropodins) by ortho-benzoquinones. They are widespread in insects and especially present in mechanically resistant structures such as the tips of mandibles. It seems highly probable that these pigments also occur in dytiscids, such as in the tips of larval mandibles (e.g., *Copelatus* (Fig. 6.17l), *Cybister* (Fig. 6.17m), and *Hyphydrus* (Fig. 6.17n; Young 1960b)).

The white to yellow colored pteridines or pterin pigments are biosynthesized by insects, vertebrates, and bacteria from a purin precursor (guanosine 5′-triphosphate). Lepidoptera and Hemiptera species are rich in pterin pigments (Kayser 1985). In beetles, only xanthopterin, isoxanthopterin, and leucopterin pigments are found (Kayser 1985). The presence of any of these pigments has to be confirmed in dytiscids. Other pigment types, including quinones, papiliochromes, purines, and isoalloxazines are probably absent in dytiscid beetles, however coloration chemistry of light brown or yellow structures (Fig. 6.17c–h) are unknown.

6.6 Microorganisms and Dytiscids

As in other insects, eggs, larvae, pupae, and adults of dytiscids may be associated with microorganisms. These microorganisms can be localized on the internal or external body surfaces. Internal microorganisms, although present everywhere in the host insect, are often found in mycetocytes or even mycetomes (=bacteriomes), and usually these microbial species either occur intra- or extracellularly (Dettner and Peters 2010). It is possible to isolate and to cultivate microorganisms from compartments within dytiscids, including the gut, rectum, or fat bodies. Due to the fact that certain bacteria are culturable, their biosynthetic capacities can be studied in the laboratory. The number and identity of such culturable (Sects. 6.6.1 and 6.6.2) and non-culturable (Sect. 6.6.3) microorganisms from Dytiscidae is described.

6.6.1 Taxonomically Identified Culturable Strains from the Dytiscid Beetle Gut, and Their Steroid Metabolism Under Laboratory Conditions

By using nutrient-rich and nutrient-poor media 30 eutrophic or facultatively oligotrophic bacterial strains were isolated from foregut and other compartments of *Agabus affinis* and *Hydroporus melanarius* (Schaaf and Dettner 1997).

Both tyrphophilous species were selected because they are found in waters that are characterized by low pH-values, high titers in humic acids, and low numbers of bacteria. Usually a higher fraction of bacterial species can be isolated and cultivated from the guts of invertebrates (about 5–10 %), as compared with other body compartments (König and Varma 2006). The aquatic habitats where both beetle species existed also contained a further 41 strains. All strains from both beetle crops and environments (71 isolates, + 5 reference strains) were compared. Overall the authors found autochthonous bacterial flora in the beetle foreguts, and a moderate influence of the aquatic microflora on the bacterial colonization of the beetles (Schaaf and Dettner 1997). How general this pattern is among other species in other habitats is unknown.

Because steroids are essential for insect physiology, it was suggested that the large amounts of dytiscid steroids from prothoracic defensive glands should be biosynthesized from dietary cholesterol through the help of microorganisms. As was evident in the foreguts of the two tyrphophilous dytiscid species (*Agabus affinis*, *Hydroporus melanarius*) that were analyzed microbiologically, several species of microorganisms in large amounts could be isolated and cultivated especially from this body compartment (see Fig. 6.19a). Based on classical methods of identification using shape and coloration of the colonies it was possible to isolate different microorganism strains. As an example, the foregut of *Agabus binotatus* contained at least four colonies [ABD1, ABD2 and ABD4 and ABD5 (Fig. 6.19a)]. In addition, high densities of *Actinomyces* were found (Fig. 6.19b). These bacteria are characterized by their air-myceliae (Fig. 6.19b) and their ability to produce melanin as a byproduct when secondary compounds are manufactured. The interior crop membrane of the beetles exhibited a lot of crypts, where rod-shaped or pleomorphic bacterial populations were attached to the gut wall (Fig. 6.19c, d). When these beetles take up food, crop bacteria subsequently show a drastic increase in number. In addition, after several days/weeks, the colonies become foamy, and aerobic crop-fluid changes from light to dark brown or black, which may indicate a significant increase of microbes and their co-occurring production of colored secondary metabolites.

The foregut microflora of *A. affinis* and *H. melanarius* mainly consists of Pseudomonads, Bacilli, and irregular, gram-positive rods (e.g., *Arthrobacter*, *Corynebacterium*). Of note is that these bacteria groups within the beetle crops are responsible for a multitude of various steroid transformation reactions (Schaaf and Dettner 1998). Generally, microorganisms are well known to modify the steroid skeleton in aqueous solvents through hydroxylations, reduction of carbonyl functions, dehydration, and hydrations, or are important in separating of racemates or asymmetric syntheses.

Two *Bacillus* strains were isolated from foreguts of *Agabus affinis* and were tested for their *in vitro* steroid transforming ability (Fig. 6.20 right; Schaaf and Dettner 1998). When incubated with androst-4-en-3,17-dione (Fig. 6.20, right) 13 transformation products were detected. Androst-4-en-3,17-dione was hydroxylated at C_6, C_7, C_{11} and C_{14} resulting in formation of 6β-,7α-, 11α- and 14α-hydroxyandrost-4-en-3,17-diones. One strain also produced minor amounts of 6β,14α-dihydroxyandrost-4-en-3,17-dione from androst-4-en-3,17-dione. Certain amounts of metabolites with a 6β-hydroxy-group were further oxidized

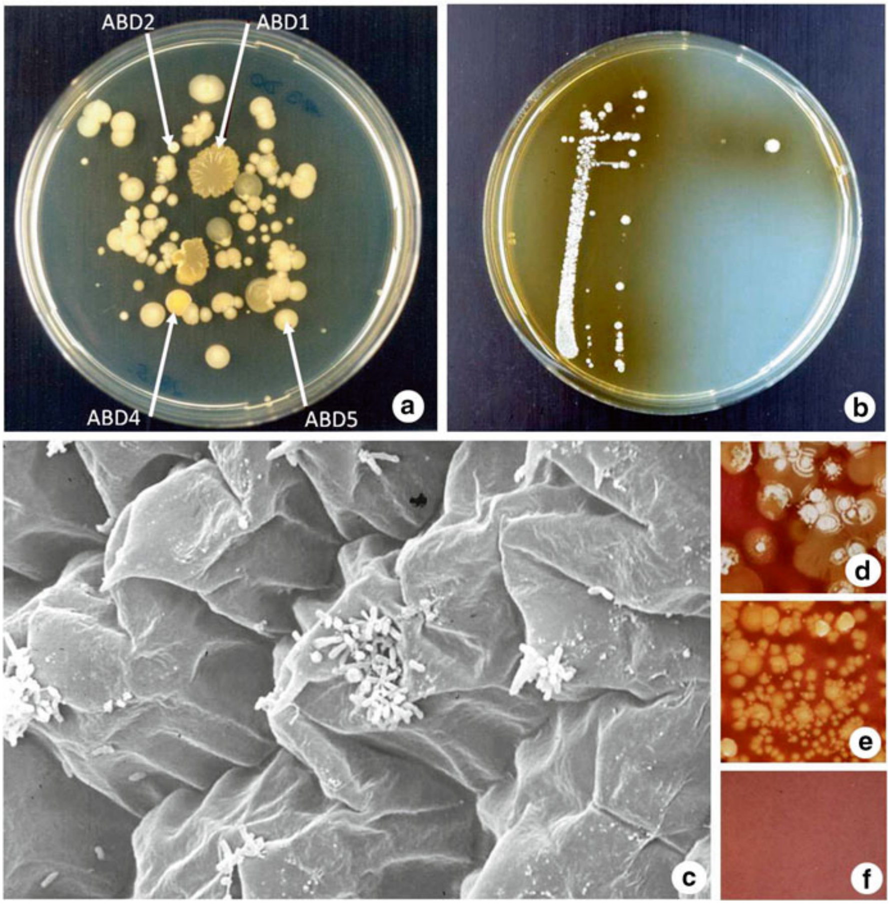


Fig. 6.19 At least four microorganism taxa (ABD1, ABD2, ABD4, ABD5) isolated from gut of *Agabus binotatus* (**a**), colony of *Actinomyces* spec. which was previously isolated from a dytiscid crop producing brown melanin within a Petri dish (**b**). REM of interior crop membrane of dytiscid beetle *Ilybius crassus* with microorganisms between the krypts (**c**). Incubated Petri dishes with isolations from the foregut (**d**), midgut (**e**) and hemolymph/fat body (**f**) of *Agabus melanarius*. There is shown at least one *Actinomyces*-species with its aerial mycelium (**d**). At least two other bacterial species are present in the midgut (**e**), whereas hemolymph/fat body host no cultivable microorganisms at all (**f**)

to corresponding 6-oxosteroids. Moreover, a specific reduction of the Δ^4-double bond resulted in production of 5α-androstane derivatives. In addition, carbonyl functions at C_3 and C_{17} were reduced leading to the formation of 3ξ-OH or 17β-OH- steroids.

If pregnenolone was used as a precursor (Fig. 6.20, left), dominating reactions were hydroxylations, with 7α-hydroxypregnenolone as major product (Fig. 6.20 left; Schaaf and Dettner 2000a). In addition both strains produced lower yields of 7β- and

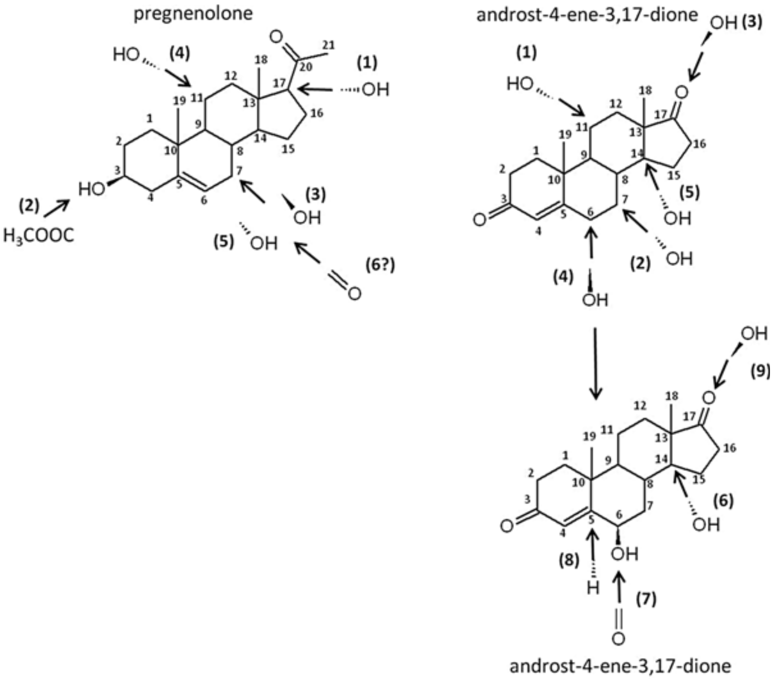


Fig. 6.20 Steroid transformation experiments with *Bacillus*-strains from guts of *Agabus affinis* water beetles. Pregnenolon (*left*) and androst-4-en-3,17-dione (*right*) were used as precursors. *Arrows* indicate those positions within steroid-skeleton where transformations occur. In addition there are indicated functional groups and the number of transformations (*brackets*)

15-hydroxypregnenolone. In contrast, 11-, 17,- and 16α –hydroxypregnenolone were only produced by strain HA-V6-3. The second strain HA-V6-11 had the capability to hydroxylate pregnenolone at C11 and C17 as well (see 7, 11α, 7β, 11α-dihydroxypregnenolone). Both strains oxidized monohydroxylated 7-OH-pregnenolones to 7-oxopregnenolone. One strain (HA-V6-3) also performed 3β-acetylation of pregnenolone in trace amounts. The major difference between the utilization of androst-4-ene-3,17-dione and pregnenolone by these *Agabus* isolates is the shift from C6 to C7, resulting in formation of 7α-hydroxypregnenolone in contrast to 6β-hydroxy-androst-4-ene-3,17-dione.

If one considers the steroidal prothoracic defensive gland compounds it seems highly probable that they are biosynthesized from cholesterol that is taken up by the beetles with their food. The above mentioned data illustrate that microorganisms in the crop may produce cholestenone and cholesteryl-3-acetate from cholesterol (Fig. 6.21). To produce defensive steroids a side chain cleavage (Fig. 6.21 scc) of cholesterol must be postulated. Pregnenolone (**67**), progesterone (**37**) and pregn-4,16-ene-3,20-dione could be present in the hemolymph (Fig. 6.21). The activity of hydroxysteroid-dehydrogenase-isomerases (Fig. 6.21, hsd), dehydrogenases (Fig. 6.21, d, h) and C_{17}-C_{20}-lyase (Fig. 6.21, ly) should be postulated. From **67**, **37**

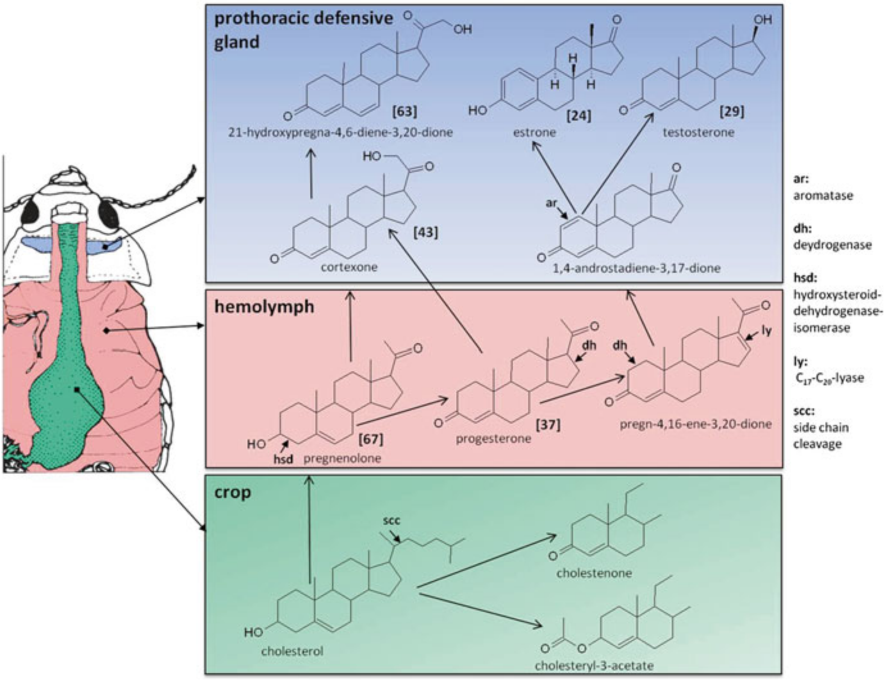


Fig. 6.21 Potential biosynthetic capabilities of microorganisms from the crop (foregut, *green*) of dytiscid water beetles to metabolize cholesterol. There are indicated further metabolites which should be present in the hemolymph (*red*) and in the prothoracic defensive glands respectively the gland reservoirs (*blue*). Numbers refer to Fig. 6.15. Important enzymes according to Swevers et al. (1991) are indicated by *abbreviations*

and pregn-4,16-ene-3,20-dione the gland cells of the prothoracic defensive glands could produce typical steroidal defensive compounds such as cortexone (**43**; biosynthesized either from **67** or **37**). 21-Hydroxypregna-4,6-diene-3,20-dione (**63**; biosynthesized from **43**), estrone (**24**; biosynthesized from 1,4-androstadiene-3,17-dione) and testosterone (**29**; biosynthesized from 1,4-androstiene-3,17-dione). To produce estrone, an aromatase (Fig. 6.21 ar) is necessary. The presence of enzymes involved in the steroid biosynthesis of vertebrate-type steroids was proven in various insect-tissues, however apart from dytiscid beetles such as *Acilius sulcatus*, the steroid concentrations are always very low (Swevers et al. 1991).

At least three investigations concerning biosynthesis of defensive steroids in Dytiscidae have been published. Schildknecht (1970) injected [4-^{14}C]-progesterone, [4-^{14}C]-cholesterol and [2-^{14}C]-mevalonolactone into *Acilius sulcatus*. In contrast to labeled mevalonolactone, cholesterol and progesterone were incorporated after 6 weeks into 6,7-dehydrocortexone (**63**), cortexone (**43**), cybisterone (**57**), 6,7-dihydrocybisterone (**50**, **51**) and 6,7-dehydroprogesterone (**56**). This indicates that these dytiscids absorb cholesterol and other steroids with their food. Biosynthetic experiments with *Agabus seriatus* and injected ^{14}C-cholesterol showed that after 3 weeks 7.5 % of incorporation occurred into deoxycorticosterone (**43**) and other prothoracic gland components (Fescemyer and Mumma 1983). In a detailed study, Chapman et al. (1977) found that pregnadiene derivatives (e.g., 6,7-dehydrocortexone (**64**)) were biosynthesized from cholesterol. The introduction of the Δ^4 and Δ^6 bonds were shown to involve the elimination of 4β and 7β hydrogens, respectively (Chapman et al. 1977). Apart from *Acilius sulcatus* and *Agabus seriatus,* a biosynthesis of vertebrate-type steroids could be only demonstrated in *Manduca sexta* (Swevers et al. 1991).

The biotechnological use of microbial steroid transformations has received increasing economical and scientific interest in the recent years. Thus, the isolation and investigation of microorganisms from 'exotic' sources associated with steroid-carrying dytiscids deserves further attention.

6.6.2 Taxonomically Identified Culturable Strains from the Dytiscid Beetle Gut and Their Secondary Metabolites Produced Under Laboratory Conditions

Nearly all insects associate with microorganisms and fungi, and sometimes these interactions are actually symbiotic. To isolate new kind of microorganisms and new natural compounds with biological activity from exotic sources various hydradephagean beetles were externally sterilized and subsequently selected compartments were analyzed for microorganisms (Gebhardt et al. 2002). Among various dytiscid hosts *Laccophilus minutus* was of interest because one bacterial strain, identified as *Bacillus pumilus*, showed remarkable activities in various bioassays. From the *L. minutus* foregut 14 bacterial strains were isolated. The *B. pumilus*-strain exhibited a pronounced herbicidal activity against both duckweed (*Lemna minor*) and a green algae (*Chlorella fusca*) (Gebhardt et al. 2002). After cultivation in a 10 L fermenter, six secondary metabolites were detected from the *B. pumilus* extract (Fig. 6.22): N-acetylphenylalanine (**112**), N-acetyltryptophane (**113**), l-isoleucine (**114**), malonic acid phenylester (**116**), 3,4-dihydroxybenzoid acid (**115**), and cyclo(propyltyrosyl) (**117**). These metabolites show some interesting biological activities. For instance, N-acetylphenylalanine (**112**) is an antidepressant and appears in large amounts in urine of individuals with phenylketonuria. Another acetylated amino acid is represented by N-acetyltryptophane (**113**), which can be used as a stabilizer of some protein solutions. l-isoleucine (**114**) represents an essential proteinogenic amino acid with various biological functions, whereas 3,4-dihydroxybenzoic acid (**115**) is antioxidant and anti-inflammatory and has tumoricidal effects. This latter compound is widely distributed in nature and occurs in various plants (Gebhardt et al. 2002; green tea), in fungi (*Agaricus, Penicillium*, *Phellinus*, Laskin and Lechevalier 1973), in bacteria (*Flavobacterium*, Kieslich 1976), as a tanning agent in the oothecas of blattid insects (Dettner and Peters 2010), and as a constituent of antimicrobial pygidial glands of dytiscids (Dettner 1985). In pygidial glands, 3,4-dihydroxybenzoic acid is found as methyl- (**7**), or ethyl- (**8**) ester.

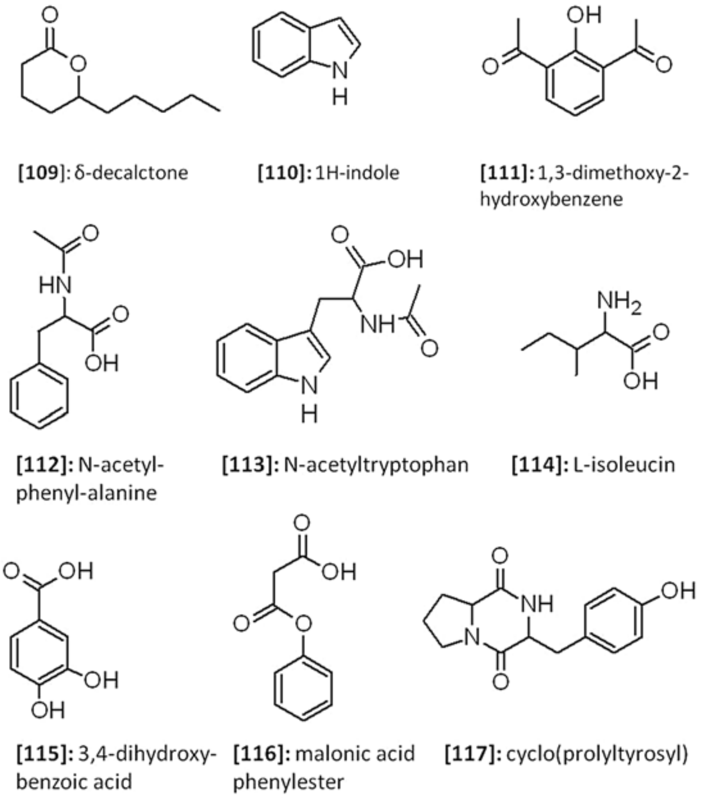


Fig. 6.22 Constituents of pupal peristigmatic glands of *Dytiscus marginalis* (constituents **109**–**111**) and secondary compounds (**112**–**117**) isolated in the laboratory from *Bacillus pumilus* which was isolated from guts of *Laccophilus minutus*

Limited data are available on malonic acid phenylester (**116**). The diketopiperazine cyclo(propyltyrosyl) (**117**) is also known as maculosin I, and was previously isolated from various other microorganisms, including the fungus *Alternaria alternata* and marine sponges (see Dettner 2011). This compound is an extremely host-specific phytotoxin from the *Alternaria-weed* pathogen, and causes black leaf blight in *Centaurea maculosa* (Strobel et al. 1990). Maculosin represents a prototype of a safe and environmentally friendly antiknapweed herbicide (Bobylev et al. 1996), which binds to cytosolic maculosin-binding proteins (Park and Strobel 1994). In addition, maculosin II (dehydrated maculosin I) and various synthetic analogues inhibit the growth of wheat coleoptiles (Bobylev et al. 2000). More recently, maculosin was found to insert into liquid crystalline phase bilayers of 1,2-palmitoyl-sn-glycero-3-phosphatidyl choline or 1-palmitoyl-2-oleoyl-sn-glycero-3-phosphatidyl choline. Its orientation within the membranes is modulated by cholesterol (Lopes et al. 2004). Because several dytiscids produce monoglycerides (Fig. 6.15) in their prothoracic glands, maculosin could also interact with these beetle compounds.

These six above mentioned compounds are produced under laboratory conditions, and thus if they are also biosynthesized under natural conditions in the foregut of *Laccophilus minutus* it would be highly interesting to know their biological significance. When the above mentioned *Bacillus pumilus*-strain from the collection of microorganisms of BASF was investigated 5 years after isolation of the microbial material from *Laccophilus* guts the six metabolites were not produced (M. Langer, unpublished data). It seems possible then that this strain was somehow stressed when it produced the six metabolites. In contrast, a different strain (LU 2644) produced small amount of phenylacetic acid, a main pygidial gland constituent (**11**) of Hydroporinae and *Copelatus* (*Liopterus*) species (Fig. 6.7, Table 6.1). In addition, incubation of a *B. pumillus* extract with phenylalanine significantly stimulated the production of phenylacetic acid, which represented the main compound of the bacterial extract. At present it is unknown if microbial metabolites, which were isolated in the lab, are also present within the intact host insect – symbiotic/parasitic bacteria systems.

6.6.3 Non Culturable Microorganisms from Predaceous Diving Beetles

According to König and Varma (2006) only low amounts of gut microorganisms can be cultivated and therefore it is of interest if non-culturable microorganisms can be also quantified. In 2009 it was reported by Küchler et al. that specimens of *Rickettsia* were detected in four species of the genus *Deronectes* (Hydroporinae). The genus *Rickettsia* is represented by gram-negative bacteria that are present in cocci, rods, or thread-like forms. All these bacteria are obligate intracellular parasites and unlike *Chlamydia* or *Mycoplasma* they possess true cell walls.

In *Deronectes platynotus*, 100 % of all specimens investigated showed association with *Rickettsia*. In other *Deronectes* species lower numbers of investigated had some associations with *Rickettsia* (e.g., *D. aubei*, *D. delarouzei*: 40 %; *D. semirufus*: 33,3 %). All individuals of *D. latus*, *D. aubei sanfilippoi*, and *D. moestus inconspectus* were *Rickettsia* negative. Within Hydroporinae *Rickettsia* could also be identified from specimens of *Hydroporus gyllenhalii*, *H. tristis*, *H. umbrosus*, and *H. obscurus*. *Rickettsia*-positive species from Colymbetinae are *Agabus melanarius*, *A. guttatus* and *Ilybius wasastjernae*. The frequencies of *Rickettsia* infection were maintained across different seasons. *Rickettsia* was also recorded from other coleopteran families including Bruchidae (Fukatsu et al. 2000), Buprestidae (Lawson et al. 2001), Coccinellidae (von der Schulenburg et al. 2001), Curculionidae (Zchori-Fein et al. 2006), and Mordellidae (Duron et al. 2008).

Analysis of 16S rRNA gene sequences revealed a phylogenetic relationship of *Deronectes* rickettsiae with *Rickettsia limoniae*, which also was isolated from the crane fly *Limonia chorea* (Diptera, Limoniidae) and tentatively classified as members of the basal ancestral group. A similarity of *Deronectes* rickettsiae was found to *Rickettsia* of *Cerobasis guestifalica* (Psocoptera, Trogiidae) and *Lutzomyia* *apache* (Diptera, Psychodinae), whereas *Rickettsia* from *D. semirufus* cluster basally with rickettsiae from leeches. Phylogenetic analysis of *gltA* (citrate synthase) gene sequences showed that *Deronectes* symbionts (from *D. platynotus*, *D. aubei*, *D. semirufus*, *D. delarouzi*) were closely related to rickettsial isolate from the spiders *Pityophantes phrygianus* and *Meta mengei*.

The distribution, transmission, and localization of *Rickettsia* in *D. platynotus* were studied using a diagnostic PCR-assay and FISH. *Rickettsia* could be identified in all compartments of *Deronectes* including the head (ommatidia), soft tissue of elytra, hemolymph, and legs. Those compartments with active metabolism, such as fat body or internal reproductive organs contain numerous Rickettsiae. Generally *Rickettsia* is more abundant in females than in males, where the bacteria dominate in accessory glands (and musculature enclosing accessory glands). When eggs of infected females of *D. platynotus* were investigated they were *Rickettsia* positive, which indicates vertical transmission. Due to the predatory lifestyle of *Deronectes*, a horizontal transmission of *Rickettsia* also seems possible, and thus aquatic prey of *Deronectes* should be analyzed in the future. The bacteria could be also found in their oocytes, follicle cells, and second and third larval stages of *Deronectes*, where the bacteria increased from earlier to later stages.

The biological role of *Rickettsia* in Coleoptera and especially in aquatic forms is largely unknown. At the moment there are no indications that *Rickettsia* infections have any effects on the fitness of the *Deronectes* host. Neither reduced body weights and fecundities (as in infected aphids) nor remarkable increases in host size as observed in leeches (Kikuchi and Fukatsu 2005) are observed. It is well known that parasitic living bacteria such as *Rickettsia*, *Spiroplasma*, *Cardinium*, and *Wolbachia* can manipulate reproduction of their hosts for their own benefit [including parthenogenesis, cytoplasmatic incompatibility, feminization, and male killing (O'Neill et al. 1997)].

6.7 Future Directions

It would be interesting if those kairomones mentioned in Sect. 6.4.1 were characterized chemically in order to perform bioassays with authentic compounds. In addition, further taxa of predaceous diving beetles should be investigated chemically in order to characterize their pygidial and prothoracic defensive gland constituents (Sect. 6.4.2). Hereby a chemotaxonomic search strategy as practiced with plants of pharmaceutical value and their biologically active natural compounds is recommended. An important question seems to be the chemical characterization of prothoracic gland constituents from Hydroporinae. In addition, both with respect to pygidial and prothoracic defensive glands several taxa of predaceous diving beetles should be investigated, including *Matus* (Matinae), *Agabetes* (Agabetinae), representatives of Methlini, Lancetinae, *Carabdytes* (Carabdytinae), *Pachydrus* (Hydroporinae), *Paroster* (Hydroporinae), *Necterosoma* (Hydroporinae) or *Laccornellus* (Hydroporinae).

Further field and laboratory bioassays are necessary to detect the effects of gland compounds on beetle relevant pathogenic bacteria, fungi and ectoparasites. In addition, the biological relevance of the plant hormone indole acetic acid from pygidial glands of Hydroporinae should be investigated. With respect to gland constituents of predaceous diving beetles biosynthetic studies, especially of aromatics and steroids, are urgently required.

Concerning microbiological data it would be worthwhile to isolate culturable microorganisms especially from the guts of other predaceous diving beetle species (see Sect. 6.6.2), in order to identify new biological active metabolites. Also, a search for cultivable microorganisms with interesting characteristics will be promising. Of great interest are those beetle species that are found in extreme habitats such as highly polluted waters or hot springs. As in bacteria from guts of larvae of *Heleomyia petrolei* (petroleum fly, Ephydridae) there might be isolated unusual microorganisms that show strong antibiotic resistance or can be grown in organic solvents (Kadavy et al. 2000).

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Chapter 7
Habitats

Margherita Gioria

No one can hunt long for water-insects without coming across the rapacious Dytiscus

(Louis Miall 1903).

Abstract Predaceous diving beetles (Dytiscidae) are a highly speciose group of insects occurring in a large variety of habitat types, where they typically form multispecies assemblages, due to their high diversity and large variation in the degree of habitat specificity. This chapter provides an overview of the characteristics of the main habitats where dytiscid species occur and summarizes the findings of previous studies aimed at characterizing the contribution of various abiotic habitat conditions in determining patterns of dytiscid species distribution, including water flow, permanency, salinity, acidity, temperature, and habitat size. Emphasis is given to the description of various lentic and lotic habitats, and springs, along gradients of habitat permanency. Given increasing evidence of the importance of biotic interactions in determining the realized niche of many dytiscid species, this review describes briefly the role of predation, food sources, and inter- and intraspecific competition as major habitat selection factors for certain dytiscid species. The significance of the structure of the vegetation as a major habitat factor determining patterns in dytiscid species distribution is discussed and new insights on plant-dytiscid relationships are provided. Some of the issues associated with developing simple habitat classifications for dytiscid species are discussed. The main characteristics of some unique habitats where dytiscids form unique assemblages, such as groundwater and interstitial habitats, rock pools, hygropetric habitats, and phytotelmata are described.

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7.1 Defining Habitats

Dytiscids are a highly diverse group of insects (~4,200 species worldwide, Nilsson A., personal communication), which vary greatly in their degree of habitat specificity. Many species display broad habitat preferences, whereas a relatively small number show high habitat specificity (e.g., Foster et al. 1992; Larson et al. 2000), with some species having evolved adaptations to extreme habitat conditions, such as stygobitic (groundwater obligates; e.g., Leys et al. 2003; Watts and Humphreys 2006; Leys and Watts 2008), acidophilic (e.g., Alarie and Leclair 1988; Hendrich 2001), and halophilic species (e.g., Jäch and Margalit 1987; Bailey et al. 2002), or those adapted to life in phytotelmata (e.g., Balke et al. 2008). High species diversity and high variation in the degree of habitat specificity among dytiscid species results in the formation of multispecies assemblages in virtually any habitat type (Larson et al. 2000, reviewed in Chap. 10 in this book), ranging from running to stagnant waters, from large lakes to rock pools, from peatland to salt marshes, from oligotrophic to eutrophic waters, from mountain to lowland ponds, and even in aquifers (e.g., Nilsson 1986; Larson 1997a; Nilsson and Holmen 1995; Foster et al. 1992; Larson 1997a; Leys et al. 2003; Foster 2010). In many habitats, dytiscids have been reported to represent the most diverse or abundant Coleoptera taxon, inlcuding in rock pools (e.g., Ranta 1985), forest ponds (e.g., Fairchild et al. 2003), farmland ponds (e.g., Gioria et al. 2010a), peatland pools (e.g., Downie et al. 1998), and hot springs (e.g., Mason 1939). Differences in habitat specificity are then reflected in large differences in the conservation status of individual dytiscid species, with some species being widely distributed and abundant in commonly distributed habitat types, whereas those restricted to uncommon or rare habitats are threatened by a number of environmental and socio-economic changes (e.g., Foster et al. 1992; Foster 2010) (reviewed in Chap. 11 of this book).

The habitat requirements of any species are a function of a range of species traits, including life history, morphology, physiology, swimming, and hunting strategies (Ribera and Nilsson 1995; Leys et al. 2003; McAbendroth et al. 2005; Yee 2010; Sánchez-Fernández et al. 2012), which determine a species' fundamental and realized niche. Within the landscape matrix, the distribution, degree of connectivity, and dynamics of habitat patches (e.g., rates of habitat formation and disappearance) determine a species' geographical distribution range, population dynamics, and emigration, immigration, extinction, and speciation rates (e.g., Hanski 1999; Ribera and Vogler 2000; Ribera et al. 2001). Knowledge of the frequency and distribution of the aquatic habitats that can be colonized by dytiscids within the landscape matrix, and understanding of the conservation value of such habitats with respect to their role in supporting individual dytiscid species and characteristic dytiscid assemblages is central to the development of sound effective habitat-based conservation measures for this group. Characterizing and classifying the habitats where dytiscid species occur and identifying the habitat variables that define the fundamental and realized niche of dytiscid species, and, subsequently, their potential distribution range, represents an important step towards acquiring such knowledge.

Providing a relatively simple habitat classification for dytiscids is complicated by several factors, including the complexity of abiotic and biotic interactions, adult dispersal, a predominance of information on adults compared to that available for larvae, and differences in the functional definition of what characterizes a habitat. First, any habitat is defined by multiple abiotic conditions that interact with each other in complex ways, such as water temperature and habitat depth, water flow and permanency, and temperature and alkalinity. Beside such interactions, the effects of abiotic conditions are often confounded by biotic factors such as predation, inter- and intra-specific competition, the availability and quality of food, and the structure of the vegetation (e.g., Wellborn et al. 1996; Lundkvist et al. 2003; Vamosi and Vamosi 2007; Gioria et al. 2010a). The distribution of certain dytiscid species has also shown strong nested patterns in some regions, with small habitats supporting a subset of species that are found in larger ones (Nilsson and Svensson 1995; Kholin and Nilsson 1998; Baber et al. 2004). Complex interactions among habitat variables and potential nesting effects make it difficult to characterize and detangle the contribution of individual habitat variables to patterns in dytiscid species distribution (e.g., Larson 1997b; Gioria et al. 2010b) and are reflected in the fact that many species have been recorded from multiple, often contrasting habitat types (see Nilsson and Holmen 1995; Larson 1997a; Larson et al. 2000; Foster 2010). This is true for eurytopic species, which are tolerant of broad environmental ranges and are widely distributed, such as various *Hydroporus* species (e.g., *H. palustris*, *H. obscurus*, *H. erythrocephalus*, *H. striola*, *H. tessellatus*, and *H. umbrosus*), or species such as *Agabus bipustulatus*, *Dytiscus marginalis*, *Ilybius fuliginosus*, and *Rhantus frontalis*. Moreover, some species occupy different habitats along altitudinal or latitudinal gradients. Examples include *Cybister lateralis marginalis*, a species that in Britain is typically found among the vegetation at the margins of lakes or in calcareous ponds, whereas it often occurs in acid bog lakes and peat ponds in Scandinavia (Nilsson and Holmen 1995). *Hygrotus quinquelineatus* is mainly associated with temporary, flooded areas in Fennoscandia and Denmark (Nilsson and Holmen 1995) and with turloughs in Ireland (i.e., calcareous temporary wetlands; Foster et al. 1992), where it is considered a moss dweller, however it is typically associated with reed-beds elsewhere in Europe (Foster et al. 2009). *Dytiscus lapponicus* can be found at high elevations in south and central Scotland, but mostly at sea level in northern Scotland (Balfour-Browne 1962; Downie et al. 1998). These and other examples (e.g., Nilsson and Holmen 1995; Larson et al. 2000; Foster 2010) indicate that much research is required to improve our understanding of the physiological and ecological requirements of many species, as well as of their phenotypic and genotypic variation.

Second, active adult flight can allow for colonization of habitats characterized by suboptimal conditions, for limited periods of time, for instance, to avoid negative biotic interactions (e.g., predation, intra-specific competition, Balfour-Browne 1962; Wiggins et al. 1980; Ranta 1985; Larson 1997b), or the negative effects of droughts (Bosi 2001) or floods (Gray 1981). Many species colonizing temporary habitats may do so to escape fish predation (e.g., *Acilius sulcatus*, Åbjörnsson et al. 1997; *Agabus bipustulatus*, De Mendoza et al. 2012), whereas some species colonize deep interstitial habitats to escape the effect of droughts (e.g., *Agabus paludosus*, Leys et al. 2003; Fenoglio et al. 2006).

An additional issue in providing simple and accurate habitat classifications and in characterizing the habitat preferences of dytiscid species is represented by the fact that, for the majority of species, our understanding of their habitat requirements is based on knowledge of the distribution and behaviour of adults (Larson 1987), with less information available on other life-history stages (Larson 1997a). In particular, few studies have examined directly the distribution of dytiscid larvae along environmental gradients. Among those studies is an investigation by Juliano (1991) who examined the abundance of both adults and larvae of *Hydroporus* species along a pH gradient within a long drainage ditch, and showed that *Hydroporus* adults and larvae have distinct habitat preferences (Sect. 7.3.4). Information on some potential habitat requirements based on correlations to rates of prey consumption by larval dytiscids has been recently provided (Yee et al. 2013). Biological and ecological notes on the habitat where dytiscid larvae have been collected can be found in the work of several authors, who described the morphology of larvae for several dytiscid species (e.g., Galewski 1973a, b, 1975; Nilsson and Holmen 1995; Alarie and Delgado 1999; Alarie et al. 1998, 1999, 2000; Larson et al. 2000; Alarie and Bilton 2001; Nilsson 2001). Because the biotic and abiotic habitat requirements of adults and larvae of dytiscids may differ substantially, and given the important role of the larval stage in determining dytiscid population dynamics, there is a need for additional information on the distribution and characteristics of the structure of dytiscid larval populations. This information is central to improve our capacity to predict distribution patterns for adults and our understanding of the overall habitat requirements of individual dytiscid species at different development stages.

Complex biotic-abiotic interactions, combined with a capacity for long-distance dispersal for many species, and knowledge skewed towards the behaviour and distribution of adults, may strongly impair our capacity to define the habitat requirements and preferences of dytiscid species. However, some of the issues in classifying dytiscids based on their habitat preferences are associated with the definition of the term habitat itself. For instance, whether or not a species is lentic or lotic has long been recognised as the primary classification criterion for dytiscid (and other) taxa (e.g., Larson 1997a; Larson et al. 2000; Ribera et al. 2001). Balfour-Browne (1962) pointed out that this classification is not always straightforward, as some typical lentic species are also found in lotic habitats, or vice versa. This can be due to low habitat specificity for some species, such as *Ilybius fuliginosus*, *Hydroporus palustris*, and *H. tessellatus*, which have been recorded from rivers, streams as well as from lentic habitats across Britain and Ireland (Foster et al. 1992; Foster and Eyre 1992) and Fennoscandia (Nilsson and Holmen 1995). Lack of clear specificity may also be due to a similarity in the habitat conditions within some lentic and lotic water bodies (Balfour-Browne 1962). For instance, within streams, sluggish areas characterized by abundant mud and vegetation can be regarded as lentic habitats (e.g., Larson 1997a), whereas open water habitats subjected to wave action at the margins of lakes or ponds resemble lotic conditions (e.g., Foster et al. 1992).

Difficulties in classifying certain dytiscid species as lentic or lotic are often associated with a tendency, particularly in earlier studies, to define a water body, such as a lake or a pond or a stream, as a habitat. In contrast, defining habitat as a suite of biotic and abiotic conditions occurring within a water body allows reconciling the presence of lentic species within lotic water bodies (in habitats with conditions resembling those of lentic habitats), and vice versa (e.g., Larson 1997b). The distinction between habitat and water body is not only important to better classify individual species based on their habitat requirements, but also to ensure the protection of specific habitats that may play a key role in supporting rare or uncommon species or in connecting habitat patches within the landscape matrix.

Based on these considerations, in this chapter, I refer to habitat as that suite of conditions that define the realized niche or ecological amplitude of a species. Water bodies can be composed of multiple habitats (e.g., lakes, rivers, ponds, streams) or single a habitat (e.g., rock pools, phytotelmata, tree holes). It is worth noting that, at present, there is no consensus on this definition, and both characterizations (habitat within a water body *versus* habitat coinciding with water body and subsequent description of microhabitats found within a habitat) can be found in the literature. As most information on the habitats where dytiscid species occur is available for adults only, descriptions of the habitat preferences for the species mentioned in this chapter refer to adult specimens, unless otherwise indicated.

7.2 Classifying Habitats

Habitat classifications for dytiscid species have been based principally on two approaches, depending on the characteristics of the data available: large-scale species distribution data *versus* community composition data, combined with detailed information on abiotic and biotic habitat conditions within a limited number of water bodies. These methods consist in (1) habitat classifications based on species distribution data and (2) characterizations of the relationship between species composition, abundance, or species richness data along a range of abiotic gradients and biotic conditions. Although the first approach is useful to identify the characteristics of species assemblages across various habitat types, the second allows a quantification of the influence on dytiscid assemblages of individual habitat variables, either quantitative (e.g., temperature, pH, salinity), or categorical (e.g., land use type, permanency, grazing regime), or a combination of both. This approach provides more detailed information on the physiological and ecological amplitude of individual species (see Gioria et al. 2010b, 2011 for a discussion on the methods that can be used to quantify habitat conditions-dytiscid distribution relationships).

The first approach has been adopted by several authors, such as Foster et al. (1992), who used water beetle distribution data as the starting point for developing a robust habitat classification for Irish water beetles. In that study, nine main community types were identified and described in terms of site, habitat, and species, using a multivariate classification method, Two-Way INdicator SPecies ANalysis (TWISNPAN: Hill 1979), and were associated with: (1) deep rivers, including dytiscids of deep running water, such as *Potamonectes depressus* and *Stictotarsus duodecimpustulatus*; (2) rivers with riffle sections and beds of unstable shingles, supporting (a) habitat specialists, such as *Oreodytes* species, (b) habitat generalists, such as *Hydroporus pubescens*, *Agabus bipustulatus*, as well as (c) species typically associated with temporary habitats (e.g., *Hydroporus palustris*, *Ilybius fuliginosus*); (3) temporary habitats such as puddles, typically dominated by habitat generalists but also by species associated with seepage, such as *Agabus paludosus*; (4) permanent open water bodies characterized by species-rich vegetation, typically enriched or eutrophic waters, as well as canals, supporting habitat generalists other than those occurring in puddles; (5) small lentic water bodies, such as ponds, ditches, and vegetated habitats within enriched lakes, supporting species of permanent habitats, including *Hyphydrus ovatus*, *Hygrotus quinquelineatus*, and *Potamonectes assimilis*; (6) fens supporting small habitat specialist dytiscids, such as *Hydroporus glabriusculus*, *H. scalesianus*, *Laccornis oblungus* and *Copelatus haemorroidalis*; (7) cutover bog and rafts of acid fen vegetation, supporting habitat specialist species and acidophilic species, such as *Hydroporus gyllenhalii* (Balfour-Browne 1940; Nilsson and Holmen 1995), *Hydroporus tristis*, *Ilybius aenecens*, as well as species indicators of eutrophic conditions, such as *Laccophilus minutus* and *Hyphydrus ovatus*; (8) montane flushes and ditches in bogs, dominated by *Hydroporus* species; and (9) turloughs and large, shallow ecosystems on base-rich substrata, supporting species associated with moss (Fig. 7.1), such as *Graptodytes bilineatus* and *Agabus labiatus*, as well as species typically found in newly created habitats where bare substratum is dominant, such as *Agabus nebulosus* and *Rhantus frontalis*.

Eyre et al. (1986) used a similar procedure to develop a habitat classification for water beetles in north-east England, based on abundance data for 384 sites. These authors identified nine habitat types, including (1) rivers with fast-flowing, shallow, probably highly oxygenated water, characterized by little vegetation, with *Oreodytes davisii* and *O. septentrionalis* being recorded from gravel; (2) large permanent lakes or ponds, typically characterized by a bare substratum, supporting species with broad habitat preferences, such as *Hydroporus palustris* and *Ilybius fuliginosus*; (3) large permanent ponds with a soft substratum, typically found on boulder clay, supporting a vegetation characterized by the presence of plant species such as *Glyceria*, *Carex*, *Juncus*, and *Phragmites* species, which provide a flooded litter zone; in this habitat, the predominant dytiscid species were *Agabus nebulosus*, *Colymbetes fuscus* and *Hygrotus inaequalis*; (4) 'transition mires', with a mixture of *Sphagnum*, *Glyceria*, *Carex*, and *Juncus* species, supporting widely distributed (e.g., *Hydroporus palustris*) and acidophilic species (e.g., *Hydroporus gyllenhali*); (5) lowland, typically permanent marshes, where *Hydroporus planus* and *Agabus bipustulatus* were the predominant dytiscid species; (6) lowland, slow-moving sections of streams and seepages, with grassy margins, where *Agabus paludosus* was the predominant species, and *Hydroporus* species (e.g., *Hydroporus striola*, *H. umbrosus*, *H. erythrocephalus*, and *H. incognitus*) were also abundant; (7) highly

Fig. 7.1 Example of a turlough located in the Burren, Co. Clare, west of Ireland, supporting a rich and unique dytiscid assemblages, mainly among moss (Photo by M. Gioria)

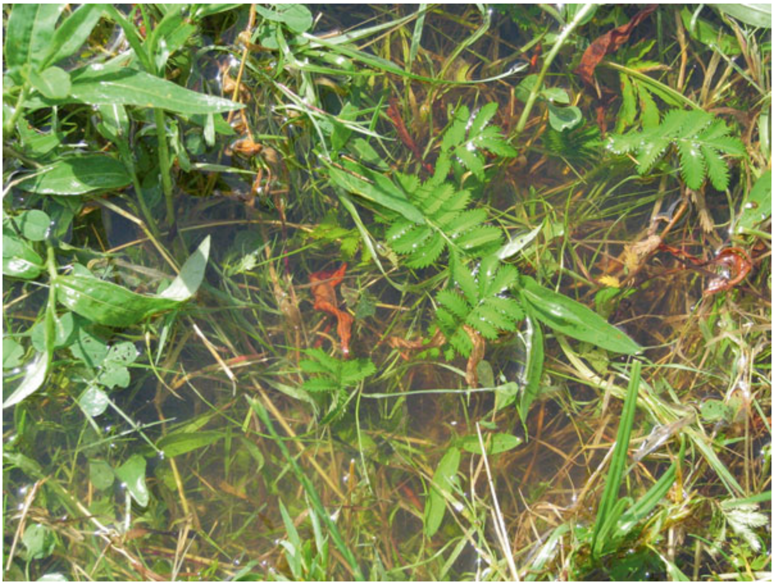

Fig. 7.2 Example of temporary flooded grassland, which had been rapidly colonized by nine dytiscid species, in Ireland (Photo by M. Gioria)

seasonal, lowland temporary pools, supporting active flying species, such as *Hydroporus planus* and *Agabus bipustulatus* (Fig. 7.2); (8) upland mires, characterized by the presence of *Sphagnum* and *Carex* species and of considerable amounts of litter, supporting species in large numbers, such as *Agabus bipustulatus* and *Hydroporus pubescens*, as well as species typical of acid conditions, such as *Hydroporus melanarius*, *H. morio*, *Agabus arcticus*, and *A. congener* (see Nilsson and Holmen 1995; Foster 2010); (9) upland running waters, typically flowing through mosses (*Sphagnum*), where *Agabus guttatus* was the dominant dytiscid species, and other species, such as *Agabus bipustulatus*, *Hydroporus pubescens*, *H. melanarius*, and *H. nigrita*, were also recorded.

Ribera et al. (1996) developed a habitat classification for water beetles in the Ebro delta and other Mediterranean coastal wetlands within the Iberian Peninsula. There, the first variable separating beetle assemblages was sea origin, with *Hydroporus limbatus* being the indicator species of habitats of mainly sea origin, including non-vegetated dune ponds and lagoons, close to the sea and filled with sea water from storms. *Rhantus suturalis* was the indicator species for sites with water from drainage, rain, or with a mixed origin. *Bidessus purnilus* was the indicator species of sites with fresh water and dense vegetation; this group also included *Rhantus suturalis*, *Hydrovatus cuspidatus*, and *Laccophilus* species. A series of small ponds in a clay substratum with marginal vegetation supported *Agabus bipustulatus*, *A. conspersus*, *A. nebulosus*, *Hydroglyphus pusillus*, *Hydroporus tessellatus*, and *Hygrotus confluens*. A group of sites with a mixture of sea water and rain water from drainage, lagoons with occasional connections with the sea, or lagoons and temporary inundated marshes supported typical coastal species, such as *Hydroglyphus signatellus*, *Agabus conspersus*, and *Hydroporus limbatus*.

Similarly, Valladares et al. (2002) examined water beetle assemblages in 12 shallow lakes in the northern Iberian Meseta and showed that permanency was the most important habitat variable determining patterns in species assemblages (Fig. 7.3). These authors identified four TWINSPAN groups, ranging from temporary habitats to semi-permanent and permanent habitats, where *Graptodytes bilineatus* and *Agabus montanus* were particularly abundant in temporary ponds, whereas the presence of *Laccophilus sinuatus* was consistently associated with permanent or semi-permanent habitats. Additional examples of studies that used a similar approach to classify habitats for water beetle assemblages include those examining patterns in fens and drainage ditches among others, including arable fenland and drains in England (Eyre et al. 1990; Foster et al. 1990), and a traditionally managed undrained fen and the ditches of a previously drained cattle-grazed fen meadow (Painter 1999).

When detailed information on the conditions found in habitats colonized by dytiscid species exists, it is possible to calculate quantitative relationships between abiotic factors and biotic interactions with distribution patterns for dytiscids. The results of various studies analysing dytiscid habitat specificity and preferences, and their distribution along environmental gradients are described below (Sect. 7.3).

Fig. 7.3 Shallow lake near the Canal de Castilla, Canal de Castilla (Palencia Province, Spain) in the northern Iberian Meseta (Valladares et al. 2002, Photo by L. F. Valladares)

7.3 Abiotic Habitat Conditions

Over the past few decades, extensive research efforts have been made to improve our understanding of the relationship between individual abiotic habitat conditions and patterns in dytiscid species distribution. The fundamental niche or physiological amplitude of dytiscid species is determined by a large number of abiotic variables, such as water flow (lentic *versus* lotic), water velocity, permanency, temperature, pH, degree of exposure or shade, salinity, nutrient levels, dissolved oxygen, type of substratum, habitat size (surface area and depth), presence of an inflow or outflow for lentic water bodies, origin (natural *versus* artificial), natural disturbance (e.g., ice, waves, wind), and by the interactions among these variables (e.g., Nilsson 1984; Larson 1985, 1997b; Ranta 1985; Eyre et al. 1986, 2005; Foster et al. 1990, 1992; Schäfer et al. 2006; De Mendoza et al. 2012). Regional variables, including landscape history and use (e.g., Foster et al. 1990; Foster 2010; Gioria et al. 2010a), and climate (Gray 1981; Williams 1983; Kholin and Nilsson 1998; Bosi 2001; Leys et al. 2003; Fenoglio et al. 2006), also play a major role in determining patterns of dytiscid species distribution. What follows is a description of some of the habitat variables that are known to have a substantial effect on the distribution and dispersal of dytiscids.

7.3.1 *Lentic* Versus *Lotic Habitats*

The distinction between lentic and lotic habitats represents one of the primary criteria of habitat classification for dytiscid species (e.g., Balfour-Browne 1940; Foster et al. 1992; Larson et al. 2000; Ribera et al. 2001). Balfour-Browne (1962) classified habitats available to water beetles into three main categories, recognizing at least two distinct lentic types of habitat: (1) large, open water areas, including water bodies such as clear lakes with little detritus and vegetation, as well as lakes with much vegetation and detritus; (2) running water; and (3) stagnant water, including silt ponds and detritus ponds. Despite variations in the classification of aquatic habitats based on water flow, this primary classification into lentic and lotic water bodies can then be used to develop finer classifications based on other habitats conditions (Balfour-Browne 1962; Williams 1979; Wiggins et al. 1980).

Within lotic water bodies, a variety of both lotic and lentic habitats can be recognized, including riffle zones, crevices, cracks, floodplains, channels or runs, springs, backwaters and side pools, waterfalls and wet rock surfaces, some of which supporting dytiscids that cannot cope with fast current. Other habitats include hygropetric habitats (i.e., films of water flowing over rocks, for instance, near the edges of streams and waterfalls) (Miller and Perkins 2012; Sect. 10.5). Various classifications of lotic habitats have been proposed; Williams (1979) identified four 'regions' along the length of a river in Canada: eucrenon (the spring region); hypocrenon (the spring brook), rithron (the region extending from the hypocrenon to the point where the mean monthly temperature rises above 20 °C), and the potamon (the region below the rithron extending to the sea or a large lake, where the mean monthly temperature rises to 20 °C) (see also Hynes 1970). Rivers, streams, lakes, and ponds with deep gravel beds are then characterized by interstitial habitats (i.e., hyporheic zone). Most dytiscids are found in the potamon, and may occupy 'potamon habitats' within the rithron in depositional areas (Williams 1979). Important traits of lotic habitats are water velocity (e.g., slow, moderate, swift, up to torrential), substrate (e.g., rubble, sand, clay, and organic debris), temperature range (e.g., minimum winter temperature and maximum summer temperature), and chemical variables (e.g., dissolved oxygen, pH, total dissolved organic and inorganic matter, nutrient concentrations) (see Pennak 1971). Permanency is also a major trait defining lotic (and lentic) habitats (Sect. 7.3). Among artificial lotic habitats, the dytiscid fauna of ditches has been examined in some studies, given their potential to support rich water beetle assemblages. In a study on water beetle assemblages in arable fenland in England, Foster et al. (1990) recognized three main types of ditches based on the assemblages they support, depending upon abiotic factors such as salinity, pH, nitrate concentrations, and permanency, and different vegetation management practices. Painter (1999) also examined the fauna of ditches in traditionally managed and grazing fen in England, where he recorded a Red Data Book dytiscid species (*Agabus undulatus*).

Lentic habitats colonized by dytiscids include lakes and ponds, marshes, fens, as well as small, temporary habitats in rock pools, bog pools, rain pools (e.g., Foster et al. 1992; Nilsson and Holmen 1995; Larson et al. 2000), and phytotelmata (e.g., Kitching 2000; Campos and Fernández 2011; Balke et al. 2008). Dytiscid species occur within the littoral zone of large lakes, which are exposed to wave action and are characterized by a substrate typically made of gravel, rock and sand, thus providing conditions similar to those found in lotic water bodies (Williams 1979; Nilsson and Holmen 1995). The majority of dytiscid species, however, occur in smaller lakes, where wave action is weak, or at the bay of larger lakes (Williams 1979), or in ponds, which are known to support species-rich dytiscid assemblages (e.g., Foster et al. 1992; Foster and Eyre 1992), even within intensively farmed regions (Gioria et al. 2010a). In the literature, ponds are often referred to as shallow lakes or pools, as several definitions for pond have been proposed, mostly based on two main criteria: a combination of surface area and depth, and topography (e.g., Biggs et al. 1998 in the UK, or Oertli et al. 2005 in Switzerland; see Biggs et al. 2005 for a list of definitions of ponds), with some definitions having local significance only. The lack of a global, general definition of a pond limits somewhat the broad applicability of the results of studies investigating the dytiscid fauna of these water bodies; therefore, the actual habitat conditions where dytiscids have been recorded from in ponds or lakes should be examined case by case. Several pond types have been identified, including farmland ponds, tundra ponds, kettle ponds, or marl holes. Beaver ponds have been shown to support several dytiscid species, with some species being commonly found in such habitats, including *Graphoderus fascicollis*, *Agabus pisobius*, *A. erythropterus*, *Dytiscus hatchi*, *D. dauricus*, and *D. harrisii*, whereas others appear to be mostly associated with beaver ponds, such as *Acilius abbreviates* (Larson et al. 2000). Tundra ponds or pools may also support various dytiscid species, including *A. elongates*, *Ilybius churchillensis* (Larson et al. 2000), *Hydroporus acutangulus*, or *A. infuscatus*, which is frequently recorded from small barren pools on tundra (Nilsson and Holmen 1995). Besides natural lentic water bodies, artificial urban or agricultural lentic waters may support various dytiscid species, including reservoirs, quarry ponds, lentic habitats in drainage and roadside ditches, golf course ponds, and fish ponds in gardens and demesnes. Cattle troughs may also support dytiscid species (e.g., *Agabus nebulosus*, *Hydroporus planus*, M. Gioria, unpublished).

Although dytiscids can be found in all the lentic and lotic habitats listed above, the majority of species occur in lentic habitats (Galewski 1971; Roughley and Larson 1991; Larson 1997a; Ribera et al. 2001), particularly within small, shallow water bodies or at the margins of running waters, in slow-moving or stagnant habitats within the emergent vegetation along shore banks, and within marshes (Balfour-Browne 1940; Jäch and Margalit 1987; Foster et al. 1990, 1992, 2009; Larson et al. 2000; Ribera et al. 2003a; Foster 2010). Relatively few species occur in lotic habitats and only a small proportion of those are exclusive. However, more habitat specialists occur in lotic habitats, and many lotic species are geographically restricted endemics (Ribera et al. 2003a). In an investigation on the habitats preferences (lentic *versus* lotic) of dytiscid species of the Iberian Peninsula, Ribera and Vogler (2000) showed that only three of 30 endemic species were exclusively found in lotic habitats (i.e., *Rhithrodytes*, *Stictonectes*, and *Deronectes*). In Britain, *Deronectes latus* is one of the few species that occurs nearly invariably in lotic habitats, within clear, gravelly rivers and streams (Foster 2010). The majority of lotic species are found in lentic water bodies, particularly at the margins of lakes characterized by some wave action, where conditions resemble those found in lotic habitats, and a strong similarity between the dytiscid fauna of rivers and lakes has long been reported (Balfour-Browne 1940). Among lotic species occurring in lakes are *Oreodytes* species, including *Oreodytes alpinus*, *O. septentrionalis* and *O. rivalis*, *O. obesus*, and *O. laevis*, and *Deronectes* species, such as *Deronectes duodecimpustulatus* (Larson et al. 2000). Widespread, eurytopic species such as *Hydroporus palustris*, *H. tessellatus*, *Ilybius fuliginosus*, *Rhantus* and *Agabus* species are commonly found in both lentic and lotic habitats (e.g., Balfour-Browne 1940; Foster et al. 1992; Nilsson and Holmen 1995; Larson 1997a; Larson et al. 2000; Ribera et al. 2001; Foster 2010).

In a comprehensive study of the water beetles of springs in Canada, Roughley and Larson (1991) provided quantitative information on the habitat preferences of 260 dytiscid species known from the Nearctic. Of these species, 71 % were recorded from lentic ‘habitats’ (lakes, ponds, marshes, saline and forest habitats) and 29 % from lotic ones, of which 37 % was also recorded from springs. In their description of the distribution, morphology, and ecology of the dytiscids of the Nearctic region, Larson et al. (2000) indicated that only 18 % (12 out of 66) of species unique to Canadian ecozones (Pacific and Atlantic Maritime, Montane Cordillera, Prairies, and Mixedwood Plains) are lotic. In the Yukon Territory, Larson (1997a) showed that only 12 % of boreal dytiscid species and 15 % of arctic species occur in lotic habitats. Conversely, the majority of species found in the Cordilleran range are lotic (82 %, 9 out of 11 species) and represent 45 % of the lotic fauna of the Yukon Territory, the westernmost territory of Canada. Lotic species in the Yukon Territory include *Agabus* species, such as *A. austinii*, *A. leptapsis*, *A. seriatus*, *A. strigulosus*, as well as *Neoscutopterus angustus*, *Stictotarsus striatellus*, and *Oreodytes sanmarkii*, although many of these lotic species also occur in cold lakes (Larson 1997a).

A larger number of lentic dytiscid species compared to lotic ones are often associated with (1) the swimming and dispersal behaviour of many species, (2) the indirect effect on the chemical and physical habitat conditions within each habitat type (e.g., water flow, water velocity, temperature, dissolved oxygen), and/or with (3) a general requirement for the presence of some vegetation. Ribera et al. (2001) suggested that the relatively low number of lotic dytiscid species compared to that of lentic ones is likely the result of differences in dispersal strategies between these two groups. This suggestion was based on previous patterns observed by Ribera and Vogler (2000), who showed an interesting correlation between habitat type (lentic *versus* lotic) and geographical ranges for water beetles. Specifically, based on 400 water beetle species of the Iberian Peninsula, these authors found that lentic species are usually distributed over the entire Peninsula and beyond, whereas the majority of lotic species are confined to a small proportion of the major biogeographical provinces of Iberia. To test this hypothesis, Ribera and Vogler (2000) used two contrasting genera, i.e., the lentic *Ilybius*, which has very broad distributional ranges, and the lotic *Deronectes*, which has typically narrower habitat requirement, with some species limited to a single mountain range. Their findings, however, provided little evidence in support of this hypothesis. Using a phylogenetic approach to examine the effect of habitat type on speciation rates and range movements for dytiscids, Ribera et al. (2001) tested the hypothesis that differences in the spatial and temporal structure of lentic and lotic habitats within the landscape matrix may select for species with specific dispersal strategies, with active flying dispersal capacity being essential for the long persistence of lentic dytiscid populations, whereas lotic populations could persist without any need for long-flying dispersal. These authors examined potential effects of these differences on clade evolution and speciation rates for the genera *Ilybius* and *Deronectes*, but also did not observed any clear pattern of distribution. These findings suggests that there are no clear mechanisms that may explain the large differences between lentic and lotic dytiscid assemblages and that additional investigations of evolutionary patterns and on the factors driving the colonization of lotic habitats are required.

7.3.2 Springs

Dytiscid species are frequent inhabitants of springs, with some species being exclusive to this habitat. Roughly and Larson (1991) classified the habitat preferences of water beetles into lentic, lotic, and springs, in recognition of the peculiar habitat conditions found in springs; in their examination of the dytiscid fauna of Canada, these authors showed that approximately 11 % of the dytiscids species known from Canada are found in springs (38 species), with 24 % of those (9 species) occurring exclusively in springs.

Springs represent a unique aquatic habitat as they originate at the intersection of groundwater, surface water, and terrestrial ecosystems (Scarbrook et al. 2007). They vary greatly in their morphology, chemistry, temperature range (from cold to hot), and permanence, and various classifications have been proposed based on such characteristics (e.g., Danks and Williams 1991; Erman and Erman 1995; White 2005), including that of Williams (1979), who recognized three types of springs: rheocrene (springs that flow from a defined opening into a confined channel), limnocrene (springs originating from a large, deep pools of water), and helocrene (springs originating from marshes or bogs).

The ecology of springs is strongly dependent upon temperature. The thermal regime defines the end of the eucrenal zone (spring) and the beginning of the hypocrenal zone (springbrook) (Smith et al. 2003), with the former being defined as the point where the annual variation in water temperature is lower than 2 °C (Erman and Erman 1995). The ecology of springbrooks, however, has also been examined and sometimes described as that of springs (see Barquín and Death 2006). Dytiscids have been reported from cold, warm, and hot springs. In a study of the fauna of thermal waters in New Zealand, Winterbourn (1968) recorded larvae of *Antiporus* species from thermal and warm spring waters of the New Zealand Central Plateau at a temperature of 34 °C. Previous records in the same region include *Rhantus pulverosus* from mineral spring water (Wise 1965) and *Liodessus plicatus* from warm pools (Ordish 1966). Stark et al. (1976) recorded both adults and larvae of *Liodessus deflectus* in the outflow of a hot spring in the South Island, New Zealand. Specifically, larvae were common at 28.5 °C, and few larvae were found at 35 °C; for adults, few individuals (1–10/0.1 m^2) occurred at 28.5 and 32.5 °C. Two species, *Hydroporus zackii* and *Dytiscus marginicollis*, have also been recorded from hot springs in North America (Larson et al. 2000). Mason (1939) showed that dytiscids were among the most important group found in Algerian hot springs.

Species that have been recorded from cold springs include *Sanfilippoides* species (Larson 1975; Larson et al. 2000), *Hydrocolus* species, whose members occur in springs or seepage (Larson et al. 2000; Ciegler 2001), various *Hydroporus* species, such as *H. fortis* and *H. transpunctatus*, whose main habitats is represented by springs and spring-fed streams (Larson et al. 2000), *H. discretus*, *H. longicornis*, and *H. obsoletus* (Nilsson and Holmen 1995; Smith et al. 2003), as well as various *Agabus* species including *A. guttatus* (Nilsson and Holmen 1995), *A. hypomelus*, *A. lugens*, *A. morosus*, *A. obliterates*, *A. perplexus A. seriatus*, and *A. verisimilis* (Larson et al. 2000). Dytiscid larvae have also been recorded from cold springs (e.g., Hilsenhoff 1993; Gioria 2002) and springbrooks (Smith et al. 2003). In an investigation on five karst springbrooks in the Peak District National Park, England, Smith et al. (2003) recorded the presence of dytiscid larvae from two intermittent springbrooks from the source (spring) or close to the source (2.5 m downstream different points in time), whereas, in permanent springbrooks, larvae were only recorded 10 m downstream the source. Larvae of *Agabus seriatus* were recorded by Hilsenhoff (1993) within small spring-fed creeks in Wisconsin.

The distribution of dytiscids in springs is strongly associated to the duration of the hydroperiod. Scarbrook et al. (2007) collected and compiled data on the ecology of 82 cold springs in New Zealand and showed that permanency plays a major role in determining dytiscid species distribution. *Huxelhydrus syntheticus*, a species that had been previously recorded from shallow temporary shingle pools at the margins of larger rivers (Ordish 1966; see Winterbourn and Gregson 1981), was the only species recorded from springs with the lowest permanence. An *Antiporous* species was the only dytiscid exclusive to temporary spring, whereas no dytiscid species were exclusive to permanent springs. Gioria (2002) recorded *Dytiscus* larvae from a small, cold spring (eucrenal zone) in a karst area in western Ireland, and their presence was strongly dependent upon rainfall patterns during the days preceding sampling collection (Fig. 7.4).

Knowledge of the dytiscid fauna of springs can provide important insights into the effects of climate change and of other global changes, particularly changes in groundwater use and water pollution arising from changes in land use and agricultural practices, urbanization, and from industrial activities, on the fauna of aquifers and springs (see Dennis and Dennis 2012; Ferguson and Gleeson 2012 for a discussion on the vulnerability of aquifers to climate change and changes in groundwater use).

7.3.3 Permanency

Permanency, i.e., the duration of the hydroperiod or wet phase, is a major determinant of patterns in dytiscid species distribution (Wellborn et al. 1996). Temporary habitats experience a recurrent dry phase of varying duration (e.g., Williams 1996)

Fig. 7.4 Cold, freshwater spring located in a karst region in the Burren, western Ireland, supporting dytiscid aduls and larvae (Gioria 2002; Photo by M. Gioria)

and can be either lentic or lotic. Williams (1996) classified the main types of naturally occurring temporary water bodies and habitats, based on their geographical distribution, into (1) ubiquitous waters (intermittent and episodic ponds, lakes, springs, rivers and streams, the margin of permanent lakes, ponds, rivers and streams, floodplains, and liquid dung); (2) arid and semi-arid regions (sections of permanent running waters, drypans, billabongs, kopjes, temporary inland saline waters, and desert rain pools); (3) humid tropical regions (e.g., tree holes, coconut shells, and rain pools); (4) temperate regions (e.g., seasonal wetlands, peatland pools, kettle ponds, woodland pools, turloughs, vernal ponds, autumnal ponds; tree holes, and rain pools); (5) maritime regions (e.g., tidal wetlands, supra-littoral tide pools, and saturated moss); and (6) Arctic and Antarctic regions (snowmelt pools, glacial streams, and aestival ponds).

For temporary, lotic habitats, Comin and Williams (1994) suggested a classification into (1) intermittent (predictable drying cycles) and (2) episodic (low degree of predictability) habitats, based on the predictability of the frequency, time of occurrence, and duration of the dry phase. Among lentic waters, temporary ponds play an important role in maintaining dytiscids diversity (e.g., Foster et al. 1992; Kholin and Nilsson 1998) and have been described using a variety of names, based on 'local' features, including seasonal ponds, ephemeral ponds, vernal pools (North America), autumnal pools (North America), billabongs (Australia), gnammas (Western Australia), playas (North America (Hall et al. 1999), Africa, Europe), rain pools (Africa, Australia), Tinajas (North America), Dayas (North Africa), vleis (South Africa), pingos, and turloughs (Ireland) (see Williams et al. 2001).

Based on their tolerance to or avoidance of droughts, Wiggins et al. (1980) classified the species of temporary vernal and autumnal pools and permanent ponds, in southern Ontario, into four groups: (1) over-wintering resident species, which are capable of passive dispersal only, and aestivate and overwinter in the dry basin; (2) over-wintering spring recruits; (3) over-wintering summer recruits; and (4) non-wintering spring migrants. *Agabus*, *Hydroporus*, and *Rhantus* species were placed in group 2 (over-wintering spring recruits), which includes species that reproduce in the pool in spring before the beginning of the dry phase, aestivate, and over-winter in the dry pool basin. These species are capable of active dispersal, although recruitment and dispersal occur in the spring only, with larvae or adults possibly surviving the dry phase. *Acilius*, *Colymbetes*, *Dytiscus*, *Graphoderus*, *Hydaticus*, *Laccophilus*, and some *Rhantus* species were, in contrast, placed in group 4 (non-wintering spring migrants); these species colonize the pools in spring during the wet phase, and then leave the pools before the beginning of the dry phase, thus over-wintering principally in permanent habitats.

Williams (1983) argued that this classification is rather confusing, as 'over-wintering residents', 'over-wintering spring recruits', and 'over-wintering summer recruits' include species that are permanently found in temporary pools, and whose active phase in temporary pools often coincide. Given detailed observations of patterns of colonization of a temporary vernal pond in southern Ontario, this author proposed a classification of its inhabitants, based on the time of occurrence as active 'forms' in this pond, into five groups: (1) species that were found during virtually the entire aquatic phase as well as during the dry phase, in the pond substratum as semi-torpid adults or immature stages; these species are capable of movement within minutes after being placed in water; two *Hydroporus* species were placed in this group; (2) species that were found in the pond as active forms within a few days from the beginning of the wet phase in the spring and that completed their life cycles within 4–6 weeks, but disappeared 4–6 weeks before the beginning of the dry phase (*Agabus* and *Neoscupterus* species); (3) species that colonized the pond ~2–5 weeks after the beginning of the wet phase in the spring; adults of *Dytiscus*, *Acilius*, and *Rhantus* species were placed in this group, but did not breed in this pond and completed their life cycle in a few weeks; (4) species that colonized the pond only 2–3 weeks prior to the beginning of the dry phase, i.e., approximately 10 weeks after the beginning of the wet phase (*Laccophilus*, *Hydaticus*, and *Hydrovatus* species); and (5) species that appeared only in the dry phase; no dytiscids species belonged to this group.

Potential inconsistencies between these two classifications are associated with differences in the colonization patterns in vernal ponds compared to those in autumnal ponds (e.g., Davy-Bowker 2002). Vernal ponds typically fill up in spring, for instance, from melting snow and rain, dry up in the summer, and remain dry until the following spring (wet phase of approximately 3–4 months). In contrast, autumnal ponds fill in autumn, due to a less permeable substrate or heavy rainfall patterns, and their wet phase of lasts approximately 8–9 months, until summer (Wiggins 1973). In a 3.5 year mark-and-recapture study in seven semi-permanent and temporary ponds in Cheshire, England, characterized by several drying and filling phases, Davy-Bowker (2002) found that the behaviour of *Acilius sulcatus* and *Dytiscus marginalis* was in accordance with that described by Wiggins et al. (1980) and Williams (1983) in Ontario, with these species dispersing from over-wintering ponds into temporary ponds in the spring, to then migrate into permanent ponds in the summer, and, in general, continue to move among ponds. In contrast, *Agabus bipustulatus* remained in the terrestrial vegetation in damp pond basins for several months after the ponds dried up in the summer, and moved back to permanent ponds only when the basin was completely dry. This is consistent with the findings of Eyre et al. (1992), who examined the effects of the duration of the hydroperiod on dytiscid assemblages (adults and larvae) and observed that the probability of occurrence of *A. bipustulatus* was higher in temporary habitats whose wet phase lasts 3–4 months, whereas it decreased at lower and higher durations.

Dytiscids represent a prominent component of the fauna of temporary habitats (e.g., Wiggins et al. 1980; Larson 1985; Foster et al. 1992; Nilsson and Svensson 1995). The main factors characterizing the ecology of temporary habitats and, subsequently, patterns in species richness and abundance, include surface area, depth, temperature, pH and alkalinity, dissolved oxygen, climate, and land use type (e.g., Nilsson and Svensson 1995; Ribera and Nilsson 1995; Nicolet et al. 2004; Gioria et al. 2010a). Kholin and Nilsson (1998) showed that pond area, depth, and temperature were among the most important determinants of dytiscid species richness in temporary ponds among three regions within the Palearctic. The composition of dytiscid assemblages in temporary habitats appears to be also correlated to the distance from permanent habitats. In an investigation on the distribution of water beetles along a Mediterranean intermittent stream in Montenegro, Pavićević and Pešić (2012) recorded five rheophilic-rheobiontic dytiscid species (*Agabus guttatus*, *Deronectes moestus inconspectus*, *Hydroporus pubescens*, *Ilybius chalconatus*, and *Scarodytes halensis*), mainly as larval instars (not identified). Adults of these species were mostly recorded from samples collected in April and May, indicative of a slow capacity of recolonization after seasonal drying, although *Agabus guttatus* and *Scarodytes halensis* were also recorded in the winter months. The majority of larvae were also recorded from samples collected in the spring.

Nested patterns for dytiscids in temporary habitats have also been reported. Nilsson and Svensson (1995) found strong nestedness in dytiscids assemblages recorded from 40 temporary snowmelt pools in Sweden, suggesting that some species may have a minimum habitat size requirement for colonization of temporary ponds. Kholin and Nilsson (1998) found significant nested patterns in northern Sweden and south Sakhalin, off the east coast of Russia. In an investigation on 42 isolated freshwater wetlands in southern New Hampshire, USA, Baber et al. (2004) showed that strong nestedness patterns were associated with hydroperiod (a proxy for risk of desiccation), wetland size, and, possibly, temperature.

Biotic habitat conditions vary substantially along gradients of permanency, including the structure and distribution of predators, that of the vegetation, and food resources. Temporary habitats typically support fewer predators, as fish and Odonata larvae are highly susceptible to habitat drying (e.g., Wiggins et al. 1980; Wellborn et al. 1996; Williams 1996). The absence of fish predators in temporary habitats is a major determinant of dytiscid distribution, and is reflected in preference for temporary habitats by species susceptible to fish predation (e.g., Fairchild et al. 2003; van Duinen et al. 2004; Foster 2010; Gioria et al. 2010a) (the importance of predation avoidance and refuge from fish predation in determining patterns of dytiscid species distribution along a permanency gradient is discussed in the context of biotic interactions, see Sect. 7.4 and in Chap. 9 in this book). Moreover, temporary habitats are often characterized by dense vegetation associated with high conductivity and nutrient concentrations (Wellborn et al. 1996; Valladares et al. 2002; Nicolet et al. 2004; Gioria et al. 2010a; Silver and Vamosi 2012) and may provide breeding opportunities (e.g., Nilsson and Svensson 1994; Batzer and Wissinger 1996) as well as abundant food resources, including mosquitoes (e.g., Lundkvist et al. 2001, 2003).

Variability in the frequency and duration of the wet phase in temporary habitats is an important factor determining the response of dytiscid species to habitat availability. In regions where intra- and inter-annual variation in the duration and frequency of the wet phase is high, the response of dytiscids to habitat availability can be very rapid. Flood frequency, duration, and magnitude were the most important determinants of patterns in dytiscid assemblages in eight temporary flooded wet meadows and two alder swamps in the River Dalälven floodplains, central Sweden, where floods are induced by snow-melt in spring and by heavy rain in summer (Vinnersten et al. 2009). In this study, the majority of dytiscid species were spring-migrants (see Batzer and Wissinger 1996). Nilsson and Svensson (1995) reported that some *Agabus* and *Ilybius* species tend to recolonize temporary habitats each spring, while several *Hydroporus* species have been recorded during the spring searching for new aquatic habitats (e.g., Lundkvist et al. 2001; Fairchild et al. 2003).

Temporary habitats typically support a lower number of species compared to permanent ones, and support dytiscid assemblages characterized by a high similarity in species richness (Kholin and Nilsson 1998) and composition, at the genus level, with *Hydroporus*, *Agabus*, and *Ilybius* species being the dominant genera, despite differences in other abiotic conditions (e.g., Nilsson 1984; Larson 1985; Foster et al. 1992; Nilsson and Svensson 1995; Lundkvist et al. 2001; Nicolet et al. 2004; Vinnersten et al. 2009; Gioria et al. 2010a). In lentic water bodies, dytiscid species are known to be distributed along a permanency gradient, from ephemeral pools to permanent lakes, with permanent habitats typically supporting richer and more abundant dytiscid assemblages compared to temporary ones (e.g., Nilsson and Svensson 1994, 1995; Schneider and Frost 1996; Lundkvist et al. 2001; Valladares et al. 2002; Fairchild et al. 2003; Schäfer et al. 2006; Gioria et al. 2010a), and a significant turnover in species composition is found along this gradient (Wiggins et al. 1980). Baber et al. (2004) recorded *Acilius*, *Dytiscus*, and *Ilybius* species from three categories of wetlands (short, intermediate, or long hydroperiod), whereas *Agabus*, *Hydaticus*, *Rhantus*, and *Colymbetes* species were absent from ‘short hydroperiod’ wetlands, despite these genera being also recorded from temporary habitats (e.g., Foster et al. 1992; Larson et al. 2000; Gioria et al. 2010a).

Lower species richness in temporary habitats compared to permanent ones has been often associated with a lower habitat stability and complexity, potentially high nutrient levels, and low dissolved oxygen. Temporary habitats are characterized by low habitat stability compared to permanent ones with respect to various biotic and abiotic conditions. Some temporary habitats can be characterized by high variability in the duration of the hydroperiod, with periodic, unpredictable drying increasing the risk of desiccation, thus threatening the persistence of certain dytiscid species (Wiggins et al. 1980; Ranta 1985; Friday 1987; Valladares et al. 2002). Flightless dytiscid species are particularly susceptible to low habitat stability with respect to permanency, and tend to occupy permanent habitats only. For instance, Larson (1997b) observed that the only flightless dytiscid known from a study area in northern Queensland, *Carabhydrus mubboonus*, was recorded exclusively in forest lotic habitats that tended to provide more stable conditions with respect to the duration and frequency of the wet phase compared to other lentic and lotic habitats (Larson and Storey 1994).

Habitat complexity is a function of several factors, including the structure of the vegetation, the presence of mosses and algal mats, that of rocks, logs or stones, the heterogeneity of the substratum (e.g., mud, gravel, rock, detritus, bare substratum or a combination of those type of substrate), depth and steepness, wave action, spatial and temporal variations in abiotic conditions (e.g., temperature, dissolved oxygen, or nutrient concentrations), the structure of predators and prey, and the number of guilds (e.g., McAbendroth et al. 2005; Tokeshi and Arakaki 2012). This habitat trait tends to be low in temporary habitats, as they typically support low plant species richness (Nicolet et al. 2004; Gioria et al. 2010a, 2011). The number of guilds is also negatively correlated to decreases in the duration of the hydroperiod. In a study on the dytiscid assemblages of 40 snowmelt pools in northern Sweden characterized by various degrees of permanency, Nilsson and Svensson (1995) showed that the number of guilds and within-guild diversity were positively correlated to increases in the duration of the wet phase for forest pools, although this pattern was not evident for clearing pools.

Despite generally supporting a lower number of species compared to permanent habitats, species-rich dytiscid assemblages in temporary ponds have been reported (Fig. 7.5). In 312 sites located in the province of Alberta, Canada, Larson (1985) documented higher dytiscid species richness in small seasonal or temporary habitats

Fig. 7.5 Seasonal, fishless pond in agricultural land, Alberta, Canada, supporting high richness and abundance of dytiscids (Silver and Vamosi 2012, Photo by D. A. Yee)

than in larger permanent water bodies such as lakes. In an investigation on a dytiscid community in a northern Swedish seasonal pond, Nilsson (1986) recorded 33 dytiscid species over a period of 7 years, with the majority (23 species) being 'satellite' species (i.e., being recorded only in certain years), and only ten species occurring each year and reproducing in the pond. Temporary habitats may also support uncommon or rare dytiscid species. In an investigation of the macroinvertebrates and plants of 71 temporary ponds in England and Wales, Nicolet et al. (2004) recorded Red Data Book dytiscid species and their conservation status, i.e., *Graptodytes flavipes* (Vulnerable), *Hydroporus rufifrons* (Vulnerable), and *Agabus labiatus* (Near Threatened).

Several dytiscid species exhibit preferences for temporary habitats. *Laccophilus* species such as *L. fasciatus* and *L. proximus* are commonly found in temporary habitats (Young 1954; Zimmerman 1959, 1960, 1970; Pitcher 2011). In 12 shallow lakes in the northern Iberian Meseta, Valladares et al. (2002) showed that temporary habitats supported species that were not found in permanent habitats, such as *Graptodytes bilineatus*. The presence of this species was negatively correlated with depth in lakes in the Pyrenees (Ribera et al. 1995), also suggesting a preference for temporary habitats. Species typically associated with temporary habitats also include *Agabus uliginosus*, which is primarily confined to highly temporary lentic waters (Foster 2010), and its larvae have been recorded from shallow water (Galewski 1971); *Hydroporus geniculatus*, which is found in various non-permanent, small, lentic habitats in Fennoscandia (Nilsson and Holmen 1995); *Ilybius fraterculus*, one of the dytiscids best adapted to warm, temporary ponds (Nilsson 1986); *Agabus* *disintegrates* and *Agabus gringo*, which are species of temporary ponds (Larson et al. 2000), and *Laccophilus* species (Zimmerman 1959, 1960, 1970; Larson et al. 2000). In a study on 12 agricultural wetlands in southern Sweden, Lundkvist et al. (2001) showed that *Ilybius ater* and *Hydroporus striola* had a preference for temporary, forested and open ponds, respectively. Dytiscids with a reported preference for permanent habitats include *Acilius canaliculatus*, *Hygrotus inaequalis*, *Hydaticus transversalis*, *Rhantus exsoletus*, and *R. frontalis* (Lundkvist et al. 2001), *Agabus tristis*, typically recorded from permanent sites of cold water, *Dytiscus dauricus*, whose main habitat is represented by permanent ponds in forested areas, and is regularly found in beaver ponds (Larson et al. 2000), *Graphoderus bilineatus*, which is confined to large, permanent ponds and lakes in Britain (Foster 2010), *G. perplexus* (Larson et al. 2000), *Agabus arcticus*, and *Ilybius guttiger* (Nilsson and Holmen 1995). Biotic interactions as well as abiotic requirements may be important in determining a preference for permanent habitats and are described more in detail later in this chapter.

Biomass of dytiscids per unit area can be higher in temporary habitats compared to permanent ones. In an investigation on the composition of lentic permanent (small lake shores) and temporary (depressional wetlands, shallow kettles, and tarns) wetlands in the South Island of New Zealand, Wissinger et al. (2009) showed that, of eight dytiscid species recorded, six (*Liodessus* species, *Antiporus* species, *Lancetes lanceolatus*, and *Rhantus suturalis*) were common in both temporary and permanent habitats and that dytiscid biomass (g ash-free dry mass/m^2) was significantly higher in temporary compared to permanent water bodies.

Dytiscids are good colonizers of temporary and newly-created habitats, with many species being active fliers capable of tracking habitats over the year (Larson 1997b), and among the first macroinvertebrate predators to arrive in newly formed habitats (e.g., Zimmerman 1960; Yano et al. 1983; Eyre et al. 1986; Foster and Eyre 1992; Fairchild et al. 2003; Lundkvist et al. 2003; Pakulnicka 2008) (Fig. 7.6; see Chap. 9 in this book). Colonization of newly created habitats may be rapid, even in the absence of any emergent or submerged vegetation, and in highly disturbed habitats (e.g., Balfour-Browne 1940; Ranta 1985; Gioria et al. 2010a). Larson (1997b) showed that dytiscids rapidly colonized rice fields and a borrow pit in northern Queensland. Rapid colonization of rice fields has been reported in other studies across different geographic regions, including southern Iberia (Picazo et al. 2010), Asia, Africa, Italy, and North America (Yano et al. 1983 and references therein). Clay pits have also been found to be rapidly colonized by dytiscid species (Pakulnicka 2008) and may support relatively species-rich dytiscid assemblage. For instance, Gioria et al. (2010a) recorded a relatively species-rich assemblage composed of 13 dytiscid species, ranging from small to large size (2.2–30 mm), in a small clay pit (~25 m^2 in surface area) that had been created only a couple of months prior to sampling. Pioneer dytiscid species include *Acilius sulcatus*, and *Agabus nebulosus* (Gioria et al. 2010a), *Agabus infuscatus*, which has been recorded from small, barren, rock pools and artificially formed habitats such as gravel pits, quarry pools and highway ditches (Larson et al. 2000), *Copelatus glyphicus*, which is abundant in small artificial pools such as gravel pit pools, and tyre ruts in

Fig. 7.6 Example of newly created, temporary habitat near a forest clear-cut, Mississippi (Photo by D. A. Yee)

peaty soils (Larson et al. 2000), *Hydroglyphus pusillus*, *Hygrotus confluens* and *H. nigrolineatus* (Nilsson and Holmen 1995), *Laccophilus proximus*, a pioneer species in newly formed or rewatered ponds (Young 1954; Zimmerman 1960), *Stictotarsus griseostriatus* (Larson et al. 2000), and *Thermonectus basilaris* in Canada (Young 1954), the only species in this warm-temperate and tropical genus being recorded at such northern latitudes.

Rapid colonization of temporary or newly created habitats may result in a temporary decrease in species richness or abundance of dytiscids in permanent habitats when adjacent temporary habitats experience a wet phase ('diluting' effect, see Larson 1997b). Thus, over the duration of the wet phase it is possible that temporary or seasonal habitats support more species than those in permanent habitats (Nilsson 1984). Dytiscid assemblages in temporary habitats are less predictable compared to those occurring in permanent habitats (Nilsson 1986). In a study of aquatic insects in Sycamore Creek, a lowland stream in the Sonoran Desert, Arizona, which is subject to recurrent floods and droughts, Gray (1981) showed that dytiscids avoided droughts principally by habitat selection of oviposition sites, by ovipositing in deep pools that retain water for the duration of larval development or in main channel segments. In contrast, dytiscids exhibited a flood avoidance behavior during floods, by leaving the stream or swimming to protected habitats, such as those protected by the vegetation along the channel edge.

Colonization patterns of temporary habitats seem to differ in temperate and tropical zones. In an investigation on habitat and community patterns of tropical Australian beetles, including dytiscids, Larson (1997b) showed that dispersal patterns for dytiscid species in *Eucalyptus* woodland regions of Queensland are somewhat different from those in forests in north temperate regions, with tropical species that occur in seasonal habitats responding rapidly to habitat availability and not showing signs of aestivation or hibernation periods during their life cycle. This author suggested that such an ability to colonize seasonal habitats is likely an adaptation to highly variable and unpredictable habitat conditions, associated with higher inter- and intra-annual variation in precipitation and temperature patterns compared to those characterizing temporary regions. For details on patterns of colonization and dispersal in different climatic zones, see Chap. 9 in this book.

Temporary habitats that support unique dytiscid species include turloughs, i.e., karst, seasonal, shallow lakes, some of which with a permanent pond in the center, with a highly restricted global distribution, occurring almost exclusively found in the west of Ireland (Campbell et al. 1992; Skeffington et al. 2006). These ‘disappearing’ lakes are characterized by a unique hydrology regulated by estavelles (holes and fissures that act both as springs) via which a turlough becomes flooded, as well as swallow holes in the spring, although the water level may raise in response to high precipitation (Skeffington et al. 2006). The majority of turloughs present an upper layer dominated by moss (Foster et al. 1992; Skeffington et al. 2006). Turloughs play a central role in the conservation of dytiscid species that are rare or uncommon in Ireland or in other regions (Foster et al. 1992, 2009; Skeffington et al. 2006). At the margins of undisturbed turloughs, Bilton (1988) recorded a moss-dwelling beetle assemblage that included a dytiscid species new to Ireland (*Graptodytes bilineatus*) as well as characteristic turlough dytiscid species, such as *Hygrotus quinquelineatus* and *Agabus labiatus*, which are regarded as species of high conservation value in Britain (Foster and Eyre 1992). A range of rock pools are present in the areas surrounding turloughs, which are also known to support diverse dytiscid assemblages (e.g., Gioria 2002).

Dytiscids known from various types of small, mossy hollows in bogs or forests include *Agabus elongates*, *A. melanarius* (Larson et al. 2000), and *A. wasastjernae* (Nilsson and Holmen 1995; Foster 2010). Snowmelt pools are also known to support dytiscid species, such as *Agabus oblungus* (Larson et al. 2000) and *Agabus uliginosus*, which are found in central Europe in ponds formed by snow melt (Foster 2010). Additional interesting temporary lentic habitats colonized by dytiscids include pools of intermittent streams, rain pools (e.g., *Neoclypeodytes cinctellus*; Larson et al. 2000), rock pools (Nilsson and Holmen 1995), and tree holes (Hendrich and Yang 1997). Water-filled tree holes, consisting of habitats formed in cavities or tree depressions by the stagnation of rain water, represent an important aquatic habitat for some dytiscid species (Kitching 1971, 2000; Hendrich and Yang 1997). Dytiscids that have been recorded in this habitat include *Agabus* (Nishadh and Anoop Das 2012) and *Copelatus* species (Yanoviak 2001). Kitching and Orr (1996) investigated the food web of water-filled tree holes in lowland mixed forest in Kuala Belalong, Brunei and recorded small dytiscids from tree holes of various origin (root pans, buttress pans, trunk pans, rot-holes, hollow trees, and log holes).

In summary, temporary habitats provide a set of habitat traits that are favorable to dytiscid colonization or dispersal, despite often lying at the extremes of the physiological requirements of a species, such as lower competition and predation, and are thus central to the conservation of dytiscids. Rigorous quantifications of the role of temporary habitats in supporting regional dytiscid diversity are now required to improve our capacity to conserve the diversity of dytiscids.

7.3.4 Salinity

Dytiscids vary substantially in their tolerance to saline conditions and are found both in fresh water and highly saline habitats (e.g., Balfour-Browne 1940; Rawson and Moore 1944; Frisbie and Dunson 1988; Ribera et al. 1996; Larson et al. 2000; Chessman 2003). Salinity is thus considered a good predictor of dytiscid composition (e.g., Rawson and Moore 1944; Galewski 1971; Larson 1975, 1985; Cuppen 1986). The number of dytiscid species along gradients of salinity tends to decrease with increases in salinity, with few species being able to tolerate highly saline conditions (e.g., Jäch and Margalit 1987). Several species possess a broad tolerance to saline conditions and are found both in freshwater and saline environments, such as *Agabus obsoletus*, *A. coxalis*, *A. rumppi*, *Dytiscus marginicollis*, *Hygrotus tumidiventris*, *Rhantus sericans* (Larson et al. 2000), *Laccophilus ponticus* (Galewski 1978), and *Hydaticus variegatus*, the latter showed a broad tolerance to salinity and was recorded from fresh as well as hypersaline habitats (Timms 1993).

Some species have a requirement for high salinity (Sánchez-Fernández et al. 2010), such as *Hygrotus salinarius*, a saline specialist that occurs exclusively in saline water, with its larvae also tolerating a wide range of salinities (Larson et al. 2000), and both larvae and adults have been recorded in habitats more saline than seawater (Tones 1978). Halophilic species or species associated with distinctly saline waters include various *Hygrotus* species, such as *H. marklini*, *H. novemlineatus*, *H. semivittatus* (Larson et al. 2000), and *H. parallelogrammus* (Nilsson and Holmen 1995). In the Ebro delta and other Mediterranean coastal wetlands in the Iberian peninsula, Ribera et al. (1996) found that sea water was the main discriminating habitat factor, with *Hydroporus limbatus* being an indicator species for sea water habitats, whereas *Rhantus suturalis* was the indicator species for the habitats with water from drainage, rain, or with a mixed origin. In an investigation on the ecology of 25 shallow, ephemeral lakes, of varying salinity in the semi-desert of north-western New South Wales, Australia, Timms (1993) also recorded *Rhantus suturalis* from fresh- to hyposaline but not in meso- or hypersaline habitats. There, three dytiscid species occurred exclusively in fresh or subsaline habitats (*Cybister tripunctatus*, *Eretes australis*, and *Hydaticus consanguineus*), and five species occurred in fresh- to meso-saline habitats (*Allodessus bistrigatus*, *Antiporus gilberti*, *Necterostoma penicillatum*, *Megaporus howitti*, and *Sternopriscus multimaculatus*). The occurrence of *Rhantus suturalis* in fresh- or hyposaline waters is also consistent with findings from the Western District of Victoria, Australia, where the fauna of 79 salt lakes, along a salinity gradient ranging from 0.3 to 343 g L^{-1}, was investigated (Williams et al. 1990). There, *Rhantus suturalis* and *Antiporus femoralis* were recorded only from a lake whose salinity was low (0.4 g L^{-1}).

The Australian Biodiversity Salt Sensitivity Database (Bailey et al. 2002) reports data for 52 dytiscid species, some of which with a tolerance to high salinity levels (up to 93 g L^{-1}), whereas some species have narrow ranges of salinity tolerance. Chessman (2003) assigned dytiscids a score of 2 (scoring system from 1 to 10, with 1 being high tolerance to a range of environmental conditions, including salinity), for species recorded in Australian Rivers. In springs of the western Dead See area, some species belonging to the genera *Hydroporus*, *Hydroglyphus*, *Hydrovatus,* and *Potamonectes* were recorded from highly saline basin springs (up to 47 g L^{-1}) (Jäch and Margalit 1987).

Among ecologically interesting but overlooked saline habitats are Mediterranean saline streams. Millán et al. (2011) compiled and summarized the results of previous investigations on saline streams in the Segura and Guadalquivir basins, southeast Iberia, Spain, where only 33 % of the streams presented a permanent flow regime, 55 % had an intermittent flow, and 12 % were ephemeral, flowing only after heavy rainfalls. These authors classified streams into hyposaline, mesosaline, and hypersaline, the former found in larger basins, at higher altitudes, and with lower maximum mean temperatures compared to meso- and hypersaline streams. Eight dytiscid species were recorded from hyposaline streams, and two of those were also found in mesosaline streams, i.e., *Nebrioporus baeticus* and *N. ceresyi*, which are characteristics of inland hypersaline systems (Toledo 2009; Sánchez-Fernández et al. 2010). These species were also recorded from the Rambla Salada, a Mediterranean hypersaline stream in south-eastern Spain (Velasco et al. 2006). Sánchez-Fernández et al. (2010) showed that salinity affects the thermal tolerance and acclimatory ability of these species hypersaline species (*Nebrioporus baetis* and *N. ceresyi*), and that lowered salinity had a negative effect on the tolerance of the adults to high and low temperatures. Additional quantitative estimates on the salinity tolerance of dytiscid species are urgently required to improve our understanding of how variations in salinity associated with climate change, groundwater use, and other agricultural and industrial activities may affect the distribution of dytiscids *via* changes in salinity.

7.3.5 pH

Besides salinity, water pH has long been considered one of the most important factors affecting the structure of dytiscid assemblages, with many studies showing a negative correlation between dytiscid species richness and abundance and pH (e.g., Balfour-Browne 1940; Galewski 1971; Cuppen 1986; Eyre et al. 1986; Friday 1987). Dytiscids, however, vary greatly in their tolerance to pH, with some species being recorded along broad pH ranges, such as *Graphoderus zonatus* (pH 4.0–7.5, Foster 2010), whereas some species are mainly associated with alkaline habitats (e.g., *Oreodytes alpinus*, found in large lochs with a pH above 7.2; Foster 2010), or with acidic habitats (e.g., Hendrich 2001; Eyre et al. 1986; Alarie and Leclair 1988; Foster et al. 1992; Larson et al. 2000; Foster 2010). These include several *Hydroporus* species (Cuppen 1986), colonizing acidic habitats such as *Sphagnum* pools (pH ~4.0–5.0; Galewski 1971; pH ~3.9–4.3; Alarie and Leclair 1988), including *H. tristis* (Nilsson and Holmen 1995), *H. gyllenhali* (Foster et al. 1992), *H. melanarius*, *H. obscurus*, *H. brevicornis*, *H. morio*, *H. geniculatus*, and *H. rectus*, which is one of the most characteristics species of peatlands within the boreal zone of North America (Larson 1975, 1987). Several species belonging to the genera *Acilius*, *Agabus*, *Dytiscus*, *Ilybius*, *Laccophilus*, and *Rhantus* have also been recorded in naturally acidic peatland habitats, including *Ilybius discedens*, which is the most characteristic water beetles of boreal peatland (Larson 1985) and *Rhantus suturellus*, the *Rhantus* species that is most frequently found in bogs and fens (Larson et al. 2000). In South-Western Australia, species belonging to the genus *Antiporus*, which appear to be restricted to acid peatland swamps, including *Antiporus mcrae*, *A. pembertoni*, *A. pennifoldae*, and the recently described *Antiporus gottwaldi*, have been classified as acidophilic (Hendrich 2001). In an investigation on the dytiscid assemblages of three acidic (pH 3.9–4.3 in bog pools) and three non-acidic (pH 5.8–7.0 in silty pools) temporary habitats in southern Quebec, Alairie and Leclair (1988) recorded 58 species, 11 of which were regarded as acidophilic, including *Agabus bifarius*, *Hydroporus badiellus*, *H. rectus*, *H. stagnalis*, and *Ilybius discedens.* In contrast, *Agabus gagates*, *Hydroporus tristis*, and *Ilybius ignarus* showed a preference for acidic habitats, despite a tolerance to broad pH ranges.

A tolerance to broad pH ranges for many dytiscid species limits our capacity to predict the role of pH in determining pattern in dytiscid distribution across habitats, such as in boreal lakes (Nilsson and Söderberg 1996) or in farmland ponds (Gioria et al. 2010a, b), and only under extreme conditions (very low pH) have strong correlations been observed (Friday 1987; Foster et al. 1990; Larson et al. 2000). Difficulties in identifying strong relationships between pH and dytiscid species distribution are associated with the fact that the effects of pH on dytiscids are mainly indirect, and mediated by those of biotic habitat variables, including the distribution and structure of predators, as the majority species are tolerant of broad pH ranges (e.g., Juliano 1991; Foster et al. 1990, 1992; Foster 1995; Arnott et al. 2006; Foster 2010), and by those on the vegetation (e.g., Foster et al. 1990, 1992; Gioria et al. 2010a, 2011, see Sect. 10.4). For instance, fish predation avoidance by *Agabus labiatus* was likely the major cause of the presence of this species in contrasting habitats with respect to pH, with individuals recorded from permanent, dystrophic waters as well as in highly alkaline habitat conditions, such as temporary turloughs and turlough-like pools (Foster et al. 1992).

The effect of pH may also be confounded by other abiotic conditions. In an investigation on the effects of calcium carbonate addition on invertebrate assemblages in peat pools, Foster (1995) observed weak effects of pH on dytiscid species distribution, with many dytiscid species that had been previously classified as acidophilic breeding successfully in calcium-enriched bog pools. This suggests that the association of certain species with acidic habitats, such as the boreal *Hydroporus morio* and *Agabus arcticus*, might be due to a broader tolerance to cold temperatures, a poor nutrient status, or to a dependence on a soft, organic substratum, rather than to a clear preference for acidic habitats (Foster 1995).

With regard to larvae, experimental studies have shown that the larvae of certain species are tolerant to extremely low pH (e.g., *Dytiscus verticalis*, pH = 3.0, Frisbie and Dunson 1988). Juliano (1991) examined patterns of total and relative species abundance for *Hydroporus* species along a pH gradient in a long ditch in North Yorkshire, England, and found that the effect of pH on dytiscid abundances differed substantially between adults and larvae. Specifically, he observed a decrease in total abundance of adult *Hydroporus* with decreases in pH, whereas larvae were most abundant at sites with the lowest pH and were absent where adults were most abundant. There was no evidence of significant differences in species richness and evenness along the pH gradient; however, a higher number of adult *Hydroporus* individuals recorded along less acidic (pH = 5.6–6.2) upstream sites, whereas larvae were most abundant along the more acidic (pH = 4.5) downstream sites. Based on these findings, Juliano (1991) concluded that pH was not the major factor affecting *Hydroporus* assemblages over the studied pH range and suggested that the absence of predators (mainly fish) from more acidic sites may have contributed to a higher abundance of larvae, as larvae were more likely susceptible to predation than adults.

7.3.6 Temperature

Temperature is a major determinant of patterns of distribution of dytiscid species (e.g., Eyre et al. 2006), to the extent that some dytiscid species have been used as paleoecological indicators to infer past temperatures (Lemdahl 2000). Eyre et al. (2006) showed that mean annual temperature was strongly correlated with distribution patterns for many dytiscid species in Britain. Although some dytiscid species have a requirement for sun-warmed habitats (e.g., *Graphoderus perplexus*, *Hygrotus suturalis*, *Liodessus affinis*, *Uvarus falli*), other species are found in cool or cold habitats only (e.g., *Agabus gagates*, *A. larsoni*, *Laccornis latens*) (Larson et al. 2000).

Based on distribution data available at the time, Winterbourn (1968) showed that the maximum water temperatures at which dytiscid species had been recorded ranged between 43 and 46 °C (Brues 1927; Mason 1939; Winterbourn and Brown 1967). In a recent study, Sánchez-Fernández et al. (2012) estimated the thermal niche of 12 *Deronectes* species based on distribution and physiological data. These species displayed broad thermal ranges in physiological experiments (thermal range = ~50 °C), greater than those estimated using distribution data, suggesting that other factors, such as biotic interactions (e.g., a preference for cold, fishless water bodies) and dispersal limitation associated with the structure of the matrix of habitats within the landscape, may be more important than a species' physiology in determining the realized niche of these species. For the species examined in this study, the maximum upper thermal limit was 54 °C, whereas the minimum lower thermal limit was −10 °C.

Temperature is strongly correlated with other abiotic and biotic conditions, such as altitude, the degree of exposure to direct sunlight, precipitation, depth, and the structure of the vegetation and predators, which act as confounding factors. For instance, in a study of the distribution of dytiscid species in 82 mountain lakes in the Pyrenees (De Mendoza et al. 2012), temperature was found to be the abiotic variable (out of 29 abiotic variables considered) that contributed most to explaining the distribution of *Platambus* species along an altitudinal (thermal) gradient, which showed a preference for warmer lakes, consistent with other investigations (e.g., Eyre et al. 1986), as well as that of *Agabus* species, which were confined to colder lakes. The presence of fish (salmonids) and vegetation cover, however, taken individually, explained more variation in dytiscid distribution than temperature for most species, indicative of a difficulty in separating the effects of biotic and abiotic habitat variables on dytiscid distribution based on observational studies only. Species that have been recorded at high altitudes include several *Agabus* species, such as *A. verisimilis* (altitudinal range 1,500–3,200 m), *A. kootenai*, *A. vancouverensis*, *A. sasquatch* (2,350–3,800 m), *A. hypomelus*, which has been recorded from sea level in Alaska to 3,000 m in Colorado, and *A. vandykei* (1,100–3,700 m) (Larson et al. 2000), as well as species such as *Colymbetes dolabratus* and *Hydroporus notabilis*, which are found above the tree line in Fennoscandia (Nilsson and Holmen 1995). The effect of temperature on dytiscid species distribution may be particularly strong in small, temporary, lentic habitats. Nilsson and Svensson (1994) showed that temperature, pool size, and hydroperiod were among the most important determinant of dytiscid species composition and distribution in boreal snowmelt pools.

7.3.7 Habitat Size and Steepness

Habitat size, expressed in terms of surface area or depth, may strongly affect the distribution of dytiscid species. Whether ‘size matters’ however, is not always clear (Oertli et al. 2002). This is likely due to a potentially strong correlation between habitat size with habitat complexity, including the structure of the vegetation, predators, and food resources, and dispersal traits. The effect of habitat size on the distribution of dytiscid species should be discussed at two levels, that of the water body itself and that of habitat within a water body. In relation to the former, surface area is generally considered an important determinant of dytiscid species richness, so that, according to the species-area relationship, more species are to be found in larger water bodies (Nilsson 1984, 1986; Larson 1985; Ranta 1985; Fairchild et al. 2003), and strong nestedness patterns have been reported (Sect. 7.3.2), possibly due to a minimum habitat size requirement for some species (e.g., Kholin and Nilsson 1998). However, patterns in dytiscid species richness along gradients of surface area in lentic water bodies, from pools to lakes, are generally better described by a unimodal humpbacked function, with dytiscid assemblages generally more abundant and diverse in intermediate size water bodies (e.g., ponds) than in large permanent lakes (e.g., Larson 1985; Ranta 1985; Nilsson 1984, 1986; Nilsson and Svensson 1994; Whiteman and Sites 2003). In a study on dytiscid assemblages in 12 wetlands in an agricultural landscape in south-eastern Sweden, Lundkvist et al. (2001) found that species-area relationships were weak, and showed that intermediate size wetlands supported the richest dytiscid assemblages. Habitat size is particularly important in determining patterns in dytiscid species distribution in small habitats. Nilsson and Svensson (1994, 1995) showed that an increase in pool size in snowmelt pools resulted in an increase in the number of guilds and in diversity within guilds. In over 200 ombrotrophic bog pools in Newfoundland, Larson (1990) found a positive, significant correlation between the size of adult dytiscids and pool size ($r=0.56$), with small species generally occurring in small pools, with the exception of *Hydroporus badiellus* and *H. obscurus*, as they occurred in moss along the water margin. In 45 permanent farmland ponds in Ireland, surface area was only a moderate predictor of dytiscid species richness and composition ($r^2=0.29$), with the richest dytiscid assemblages (18–22 species) being recorded from intermediate size ponds (80–120 m^2); the smallest ponds (<25 m^2) supported 12–13 species whereas ponds larger than 200 m^2 supported between 10 and 21 species (Gioria et al. 2010a; Fig. 7.7). In these ponds, the effect of habitat depth on dytiscid assemblages was greater than that of surface area, with shallow habitats being generally richer than deep ones, likely due to a moderate correlation between depth with the structure of predators and with the physical structure provided by the vegetation, with shallower habitat characterized by dense vegetation (Fig. 7.8).

Larger species often have a preference for large water bodies (Ribera and Nilsson 1995), although the presence of fish in larger or deeper habitats may force these species to colonize shallower or smaller habitats to avoid fish predation (Sect. 7.4). For instance, the large-bodied *Dytiscus marginalis* was recorded in small, shallow ponds at high altitudes in the Pyrenees (Ribera et al. 1997), despite a preference for relatively deep, open waters (with an optimum depth of 60 cm) in the area (Ribera et al. 1995). This species was also recorded from a shallow, densely vegetated, temporary pond/pool (6 m^2 in diameter) (Fig. 7.9), probably to avoid the presence of fish occurring from adjacent permanent ponds. Foster (1995) showed that *Hydroporus* species were most abundant in shallow bog pools, whereas larger dytiscid species, such as *Agabus* and *Ilybius* species, were more abundant in deeper bog pools. Such an effect was likely mediated by biotic interactions, as deeper pools were dominated by odonates, to which smaller species such as *Hydroporus* species are more susceptible. Similar patterns were reported by Juliano (1991) in a long ditch, where larvae and adults of *Hydroporus* species were more abundant in shallow water, possibly to avoid predation by larger dytiscid species, odonates, and notonectids (see also Fairchild et al. 2003). Juliano (1991) also suggested that, in shallow waters, small dytiscids species may replace their oxygen storage more easily, and that differences in the distribution of prey may also account for such patterns.

The steepness of habitats such as the margins of ponds and stream banks may also have a strong effect on patterns in dytiscid species assemblages, although the interaction of this factor with both depth and plant density makes it difficult to detangle the effects of this factor from those of other abiotic conditions. Nilsson et al. (1994) showed that shallow water bodies with gentle profiles supported richer dytiscid assemblages compared to those found in steep-sided lakes and pools. Habitat steepness is strongly correlated to other abiotic habitat variables, such as depth, temperature, light, and nutrient levels, as well as with biotic conditions, including grazing and the structure of the vegetation, with shallow-water plant species being not capable of growing on the margins of steep-sided habitats

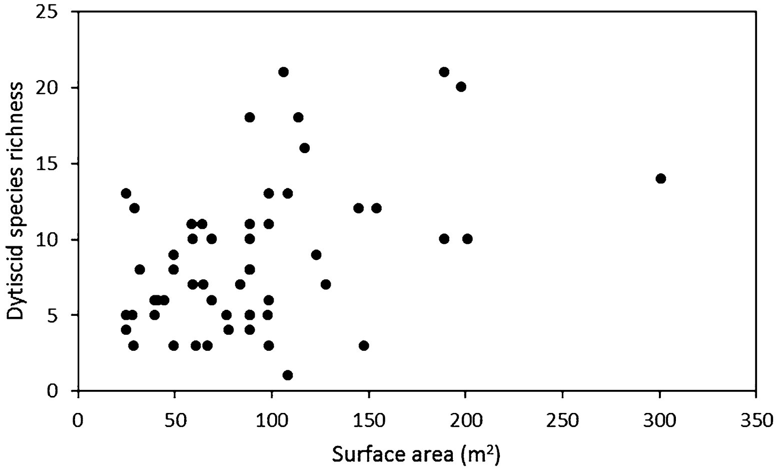

Fig. 7.7 Relationship between pond surface area and dytiscid species richness in 45 farmland ponds in two intensively farmed regions in Ireland (Gioria et al. 2010a)

Fig. 7.8 Example of a species-rich, dense plant assemblage, at the margins of a permanent pond, from where a species rich dytiscid assemblage (18 species) was recorded, in Ireland (Photo by M. Gioria)

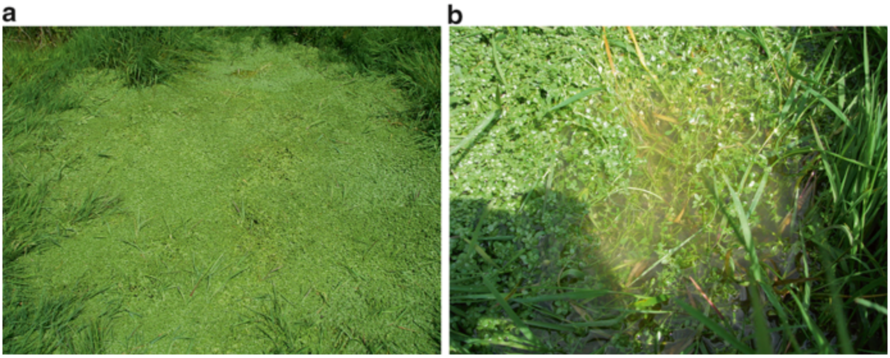

Fig. 7.9 Example of a (a) temporary pool and (b) detail of its dense vegetation, Ireland. A male individual of *Dytiscus marginalis* was recorded from this small pond or pool (diameter ~2.5 m, depth ~40 cm), together with three *Hydroporus species* and *Hyphydrus ovatus* (Photo by M. Gioria)

(Newbold et al. 1989; Painter 1999). Dispersal limitation in habitats with steep margins may also play an important role in determining patterns of dytiscid species distribution (see Yee et al. 2009).

7.3.8 Additional Abiotic Habitat Variables

Additional abiotic factors may determine the distribution of dytiscid species in aquatic habitats, such as the degree of shading, exposure, nutrient concentrations, and pollution by heavy metals, although their effects are often strongly correlated to those of the habitat variables described previously. The degree of shading affects the distribution of dytiscid species typically indirectly, via its interaction with a range of abiotic and biotic conditions, such as temperature, habitat productivity, and vegetation structure (Lundkvist et al. 2001; Schäfer et al. 2006; Vinnersten et al. 2009), with shaded habitats being often cooler than open habitats or characterized by a large amount of debris accumulating on the substrate, potentially leading to eutrophic or even hypertrophic conditions (e.g., Gioria et al. 2010a). Habitats exposed to sunlight are more visible to migrating species than shaded ones (Nilsson and Svensson 1995), so that, in general, more species have often been recorded in open, sun-exposed wetlands (e.g., Nilsson and Svensson 1994; Gee et al. 1997). Some species that have a requirement for unshaded habitats include *Agabus punctulatus*, *Graphoderus perplexus* (Larson et al. 2000), *Rhantus bistratus* (Nilsson and Holmen 1995; Foster 2010), *Ilybius ater* (Lundkvist et al. 2001), *Hygrotus marklini*, *Hygrotus confluens*, and *Hydaticus continentalis* (Nilsson and Holmen 1995). Species that have a preference for shaded habitats include *Hydroporus striola*, which seem to be dominant in temporary forested wetlands in southern Sweden (Lundkvist et al. 2001), *Agabetes acuductus*, *Agabus larsoni*, *Acilius fraternus*, *Hydaticus pisceus*,

Fig. 7.10 Example of eutrophic, permanent pond, dominated by *Cladophora algae*. Despite the high nutrient levels and the presence of a tick mat of algae, seven dytiscid species, belonging to the genera *Agabus, Hydroporus, Hyphydrus* and *Ilybius* were recorded from the emergent vegetation (Photo by M. Gioria)

Ilybius vittiger, and *Laccornis latens*, all of which have been recorded in woodland pools (Nilsson and Holmen 1995; Larson et al. 2000).

Nutrient concentrations, which are a function of various abiotic conditions, management practices, and land use history, may have a major effect on dytiscid species, via its effects on habitat productivity and on the structure of the vegetation structure, as well as on other habitat conditions, such as dissolved oxygen, turbidity, and chlorophyll a density (e.g., Gioria et al. 2010a). Habitat productivity, in turn, affects food availability and quality, the structure of predators, and inter-and intra-specific competition. Some dytiscid species are tolerant of high nutrient concentrations and may colonize eutrophic habitats (e.g., Foster 2010; Gioria et al. 2010a; Silver and Vamosi 2012; Fig. 7.10), including constructed wetlands, where they tend to form assemblages dominated by *Hydroporus* species (e.g., Becerra-Jurado et al. 2009). Species that have been frequently recorded from eutrophic habitats include *Hydroporus tenebrosus*, *Agabus serricornis*, *A. subfuscatus*, whose main habitat is represented by eutrophic marshes (Larson et al. 2000), *Hydaticus seminiger* (Painter 1999), *Hydroporus planus*, and *Hyphydrus ovatus*, the latter being even recorded from hypertrophic ponds (Gioria et al. 2010a). Dytiscid species also occur in oligotrophic habitats, such as *Laccophilus biguttatus*, *Hygrotus novemlineatus*, and *Oreodytes alpinus* (Nilsson and Holmen 1995), as well as in dystrophic habitats, such as *Dytiscus latissimus*, which has been recorded from large, slightly dystrophic lakes (Nilsson and Holmen 1995).

The presence of heavy metals strongly affects the distribution and survival of dytiscid species. Due to their role as predators in the food web, dytiscid species are prone to accumulating trace elements and vary substantially in their capacity to uptake pollution and heavy metals (Burghelea et al. 2011). In an investigation on the use of certain dytiscid species as bioindicators of trace elements in rice fields and reservoirs, Burghelea et al. (2011) showed that *Rhantus suturalis* has a high capacity to bioaccumulate Al, Mo and Pb in rice paddies*,* whereas *Laccophilus minutus* is prone to accumulate Se in reservoirs. *Hydroglyphus pusillus* exhibited the highest metal uptake in both habitats, but proved to be less efficient in discriminating the effects of habitat management/type (rice fields *versus* reservoirs), whereas *Rhantus suturalis* proved to be suitable as a bioindicator of trace element pollution.

Knowledge the relative importance of individual abiotic conditions on the distribution of dytiscid species using species distribution data is limited by the often strong interactions among abiotic factors. While extensive surveys of the dytiscid fauna provide us with important information on the length of the abiotic gradients along which individual species may occur, experimental studies are needed to improve our understanding of the contribution of individual abiotic conditions to determining the physiological amplitude and the habitat requirements of individual dytiscid species.

7.4 Biotic Interactions

For a long time, investigations on distribution patterns for dytiscid and other invertebrate species focused on characterizing the main physico-chemical determinants of such patterns. Observational studies have, however, shown that abiotic habitat conditions often have a low capacity to explain or predict distribution patterns for dytiscids, in the absence of extreme abiotic conditions. In contrast, biotic interactions seem to play a prominent role in determining the magnitude of the differences between the fundamental and the realized niche of several dytiscid species.

Predation represents a major mechanism determining the realized niche of dytiscids. Many dytiscid species are highly susceptible to predation by other aquatic predators, particularly fish and Odonata larvae (e.g., Ranta 1985; Larson 1988, 1990; Bosi 2001). These predators, like their dytiscid prey, are typically distributed along gradients of permanency, pH and temperature, so that the effects of abiotic conditions on dytiscid assemblages typically covary with those associated to the presence and density of predators. Several studies have shown that the identity and density of predators may change with small differences in permanency (Eyre et al. 1992; Jeffries 1994; Larson 1985), with the potential pool of predator species typically decreasing with decreases in habitat permanency and stability (Wellborn et al. 1996). Fish predation appears to be a major factor driving dytiscid species distribution, with many species displaying a strong fish predation avoidance behavior. The susceptibility of dytiscid species to fish predation is species-specific and is generally assumed to be a function of body size (mean body length), level of activity, and macrophyte cover, among others (Juliano and Lawton 1990; Larson 1990; De Mendoza et al. 2012). Species that are highly susceptible to fish predation are known to migrate to temporary habitats during the wet phase or to newly created habitats to avoid fish predation, even when abiotic conditions are suboptimal, such as more acidic, shallower, or colder habitats compared to those they would occupy based on their physiological requirements (Wiggins et al. 1980; Jeffries and Lawton 1984; Foster et al. 1992; Foster 1995; Larson 1997b; Knapp et al. 2001; Fairchild et al. 2003; Arnott et al. 2006; Schilling et al. 2009; De Mendoza et al. 2012; Gioria et al. 2010a). The presence of Odonata larvae also represents a major habitat factor affecting the structure of dytiscid assemblages (Larson 1985; Nilsson 1986; Larson 1988, 1990; Bosi 2001). Odonata larvae are major predators of dytiscids, with interactions between larval stages being most important, whereas adult dytiscids are relatively protected by size, hard cuticle, and, possibly, defensive secretions (Larson 1990).

Understanding of the role of predation in determining species distribution and evolutionary patterns requires quantitative data on predation rates on dytiscids by fish and Odonata larvae, in different habitat types. Although the majority of studies have suggested predation as a major mechanism driving patterns in dytiscid assemblages, rigorous quantifications of predation rates are central for characterizing the contribution of predation to determining the ecological amplitude of individual dytiscid species (see Larson 1990; Larson and House 1990). Clearly, additional information is required to improve our understanding of how the presence and structure of predator populations affect the habitat preferences of dytiscid species. The effects of predation on dytiscid species distribution are described and discussed in Chap. 8 in this book.

Food availability and quality also represent a major habitat trait and an important dimension of habitat complexity and is discussed in Chap. 8 in this book. Dytiscid larvae are strictly predators, whereas adults may also scavenge (e.g., Nilsson and Svensson 1994, 1995; Larson et al. 2000; Nilsson 2001). Dytiscids are typically regarded as general predators, but for some species, the identity of their prey may be important in defining their realized niche (e.g., Deding 1988; Nilsson and Svensson 1994; Lundkvist et al. 2003; Culler and Lamp 2009).

Within agricultural regions, livestock grazing (hereafter grazing) can also be a major habitat variable affecting the structure of dytiscid assemblages (Gioria et al. 2010a; Silver and Vamosi 2012). Specifically, grazing may affect dytiscid species directly, via (1) increases in nutrient levels; (2) the deposition of cow dung either on the marginal vegetation or in the water; and (3) increases in turbidity due to the creation of open zones of bare ground by trampling (Gioria et al. 2010a; Gioria 2011). Trampling by cattle affects directly those species whose larvae occur at the edge of the water in damp soils. Indirectly, grazing suppresses the growth of marginal and emergent plants and simplifies habitat structure, with detrimental effects on dytiscid species richness and abundance (Gioria et al. 2010a, Fig. 7.11). In a study on 54 farmland ponds in Ireland, Gioria et al. (2010a, b) showed that

Fig. 7.11 Example of permanent pond where the marginal and emergent vegetation was suppressed by cattle. Two *Hydroporus* species, *Agabus nebulosus, Hyphydrus ovatus* and *Rhantus frontalis* were recorded from this pond (Wexford, Ireland) (Photo M. Gioria)

grazing was a major determinant of dytiscid species composition, with grazed ponds supporting significantly less species and individuals compared to ungrazed ponds. In particular, dytiscid assemblages in grazed ponds were species-poor and dominated by few species, mainly *Hydroporus planus*, *Agabus nebulosus,* and *Agabus bipustulatus*, which are relatively tolerant of eutrophic conditions (Eyre et al. 1986; Foster et al. 1992; Foster and Eyre 1992; Foster 2010). The negative effect of grazing on dytiscid species richness and abundance via changes in the vegetation was evident when a comparison between dytiscid assemblages in grazed and fenced ponds was made. There, the presence of a fence preventing direct cattle grazing was beneficial only when the distance between the pond margin and the fence allowed the growth of some emergent and marginal vegetation, indicative of the central role of the vegetation in determining patterns in dytiscid assemblages. Evidence of the detrimental effect of grazing on dytiscid species richness and abundance was also provided by Silver and Vamosi (2012), who conducted an investigation on macroinvertebrate assemblages in 13 temporary wetlands subjected to rotational grazing, in Alberta, with no dytiscids occurring in early grazed wetlands (wetlands that are grazed during the wet phase). In contrast, *Dytiscus*, *Ilybius*, and *Rhantus* species were indicator taxa for late grazed wetlands (wetlands that were grazed during the dry phase).

The detrimental effects of grazing on dytiscid assemblages are well understood and the use of fences can be very effective at conserving the dytiscid fauna of habitats supporting diverse dytiscid assemblages (Gioria et al. 2010a, b; Gioria 2011). Such knowledge should be incorporated in specific policies aimed at the conservation of dytiscids and other taxonomic groups. Conservation issues are discussed in Chap. 11 in this book.

7.5 Plant-Dytiscid Relationships

The characteristics of the vegetation represent a major determinant of habitat structure and complexity (e.g., Ranta 1985; Friday 1987; Foster et al. 1990, 1992; Nilsson et al. 1994). Vegetation plays a range of functional roles in aquatic habitats and at the interface of aquatic-terrestrial habitats (Gioria et al. 2010a, 2011). Plants determine directly the physical structure available to dytiscids, providing oviposition sites, and mitigating the effects of inter- and intra-specific predation (e.g., Crowson 1981; Foster et al. 1992; Gee et al. 1997; Painter 1999; McAbendroth et al. 2005; Yee 2010; De Mendoza et al. 2012). Moreover, for certain species, vegetation may represent a food source (e.g., *Graphoderus cinereus*; Deding 1988). Plants also affect the stability of a habitat's substrate, the cycling of nutrients, and filter the amount of nutrients and pollutants reaching the water (e.g., Becerra-Jurado et al. 2009; see Keddy 2000 for a review).

The structure of the vegetation can be defined by various vegetation traits, including plant species richness, vegetation cover, plant biomass, presence and size of vegetation gaps, rigidity, the number and arrangement of stems and leaves, and shoot density (e.g., McAbendroth et al. 2005; Tokeshi and Arakaki 2012). The relationship between individual dytiscid species and the structure and density of the vegetation are strongly dependent upon their swimming strategy (Ribera and Nilsson 1995). In a comprehensive study on morphometric patterns for diving beetles, Ribera and Nilsson (1995), investigated the correlation between body size and shape with swimming strategies, and identified four main morphometric groups, each with a clear habitat preference depending upon their morphology and swimming behaviour: (1) large to medium-sized, streamlined, wide species with the maximum width in the rear part of the body and the maximum height in the front part, with short tibiae and long tarsi; species belonging to this group are considered to be fast swimmers and seem to have a preference for open waters, such as *Acilius sulcatus*, *Cybister lateralimarginalis*, *Eretes sticticus*, most Colymbetinae species, and all Dytiscinae; (2) small to medium-sized species with a spherical body and long femora; species belonging to this group are considered to be adapted to manoeuvring in stagnant waters, and all the species in this group belong to the Hydroporinae; (iii) small species with a discontinuous outline, a narrow body, and long, slender legs; they are considered to be poor swimmers in running waters, thus, they are typically found in lentic habitats; this group includes *Yola bicarinata*, *Bidessus goudoti*, and *Hydroglyphus pusillus*; (iv) small to medium-sized species, usually with a streamlined, relatively high body, and short, wide legs; these

Fig. 7.12 Example of a fishless, permanent pond characterized by a species-poor plant assemblage, dominated by *Typha latifolia*, but supporting a species-rich dytiscid assemblage (22 species), in Ireland (Photo M. Gioria)

species crawl among detritus and rotten or dense vegetation, such as *Hydrovatus* species and *Methles cribatellus*, and are considered to be poor swimmers, with exception of few species, including *Laccophilus minutus* and *L. hyalinus*.

In general, habitats characterized by complex vegetation tend to support species-rich dytiscid assemblages (Downie et al. 1998; Painter 1999; Armitage et al. 2003). For instance, Nilsson et al. (1994) showed that dytiscid species richness was largely dependent upon the structure of vegetation in 30 lakes in Sweden. However, complex vegetation structure, expressed by high plant species richness, is not a necessary condition for supporting high dytiscid species richness or abundance. For instance, Gioria et al. (2010a) showed that habitats dominated by species-poor plant assemblages, such as swamp zones dominated by *Typha latifolia*, supported species-rich dytiscid assemblages (up to 22 species) (Fig. 7.12). McAbendroth et al. (2005) also showed that habitat complexity, defined in terms of species richness, plant surface area, and complexity indices based on plant fractal dimensions, was unrelated to dytiscid species richness in two semi-permanent ponds on the Lizard Peninsula in Cornwall.

Gioria et al. (2010a, 2011) made a rigorous evaluation of the strength of plant community data (species richness and composition), in predicting patterns in water beetle assemblages in Irish farmland ponds. When these data were analyzed for

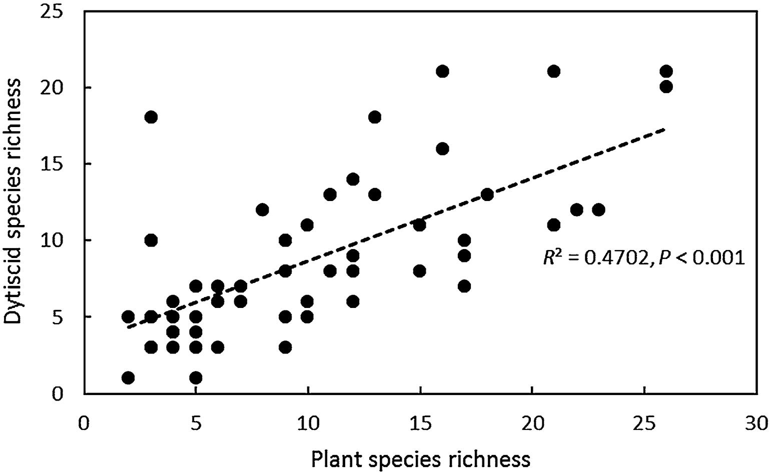

Fig. 7.13 Relationship between dytiscid and plant species richness, based on the Pearson correlation, in assemblages recorded from 54 farmland ponds, Ireland (Gioria et al. 2011)

dytiscid species only, a moderate correlation (~47 %) was found between plant species richness and dytiscid species richness (Fig. 7.13), suggesting an important role of plant diversity in supporting diverse dytiscid assemblages in many habitat types. This correlation is greater than that recorded when whole water beetle assemblages were examined, suggesting that dytiscids are more strongly correlated to the complexity of the vegetation compared to other aquatic Coleoptera. Plant species composition and, to a lesser extent, plant community type composition (*sensu* Rodwell 1995) were good predictors of patterns in dytiscid assemblages (~15 and 8 % fit). A positive capacity of plant species composition data in predicting dytiscid species composition was likely the result of a strong similarity in the response of plant and dytiscid assemblages to abiotic factors, as well as a capacity for the vegetation to 'summarize' information on local habitat conditions (see also Gioria et al. 2010a, 2011). For instance, *Juncus* species were characteristic of highly degraded, eutrophic ponds grazed by cattle, and were good predictors of the presence of species such as *Hyphydrus ovatus, Hydroporus planus*, *H. palustris*, and *Agabus nebulosus*. In contrast, species-poor plant assemblages dominated by *Typha latifolia* were good indicators of high dytiscid species richness, often supporting dytiscid assemblages composed of more than 20 species. The beneficial effect of *Typha latifolia* on dytiscid species richness is likely associated with the provision of an ideal physical structure for many species, as it provides shelter from predators but, at the same time, allows free movement for active species (Fig. 7.12). It is interesting to note that the capacity of plant species richness and composition in predicting patterns in species richness and composition for dytiscids was nearly twice than that reported by Gioria et al. (2010a) for all water beetle species recorded in this study. This suggests that, even if the majority of dytiscid are not host specific, some plant species or community types provide an ideal physical structure to many dytiscid species.

In addition to measures of species richness and composition, plant density also plays a role in dispersal patterns of dytiscids species. In an investigation on dytiscid and plant density as cues initiating dispersal in *Graphoderus occidentalis* and *Rhantus sericans*, Yee et al. (2009) showed that the latter was more strongly associated with low plant density and, in both species, low plant density appeared to increase their dispersal.

The capacity of the vegetation to provide shelter from predators is dependent on dytiscid species morphometric patterns and swimming behaviour (McAbendroth et al. 2005). In their study on the dytiscid assemblages of mountain lakes in the Pyrenees, De Mendoza et al. (2012) showed that even sparsely vegetated lakes could act as refuges for dytiscids. There, the refuge effect of the presence of some vegetation in mountain lakes was, however, highly species-specific, being strong for *Boreonectes ibericus*, but not for *Agabus*, *Platambus*, and *Hydroporus* species. In this study, vegetation cover was the most important factor affecting the distribution of *Boreonectes* species. Some species tolerated dense vegetation, such as *Graphoderus cinereus*, which is usually found in fens or ponds with dense vegetation and, compared to other species belong to the sub-family Dytiscinae, is considered to be adapted to crawl among dense vegetation or detritus (Ribera and Nilsson 1995; De Mendoza et al. 2012). In addition to provide shelter from predators, the vegetation also provides dytiscids with some degree of protection from wave action. In 98 lakes in northern Sweden, Nilsson and Söderberg (1996) showed that the majority of dytiscid species were found more frequently in samples from protected sites with vegetation than in those from exposed sites without vegetation, with the principal exceptions of *Hydroporus obscurus*, *Hydroporus palustris*, and *Nebrioporus depressus*.

In addition to providing a physical structure to an aquatic habitat, plants may originate habitats representing whole, island-like, ecosystems, such as phytotelmata and water-filled tree holes. Phytotelmata are small pools impounded within terrestrial plants (Varga 1928; Kitching 2000) and support unique dytiscid species. These habitats are distributed in all continents except Antarctica, with their diversity being larger in the tropics and subtropics (Campos and Fernández 2011). Phytotelmata represent an ancient habitat, which has maintained a specialized dytiscid fauna over evolutionarily extended periods (Balke et al. 2008). The insect fauna of bromeliad (Bromeliaceae) phytotelmata (Frank and Lounibos 2009) and the origin and specificity of bromeliad-associated Copelatinae have been recently reviewed. Bromeliad-associated dytiscids are represented by the genus *Desmopachria* and the genus *Copelatus* (bromeliad-inhabiting species formerly placed in *Aglymbus* are now assigned to *Copelatus*), which is represented by six species that are strictly specialized to bromeliad tanks, despite being highly mobile and related to species occurring in small water bodies in tropical forests (Balke et al. 2008). Both adults and larvae have been recorded in bromeliad tanks. Phylogenetic studies have shown that one lineage of bromeliad-associated *Copelatus* species is morphologically distinct, and was estimated to originate 12–23 Ma ago, comparable to the age of the tank habitat itself. Bromeliads colonized by dytiscids belong to the genera *Aechmea*, *Brocchinia*, *Guzmania*, *Hohenbergia*, *Nidularium*, *Tillandsia*, and *Vriesia* (Balke et al. 2008; Campos and Fernández 2011). In temperate Argentina, adults of *Copelatus* species

Fig. 7.14 *Eryngium cabrerae* (Cyperaceae) in temperate Argentina, where *Copelatus* and *Liodessus* species were recorded (Photo by R. E. Campos)

have been recorded within *Eryngium cabrerae* Pontiroli (Cyperaceae, Fig. 7.14), whereas adults of *Liodessus* species have been found within *Eryngium cabrerae*, *E. elegans* Cham. & Schltdl (Fig. 7.15), and *Aechmea distichantha* Lemaire (Bromelidae) (Fig. 7.16; Campos and Fernández 2011). Phytotelmata also occur in the inflorescescences and infructescences of *Xanthosoma* (Araceae) species (García-Robledo et al. 2005). In an investigation on the composition and abundance of arthropods during the anthesis of inflorescences and the development of infructescences of three *Xanthosoma* species at three different geographic locations (populations of *X. undipes* in a tropical cloud forest of Costa Rica, Central America; *X. daguense* in a tropical cloud forest in the central Andes of Colombia; *X. poeppigii* in the Peruvian Amazonas), recorded dytiscid larvae only from older inflorescences (García-Robledo et al. 2005).

Fens also represent an important habitat for various dytiscid species (Foster et al. 1990). Dytiscids found in fens include *Laccornis oblungus*, which is confined to shallow, mossy areas of temporary base-rich fens (Foster 2010), *Agabus biguttulus*, *Copelatus haemorrhoidalis*, various *Hydroporus* species (e.g., *H. elongates*,

Fig. 7.15 *Eryngium elegans* (Cyperaceae) in temperate Argentina, where *Liodessus* species were recorded (Photo by R. E. Campos)

Fig. 7.16 *Aechmea distichantha* (Bromeliaceae) in temperate Argentina, where adults of *Liodessus* species were recorded (Photo by R. E. Campos)

H. glabriusculus, and *H. semenowi*), and species typically found in peatland, such as *Hydaticus aruspex*, *Hydrocolus rubyae*, and *Rhantus suturellus* (Nilsson and Holmen 1995; Larson et al. 2000).

The presence of mosses and algal mats may also represent an important dimension of habitat structure and complexity. Certain dytiscid species have a requirement for the presence of mosses, particularly within lotic habitats, in springs, in peatland, or at the margins of lakes and ponds. Mono-specific habitats composed of *Sphagnum* moss support high densities of *Agabus* and *Hydroporus* species (e.g., Foster et al. 1992; Larson et al. 2000; Gioria 2002). Species that are commonly found among mosses include several *Hydroporus* species, such as *H. scalesianus*, typically found within floating *Sphagnum* carpets surrounding small lakes (Nilsson and Holmen 1995), *H. obscurus*, *H. brevicornis*, and *H. morio* (Larson et al. 2000; Nilsson and Holmen 1995); *Agabus* species, such as *A. wasastjernae*, recorded from small, mossy hollows in bogs or spruce forests (Larson et al. 2000), and *A. zetterstedti* (Nilsson and Holmen 1995); and *Hydrocolus* species, such as *H. lupines*, recorded from saturated mosses of a seepage at the margins of a waterfall on Daniel Creek (Larson et al. 2000), *H. filiolus*, and *H. rubyae* (Nilsson and Holmen 1995). Other species include *Laccornis oblungus*, which appears to be restricted to shallow, mossy areas in temporary alkaline fens (Foster 2010), *Bidessus grossepunctatus*, whose main habitat is associated with moss carpets surrounding various water bodies, such as lakes, ponds, and springs, and *Iybius crassus* (Nilsson and Holmen 1995). Few species are also found within algal mats, such as *Hydrotrupes palpalis*, a lotic species that has been also recorded from hygropetric habitats, where there is a growth of filamentous algae, and *Liodessus flavicollis*, which is found in algal mats in relatively deep water, from clear-water pools or ponds with sandy substrates (Larson et al. 2000). However, the presence of dense algal formations is detrimental to the majority of dytiscid species in lentic habitats. For instance, Gioria et al. (2010a) recorded only few specimens of *Hydroporus planus* and *H. palustris* within ponds characterized by dense *Cladophora* formations.

7.6 Habitat Specificity

Although the majority of dytiscid species are habitat generalists, some have stricter habitat requirements or have adapted to harsh habitat conditions, and the degree of habitat specificity varies substantially among dytiscid species (Larson et al. 2000). In regions where habitat diversity is high and where habitats characterized by 'extreme' abiotic conditions are present, dytiscid diversity tends to be high, such as in the southeast of the Iberian Peninsula, where a variety of habitats, including fresh, saline, temporary, permanent, karstic, endorheic, and artificial habitats, are found (e.g., Picazo et al. 2010). In certain habitats characterized by unstable or harsh abiotic conditions, dytiscids represent the richest or more abundant Coleoptera or insect group, such as groundwater, interstitial habitats, rock pools, and hygropetric habitats.

Fig. 7.17 A collapsed sinkhole in Western Australia showing the nature of the substrate of the calcrete aquifer that is home to many species of subterranean dyticsid, including *Limbodessus cueensis* and *L. bigbellensis* (Photo courtesy of Bill Humphreys, Western Australian Museum)

Groundwater is known to support several stygobiont dytiscid species (i.e., species associated with and highly adapted for life in groundwater) (e.g., Leys et al. 2003; Watts et al. 2007). In recent years, an increasing number of studies have shown that groundwater in arid inland Australia supports the world's most diverse community of stygobiont dytiscid species, where dytiscids have been recorded from peculiar habitats such as salt lake groundwater estuaries and groundwater calcretes (i.e., carbonate deposits whose formation is directly associated with groundwater) (e.g., Watts and Humphreys 1999, 2000, 2001, 2003, 2004, 2006, 2009; Balke et al. 2004; Leys et al. 2010) (Fig. 7.17). In the Yilgarn region of western Australia and the Ngalia basin in central Australia, more than

100 species of stygobitic (groundwater obligate) dytiscid species have been recorded from calcretes on inland and coastal drainages (Watts and Humphreys 2006, 2009; Watts et al. 2007).

Over the past decade, the majority of stygobitic species have been recorded from northern, western, and central Australia (Watts and Humphreys 2003, 2004, 2006, 2009). Watts et al. (2007) reported the first truly stygobitic dytiscid species from eastern Australia, *Carabhydrus stephanieae*, which was collected from the alluvial aquifers of two tributaries of the Hunter River in eastern New South Wales. Soon after that, a second stygobitic dytiscid species was described by Watts et al. (2008) and collected from eastern Australia from alluvial gravels in the Peel River aquifer. Recently, Leys et al. (2010) described the first stygobitic species recorded from southern Australia, in a well in the bank of Reedy Creek at Willow Spring, suggesting that the number of dytiscid species recorded in underground habitats will increase with increases in the number of investigations on the fauna of these habitats.

Leys et al. (2003) suggested that the process of colonization of groundwater habitats has been driven by aridification, with some dytiscid species, and particularly larvae, moving into interstitial habitats when the surface water dries out to avoid the effects of droughts. Fenoglio et al. (2006) also suggested that the use of interstitial habitats as a refuge from droughts could be a first step towards the colonization of groundwater aquifers, based on their recording of specimens of *Agabus paludosus* in the interstitial zone of the streambed of the Po River (NW Italy) during a prolonged drought. According to Leys et al. (2010), evolution of stygobitic species is an on-going process. Stygobitic species possess a range of adaptations to darkness as well as typically low and heterogeneous food input, in space and time, and a relatively constant climate (Balke et al. 2004; Moldovan 2004). Such adaptations include depigmentation, with the cuticle becoming thinner, a reduction or a complete lack of eyes, and elongation of the body and antennae, a loss of wings and fusion of the elytrae, as well as anatomical internal alterations (Balke et al. 2004; Moldovan 2004).

Outside Australia, stygobitic dytiscid diversity appears to be poor, and few genera have been recorded within each continent (Spangler 1986), including France (*Siettitia* species, Abeille de Perrin 1904; Deharveng et al. 2009), Spain (*Iberoporus cermenius*; Castro and Delgado 2001), Mexico (*Sanfilippodytes sbordonii*; Franciscolo 1979), Venezuela (*Trogloguignotus concii*; Sanfilippo 1958), China (*Sinodytes hubbardi*; Spangler 1996; *Microdytes trontelji*; Wewalka et al. 2007), Japan (*Morimotoa phreatica*, Uéno 1957), west Africa (*Uvarus chappuisi*; Peschet 1932), New Zealand (e.g., *Phreatodessus hades*, *P. pluto*, and *Kuschelydrus phreatic*; Ordish 1976, 1991), and Thailand (*Siamoporus deharuengi*; Spangler 1996). In North America, four stygobiontic species, belonging to four genera, have been recorded: *Comaldessus stygius*, from Coal Springs, Texas (Spangler and Barr 1995); *Stygoporus oregonensis*, from a shallow well in Oregon (Larson and Labonte 1994), *Haideoporus texanus*, within the San Marcos pools, Texas (Young and Longley 1976), and *Ereboporus naturaconservatus*, from Caroline Springs, Texas (Miller et al. 2009).

Rock-pools also possesses unique habitat characteristics, which are associated with the highly unpredictability of the hydroperiod and, often, with saline conditions.

In an investigation on water beetles in the littoral zone of the Baltic Sea and rock-pools on Baltic islands, Ranta (1985) showed that littoral rock-pools supported dytiscid species that might have developed some adaptations, including a tolerance to saline water as well as a capacity to cope with temporary and unpredictable drying out phases (Ranta 1982). Despite being highly unstable, rock pools support exclusive dytiscid species, with three species (*Hydroporus melanocephalus*, *Potamonectes griseostriatus*, *Ilybius subaeneous*) contributing ~84 % of all the specimens recorded in this habitat (Ranta 1985). Additional records of species from rock pools include *Oreodytes* species, *Agabus infuscatus*, and *Rhantus monteithi*, which have been recorded from rock pools of clear streams of high mountains (Larson et al. 2000). In Fennoscandia, *Hygrotus polonicus*, *Hydroporus nigellus*, and *H. morio* have been recorded from freshwater or brackish rock pools, whereas *Stictotarsus griseostriatus* appears to be restricted to coastal rock pools (Nilsson and Holmen 1995).

Finally, among those habitats that have been long overlooked or under-investigated are hygropetric habitats (Miller and Perkins 2012), which consist of running water films or small springs flowing over exposed bedrock or flowing through mosses (Larson et al. 2000). These habitats include a variety of habitats ranging from small waterfalls or margins of larger waterfalls, large boulders in streams, springs, and seepages on vertical cliffs (Miller and Perkins 2012). Dytiscids appear to be relatively well represented in hygropetric habitats and include several species from the Bidessini (Miller and Spangler 2008; Miller 2012), *Africophilus*, *Hydroporus*, *Hydrotarsus*, and *Hydrotrupes* species (Larson et al. 2000; Ribera et al. 2003b; Miller and Perkins 2012). *Africophilus* species have been recorded from hygropetric habitats in Madagascar, the Ivory Coast, and Tanzania (e.g., Holmen 1984, see Alarie et al. 2000); these species are poor swimmers and tend to be found among the vegetation, debris, or gravel, moistened by trickles of water (Holmen 1984). Holmen (1984) described two species from Tanzania, *Africophilus stoltzei* and *A. uzugwai*, which were recorded 'among tufts of vegetation or dead leaves moistened by trickles of water on rock faces or at the edges of small streams in the rain forest', at altitudes comprised between 750–1,600 m and 1,000–1,650 m, respectively. The genus *Hydrotarsus* is the only genus of dytiscids endemic to Macaronesia, and presently includes three species, *H. compunctus*, *H. pilosus*, and *H. lundbladi* (e.g., Alarie and Bilton 2001; Ribera et al. 2003b), with both larvae and adults being restricted to hygropetric habitats. *Hydrotrupes palpalis* is the only confirmed hygropetric dytiscid species in North America (Miller and Perkins 2012), with most specimens being collected from hygropetric habitats (Larson et al. 2000).

7.7 Future Directions

Dytiscids are a highly diverse group that is found in a wide range of aquatic habitats, including 'extreme' habitats, where they often represent the dominant Coleoptera or insect group, in terms of species richness or abundance. Some dytiscid habitat specialists have developed a range of adaptations to cope with extreme habitat conditions in terms of acidity, salinity, permanency, or temperature, and have colonized habitats such as groundwater, temporary, eutrophic, acidic, highly saline habitats, or highly unstable habitats, such as rock pools. Over the past few decades, there have been increasing research efforts aimed at assessing patterns in dytiscid diversity and, in general, in aquatic diversity, along various habitat gradients. Our capacity to predict the distribution of dytiscid species based on habitat traits, regional, and local species pools is, however, hampered by a variety of factors, including (1) a high mobility of adults, which may migrate to less preferred habitats for part of their life cycle only, and random colonization events; (2) a high spatio-temporal variation in habitat conditions at different times of the year; (3) the tolerance of many species to large abiotic gradients; (4) a strong interaction between abiotic and biotic habitat conditions, particularly in relation to the distribution and structure of predators and that of the vegetation; and (5) the observational nature of the majority of studies examining dytiscid species distribution, with many studies focusing on gradients too narrow to detect strong effects or to detangle the individual effects of multiple variables.

Future investigations should include the collection of data on both biotic and abiotic conditions in the habitats to be investigated, and, where possible, these studies should be combined with laboratory experiments, to characterize properly the physiological and ecological amplitude of dytiscid species and predict their potential realized niche. Due to the heterogeneity in the biotic and abiotic conditions found in most habitat types, the use of large-scale species distribution data could help improve our capacity to predict the preferred habitat conditions of each species. To comprehensively characterize the habitat requirements of individual species, information on the habitat preferences of larvae should also be included, where possible. Habitats that have been overlooked, such as hygropetric habitats, groundwater, and unstable habitats such as rock pools and phytotelmata should be more consistently examined for dytiscids.

Meta-analysis studies could provide important insights into the role of various habitat variables in determining the habitat preferences of dytiscids. However, two main issues limit the possibility of using the extensive body of available literature on dytiscids, and, in general, on invertebrate assemblages. First, many studies of water beetles or macroinvertebrate assemblages do not separate clearly data for dytiscids from those of other families, and do not provide full species lists; second, a multiplicity of statistical protocols has been used to examine dytiscid distribution data (see Gioria et al. 2010b) and have relied on ordination techniques such as canonical correspondence analysis, which make it difficult to extract the actual contribution of individual explanatory variables to species distribution and does not allow comparisons among the results of multiple studies. These issues can be addressed by keeping separate information on various invertebrate families and by the use of commonly agreed sampling protocols and analytical procedures. Increasing information on how phylogenetic attraction affects habitat preference in dytiscids (e.g., Vamosi and Vamosi 2007), should be used to complement information on species community data, as it can provide important insights into the determinants of dytiscid distribution across habitats.

Ultimately, knowledge of the habitat requirements of dytiscid species and assemblages is central to the conservation of this highly diverse, fascinating taxonomic group. Despite much information now available on the distribution of dytiscids along various abiotic gradients, there is an urgent need to improve our understanding of how global environmental and socio-economic changes, including the intensification of agricultural and industrial activities, fish stocking, water use, urbanization, nitrification, climate change and extreme climatic events will affect the distribution of dytiscid species across habitats, and identifying the habitats are most likely to be affected by such changes with respect to the dytiscid fauna they support.

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Chapter 8
Predator-Prey Interactions of Dytiscids

Lauren E. Culler, Shin-ya Ohba, and Patrick Crumrine

> *With creamy margined, bronze green wing covers, oarlike hind legs fringed with chestnut-colored hairs, and a pair of formidable, meat-tong mandibles, what a well-fashioned submarine predator the diving beetle is.*
>
> (Wayne H. McAlsiter 2004)

Abstract As conspicuous predators throughout ontogeny, dytiscids are central to freshwater food webs, particularly in lentic systems such as wetlands and ponds. Adult and larval dytiscids are considered to be generalists, feeding on zooplankton, aquatic invertebrates, larval amphibians, and fish, but some dytiscid species selectively feed on certain prey types relative to others. Selective predation, cannibalism, intraguild predation, and non-consumptive effects on prey are attributes of dytiscid feeding that are known to shape food web structure and composition and influence species coexistence. Larval and adult dytiscids are also predators of mosquito larvae and thus frequently investigated as potential agents for mosquito suppression, particularly in northern areas and in areas where mosquitoes vector diseases. The effects of dytiscid predation on food webs and mosquito populations are dependent on several abiotic and biotic conditions, including vegetation structure, habitat

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complexity, and temperature. Dytiscids are also food for other organisms. Odonate nymphs, fish, amphibians, reptiles, birds, and mammals are known predators of dytiscids, although the extent to which these organisms rely on dytiscids for food remains unclear. Given the prominent role of dytiscids in freshwater food webs, future research should be aimed at improving basic knowledge of dytiscid feeding ecology, using dytiscids to test predator-prey and trophic theory, and examining how environmental change affects the role of dytiscids as predators of vector and nuisance species.

Keywords Predation • Trophic ecology • Community structure • Cannibalism • Biological control • Mosquitoes • Predator-prey interactions • Non-consumptive effects

8.1 Introduction

Predation is an important component of aquatic systems and plays a critical role in structuring communities (Batzer and Wissinger 1996; Batzer and Sharitz 2006) via consumptive and non-consumptive effects on prey. Knowing the direction and intensity of predation is vital for understanding the processes that structure communities (Klecka and Boukal 2012) and for cascading predator effects on other ecosystem characteristics (e.g., secondary production). Cannibalism and intraguild predation, special cases of predation that are prevalent in aquatic systems, can further influence community structure through density-dependent and size-structure effects and can help to explain species diversity (Yee 2010). Although fish and odonates as predators have received a great deal of attention (e.g., Crowder and Cooper 1982; Gillinsky 1984; Mallory et al. 1994; Batzer et al. 2000; Crumrine et al. 2008), dytiscids are ubiquitous predators in most freshwater habitats (Bay 1974). Dytiscids exert strong top-down impacts on prey assemblages and affect other ecological attributes of aquatic food webs.

All dytiscid beetles are carnivorous for at least part of their life-cycle. Larvae are exclusively predaceous, whereas adults may also feed as scavengers (Johnson and Jakinovich 1970; Larson et al. 2000; Bofill 2014). Detection of prey by dytiscids is via visual (Maksimovic et al. 2011), tactile (Friis et al. 2003), or chemical (Formanowicz 1987) cues and varies between species, life stages, and habitats (Michel and Adams 2009). Adults dytiscids are clumsy and inept at capturing active prey (Larson et al. 2000) but larvae use a variety of hunting modes, including sit-and-wait and active hunting (Yee 2010), and can be broadly classified as swimmers, floaters, and crawlers (Wichard et al. 2002). Larvae of many of the larger dytiscids, such as in the genus *Dytiscus*, are swimmers that pursue their prey by ambushing and trapping it against vegetation or the water's surface (Wichard et al. 2002). Floating larvae (e.g., *Graphoderus*, *Acilius*) are more specialized swimmers that move elegantly through open water and thus are more active during hunting (Wichard et al. 2002). Crawlers, including larvae in the Hydroporine group, tend to be broad bodied and cling to vegetation and

Fig. 8.1 Larval *Dytiscus* sp. sinking its mandibles into a small fish in a laboratory aquarium (Photo courtesy of Siegfried Kehl 2012)

sediment rather than pursuing prey by swimming (Wichard et al. 2002). Once detected and encountered, larval dytiscids grasp their prey with falcate piercing-sucking mandibles. They pre-orally inject digestive protease enzymes that liquefy their prey's body contents and then proceed to suck the resulting mixture back up through their mandibles for ingestion (Young 1967; Formanowicz 1987). This type of feeding permits tackling prey items that may be quite large, including vertebrates like fish (Fig. 8.1) and the tadpoles of bullfrogs and toads (Fig. 8.2, Smith and Awan 2009). Adults have chewing mouthparts like those of other Coleoptera and thus are less efficacious and more gape limited than their larval counterparts.

The diet of any predator is determined by its ability to detect, encounter, attack, capture, subdue, and digest the various types of prey in its habitat. Any one of these behavioral interactions may limit a predator's ability to successfully consume individuals of a given prey species. For example, prey of a given species may be consumed because they are more abundant relative to other species in the habitat and therefore encountered most often. Alternatively, the most abundant prey might be difficult for a predator to successfully capture so alternative prey are pursued. For adult dytiscids, gut contents can be discerned by dissection of the foregut and inspection of the contents using a microscope (see Bosi 2001; Kehl and Dettner 2003). As with any examination of gut contents, care must be taken in interpreting the results as some of the material could have been ingested via the guts of other prey organisms (Kehl and Dettner 2003) or could have been accidentally ingested. Visual examination of gut contents is not possible for dytiscid larvae because the prey are liquefied during ingestion. Polyacrylamide gel electrophoresis has been used to asses gut contents of

Fig. 8.2 A larval *Cybister chinensis* grasps and consumes a tadpole in the field (Photo by Shin-ya Ohba 2007)

other piercing-sucking predators, such as notonectids (Giller 1984, 1986), and could be used for studying the diets of larval dytiscids. Laboratory feeding experiments and preference trials are therefore a common way of assessing what larval and adult dytiscids consume. Individuals are offered different types of prey in different proportions and if consumption deviates from the offered proportion the individual is considered to exhibit selective predation (e.g., Peckarsky 2006; Culler and Lamp 2009).

8.2 What Do Dytiscids Eat?

Dytiscids are considered to be generalists that feed opportunistically on whatever is available, including conspecifics and hetorespecifics. Gut content studies, preference trials, and field observations have shown that zooplankton (Arts et al. 1981), insects (Figs. 8.3 and 8.4, Johansson and Nilsson 1992; Hicks 1994), fish (Balfour-Browne 1950; Dillon and Dillon 1961; Le Louarn and Cloarec 1997), amphibians (Formanowicz and Brodie 1982; Brodie and Formanowicz 1983; Resetarits 1998; Rubbo et al. 2006; Smith and Awan 2009; Inoda et al. 2009), reptiles (snakes) (Drummond and Wolfe 1981), and even decaying animal carcasses (Velasco and Millan 1998; Barrios and Wolff 2011) are part of their diets. Occasionally, plant material and algae can also be found in the guts (Deding 1988), but plants are considered to be accidentally ingested (Bosi 2001).

Fig. 8.3 A dragonfly nymph succumbs to predation by an adult *Cybister brevis* (Photo courtesy of Naoto Goto 2003)

Fig. 8.4 Backswimmers (Notonectidae) in a pond serving as prey for a *Cybister brevis* larva (Photo by Shin-ya Ohba 2008)

Several studies have indicated that both larval and adults stages of certain dytiscid species selectively feed on certain types of prey relative to others (Koegel 1987; Kehl and Dettner 2003; Tate and Hershey 2003; Ohba 2009a, b; Cobbaert et al. 2010; Ohba and Inatani 2012), sometimes even preferring dead prey to live prey, as is the case with adults of *Thermonectus marmoratus* (Velasco and Millan 1998). Aditya and Saha (2006) showed that adult *Rhantus sikkimensis* preferentially fed on chironomids versus culicids. *Dytiscus circumcinctus* larvae preferred mayfly nymphs and isopods to caddisfly larvae whereas the co-occurring *D. latissimus* had just the opposite preference (Johansson and Nilsson 1992). Yee et al. (2013) demonstrated a preference by larval *Graphoderus* for corixids compared to chironomids or damselflies, but larval *Rhantus* consumed similar proportions of corixids and chironomids. In temporary ponds in North Carolina, *Dytiscus* larvae had a negative effect on the survival of *Pseudacris triseriata* tadpoles relative to *Bufo americanus* tadpoles (Pearman 1995). A few studies have tested the preference of adult and larval dytiscids feeding on dipterans versus microcrustaceans, with preference noted for dipterans, including chironomids by adult *Potamonectes griseostriatus* (Ranta and Espo 1989) and culicids by larval *Agabus* (Culler and Lamp 2009). Some groups of dytiscids, such as the Hydroporinae, have larvae with elongated nasales that resemble a pig's snout (Friis et al. 2003) and are presumed adaptations for capturing microcrustaceans over other types of prey (Galewski 1971; de Marzo and Nilsson 1986). In addition to unique morphological adaptations, hunting mode (Yee 2010; Yee et al. 2013), hunger level (Hileman et al. 1995), visual cues (Nilsson 1986), and ontogeny (Friis et al. 2003; Ohba 2009b) are often cited as reasons for greater consumption of certain prey species relative to others.

8.3 Selective Predation and Effects on Community Attributes

When explored within a community context, the consequences of selective predation include effects on prey abundance and prey taxa richness. In general, and not surprisingly, dytiscids have high feeding rates and therefore can decrease total macroinvertebrate abundance or biomass (Arts et al. 1981; Arnott et al. 2006; Magnusson and Williams 2009; Cobbaert et al. 2010), with some macroinvertebrate groups reduced more than others. In fishless ponds in north-central Alberta, adults of *Dytiscus alaskanus*, via preferential consumption, lowered biomass of several groups including amphipods, leeches, water bugs, damselflies, dipterans, and snails (Cobbaert et al. 2010). Higher zooplankton biomass was also noted, indicating a possible trophic cascade (Cobbaert et al. 2010). Similarly, Tate and Hershey (2003) used lab experiments and molecular analyses to demonstrate preferential feeding by larval dytiscids (*Agabetes*, *Celina*, *Colymbetes*, *Derovatellus*, *Dytiscus*, and *Rhantus)* on larger prey species, including caddisflies, fairy shrimp, water bugs, diptera, amphipods, and also young-of-year grayling. Neither of these studies reported changes in taxa richness, but Arnott et al. (2006) found that *Graphoderus liberus* adults reduced zooplankton biomass by 21 % and lowered taxa richness and values of the Shannon-Wiener diversity index for zooplankton. In general, aquatic invertebrate predators have been shown to affect community attributes due to selective predation

Fig. 8.5 Larval *Colymbetes dolabratus*, collected from a pond near Kangerlussuaq, Greenland, engaging in cannibalistic interactions (Photo courtesy of Gifford Wong 2010)

(e.g., Murdoch et al. 1984; Runck and Blinn 1994), although studies directed at dytiscids are limited (Arnott et al. 2006) and the consequences of dytiscid predation on communities are not yet fully understood.

8.4 Cannibalism and Intraguild Predation

Intraspecific predation (cannibalism) is quite common among aquatic organisms (Fox 1975) and has been documented among larval dytiscids (Pajunen 1983; Juliano and Lawton 1990; Culler and Lamp 2009; Yee 2010). There is much less evidence for cannibalism between adults, most likely due to gape limitation (Johnson and Jakinovich 1970). Cannibalism during the larval stage is probably even more prevalent than the literature suggests given the generalist foraging patterns and voracity of many dytiscid species (Fig. 8.5). Cannibalism has the potential to function as a density dependent control on dytiscid populations (Juliano and Lawton 1990) and this effect may be more pronounced when alternative prey is limited in abundance (Culler and Lamp 2009). Under these conditions, cannibalism can be viewed as a lifeboat strategy that allows individuals to persist under sub-optimal ecological conditions and even accelerate development in temporary ponds that are prone to drying (Batzer and Wissinger 1996). In some species, such as *Potamonectes griseostriatus*, conspecifics make up nearly 10 % of the diet and are among the more common prey items in the diet of larvae (Pajunen 1983).

In general, the factors influencing the occurrence and frequency of cannibalism within Dytiscidae are not unlike those across other orders of aquatic insects. In most aquatic insects, population size structure plays a key role in determining the frequency of cannibalism and larger individuals are almost always the cannibal and smaller individuals the victim (Wissinger 1992; Fagan and Odell 1996; Hopper et al. 1996; Wissinger et al. 1996; Yee 2010). However, the relatively large mandibles possessed by larval dytiscids confer the ability to subdue large prey items including similar-sized conspecifics (Pajunen 1983) and perhaps even larger individuals. Avoidance of cannibalism may be influenced by large differences in size between larvae (Pajunen 1983) and the ability to recognize and avoid conspecifics (Inoda 2012). Given the dearth of studies on cannibalism among dytiscids, these and other aspects of cannibalism deserve further inquiry. This is particularly true for dytiscids because they occupy relatively high trophic positions within fishless systems and recent modeling studies have demonstrated the potential for cannibalism to strongly influence coexistence among predators and structure communities (Rudolf 2007; Ohlberger et al. 2013).

Besides cannibalism, intraguild predation (IGP) is likely to be a common interaction among dytiscids, particularly among larvae for the reasons noted above. IGP is a mixed competition-predation interaction that occurs when species that compete for a common resource also interact as predator and prey (see Figs. 3, 4, and 6 in Polis et al. 1989). Simple mathematical models suggest that IGP should be relatively rare in nature (Holt and Polis 1997), but food web studies indicate that IGP is common across terrestrial, marine, and aquatic systems (Arim and Marquet 2004). More recent theoretical and empirical work indicates that size-structured interactions such as cannibalism may promote the coexistence of predators in IGP systems (Crumrine 2005; Rudolf 2007). There are few studies that specifically examine IGP among larval dytiscids (e.g., Nilsson and Soderstrom 1988; Culler and Lamp 2009; Yee 2010). As is the case with cannibalism, IGP is probably more prevalent than the literature suggests given the generalist foraging patterns of larval dytiscids and high spatial and temporal overlap among species (Yee 2010). Of the studies that have examined IGP among larval dytiscids, not surprisingly, size differences between individuals influence the outcome of predator-prey interactions between intraguild predators. In some cases larger larvae consume smaller larvae (Nilsson and Soderstrom 1988; Yee 2010), but there are also examples of IGP between individuals similar in size (Culler and Lamp 2009; Yee 2010). In fact, some genera (e.g., *Dytiscus*) do not appear to consume dytiscid prey smaller than themselves and this may promote coexistence between relatively large- and small-bodied dytiscids (Yee 2010). IGP among larval dytiscids can be symmetric; that is, both predators consume each other (Culler and Lamp 2009; Yee 2010). This appears to be most common among congeneric species that are similar in size; although higher levels of aggression may also lead to greater frequency of IGP among some species (Culler and Lamp 2009). Asymmetric IGP appears to be most common when there is a distinct size difference between individuals (Nilsson and Soderstrom 1988; Yee 2010). Large-bodied dytiscids, such as those in the genera *Dytiscus* and *Cybister*, are within the guild of top predators in fishless ponds and likely function as intraguild predators of larval dytiscids as well as other large predatory aquatic insects such as odonate nymphs. Despite this, there are surprisingly few studies that have examined IGP within this group of insects. Future studies are warranted because IGP among dytiscids is likely to influence coexistence between competing species and it may help to explain the diversity of species found in some aquatic systems (Yee 2010).

8.5 Non-consumptive Effects of Dytiscid Predation

In addition to consumptive (i.e., lethal) predator effects that change prey abundance and taxa richness, non-consumptive (i.e., non-lethal) effects are a major component of predator-prey interactions (Preisser et al. 2005). The presence of a predator can trigger a cascade of changes in prey foraging behavior, physiology, and the timing of life history events, with consequences for prey fitness. These non-consumptive effects can sometimes outweigh consumptive effects (McPeek and Peckarsky 1998) and often cascade to influence ecosystem properties and functions (e.g., Schmitz et al. 2010). Removal of aquatic insect predators, including some dytiscids, resulted in altered migration strategies and an increase in body size of daphnids in fishless ponds (Herwig and Schindler 1996). Although specific investigations of non-consumptive effects of dytiscids are uncommon, they do offer insights into how these predators may affect aquatic prey communities. Ohba et al. (2012) reported that *Culex tritaeniorhynchus* female mosquitoes avoided laying eggs in dytiscid-conditioned water and that smaller mosquitoes emerged from dytiscid-conditioned water as a result of lowered larval activity. Smith and Awan (2009) found that American toad and bullfrog tadpoles altered activity levels and avoided vegetation when dytiscids were present, presumably to avoid detection and because dytiscids use vegetation as an ambush perch. Similarly, wood frog tadpoles avoided areas containing caged dytiscids in experimental mesocosms (Rubbo et al. 2006). Johnson et al. (2003) found that the presence of dytiscid larvae and other predators of southern leopard frog eggs shortened the time to hatching and decreased hatchling size. In these preceding examples, dytiscid-induced changes in a prey's behavior and size could be energetically costly and have fitness consequences, but dytiscid predators can also increase prey fitness. For example, in temporary pools adult dytiscids facilitated dispersal of their prey (Beladjal and Mertens 2009); consumption, mastication, and the passage of fairy shrimp through the digestive tracts of adult dytiscids (*Ilybius fenestratus* and *Colymbetes fuscus*) led to increased fairy shrimp hatching (Beladjal and Mertens 2009). Given their numeric and taxonomic dominance in many aquatic systems, non-consumptive predator effects, positive or negative, should be further explored in dytiscids, especially because non-consumptive effects of predation on prey have been shown to result in changes to population and community dynamics (McPeek and Peckarsky 1998) and ecosystem function (Schmitz et al. 2008).

8.6 Dytiscids as Predators of Vector and Nuisance Species

Of Coleopteran predators, dytiscids are the most commonly reported predators of vector and nuisance species, specifically mosquito larvae and pupae (Fig. 8.6, James 1961, 1964, 1965, 1967; Lee 1967; Young 1967; Borland 1971; Notestine 1971; Swamy and Rao 1974; Akmetbekova and Childibaev 1986; Sugiyama et al. 1996; Mogi 2007; Quiroz-Martínez and Rodríguez-Castro 2007; Shaalan and Canyon 2009). Consumption rates can be as high as 86 mosquito larvae per predator per day

Fig. 8.6 A larval *Dytiscus* sp. eats a mosquito larva (Photo courtesy of Ary Farajollahi 2009)

(Aditya et al. 2006), thus warranting their consideration as agents for natural mosquito suppression. The most commonly reported predators of mosquitoes in field studies include the genera *Laccophilus*, *Agabus*, and *Rhantus* (Sailer and Lienk 1954; Kuhlhorn 1961; James 1964, 1965; Lee 1967; Roberts et al. 1967; Ohba et al. 2010, Table 8.1). Laboratory observations have confirmed that adult and larval dytiscids attack mosquito larvae (Table 8.1). For example, Bofill (2014) found that although adult and larval *Laccophullis faciatus rufus* consumed early and late instar *Culex quinquefasciatus*, adults consumed more later instars, suggesting a potential synergistic effect of dytiscids on mosquito populations. Mosquito larvae have been found in the guts of field collected dytiscids (Deding 1988; Bosi 2001). Radioisotope studies (James 1965) and precipitin tests (Service 1973) have confirmed the prominent roles of dytiscids as mosquito predators. Moreover, serological methods (Service 1977, 1993) and DNA analysis (Ohba et al. 2010) revealed that some species consumed malaria vector mosquitoes in their natural wetlands.

The effects of dytiscids on mosquitoes have been studied in diverse habitats (Walton et al. 1990; Campos et al. 2004; Carlson et al. 2009; Ohba et al. 2013) including rice ecosystems (Mogi and Miyagi 1990; Mogi 1993; Takagi et al. 1996; Mogi et al. 1999; Mwangangi et al. 2008; Ohba et al. 2011), areas where mosquitoes vector disease (e.g., Chandra et al. 2008; Hassan et al. 2010), and in northern areas, where dytiscids often dominate as top predators and have life cycles that are synchronous with those of their mosquito prey (e.g., James 1964; Nilsson and Svensson 1994). In a field study in India, Chandra et al. (2008) showed that *Acilius sulcatus* larvae significantly impacted mosquito larvae that prevail in cement tanks. A significant decrease in larval density of different mosquito species was observed 30 days after the introduction of *A. sulcatus* larvae, while the removal of *A. sulcatus* resulted in a significant increase in larval density. These results highlight the efficacy of *A. sulcatus* in suppressing larval mosquito populations (Chandra et al. 2008). Using artificial ponds in Sweden, Lundkvist et al. (2003) showed that after colonization by large adult dytiscid predators (*Ilybius*, *Rhantus* and *Agabus* spp.), larval mosquito abundance was significantly reduced.

Interest in dytiscids for their mosquito suppression abilities has spurred research that examines natural patterns in assemblages of dytiscids and culicids (e.g., Nilsson and Svensson 1995). In northern areas, many species of dytiscids have lifecycles that coincide with mosquito development. In snowmelt ponds in Greenland, larvae of *Colymbetes dolabratus* hatch early in the spring just after pond thaw when mosquito larvae are abundant and one of the only food sources available (Culler 2013).

Table 8.1 Summary of predaceous diving beetles and species of mosquito prey

Dytiscid species and stage[a]	Mosquito species	Method[b]	Reference
Acilius sulcatrus L	*Culex quinquefasciatus*	LE, FE	Chandra et al. (2008)
Agabus bipustulatus A	Not reported	FCG	Bosi (2001)
Agabus conspicuous A	*C. tritaeniorhynchus*	LE	Ohba and Takagi (2010)
Agabus disintegratus L	*Aedes albopictus*	LE	Culler and Lamp (2009)
Agabus erichsoni L	*A. communis*	LE, FE	Nilsson and Soderstrom (1988)
Agabus japonicus A	*C. tritaeniorhynchus*	LE	Ohba and Takagi (2010)
Agabus opacus L	*A. communis*	LE, FE	Nilsson and Soderstrom (1988)
Agabus punctatus L	*A. albopictus*	LE	Culler and Lamp (2009)
Colymbetes dolabratus L	*A. nigripes*	LE, FO	Culler pers obs
Colymbetes paykulli A	*Culex.* spp.	LE	Lundkvist et al. (2003)
Cybister brevis A	*C. tritaeniorhynchus*	LE	Ohba and Takagi (2010)
Cybister brevis L	*C. mimeticus*	FO	Ohba (2009)
Cybister japonicus A	*C. tritaeniorhynchus*	LE	Ohba and Takagi (2010)
Dytiscus marginicolis	*C. incidens*	LE	Lee (1967)
Eretes griseus A	*C. tritaeniorhynchus*	LE	Ohba and Takagi (2010)
Eretes sticticus A	Not reported	LE	Swamy and Rao (1974)
Graphoderus adamsii A	*C. tritaeniorhynchus*	LE	Ohba and Takagi (2010)
Hydaticus bowringii A	*C. tritaeniorhynchus*	LE	Ohba and Takagi (2010)
Hydaticus grammicus A	*C. tritaeniorhynchus*	LE	Ohba and Takagi (2010)
Hydaticus grammicus A, L	*C. tritaeniorhynchus*	LE	Sugiyama et al. (1996)
Hydaticus rhantoides A	*C. tritaeniorhynchus*	LE	Ohba and Takagi (2010)
Hydroglyphus japonicus A	*C. tritaeniorhynchus*	LE	Ohba and Takagi (2010)
Hydroglyphus japonicus A	*C. tritaeniorhynchus*	LE	Sugiyama et al. (1996)
Hydroglyphus pusillus A	*C. pipiens*	LE	Bellini et al. (2000)
Hyphydrus japonicus A	*C. tritaeniorhynchus*	LE	Ohba and Takagi (2010)
Ilybius ater A	*Culex.* spp.	LE	Lundkvist et al. (2003)
Ilybius fuliginicolis A	*Culex.* spp.	LE	Lundkvist et al. (2003)
Ilybius subaeneus A	Not reported	FCG	Bosi (2001)
Laccophilus difficilis A	*C. tritaeniorhynchus*	LE	Ohba and Takagi (2010)
Laccophilus fasciatus A	*C. pipiens*	LE	Roberts et al. (1967)
Laccophilus fasciatus rufus A, L	*A. vexans*, *C. quinquefasciatus*	LE	Pitcher and Yee (2014), Bofill (2014)
Laccophilus maculosus L	*A. atropalpus*	FCR	James (1965)
Laccophilus maculosus A	*C. pipiens*	LE	Roberts et al. (1967)
Laccophilus proximus A	*A. vexans*	LE	Pitcher and Yee (2014)
Laccotorephes punctipennis L	*A. albopictus*	FE	Sulaiman and Jeffery (1986)
Rhantus pulverosus A, L	*C. tritaeniorhynchus*	LE	Sugiyama et al. (1996)
Rhantus sikkimensis A	*C. quinquefasciatus*	LE	Aditya et al. (2006)
Rhantus suturalis A	*C. tritaeniorhynchus*	LE	Ohba and Takagi (2010)
Rhantus suturalis A	Not reported	FCG	Bosi (2001)
Unknown	*C. annulirostris*	NR	Rae (1990)
Laccophilus spp. A	*Anopheles gambiae*	FCP	Ohba et al. (2010)

[a] L larvae, A adults

[b] LE lab experiment, FE field experiment, FO field observation, FCG field collection and gut contents, FCP field collection and PCR, FCR field collection and radioisotopes, NR not reported

Similar patterns are found elsewhere in northern regions. *Agabus erichsoni* completes its life cycle in woodland pools, overwintering as both eggs and adults, the appearance of the latter coinciding with the winter hatch of mosquitoes (James 1961; James 1967). Nilsson and Svensson (1994) compared assemblages of dytiscids and mosquitoes in two boreal snowmelt pools that differed in temperature. Although dytiscid abundance was similar, dytiscid species richness was higher and mosquito larvae suffered higher mortality in the warmer pools (Nilsson and Svensson 1994). In Canadian rock pools, James (1964) found *Laccophilus maculosus* to be the most abundant predator of the mosquito *Aedes atropalpus,* with a significant inverse correlation between densities of *Ae. atropalpus* and larval *L. maculosus*. Smaller pools supported high densities of immature mosquitoes but no larval dytiscids, suggesting that dytiscids may restrict mosquitoes to certain parts of the potential breeding habitat (James 1964). Based on associations between landscape structure, including forest cover and water permanence, and mosquito and dytiscids assemblages, Schafer et al. (2006) suggested that creating permanent wetlands in an open landscape would favor colonization by diverse dytiscid assemblages and therefore reduce mosquito colonization. Other studies have also suggested that construction of aquatic habitats with the goal of attracting a diverse and abundant predator assemblage may help to reduce pest abundance (Walton 2012). Similar to ideas proposed in conservation biological control (Barbosa 1998), these techniques may be useful because dytiscids are difficult to rear and do not lend themselves well to use as classical biological control agents.

8.7 Environmental Constraints on Predation

Predation is dynamic in response to changing abiotic and biotic environmental conditions. Factors such as vegetation structure, the presence and abundance of intraguild predators, and environmental temperature, via behavioral and physiological modifications, can limit or enhance the ability of a predator to consume prey. Habitat complexity and structure have been shown to shift dytiscid hunting mode from actively foraging to sit-and-wait (Michel and Adams 2009; Yee 2010), though do not necessarily affect overall prey capture rates (Michel and Adams 2009). Environmentally-induced shifts in predator behavior can have multiple effects on ecological communities (Michel and Adams 2009), including consumptive (Preisser et al. 2007) and non-consumptive effects, the occurrence of trophic cascades, and even changes in ecosystem function (Schmitz 2008). Habitat structural complexity has also been suggested to enhance predation due to a reduction in negative intraspecific interactions that are a component of dytiscid interactions (i.e., cannibalism and intraguild predation, Culler and Lamp 2009; Yee 2010). Given the increasing numbers of freshwater habitat restoration projects, such as construction of mitigation wetlands and restoration of drained wetlands on agricultural fields, understanding effects of habitat structure and complexity on dytiscid predation and effects on food webs remains a high priority for research. For example, wetland construction techniques that include adding coarse woody debris or planting diverse aquatic vegetation could be useful for projects that have goals of encouraging predator colonization to reduce pest abundance (e.g., Walton 2012). This idea largely parallels a practice used in agricultural habitats known as conservation biological control, which is defined as the manipulation of habitats to favor the natural enemies of pests, as to conserve biodiversity and reduce pest problems (Barbosa 1998).

Temperature, as a fundamental driver of many biological processes, especially in poikilothermic animals like insects, can also affect dytiscid predation. Calosi et al. (2007) showed that temperature can alter the diving behavior of dytiscids, with frequency of diving increasing at higher temperatures, thus decreasing the amount of time available for other activities such as foraging. Furthermore, temperature, due to basic effects on the metabolism of ecothermic animals, can also directly affect consumption rates, with higher intakes necessary to maintain metabolic activities at higher temperatures (Brown et al. 2004; Rall et al. 2010). This is consistent with results from Nilsson and Svensson (1994) who showed that prey mortality from dytiscid predation was higher in warmer pools. In addition to direct effects on rates of predation by dytiscids, temperature can indirectly affect predation via shifts in the behavior and phenology of the predators and prey (Culler 2013). Understanding these temperature effects is a research priority, particularly in regions where there is significant warming occurring (e.g., Arctic and alpine regions) and where dytiscids occur as top predators and have a strong influence on the prey community, particularly mosquito abundance.

8.8 Dytiscids as Prey

The role of dytiscids in the trophic ecology of freshwater food webs is often investigated from the standpoint of dytiscids as top predators, but dytiscids also make up parts of the diets of many other organisms, both aquatic and terrestrial. Odonates are known predators of dytiscids (Fig. 8.7, Larson 1990 R. Roughley personal communication), but there are few, if any, published reports of other aquatic invertebrates feeding on dytiscids. Dytiscids cuticle has been recovered from dissected fish guts (Laufer et al. 2009), suggesting that that adult and larval dytiscids are consumed by fish (e.g., Closs 1996; Laufer et al. 2009). There is evidence, however, that some fish and dytiscids do not typically co-occur (Schilling et al. 2009; de Mendoza et al. 2012) and thus the extent to which fish rely on dytiscids for food is not well known. In mountain lakes, the distribution of *Agabus bipustulatus* is constrained due to predation by salmonid fish, and thus they are found to only inhabit colder lakes where fish are unlikely to occur (de Mendoza et al. 2012). Gerhart et al. (1991) also showed that dytiscids can secrete defensive hormones that inhibit feeding by fish. Dytiscids are part of the diets of turtles (Chessman 1984; Georges et al. 1986; Demuth and Buhlmann 1997), bullfrogs (Korschgen and Moyle 1955; Bruggers 1973), toads (Whitaker et al. 1977), salamanders (Whiles et al. 2004; Dasgupta 1996), and snakes (Peddle and Larson 1999).

Fig. 8.7 Dragonfly nymphs and dytiscids frequently co-occur and engage in intraguild predation. Here, a large *Anax* dragonfly (Odonata: Aeshnidae) nymph consumes a *Graphoderus* larva (Photo courtesy of Donald Yee 2007)

The evidence for snake predation comes from postulation that scratch marks on the beetle's cuticle were caused from predator attacks in areas with known snake populations (Peddle and Larson 1999).

Dytiscids transcend the aquatic food web by virtue of bird and mammal diets. Numerous studies have confirmed the role of adult and larval dytiscids in the diets of birds, particularly in birds species that are associated with water (e.g., Schubart et al. 1965; Abensperg-Traun and Dickman 1989; Goutner and Furness 1997; Elmberg et al. 2000), but also in hawks (Munro 1929) and finches (Montalti et al. 2005). Pellets collected from colonies of grey herons in northern Poland consisted of 26–51 % invertebrate remains, mainly the dytiscid beetle *Dytiscus marginalis* (Jakubas and Mioduszewska 2005). Forty-one percent of regurgitate material from Glossy Ibises in Spain were dytiscids, primarily *Cybister* (Macías et al. 2004). In Arkansas, dytiscids make up 19 % of the King Rail's diet during the winter months (Meanley 1956). Brooks (1967) presented data on the diets of various species of shorebirds in Illinois, the majority of which contained adults of the dytiscid beetles *Agabus disintegratus* and *Hygrotus*. Raccoons (Capinera 2010) and otters (Brzeziński et al. 1993) are also noted predators of dytiscid beetles. During the warm season, dytiscids are the third most important prey item in terms of biomass for river otters in eastern Poland (Brzeziński et al. 1993). The only other mammals known to ingest dytiscids are humans. Several species in the genus *Cybister* are regularly consumed in parts of China (Jäch 2003), Thailand (Chen et al. 1998), New Guinea (Gressitt and Hornabrook 1977), and Japan (S. Ohba, personal observation).

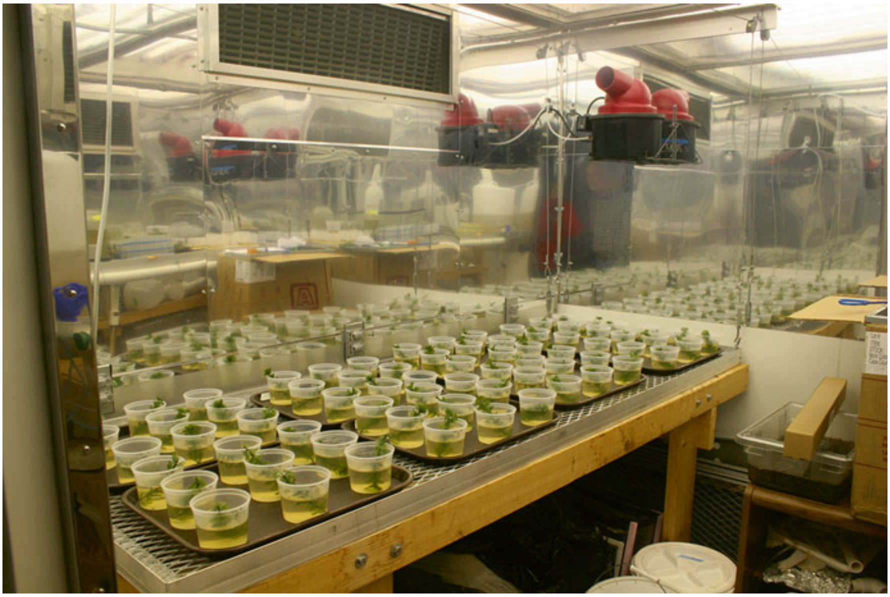

Fig. 8.8 Dytiscids are ideal for use in laboratory experiments where various factors can be manipulated, including habitat structure, temperature, and relative abundance of different types of prey. Here, small plastic cups housing dytiscid larvae are used as microcosms to test the effects of structure and prey density on antagonistic predator-predator interactions (Photo by Lauren Culler 2008)

8.9 Future Directions

Dytiscids are an ideal study organisms for basic and applied ecological research due to their ubiquitous and global distribution and ease of handling in the laboratory (Fig. 8.8) and field (Fig. 8.9). Freshwater food webs in lentic habitats, particularly in fishless ponds, are much less studied than those in streams and lakes (Klecka and Boukal 2012). Given the role of dytiscids in these habitats as top predators, predators of mosquitoes, and as food for other organisms, future studies are essential for understanding the processes that structure freshwater lentic communities.

Basic information about dytiscid trophic ecology remains largely unknown. For example, we do not know the prevalence of generalist versus specialist type feeding in dytiscids and how this changes with ontogeny, and the role, if any, of plants in the diets of dytiscids. We also do not know the extent to which fish and other aquatic or terrestrial organisms rely on dytiscids as a part of their diets. Improved basic knowledge about the position and relative importance of dytiscids in freshwater food webs will promote the design of studies that address basic and applied questions.

Fig. 8.9 Field experiments are useful for measuring effects of dytiscid predation on prey. Here, white pans are set up adjacent to a tundra pond and used to measure consumption rates of mosquito larvae by dytiscid predators (Photo by Lauren Culler 2012)

Dytiscids are easily handled and observed and thus are ideal for testing ecological theories of predator-prey interactions, species coexistence, and consumptive and non-consumptive effects of predators on prey. Future studies should address prey choice and the mechanisms underlying selective predation. These studies are needed for understanding the relative intensity of intraguild predation and cannibalism among dytiscids and the role of size structure in shaping these interactions. Behavioral studies are needed to elucidate the non-consumptive effects of dytiscid predation on the behavior and life-history traits of prey. The consequences of selective predation, intraguild predation, cannibalism, and non-consumptive effects by dytiscids remain largely unknown but have the potential to strongly influence population dynamics and species coexistence (Yee 2010).

Environmental changes that are occurring at local and global scales, including habitat degradation and restoration and climate change, necessitate further study of how environmental factors shape dytiscid effects on prey, particularly factors such as habitat structure and temperature. As predators of vector and nuisance species, some dytiscids have potential as biological control agents. Measuring their effects on nuisance prey populations and testing how habitat and environmental factors influence these effects are essential for projects that aim to construct or restore natural lentic habitats while minimizing increased threats from vectors.

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Patrick Crumrine earned his B.S. in Biology in 1998 from SUNY Plattsburgh and his Ph.D. in Biology from the University of Kentucky in 2003. The primary focus of his research is to understand how size-structure influences competition and predation among aquatic organisms, particularly odonates and dytiscids. Other research interests include disease ecology of amphibians and population/community structure of aquatic turtles. Most of his work is conducted in small ponds and wetlands in the mid-Atlantic region of the United States.

Chapter 9
Dispersal in Dytiscidae

David T. Bilton

> *"I was reading in bed in Sussex in July, 1937, at 11.15 p.m. when a male* Ilybius fuliginosus *flew in at the window and settled on my pillow….."*
>
> F. Balfour-Browne (1953)

Abstract Dytiscid beetles live in spatially discrete habitat patches of varying temporal duration and ecological stability. Many species are exemplary active dispersers, moving between suitable localities, sometimes on multiple occasions within an individual's lifetime. Despite this there is apparently much variation in the ability of individual species to disperse by flight, this having far-reaching consequences for their evolution and persistence. This chapter examines the mechanisms, causes, and consequences of dispersal in predaceous diving beetles, reviewing work on flight and flightlessness, ultimate and proximate triggers of dispersal, and the biogeographical/macroecological consequences of movement, as well as suggesting areas where further research is required. Most predaceous diving beetle species fly, but some do so far more readily and over longer temporal windows than others. The degree to which individual species disperse may be shaped largely by habitat stability and persistence something which has significant consequences for the composition of regional faunas.

Keywords Dytiscidae • Dispersal • Flight • Colonization • Biogeography

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9.1 Introduction

Like Frank Balfour-Browne's nocturnal *Ilybius*, many dytiscid beetles are active fliers, something that is rarely observed, but nevertheless fundamental to their way of life, allowing them to colonize new areas of habitat (Fernando 1958; Fernando and Galbraith 1973), track the seasonal availability of water (Hilsenhoff 1986; Miguelez and Valladares 2008), or move to terrestrial overwintering sites (Galewski 1971). Almost all inland waters on earth contain predaceous diving beetles, including those on isolated oceanic islands such as the Azores and Hawaii. New water bodies are colonized by a suite of pioneer dytiscids, which often arrive within days of their creation. Even the small pockets of water found in phytotelmata, such as bromeliad tanks, harbor specialist diving beetles (e.g., Balke et al. 2008). Like all freshwater organisms, dytiscid beetle populations live and reproduce in discrete localities, surrounded by a relatively inhospitable terrestrial landscape. Whilst the ecophysiology and gas exchange mechanisms of adult dytiscids (Verberk and Bilton 2013) mean that crossing this matrix may be less insurmountable than it is for some freshwater animals, moving between suitable patches nevertheless constitutes a significant challenge.

As with other pterygotes, most dytiscid species possess functional flight wings, and utilize these to overcome the challenge of inter-patch dispersal. As such, dytiscids can generally be considered active dispersers, powering their own movement between suitable habitat patches. Such active inter-habitat dispersal involves behaviors that are predominantly initiated, and at least partly controlled, by the individual beetle. Actively dispersing predaceous diving beetles may therefore use sensory cues to seek out new areas of habitat, or patches occupied by conspecifics. The degree to which dispersal movements can truly be considered active, however, will depend on species, situation, and the prevailing environmental conditions – for many small beetles much of their time in the air may be at the mercy of the wind, giving them little control over their direction.

Following a brief general consideration of the evolution of dispersal, and its consequences, this chapter will focus on aspects of dispersal biology fundamental for dytiscids, as well as some areas where studies of these beetles have contributed to wider ecological and evolutionary ideas. Specifically, I start by revisiting studies of flight and flying ability, which directly examine the dispersal apparatus and behavior of predaceous diving beetles. Continuing with the behavioral theme, I review studies of dispersal triggers and timing in predaceous diving beetles, considering what cues individuals may use when making the decision to leave an occupied patch. Finally, I consider the large-scale ecological and evolutionary consequences of dispersal evolution in dytiscids, and show how the origin of both widespread species and narrow-range endemics ultimately depends on the relative strength of selection for dispersal – itself dictated by habitat.

9.2 The Evolution, Maintenance, and Consequences of Dispersal

9.2.1 *Why Disperse?*

Viewed from the perspective of the individual dytiscid, there are both advantages and disadvantages that may result from dispersing from one site to another (see Bilton et al. 2001; Bonte et al. 2012). Advantages include escape from unfavorable conditions, e.g., limited resources, predators, pathogens and parasites, and inbreeding and the possibility of locating a new site with low density occupation and fewer direct competitors. Disadvantages include an inability to locate a suitable new site, a risk of predation en route, an inability to locate a mate, outbreeding depression and lack of adaptation to the new habitat. The most likely risks to sexually reproducing organisms such as dytiscids in failing to disperse in the short-term are inbreeding, overcrowding and increased competition, predation, and exposure to pathogens and parasites. In the long term, failing to disperse is likely to increase extinction risk at the population and lineage level, if nothing else as a result of stochastic effects.

9.2.2 *The Evolution and Maintenance of Dispersal*

The evolution of dispersal has received a great deal of theoretical investigation, including the development of numerous mathematical models, and although none of this work has considered dytiscids, the ideas clearly apply when considering these beetles (see e.g., Hamilton and May1977; Levin et al.1984; Johnson and Gaines1990; Cohen and Levin1991; McPeek and Holt1992; Dieckmann et al. 1999; Ferriere et al. 2000; Clobert et al. 2001; Ronce 2007). Most models assume that local populations occur in discrete habitats and identify evolutionarily stable strategies based on game theory.

Factors such as habitat stability and permanence are likely to be key in shaping the dispersal strategies of dytiscids over evolutionary timescales, dispersal being more strongly selected for in taxa of relatively unstable habitats, such as the small standing waters that typically hold the bulk of local dytiscid diversity. Such habitats may dry seasonally, forcing the adults of some species to disperse locally to more permanent sites, but are also short-lived on geological timescales (Ribera 2008) – a point I return to below. In addition to the above-mentioned costs and benefits associated with dispersal from the point of view of an individual, the dispersal ability of aquatic invertebrates such as dytiscids is likely to influence the long-term persistence of local populations (e.g., Avise 1992; Hogg et al. 1998), an association that may ultimately influence the success of species. Dispersal ability may be a critical predictor of a species' ability to escape environmental change, such as climate warming, where movement to a more suitable site may be necessary for long-term survival. The climatic changes of the Pleistocene have provided repeated natural experiments that allow us to examine how fauna and flora, including dytiscids, have responded to shifts in temperature, this being particularly well-studied in the northern hemispheres (see Elias 1997 for a review). Whilst there are a number of examples of massive range shifts in beetles in response to Pleistocene climatic changes, including the occurrence of the Mongolian and Canadian *Hygrotus unguicularis* (Crotch) on the Isle of Man (between Ireland and Britain) in the Late Glacial period 12,000 years ago (Joachim 1978), almost all of these concern species occurring at high latitudes. Very few examples are known of large-scale range movement in species occupying lower latitudes – most endemic species appear to have evolved in, or close to, the areas where they currently occur, and many may have limited dispersal ability compared to their more widespread relatives, particularly with lotic taxa (Abellan et al. 2011; Sánchez-Fernández et al. 2012a).

9.2.3 Consequences of Dispersal

Dispersal only makes a difference in an evolutionary sense if it results in successful colonization of a site – something that involves successful reproduction. When dispersing individuals enter an existing population, such reproduction results in gene flow, i.e., the transfer of genes from one population to another. The effects of dispersal and gene flow are varied. Dispersal can result in the expansion of ranges following the colonization of new sites. An interesting question here is what ultimately sets the limits to dispersal and range expansion in individual species? Whilst there is finally good evidence, including recent meta-analyses (Slatyer et al. 2013) linking geographical range size to niche breadth, a key question is what limits niche breadth evolution itself, particularly at range edges (Kirkpatrick and Barton 1997; Kubisch et al. 2013)? Dispersal can reduce the amount of genetic differentiation amongst populations (Avise 1992; Bohonak 1999), producing panmixia with relatively few successful colonists (Crow and Kimura 1970). On the other hand, in the absence of gene flow, populations are free to evolve along independent trajectories, something that in sexual organisms may lead to the direct or indirect evolution of reproductive isolation and so biological speciation (see Coyne and Orr (2004) for a recent review). Such dispersal limitation processes are believed to have contributed to the diversity of a number of predaceous diving beetle radiations, particularly those in running waters (Ribera 2008) and subterranean aquifers (e.g., Vergnon et al. 2013) – indeed the way in which habitat type shapes dispersal evolution, and the way this in turn moulds the evolutionary fate of individual clades is a fundamental feature of freshwater faunas, and something first postulated from studies of water beetles, including dytiscids (see below and Ribera and Vogler 2000; Ribera 2008).

In an ecological sense, dispersal will clearly have important consequences for dytiscid assemblage composition, and how species are distributed across patches within a region. Resetarits (2001) points out that random movement among ponds will result in homogenized assemblages, whereas different assemblages will result if adults chose sites in response to their environmental characteristics (see below and Chap. 7 in this book). Given the spatial and environmental structure observed in real dytiscid communities (e.g., McAbendroth et al. 2005; Florencio et al. 2011; Picazo et al. 2012), there are no prizes for guessing what most beetles do!

9.3 On Flight and Wings and Flightlessness

Dytiscid hind wings are their primary means of dispersal, and have a long history of scientific study; Goodliffe (1939) and Balfour-Browne (1944) outlining key features of venation, and discussing its possible taxonomic significance, albeit with differing conclusions. The work of Dorothy Jackson in the 1950s, however, represents the most complete direct investigation of the flight capacity of diving beetles, investigations which have been complemented by Kehl and Dettner (2007). Whilst such work has almost exclusively been concerned with European species, it is worth revisiting here, as such exhaustive studies have not been undertaken elsewhere, and these findings have much wider relevance. In addition to direct observations of the wings, Jackson also studied the flight musculature and metathoracic exoskeleton associated with flight in predaceous diving beetles, and subjected living specimens to direct flight tests in the laboratory. As was extensively documented by Smith (1964), modifications, especially reduction in size, of certain elements of the metathoracic skeleton such as the pre- and postphragmata on which the flight muscles attach, can indicate flightlessness even if a beetle is fully winged. Jackson published her observations in a series of papers (Jackson 1950, 1952, 1956a, b, c, d, 1958, 1973a, b), categorizing the species studied into those which were strongly-flying, apparently flightless, and variable. Similar approaches were adopted by Kehl and Dettner (2007), who, in addition to dissection of flight musculature in selected taxa, provide an exhaustive compilation of flight records, as well as incidences of a species' capture outside its normal habitat – itself highly suggestive of flight.

Jackson's strong fliers are species that readily flew in the laboratory, and in which wings, flight musculature, and thoracic skeleton were always well developed. This category includes the majority of larger lentic water dytiscids examined, classic pioneer and generalist species such as *Hygrotus confluens* (Fabricius), *Hydroporus nigrita* (Fabricius), and *H. tessellatus* Drapiez, as well as *Stictonectes lepidus* Olivier, a species usually associated with lotic habitats. Species Jackson noted as apparently being flightless are a mixed bag of running and standing water species, including the temporary pond agabines *Agabus labiatus* Brahm, *A. uliginosus* (L.) and *A. undulatus* Schraum. In only one of these species, *Hydroporus ferrugineus* Stephens (Jackson 1956a), is significant wing reduction noted (see Fig. 9.1), and even here Jackson reports that whilst there was no trace of flight muscles in the few specimens dissected, and a weakly developed thoracic skeleton, the beetles did show some variation in relative wing size. Although such taxa may indeed be relatively poor aerial dispersers, it is difficult to state with certainty that such species *never*

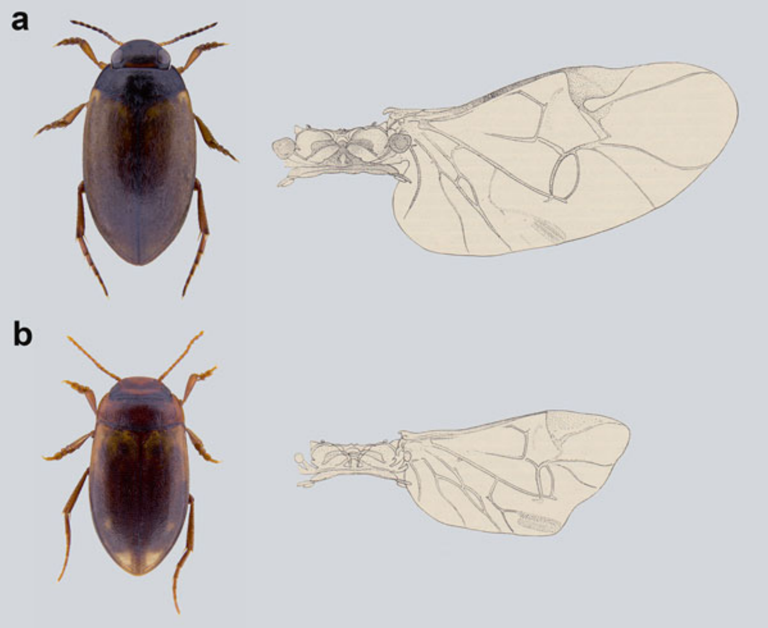

Fig. 9.1 Wings and internal views of metaterga of *Hydroporus* species, with pleural discs attached, drawn to the same scale. (**a**) *Hydroporus planus* – a strongly flying species, (**b**) *Hydroporus ferrugineus* – a species considered flightless by Jackson. See text for details (After Jackson 1956a)

disperse by flight. Wing polymorphism is known elsewhere in Dytiscidae, including *Agabus bifarius* (Kirby) in which fully-winged and brachypterous individuals have been reported (Leech 1942). Jackson's final category covered variable species in which at least some individuals were considered able to fly. In some cases variation was only observed in flight musculature, in others reductions to the thoracic skeleton were also reported in some individuals (e.g., *Agabus paludosus* Fabricius – see Fig. 9.2).

Whilst there can be no doubt about the strong fliers, it is difficult to be certain that many species considered flightless by Jackson (1950–1973) and Kehl and Dettner (2007) are not variable ones with a low proportion of flying individuals, or at least in the populations examined to date. There are a handful of dytiscids, such as the semi-subterranean *Rhithrodytes agnus* Foster (Bilton and Fery 1996), the island endemic *Agabus maderensis* Crotch (Balfour-Browne 1950), and some fully subterranean taxa (Spangler 1986), where flight wings are so strongly reduced that flight would be impossible. On the other hand, if species have full wings it is hard to discount the possibility that they sometimes use them! Indeed, some species considered flightless by Jackson have subsequently been shown to fly on occasion. As stated above, *A. uliginosus* is described as flightless by Jackson (1956b) on the basis of abnormal flight musculature and reduced metaterga and pleural discs, but it is now known that this species does indeed sometimes fly, soon after the emergence

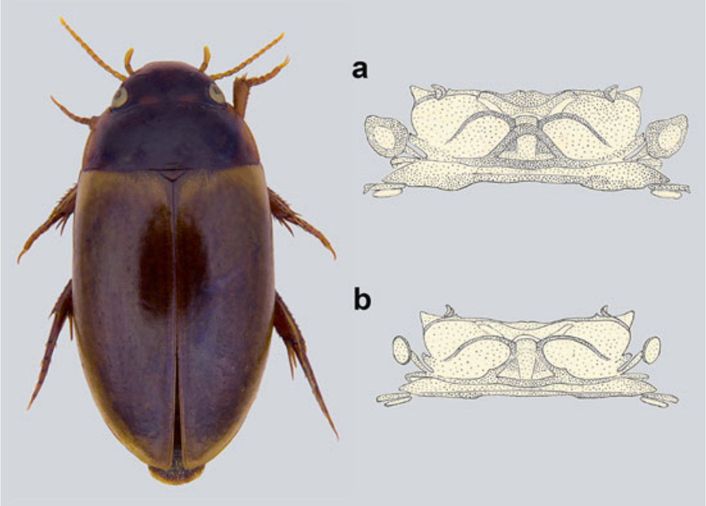

Fig. 9.2 *Agabus paludosus* – one of Jackson's variable species. Internal views of metaterga, with pleural discs attached, drawn to the same scale, (**a**) from a female with normal flight muscles, (**b**) from a male with no flight muscles (After Jackson 1956a)

of teneral adults (whose morphology was not, unfortunately, examined – Kirby and Foster 1991). In a similar fashion, *Agabus labiatus* has been observed in flight (Kehl and Dettner 2007), and *Agabetes acuductus* (Harris), considered flightless by Jackson (1956d), has been subsequently suggested to fly, being captured in UV light traps operated close to occupied woodland pools (Spangler and Gordon 1973). Indeed, it is difficult to see how species of small isolated lentic waters could adequately disperse and recolonize large tracts of previously glaciated terrain in some cases in the complete absence of flight, or indeed how flightless species could persist in such habitats given their geological instability (Ribera 2008). When looked at from an ecological and biogeographical perspective, many of the species listed as flightless by Jackson (1950–1973) and Kehl and Dettner (2007) probably are capable of flight, or at least some individuals, in some populations are, for part of their adult life. Recent observations on *Hydroporus rufifrons* (Müller) (Fig. 9.3), an inhabitant of seasonally fluctuating pools in northern Eurasia, reveal that despite being fully winged, the species usually has poorly developed flight muscles, and cannot be coaxed into flight in the laboratory (Foster 2000, D. T. Bilton, personal observation). Despite this, the beetle occurs in isolated ponds in hill country, in both central Europe and the UK (Hess and Heckes 2004; Foster et al. 2008), and it is hard to explain its site occupancy without occasional flight. *Hydroporus rufifrons* appears to show a core-satellite metapopulation structure in most regions, being rare in most occupied localities, but superabundant in others, where it can be the dominant dytiscid (D. T. Bilton, personal observation; G. N. Foster, personal communication). If only a small proportion of beetles in these high density populations are capable of flight this would fit with both field and laboratory observations. As discussed in

Fig. 9.3 *Hydroporus rufifrons*, a northern Palaearctic specialist of temporary and fluctuating waters that has declined significantly in recent decades in much of western Europe in response to agricultural intensification. *Hydroporus rufifrons* occupies isolated water bodies but is apparently an infrequent flier, having never been coaxed into the air in the laboratory (Photo courtesy of Franz Hebauer)

Bilton (1994), it has often been assumed that a number of the dytiscids associated with primary fen habitats in western Europe are flightless (e.g., Foster 1979), following on from the studies of Jackson (e.g., negative flight tests) and the fact that they are typically absent from apparently suitable secondary habitats in many regions, including the United Kingdom. Whilst species such *Hydroporus scalesianus* Stephens are indeed restricted to relict patches of primary fen in highly fragmented landscapes such as the United Kingdom, the same species are apparently capable of colonizing relatively new habitats in other parts of their range, and it is difficult to envisage how this happens without flight. In central Sweden, for example, classic relict species such as *Hydroporus glabriusculus* Aubé and *H. scalesianus* occur in small fens formed in the last 200 years as a result of isostatic land uplift around the central Baltic Sea, and in the case of *H. scalesianus*, artificial ponds created *de novo* within the last 50 years (D. T. Bilton, personal observation). Whilst flight tests on *H. scalesianus* in the United Kingdom have always proved negative (Foster 2000), the capture of a Swedish specimen in a window trap (Lundkvist et al. 2002) demonstrates that some beetles in some populations can indeed fly. In regions such as Scandinavia the density of suitable fen habitat remains relatively high, and there is the possibility that elsewhere reduced dispersal ability has evolved recently in response to habitat fragmentation, as suggested in *H. glabriusculus* in Britain and Ireland (Bilton 1994). Some species may indeed behave as relicts over part of their distribution, such populations perhaps representing the ‘living dead’ in a metapopulation sense (Hanski et al. 1996). In a similar vein Iversen et al. (2013) suggested that viable population networks of low-dispersing species such as *Graphoderus bilineatus* (DeGeer) depend on a relatively high density of habitat in the landscape.

At least some reports of absent or variable flight musculature in dytiscids may be related to the oogenesis-flight syndrome (Johnson 1969), in which individuals disperse early in adult life, often as tenerals, then utilize energy from autolyzed flight musculature in reproduction (e.g., Hocking 1952). Although not directly studied to date in dytiscids, such autolysis of flight musculature in fully-winged individuals has been observed on commencement of reproductive activity in *Mesovelia* and a range of pond skaters (Galbreath 1975; Vespäläin 1978). In the hydrophiloid beetle *Helophorus brevipalpis* Bedel, fully functional flight musculature is present throughout adult life, as in Jackson's strong fliers. In Spring, flying *H. brevipalpis* females contain mature oocytes, and at this time of year, after snow-melt, dispersal to newly-available temporary water occurs, an individual female that has mated and contains mature eggs representing a very effective colonizer. In the related *Helophorus strigifrons* Thompson flying females are mainly gravid, but with small oocytes, and flight muscle degeneration occurs after dispersal (Landin 1980). Similar processes probably account for many observations of flightless and variable species flight muscle development, and ability to actively disperse, varying over the course of an adult's lifetime.

9.4 Proximate Drivers of Dispersal and How to Find Water

9.4.1 Dispersal Triggers at the Individual Level in the Field and the Lab

Factors triggering and regulating dispersal in dytiscids, and indeed freshwater insects in general, have received only limited attention. In many species, dispersal flights are undertaken by teneral individuals (Bilton 1994), this possibly relating to the oogenesis-flight syndrome as discussed above. The proximate cues that may trigger an individual predaceous diving beetle to leave a water body are poorly known, although both decreasing water depth and increasing temperature appear to play important roles. Whilst flight in *Dytiscus marginalis* L. has been seen in the field at temperatures as low as 6.4 °C (Nilsson and Svensson 1992), most observations suggest flight is most common at higher temperatures, even in temperate taxa. In some cases, mass emigrations have been observed in response to changing conditions, such as with *Agabus disintegratus* (Crotch) (Young 1960) and *Eretes sticticus* L. (*sensu lato*) (Kingsley 1985). In other instances, dytiscids, including *Hygrotus wardii* (Clark), have been reported as forming a significant portion of diurnal mass swarms of aquatic Heteroptera and Coleoptera, which, when hitting a tin roof, have been likened to hail (Stevens et al. 2007). In one of the few studies of its kind, Velasco and Millán (1998) examined the response of a number of desert stream dwelling beetles and bugs to simulated drought conditions, by increasing temperature and decreasing water depth in the laboratory. They demonstrated than reduced water depth was the principal trigger of dispersal in the beetles studied, including *Stictotarus roffii* (Clark) and *Laccophilus maculosus* Say, the threshold depth for dispersal initiation being around 1 cm. More limited dispersal activity was observed in response to warming from 24 to 40 °C, and here exit responses only occurred at temperatures of 28 °C and above. In a study of the saline water diving beetles *Nebrioporus baeticus* (Schaum) and *N. cereysi* (Aubé), Pallares et al. (2012) found that flight activity in the laboratory increased to a maximum at 40 and 35 °C respectively, declining significantly thereafter, when high mortality was observed in

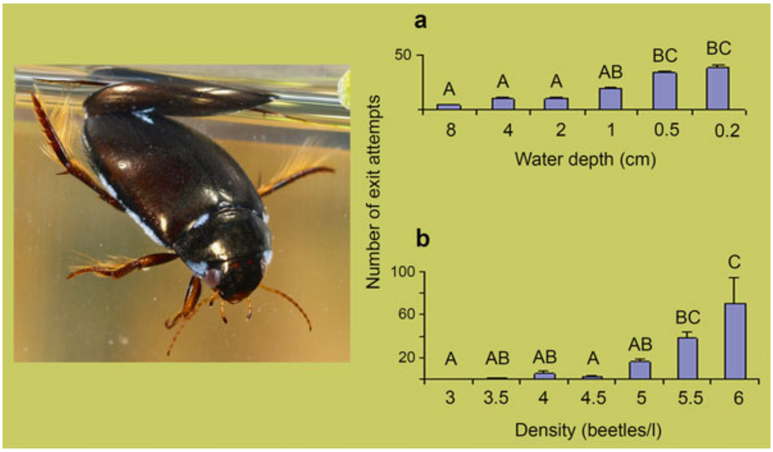

Fig. 9.4 Exit behaviour of *Agabus bipustulatus* in the laboratory. Beetles were placed in 2 l aquaria at 28 °C, and after a 5 min acclimation period the number of exit attempts recorded over a 30 min window. A beetle was deemed to have attempted to disperse if it left the water, via the tank margin, or the crossed bamboo sticks supplied. (**a**) The influence of depth on exit behaviour (ANOVA $F = 4.798$ *d.f.* = 5,31 $P = 0.003$) – letters above bars indicate significant differences between means (Fisher's LSD), (**b**) The influence of density on exit behaviour (ANOVA $F = 4.375$ *d.f.* = 6,39 $P = 0.002$) – letters above bars indicate significant differences between means (Fisher's LSD). Data in **b** are for total number of exit responses recorded, for convenience, but statistical tests were conducted on data rescaled per individual beetle (Vosper and Bilton, unpublished) (Photo courtesy of Jonty Denton)

both species. In the widespread Palaearctic dytiscid *Agabus bipustulatus* (L.) both water depth and individual density influence exit behaviour from aquaria. In response to density, exit rates increased significantly at a density>5/l (Fig. 9.4). Decreasing depth also triggered exit behaviour, this increasing significantly below a threshold of around 0.5 cm at 28 °C (Fig. 9.4). At this depth beetle elytra were frequently in contact with the surface film during normal activity, and it is thought that this stimulus may have triggered the shift in behavior observed in the laboratory. It would be interesting to see how such responses are modified by the presence of heterospecifics, and changes in habitat complexity/quality. Using a combination of field and laboratory experiments, Yee et al. (2009) showed that higher conspecific density and lower macrophyte density both triggered dispersal in *Rhantus sericans* (Sharp) and *Graphoderus occidentalis* (Horn), and that this effect was modulated by the presence or absence of food, all suggesting that the beetles responded to perceived patch quality.

9.4.2 Weather, Season and the Timing of Field Flights

Some attention has been given to the habitat and climatic conditions that limit flight in water beetles in the field, with temperature and wind speed being important (Landin 1968; Landin and Stark 1973; Zalom et al. 1980; van der Eijk 1983; Williams 2005;

Nilsson and Svensson 1992; Weigelhofer et al. 1992). In some cases, diurnal flight periodicity has been detected, flight activity peaking in either the mid morning, around noon, or at nightfall (Nilsson 1997; Csabai et al. 2012). Many species change their diel flight behavior seasonally, diurnal dispersal being the norm in spring, with evening dispersal becoming more common in summer and autumn. Csabai et al. (2012) suggest that seasonal changes in air temperature may drive such shifts in behavior, something in keeping with the threshold temperature response observed in many species in the laboratory (see above). As discussed by Csabai et al. (2006), the ability of aquatic insects to detect water polorotactically is at its maximum at high and low angles of solar elevation – i.e., at noon and dawn and dusk. It is thought that this 'polarization sun-dial' interacts with air temperature to shape the timing of dispersal movements in such animals. Of the dytiscids studied by Csabai et al. (2006) most were evening dispersers, with one, *Rhantus suturalis* (MacLeay) dispersing in both morning and evening windows.

The seasonal timing of dytiscid dispersal is poorly understood. Temporary pond breeders appear to disperse mainly in spring, whilst many inhabitants of permanent water predominantly disperse during summer and autumn. Some Nearctic agabines may move between temporary ponds for reproduction in Spring, and more permanent ponds in summer when vernal pools dry (e.g., Hilsenhoff 1986), a phenomenon also seen with some Palaearctic taxa, and in the Western Cape of South Africa, where species such as *Hydropeplus trimaculatus* (Laport) occupy temporary ponds in spring, and permanent stream pools in summer (D. T. Bilton, personal observation).

9.4.3 How Do the Beetles Find New Water Bodies?

How dispersing dytiscids detect suitable water bodies is, again, incompletely understood, although recent work has emphasized the part played by patterns of polarized light. Observations that many water beetles were more strongly attracted to some color of car than others, particularly red ones (Jäch 1997; Nilsson 1997) were followed up by some elegant experiments by Kriska et al. (2006), who demonstrated that this effect is driven the degree and direction of light polarization from the surface. Because aquatic insects detect water largely on the basis of the horizontal polarization of light reflected from water surfaces, they are strongly attracted to red, and other dark, shiny surfaces, such as car bonnets and roofs. Why red in particular should be attractive to some species, such as *Hydroporus incognitus* Sharp, remains unclear. In addition, habitat detection is clearly a process in which different cues may operate at different spatial scales. In addition to the visual, aquatic insects can rely on olfactory cues to detect patches of suitable microhabitat, although such processes remain unstudied to date in predaceous diving beetles. Within a water body the presence of con- and heterospecifics, vegetation, and predators (e.g., Åbjörnsson et al. 1997; Yee et al. 2009), as well as a species niche breadth (see Arribas et al. 2012 for a water beetle example) will clearly be important in determining whether a dispersal event becomes a colonization event, although detailed investigations of these factors in this regard are lacking.

9.5 The Macroecology of Movement in Predaceous Diving Beetles

9.5.1 Dispersal and Geographical Range Size

It is a longstanding observation that most species on Earth are rare, and restricted in their geographical occurrence, but despite numerous reviews (e.g., Gaston 1994, 2003, 2009), our understanding of what drives these patterns remains limited and not just in the case of dytiscids. A factor that intuitively *should* be involved in many cases, however, is relative dispersal ability, in terms of the ability of a species to establish a new population in a new, discrete, habitat patch (i.e., emigration plus interpatch movement plus immigration, *sensu* Bowler and Benton 2005). A number of recent studies (e.g., Malmqvist 2000; Böhning-Gaese et al. 2006; Rundle et al. 2007) have suggested a relationship between dispersal potential (as assessed by relative wing size) and geographical range, some of these concerning aquatic insects. In the case of dytiscids, Calosi et al. (2010) examined the relative importance of estimated dispersal potential, as assessed from relative wing size, and a number of thermal physiology traits in driving latitudinal range extent in European species of *Deronectes*, a genus of lotic dytiscids. They concluded that thermal physiology, rather than relative wing size, was the best predictor of geographical range extent, with rare species having much narrower thermal limits than common ones, with the highly successful Postglacial colonist *Deronectes latus* (Stephens), distributed from Scandinavia to the Balkans, being by far the most thermally tolerant and plastic species examined. Whether relative dispersal ability plays *any* role in shaping the biogeography of this genus remains unclear, however. Sánchez-Fernández et al. (2012b) examined the fit between actual and potential geographical ranges in the same species, comparing range estimates based on climatic data of occupied areas, with those based on data from physiology experiments. They found that neither approach predicted ranges that closely matched those observed, suggesting a possible role for dispersal limitation. Perhaps when comparing closely related species, measures of wing size tell us little about what species actually do – taxa with similar wings may behave very differently in terms of how frequently they fly, and the thresholds which trigger such movements (see above).

Whatever the role of dispersal in shaping relative range sizes in some individual dytiscid clades, it is difficult to imagine how a widespread diving beetle could colonize large areas without an ability to fly well, particularly given the isolated nature of most inland waters. Perhaps the most widely distributed dytiscid on earth is *Rhantus suturalis*, known almost throughout the old world, from the Azores to New Zealand. Balke et al. (2009) suggest that this species has arisen from within a clade of closely related taxa endemic to the New Guinea highlands between 6 and 2.7 MYA, and has subsequently spread over much of the globe, in a rather complex pattern (Fig. 9.5).

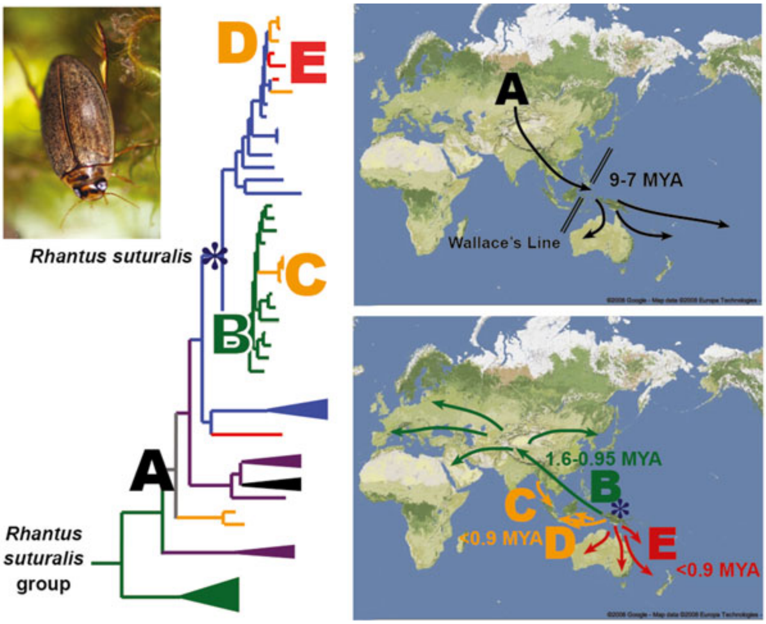

Fig. 9.5 Phylogeography of the supertramp *Rhantus suturalis* and its relatives, showing major colonization events (A–E). Branch/letter colors: *orange*, Oriental region *blue*, New Guinea *red*, Australia, New Zealand and New Caledonia *purple*, Melanesia *black*, Oceania (Polynesia) *green*, Holarctic. *R. suturalis* itself originated in the New Guinea highlands (*asterisk*) and has expanded its range northwards (*green arrows* – B) and colonized Wallacea, Sumatra and the Australian region (*orange* and *red arrows* – C, D, E) (Modified after Balke et al. 2009) (Beetle photo courtesy of Jonty Denton)

Data from the British and Irish biological recording schemes for water beetles suggest that *R. suturalis* has also responded rapidly to climatic warming (Fig. 9.6), the species reaching northern Scotland and parts of Ireland for the first time in recent decades. This 'supertramp' (*sensu* Diamond 1974), is a very active flier (Jackson 1956b, D. T. Bilton, personal observation), and one which has a relatively wide diurnal window for flight activity (Csabai et al. 2006). At the other extreme, dispersal limitation could clearly be an important driver of diversification in dytiscid clades, lineages that are weak dispersers being likely to contain large numbers of narrow-range taxa. Whilst pointing to the importance of long-distance dispersal in island colonization, Balke et al. (2007) point out that the majority of *Exocelina* species are endemic to small areas, with over 150 such species likely to be present on New Guinea. With one exception so far (Shaverdo et al. 2013) all these New Guinea species occur in running waters. Indeed, as discussed below, habitat type seems to be *the* major ecological/evolutionary driver of range size in dytiscids (and most freshwater organisms for that matter), this effect of habitat being mediated largely through the relative strength of selection for dispersal.

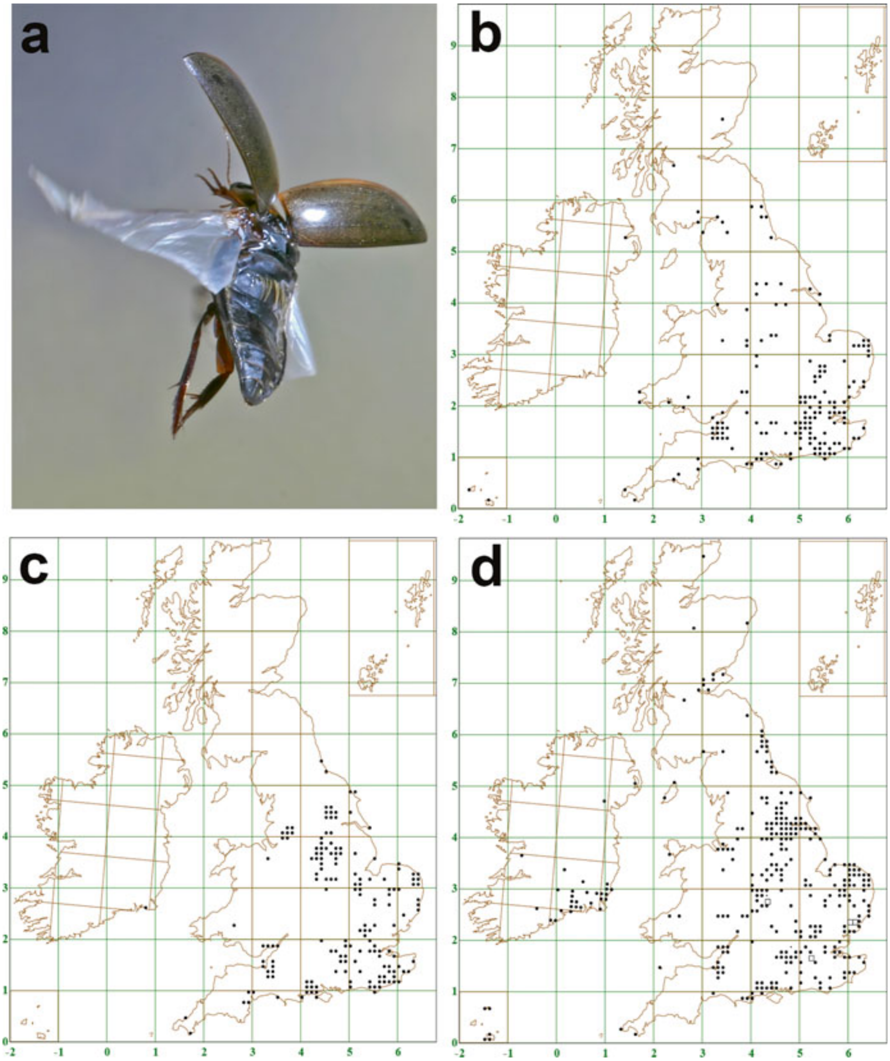

Fig. 9.6 The supertramp *Rhantus suturalis* in Britain and Ireland. (**a**) Adult beetle in flight (Photo courtesy of Geoff Nobes), (**b–d**) records from the UK and Irish water beetle recording schemes, by 10 km^2. (**b**) Nineteenth century – 1979, (**c**) 1980–2000, (**d**) 2000–August 2013. This strong flier has shown apparently rapid shifts in range, at this, the northwestern edge of its global distribution. Whilst apparently present in Scotland and Ireland in the nineteenth century, *R. suturalis* was rarely reported in these countries, and relatively southern in distribution in England and Wales between 1980 and 2000. In the current century it has colonized the northernmost regions of Scotland and expanded greatly in SE Ireland, these expansions likely being a response to recent climate change

9.5.2 Predaceous Diving Beetles and the Lentic-Lotic Divide

In recent years studies of water beetles, including dytiscids, have been instrumental in the development of a novel macroecological framework for understanding diversity and evolution in freshwater organisms – the lentic-lotic divide (see Ribera 2008 for a review of this topic). First suggested through the study of Iberian aquatic beetles, it is now generally established that in many inland water organisms (e.g., Hoff et al. 2006, 2008), running water species have smaller geographical ranges, and more spatially structured populations, than their standing water relatives. The divide is believed to be driven by differences in the geological persistence of running versus standing waters. Most small isolated standing water bodies have relatively short lifespan, in geological or evolutionary terms, requiring their occupants to have relatively good powers of dispersal, which result in relatively large geographical ranges. The short lifespan referred to here is not related to short-term seasonal drought, because species have a variety of strategies to cope with these, including, in dytiscids, short larval lifespan (Peters 1972), diapausing eggs/adults (Nilsson and Soderstrom 1988), or moving to more permanent water bodies (Hilsenhoff 1986). Instead it refers to the fact that many small standing water basins disappear relatively rapidly through, for example, successional processes. In contrast, running waters are firstly more connected through a drainage network, and crucially much longer-lived in geological terms, tending to persist as long as there is rainfall and a gradient. In such habitats, there is therefore less need to disperse, and indeed reduced dispersal may in some cases be advantageous due to trade-offs with other life-history traits such as reproduction (e.g., Zera and Denno 1997; Zera and Zhao 2003). The lentic-lotic framework also allows other predictions, including more rapid speciation and greater vulnerability to global change in lotic taxa (Ribera 2008), traits which are a result of their lower ability to disperse.

Since first proposed, these ideas have gained broad acceptance, being supported by a number of empirical studies, some of which have concerned dytiscids. In a study of species of inland saline waters, for example, Abellan et al. (2009) compared phylogeographic structure in two closely related southern European diving beetles *Nebrioporus baeticus* and *N. cereysi*, which are lotic and lentic, respectively. *N. baeticus* had a higher proportion of its observed nucleotide diversity amongst than within populations, and a faster rate of accumulation of haplotype diversity than its standing water relative, as well as showing higher phylogenetic diversity, despite having a much smaller geographical range. In one of the few papers to question the predictions of this framework, Short and Caterino (2009) compared phylogeographic structure in the dytiscid *Stictotarsus striatellus* (LeConte) with that seen in the hydrophilid *Anacaena signaticollis* Fall, and the psenid *Eubrianax edwardsii* (LeConte), in southern Californian running waters. These authors argued that the fact that the species examined spanned observed extremes of genetic and phylogeographical structure argued against the importance of habitat type in structuring aquatic populations. Such a conclusion makes the assumption that dispersal ability/propensity is broadly similar across these taxa, however, something which is unlikely given, for example, their different ecologies and adult lifespan. To effectively test the predictions of the lentic-lotic framework one needs to compare related taxa which live on either side of the divide.

9.6 Future Directions: Where Do We (and the Beetles) Go from Here?

While our understanding of the causes and consequences of dispersal in dytiscids has improved in a number of ways since Frank Balfour-Browne was disturbed by a nocturnal *Ilybius fuliginosus,* a number of questions remain unanswered, both in terms of the natural history of movement, and the role of dispersal in shaping large-scale patterns. There remains a need for empirical studies of individual species and assemblages, particularly those which take a comparative approach. The works of Jackson (1950–1973) and Kehl and Dettner (2007) remain the only attempts to examine comparative flight ability in a regional species pool, and both deal with the western Palaearctic fauana. Similar data are lacking from other regions, as are studies using a suite of approaches, such the integration of direct observations of anatomy and behavior with comparative phylogeography. In this sense, dytiscids provide excellent models, and could be more widely used by researchers, the resulting data allowing better parameterization of dispersal models. Studies such as those of Svensson (1998, 1999) on rock pool whirligig beetles set the standard for understanding local dispersal movements, and there is still the need for such work on predaceous diving beetles occupying patchy landscapes, particularly if mark-release-recapture (e.g., Davy-Bowker 2002) can be integrated with population genetic approaches. At a larger scale, dytiscids again provide excellent models with which to test biogeographic and macroecological ideas. Diving beetles have featured in a number of recent attempts to understand range size evolution, but there remains a need for further work in this area. Arribas et al. (2012) show that habitat transitions from lotic to lentic waters were accompanied by huge increases in geographical range size, driven by shifts in dispersal potential, in a clade of European *Enochrus* (Hydrophilidae). Dytiscid lineages (e.g., *Hydroporus*), which show similar habitat transitions, could be used to test the generality of such observations. To date, most published work on relative dispersal ability infers this from studies of wing or flight muscle morphology. As stated above, species could also differ in the thresholds that trigger dispersal flights. Comparative studies of such features, particularly if conducted on a suite of ecologically similar species, may prove highly illuminating.

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David Bilton has worked on water beetles one way or another for approximately 30 years. He has a particular interest in understanding biogeographical patterns, including the role of dispersal, and never tires of finding new beetles. After studying Zoology at the University of Oxford he obtained his Ph.D. on *Hydroporus* population genetics and phylogeography from the University of London and is currently a Reader in Aquatic Biology at Plymouth University in the southwest of England.

Chapter 10
Community Patterns in Dytiscids

Steven M. Vamosi and Bianca Wohlfahrt

> *What governs the nature of natural communities? This question has generated much interest among biologists. The major conclusion to come out of the considerable research conducted on the questions seems to be that there is no simple answer.*
>
> Larson 1990

Abstract Understanding the relative contributions of biotic and abiotic factors to community structure remains a fundamental aim of community ecology. Dytiscid beetles, which occur in a diverse set of aquatic habitats and display considerable variation in their abundance and composition among locales, would appear to be a model system for investigating such questions. Here, we present an overview of investigations into community structure in dytiscids, which reveals that they are understudied relative to their typically high abundance in ditches to bogs to lakes. We discuss emergent trends in the co-occurrence of dytiscids with regard to ecological and phylogenetic similarity, briefly present some investigations into the influence of dispersal on community structure, and discuss some prospects for future progress in this area.

Keywords Competition • Community dynamics • Dispersal • Phylogenetic ecology • Predation

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10.1 An Introduction to Natural Communities

If there is no simple explanation of the mechanisms that shape the structure of communities, let's start by defining what natural communities are. In ecology, a community is generally considered to be a group of interacting species coexisting under natural conditions in a defined area. This definition may inspire an examination of the major components of natural dytiscid communities: habitats in which communities tend to be found, important interactions between dytiscids and the abiotic environment, and species interactions that influence the abundance and distribution of (sets of) dytiscid species.

In general, patterns of species coexistence and diversity in natural communities may be shaped by complex interactions among organisms, and between organisms and the environment (e.g., Vamosi 2005; Östman et al. 2007). Important interactions include competition for limited resources (e.g., Tilman 1982; Schluter and McPhail 1992), predator–prey relationships (e.g., Sih 1987; Vamosi 2005) and their associations (e.g., intraguild predation; Polis et al. 1989, keystone predation; Leibold 1996; Chase 1999), whereas important environmental variables may include the permanence (Wellborn et al. 1996), size (Poethke and Hovestadt 2002), or isolation of a certain habitat (Brown and Kodrik-Brown 1977). Freshwater systems are well suited for community studies because it is well established that the composition of freshwater communities can be dramatically influenced by environmental gradients associated with habitat area size, permanence, and with the presence or absence of dominant predators (reviewed by Wellborn et al. 1996).

Public interest in the investigation of wetland insect communities was raised in the 1960s, when researchers examined the role of aquatic insects as food for fish (e.g., Macan 1966a, b) and waterfowl (Murkin and Blatt 1987, reviewed by Batzer and Wissinger 1996). Classic studies often focused on few local water bodies in order to examine the structure of aquatic insect communities (e.g., Macan 1966a, b), whereas more recent studies frequently take into account a larger number of local habitats and/or spatial scales (e.g., Fairchild et al. 2000; Schäfer et al. 2006).

Before we provide an overview of community studies focused on dytiscids, we consider how they tend to be sampled for such studies. Dytiscids are generally more abundant in shallow and densely vegetated microhabitats compared to deeper and more sparsely vegetated parts of water bodies (Larson et al. 2000). Thus, the sweep-net technique is the classic method of dytiscid capture. Following the established method of Larson (1990), dytiscids can be sampled within a defined space among submerged macrophytes along the shoreline with repetitive swipes using a sweep net (e.g., Nilsson and Svensson 1994; Nilsson and Söderberg 1996). To prevent beetles from the surrounding to be sucked into the sampled space during sweeping, a plastic frame can be placed into the water, with the walls of the frame pressed into the sediment (e.g., Fairchild et al. 2000; Yee et al. 2009). The use of the plastic-frame sweep-netting technique is expected to deliver a more accurate number of specimens per m^2, except for sediment dwelling species and for large active dytiscids (Fairchild et al. 2000). Another method of dytiscid capture is the use of traps consisting

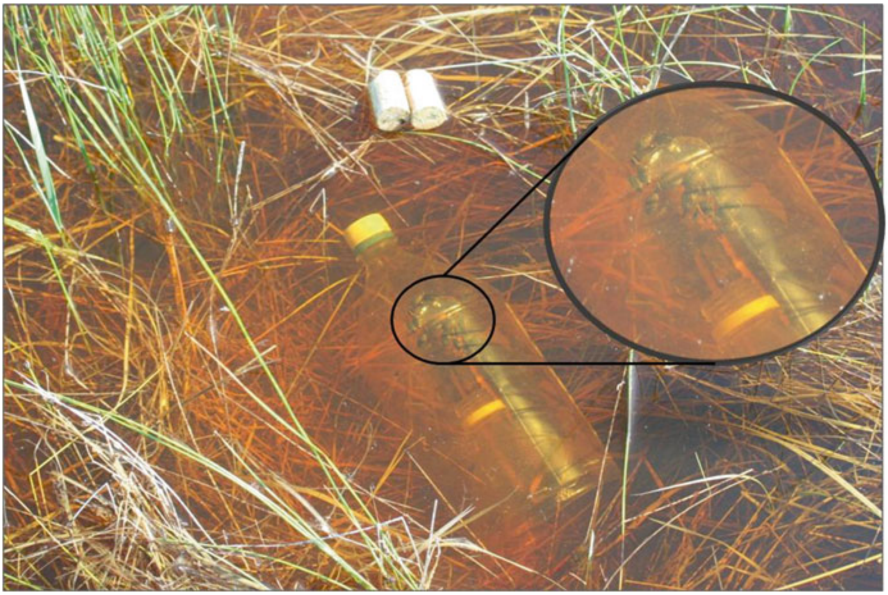

Fig. 10.1 Bottle trap in shallow water, with zoomed inset showing several dytiscid specimens that were successfully captured (Photo courtesy of Don Yee 2007)

of 1.5–2.0 L plastic jars or bottles with inverted funnels, which have been found to be effective at capturing active dytiscids with a sampling range of approximately 10 m (Schäfer et al. 2006, Fig. 10.1). The downside of these "bottle traps" is that not only may dytiscids be caught, but also predators of dytiscids such as large dragonfly larvae, newts, or small fish (personal observation). These predators may simply eat the trapped dytiscids, or worse, might prevent dytiscids from entering the traps; each sampling technique has pros and cons.

Likely owing to their near-cosmopolitan distribution, high global species richness and marked among-site variance in species richness at local scales, there is a rich history of studying community patterns in dytiscids. Curiously, we note that there appears to be little attention paid to whether the usual latitudinal biodiversity gradient is observed in dytiscids (but see Nilsson et al. 1994). Anecdotally, it appears it may not exist or, at least, not be very strong, with approximately 500 of the total 4,200 species (Nilsson, personal communication) being found in North America, and 276 of the former being present in Canada (Larson et al. 2000). Rather than attempting to present a comprehensive review of all the community investigations we are aware of, we focus on the main findings of a coordinated series of investigations by a few key groups, namely Nilsson and colleagues (Nilsson 1984, 1986; Nilsson and Svensson 1994, 1995; Nilsson et al. 1994; see also Nilsson and Söderberg 1996), Ribera, Vogler, and colleagues (Ribera et al. 2003; see also Baselga et al. 2013), Eyre and colleagues (Eyre et al. 1986, 1992, 1993, 2003; Foster et al. 1990), and Larson and colleagues (Larson 1985, 1990; Larson et al. 2000), primarily in Sweden,

Table 10.1 Key features of some dytiscid community investigations; see main text for more detail

Locale	Number of sites	Total number of species	Mean species richness	Significant abiotic and biotic associations	Raw data available?	Reference
Sweden	10	46	~25	Pond successional stage; pond area (but only when fens excluded)	No	Nilsson (1984)
	30	59	10.7	Vegetation structure; prey abundance; relative shore depth	Yes	Nilsson et al. (1994)
	9	69	Not reported	Water permanence; forest cover	No	Schäfer et al. (2006)
England	384	Not reported	7–13[a], depending on habitat type	Water pH; dissolved oxygen levels	No	Eyre et al. (1986)
	157	130[a]	Not reported	Water pH; nitrate levels; water depth; abundance of submerged vegetation	No	Foster et al. (1990)
Canada	312	145	2.4–25.0, depending on cluster	Water salinity; productivity; permanence; temperature; substrate type; flow; vegetation	No	Larson (1985)

[a] Water beetles, of which dytiscids were one component

western Europe, the United Kingdom, and Canada, respectively. We present a brief summary of some of the community investigations described in detail in Table 10.1. For interested readers, other studies include Lancaster and Scudder (1987), Aiken (1991), Bosi (2001), Arnott et al. (2006), Vamosi et al. (2007), and Vinnersten et al. (2009).

Nilsson (1984, 1986; Nilsson and Svensson 1994, 1995; Nilsson et al. 1994) documented community structure patterns at a series of sites and, in many cases, correlated these with various environmental features. Nilsson (1984), for example, investigated community patterns in 10 kettle-hole ponds located in a very restricted region, which were arrayed along a successional gradient correlated with changes in dominant vegetation. Consistent with other studies, species richness of aquatic beetles was quite high, with 61 species overall (of which 46 were dytiscids), and 14–34 species in the individual ponds. Species richness was negatively associated with successional stage (Fig. 6 in Nilsson 1984), although close inspection reveals that the pattern was largely driven by reduced species richness in the three fen ponds (14, 16, and 24 species), compared to the others (27–34 species). Nilsson et al. (1994) again investigated factors predicting dytiscid abundance and species richness, but on a much larger spatial scale, with 10 lakes each in south, central, and north Sweden. Species richness in these lakes was comparable to that observed in the kettle-hole ponds, ranging from 0 to 32 species, with 17 lakes having 10 or fewer dytiscid species. Partial least square regressions revealed positive associations for abundance and species richness with vegetation, structural complexity, and abundance of two taxa (*Asellus* and immature dipterans) and a negative association with relative shore depth on the first component, as well as weaker positive associations with fish abundance and negative associations with lake area on the second component. We do not review the other three studies here because they either considered a very small number of sites (a single seasonal pond, Nilsson 1986; two boreal snowmelt pools, Nilsson and Svensson 1994) or were comparing clear-cut to natural boreal swamp forest pools in a restricted geographical area when sample size ($N=40$) was high (Nilsson and Svensson 1995). However, one final remarkable feature about the five studies bears noting here, which is that raw species lists were provided for all water bodies in all cases as well as number of individuals per species in all but Nilsson (1984). The availability of these data, along with key environmental parameters, makes them especially amenable to future phylogeny-informed community ecology analyses (e.g., Vamosi and Vamosi 2007) or meta-analysis approaches.

Although primarily concerned with improving our understanding of speciation in, and relationships among, dytiscids (e.g., Ribera et al. 2004, 2008), other researchers have also delved into related investigations of patterns in species richness. For example, Ribera et al. (2003) investigated large-scale factors associated with species richness in lotic and lentic water beetles (i.e., not just dytiscids) from 15 regions in western Europe, finding an influence of latitude for the former group and influences of geographic connectedness and total area size for the latter group. We will discuss the application of DNA barcoding to related questions by Baselga et al. (2013) near the end of this chapter.

In a series of interrelated studies, Eyre et al. (1986, 1993, 2003, 2006; also Foster et al. 1990) have studied predaceous diving beetles in Scotland and England, with the aim of defining associations between their distributions and environmental conditions to guide environmental monitoring or conservation efforts. Because we are focusing on community patterns here, we will not go into detail on those that used presence/absence from, for example, 10-km national grid squares for distribution data (Eyre et al. 1993, 2003, 2006). Eyre et al. (1986) analyzed the assemblages of dytiscids and other water beetles from 384 sites in northeast England that had been sampled over nearly two decades. Using a largely deprecated clustering algorithm, they produced nine "habitat groups" and the indicator species most representative of each type. Although analyses were not formally presented, they interpreted these habitat groups to suggest that water pH and oxygen levels were dominant influences on water beetle community patterns. In a related analysis, Foster et al. (1990) characterized community patterns for water beetles from 157 sites (primarily ditches in arable land) in England. Using the same clustering techniques, they produced eight habitat groups, which they correlated with nine environmental variables and an index of vegetation management. These analyses revealed that the variables with the greatest influence were water pH, nitrate levels, depth, and abundance of submerged vegetation. Site-specific species lists and environmental conditions were not presented in either paper, but the sample sizes suggest that these would otherwise be excellent candidates for additional analyses.

A trio of researchers have carried out the bulk of the investigations on community patterns in Canada (e.g., Larson 1985; Alarie and Maire 1991; Roughley and Larson 1991; Paquette and Alarie 1999). Building on these works, various aspects of the biology of Nearctic dytiscids were summarized by Larson et al. (2000). Nearctic dytiscids are found to be abundant in a large variety of temporal and permanent freshwater habitats and, correspondingly, display diverse patterns in life history, morphology, and microhabitat use (Larson et al. 2000). One of the main findings of these works relevant to community patterns was documenting significant differences in the distribution of dominant predators such as fish, large active dragonfly larvae (Odonata: Anisoptera), and dytiscid beetles among different lake types: whereas most fish species may only persist in permanent waters, large odonates are more abundant in permanent fishless waters, and dytiscids dominate in temporary ponds (Larson 1990).

Fish are important top predators in many aquatic systems (Wellborn et al. 1996) including important consumers of dytiscids (see Chap. 8 in this book). A number of factors lead to the exclusion of many fish species from shallow water bodies, including seasonal increases in water temperature (Magalhães et al. 2002), decay of organic matter, and associated anoxia (Meding and Jackson 2003), and/or oxygen stress due to ice cover (Wellborn et al. 1996). Larger sized fish are typically able to catch and devour large sized prey. Large predaceous fish thus tend to select for small-bodied prey organisms (McPeek 1990; Wellborn et al. 1996). However, frequently abundant species in shallow ponds may be small-bodied fish species, such as fathead minnows (*Pimephales promelas*) and brook stickleback (*Culaea inconstans*) (Peterka 1989). Although smaller fish may be gape limited, abundance of fathead minnows has been shown to be associated with decreases in the abundance of aquatic invertebrates and with changes in the pond-community composition (Zimmer et al. 2001).

The aquatic larvae of predaceous dragonflies are less susceptible to oxygen stress than many fish species (Wellborn et al. 1996). However, the larvae of many dragonfly species can be excluded from fish dominated habitats via predation (Larson 1990; McPeek 1990). In temperate regions, dragonflies may over winter in the egg stage (i.e., diapause) or as larvae. Large predaceous dragonfly larvae, such as aeshnids (Anisoptera, Aeshnidae), may require 1 year to several years to complete larval development (Cannings 2002; Askew 2004).

Unlike dragonflies, both the larval and adult stages of dytiscids are aquatic. Dytiscids often inhabit the shallow, vegetated parts of various water bodies, including temporary ponds (Larson et al. 2000). During both life stages, dytiscids need to break the water surface with the tip of their abdomen to take air; thus, most dytiscids in temperate regions leave the water for overwintering in the adult stage (Larson et al. 2000). Dispersing female dytiscids that fly to new habitats may select oviposition sites based on the presence or absence of predators, ovipositing more eggs into fishless habitats (Brodin et al. 2006). Dytiscids in the adult life stage are less susceptible to predation than larvae, and possess antipredator defences such as hardened bodies and cryptic colouration (Larson et al. 2000) or chemicals (Chap. 6 in this book). Despite these defences, small dytiscids may regularly fall prey to large dragonfly larvae (Larson 1990).

Correspondingly, Larson (1990) observed increased abundances of large sized dytiscid species that may avoid predation due to their large body size (e.g., species of *Dytiscus*), and of very small sized dytiscids that may hide from predators among dense patches of vegetation in ponds dominated by large predaceous dragonfly larvae. Thus, in addition to habitats dominated by different predator types, Larson (1990) divided dytiscid communities within dragonfly-dominated ponds into three microhabitat types and prey size morphs: (i) very small dytiscid species, occurring amongst dense submersed vegetation, (ii) very large dytiscid species, and (iii) open water species. Overall, although community composition may vary dramatically among water bodies within and among regions, studies to date (Table 10.1) point to recurring influences of key physicochemical features, such as water permanence, vegetation structure and water chemistry, along with additional effects of species interactions, especially with predators, on shaping community assembly in dytiscids.

10.2 Random vs. Non-random Distributions

As exemplified by the studies reviewed above, the traditional approach to understanding communities has been to group individuals into species, without reference to phylogenetic relatedness or functional trait values, when attempting to understand their presence or abundance in certain locales (e.g., Hutchinson 1959; Hubbell 1979). Niche theory, for example, assumes that multiple species are able coexist in the same living space, or in their habitat, because different species possess contrasting ecological requirements (Hutchinson 1959). Interspecific competition for limited resources is the classic reason for niche diversification (e.g., Hairston 1949; MacArthur 1958). Thus, it is assumed that over the long term no two species are able to occupy exactly the same niche in the same habitat. Hutchinson (1959) defined the ecological niche as a multidimensional space or hypervolume that is not shaped by competition alone, but contains the biological requirements of any species. Within its niche, a species is assumed to experience environmental conditions that allow the species to persist in the habitat. Outside the specific niche, they are expected to experience environmental conditions that prohibit their long-term persistence.

The classic niche theory has not been without its detractors. Hubbell's (1979) main criticism was that high species diversity can be found in many natural habitats, combined with a relatively low number of limiting environmental factors. For example, the high diversity of tree species in tropical forests appears to be at stark odds with the low number of limiting factors such as water, light, and nutrients (Hubbell 1979). In other words, it has been argued that the diversity of species coexisting in a community cannot always be explained by the number of limiting environmental factors. According to the neutral model, species are ecologically identical in the sense that there are no niche differences. Thus, all species are assumed to possess equal ecological requirements and equal per capita fitness (e.g., Hubbell 1979, 2001; Bell 2001; Alonso and Mc Kane 2004). Following the neutral approach, communities are random collections of species, with a composition mainly shaped by metacommunity size, speciation rate, and dispersal among communities (Bell 2001; Hubbell 2001).

More recently, Chase (2005) suggested a synthetic approach to investigating species coexistence within communities. This synthesis would take into account aspects from the niche approach, such as the existence of limiting environmental factors, combined with aspects from the neutral model, such as dispersal effects. Although Chase (2005) has been well received and fruitfully applied to some aquatic systems, literature searches suggest that this integrated approach has not yet been specifically applied to dytiscid communities.

Another approach to investigating community composition that differs from the classic niche perspective is a consideration of metacommunity dynamics. A metacommunity is defined as a set of local communities, which are linked by dispersal and contain groups of interacting species (Wilson 1992). Theory (Hastings 1980; Amarasekare 2003) predicts that if the species within a community differ in their competitive ability, local coexistence is possible in presence of limiting factors, which may be abiotic (e.g., wave action) or biotic (e.g., predator presence). However, species may differ in their ability to tolerate environmental factors and, thus, can experience favorable conditions in one habitat type and unfavorable conditions in another habitat type, leading to habitat partitioning (Kneitel and Chase 2004). Thus, spatial heterogeneity among local communities may result in local exclusion and regional coexistence of species within the metacommunity. Habitat partitioning among lake types has been shown in larval dragonflies of the genus *Leucorrhinia*. Shifts from fish lakes to dragonfly lakes have resulted in the loss of abdominal spines, a morphological defense effective in fish presence, but increased the vulnerability of prey in presence of large predaceous dragonflies (Hovmöller and Johansson 2004). Because adaptations exist that increase a species ability to cope with limiting environmental factors, but may have no or opposing effects in different habitats (McPeek 1990; Richardson 2001), species that occur in heterogeneous habitats may be subject to antagonistic selection (Wohlfahrt and Vamosi 2009), which in turn can promote habitat partitioning (Davidowitz et al. 2005).

In contrast, in a spatially homogeneous competitive environment, regional coexistence is expected when a trade-off between competitive ability and dispersal ability exists. In that case, the species that is the weaker competitor must be the better disperser to persist at the regional scale (Hastings 1980). However, local patch densities and habitat fragmentation are predicted to affect the competition-colonization trade-off (Tilman 1994; Yu and Wilson 2001). If local habitat density is reduced, a superior colonizer is more likely to invade the habitat and suppress the stronger competitor. On the other hand, in case the number of isolated habitats declines, it is the better colonizer that is expected to go extinct. Brown and Kodric-Brown (1977) examined the effect of dispersal and immigration on species extinction in patchy habitats. Using island populations as model systems, they found that high immigration rates could reduce extinction rates of conspecifics within habitats. This observation was referred to as the rescue effect. Thus, immigration and recolonization are expected to stabilize the abundance of species, even if these species are not favored by the limiting factors present. This provides researchers with a problem, because locally stable communities may be difficult to tell apart from unstable, dispersal-maintained communities. The question every researcher faces when taking samples from a local habitat patch is to what degree a community was composed as the non-random result of limiting factors and to what degree the community was composed by random dispersal events. Hence, it may be necessary to sample a large number of local habitat patches for patterns in community composition to become evident (Larson 1985). Ultimately, resolving such questions requires the use of manipulative experiments to test the associations observed in the field.

With samples from a series of communities in hand, one can ask several questions, including: (i) are sampled habitat patches occupied by a non-randomly composed community? and (ii) does community composition differ among habitat patches? In an extensive study of water bodies in Alberta, Canada, Larson (1985) used cluster analysis to examine the sampled sites for patterns of similarity in dytiscid species distributions. He found twelve clusters, which were interpreted as communities with contrasting dytiscid species composition, although there were also unclustered sites. Further analyses revealed that certain environmental factors also varied among the sampled habitat patches that had well-defined community clusters: salinity, productivity, stability, water temperature, substrate type, flow, and vegetation. These differences in the environment may form ecological gradients, which in turn can be associated with differences in dytiscid species distribution. Because communities are typically influenced by a large number of environmental factors, it is often not possible to explain associations between the composition of species and the environment by a single dimension in a statistical analysis (Larson 1985). In more recent studies, the association among multiple gradients in community composition and the environment has been analysed using ordination analyses, such as redundancy analyses (e.g., Schäfer et al. 2006). Alternatively, canonical correspondence analyses (e.g., Fairchild et al. 2000; Wohlfahrt and Vamosi 2012) can be conducted to identify variance in community data with long gradient lengths (Lepš and Šmilauer 2003).

Recent community analyses have confirmed Larson's (1990) hypothesis that the presence of predaceous fish can be an important biotic factor influencing the composition of dytiscid communities (Wohlfahrt and Vamosi 2012) and of water beetle communities in general (Fairchild et al. 2000). The negative effects of fish can be mitigated to some extent by the presence of submerged macrophytes, which can serve as refuges from predation (Dionne and Folt 1991) and support high densities of potential prey, such as epiphytic insects (Batzer and Wissinger 1996), for dytiscids (see Chap. 7 in this book for more details on the influence of macrophytes). Other environmental factors, such as pond surface area (species richness: Nilsson and Svensson 1994, abundance: Fairchild et al. 2000), pond permanence (species richness: Nilsson and Svensson 1994; Bosi 2001) and habitat isolation (species richness: Suhlman and Chase 2007) may influence dytiscid communities as well.

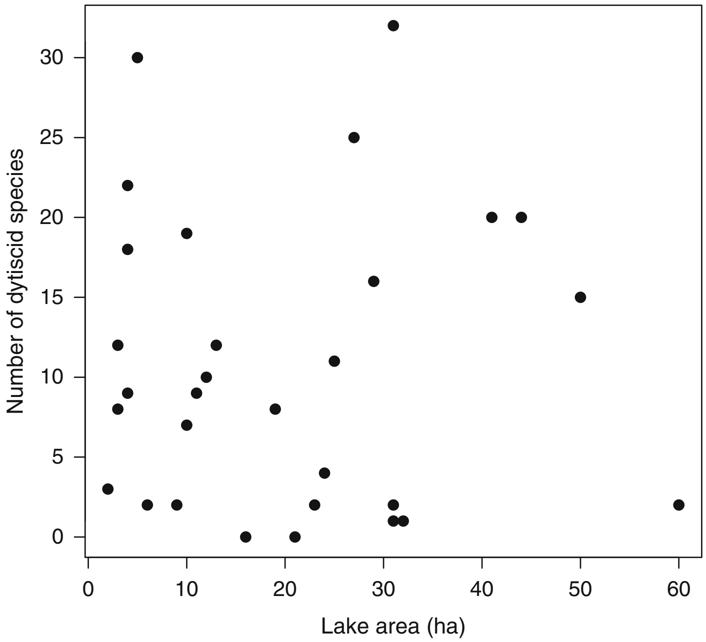

Fig. 10.2 Species richness as a function of lake surface area in 30 Swedish lakes (Data from Nilsson et al. 1994)

The number of organisms any habitat can accommodate is typically positively correlated with habitat area size (Poethke and Hovestadt 2002). Dytiscids do not cleanly follow the usual species richness-area relationship, however, likely owing to the presence of more diverse predator communities in larger water bodies. For example, we present a novel examination of the relationship between lake area and species richness for the 30 lakes considered by Nilsson et al. (1994). There was a negative relationship for the 10 Scania lakes, and a weakly positive but mostly variable relationship for the 10 Södermanland lakes, and no obvious relationship for the 10 Västerbotten lakes. Plotting all the data together reveals considerable variability in species richness for smaller lakes (i.e., those with a surface area <35 ha), and possibly a negative relationship between lake area and species richness for larger lakes (Fig. 10.2). Minimally, the lack of a strong positive relationship deviates from the typical "textbook" pattern (e.g., Smith et al. 2005). We encourage others to carry out more systematic investigations of the relationship between species richness and area for dytiscids, likely in conjunction with additional investigations of latitudinal species richness patterns (Vamosi et al. 2007).

Increasing habitat isolation can result in decreased species richness (Suhlman and Chase 2007) especially if species coexistence is dependent upon immigration from neighbouring habitats (reviewed by Taylor 1990), whereas habitat heterogeneity may facilitate species coexistence (e.g., Macan 1966b; Amarasekare 2003) to the point of outweighing the effects of habitat area and isolation on species diversity (e.g., Báldi 2008; Kallimanis et al. 2008; Jonsson et al. 2009; Kruk et al. 2009; Wohlfahrt and Vamosi 2012). In heterogeneous habitats, differences in area, isolation, and dominant predator presence still affect the composition of dytiscid communities, and may thus act as environmental gradients (Wohlfahrt and Vamosi 2012). Specifically, the composition of dytiscid communities may differ among habitats depending on both the effect of predator presence or absence, and on the degree of habitat isolation, with different species composition in isolated ponds with the dominant predator present, in isolated ponds with the dominant predator absent and in less isolated ponds with the dominant predator present or absent. Similarly, the presence of large predaceous dragonfly larvae may affect dytiscid species composition depending on the pond surface area size (Wohlfahrt 2010).

Overall, these results illustrate that differences in the composition of dytiscid communities depend not only upon multiple environmental gradients, but can also be organized along community gradients, from apparently random dytiscid assemblages to patches with significantly contrasting sets of coexisting species. The interpretation of the results from community analyses has evolved from observations of richness and abundance of individual species to investigations of community clusters and community gradients. However, in a world full of scaling issues there still remains the question of where a community starts and where it ends. Thus, in a variable environment, a dytiscid "community" may represent no more and no less than a certain point along a dynamic continuum of species coexistence (Larson 1985).

10.3 Ecological Similarity

In the previous section we explored how dytiscid communities may be influenced by environmental gradients, but what kind of species coexist in communities structured by different biotic interactions and why? Would coexisting species resemble each other or would they differ in their phenotypic traits? A long-standing assumption in community and evolutionary ecology is that organisms with contrasting ecological requirements are better able to coexist in the same habitat (e.g., Hutchinson 1959; Grant 1986; Schluter 2000). Individuals are expected to compete more strongly for limited resources when they share the same ecological niche and, thus, use the same resources in similar ways. To predict the outcome of resource competition, Tilman (1982) developed the R* rule for competitive exclusion. According to this rule, the species that suppresses resources to the lowest amount wins in competition – i.e., becomes the dominant competitor. Thus, resource competition may lead to the exclusion or extinction of inferior competitor species, and is considered an important factor in structuring communities (Losos 1990; Schluter and McPhail 1992).

Species that occupy similar niches and positions within a community can be grouped into guilds, which have been used in multiple studies to investigate the effects of ecological similarity on patterns of species co-existence (e.g., Williams and Hero 1998; Webb 2000; Gurd 2007). In dytiscids, ecologically similar species can be

Fig. 10.3 A ditch near York, England, sampled by Juliano and Lawton (1990) to test the role of competition in structuring communities of dytiscids. This type of habitat is home to many species of dytiscids, although the ecological mechanisms that explain their coexistence are still unknown (Photo courtesy of Steve Juliano 1990)

grouped into guilds by using the criteria of body size and life cycle length (Nilsson 1986; Nilsson and Svensson 1994). Morphological traits are well suited to assess ecological similarity of a species, because morphology is often closely correlated to the species' resource use (e.g., Schluter and McPhail 1992; Gurd 2007). Thus, morphologically similar species are expected to compete more strongly for resources compared to species with contrasting morphology (Juliano and Lawton 1990). Despite this, coexistence of species with similar phenotypic traits has often been observed in natural communities (e.g., Nilsson and Svensson 1994; McPeek and Brown 2000; Hubbell 2001; Scheffer and van Ness 2006).

For dytiscids, competition among coexisting species with similar body size has not been detected (Juliano and Lawton 1990, Fig. 10.3; see also Nilsson 1986). Larson (1985) found generally high species richness in dytiscid communities of the north temperate regions. Combined with high productivity observed in many water bodies, it was concluded that other factors, such as predation, may be more important in shaping dytiscid communities in the temperate regions (Juliano and Lawton 1990; Larson 1990). Body size distributions of dytiscids have also been used to investigate patterns in the composition of communities. For example, Larson (1985) revealed differences in dytiscid size distributions among regions with contrasting climate, such as northern temperate climate in Alberta (Canada) and warm temperate climate in Florida (USA). In general, dytiscid species with small body size (body length: 3–10 mm), such as species of *Hygrotus*, *Hydroporus*, *Laccophilus*, *Rhantus*, and *Agabus*, were found to be more abundant in communities compared to larger species. In contrast to dytiscid communities in Florida, a relatively high number of medium sized dytiscids (body length: 5–10 mm) coexisted in communities in Alberta. It was suggested that the presence of large dragonfly larvae in the more stable habitats in Florida prevented medium-sized dytiscids from coexisting in these communities. However, other studies on dytiscids have found no relationship between body size and frequency of occurrence in dytiscids (e.g., Nilsson et al. 1994; Vamosi and Vamosi 2007).

Although the coexistence of similar species may be limited by the degree of resource competition and may result in competitive exclusion, certain environmental factors may facilitate their coexistence. If phenotypic characters represent adaptations to particular environmental conditions and environmental factors act as filters, the community may be restrained to species with certain sets of phenotypic traits (e.g., Webb 2000; Webb et al. 2002; Vamosi and Vamosi 2007). However, when the environment changes or a species colonizes a new habitat, these traits may no longer be beneficial or may even decrease the species ability to persist (McPeek 1990; Richardson 2001; Mikolajewski et al. 2006). Thus, species that occur in heterogeneous habitat patches may be subject to antagonistic selection. Antagonistic selection can promote habitat partitioning, and with this, increase the coexistence of ecologically similar species (Davidowitz et al. 2005).

Also within in the realm of ecological similarity, predation is an important limiting factor that may instantly reduce the fitness of prey (e.g., Sih 1987, reviewed by Vamosi 2005). Sih (1987) suggested that prey species could coexist with predators by possessing particular antipredator adaptations, such as morphological and/or behavioral traits or, in case heterogeneous local habitats are present, occupy habitats free of predators. For example, habitat heterogeneity can be defined in a region that contains local habitat patches dominated by different top-predator types, such as fish or large active dragonfly larvae (McPeek 1990; Hovmöller and Johansson 2004). Among these heterogeneous habitats, prey body size is likely to be affected by antagonistic selection, because fish and large dragonfly larvae may select for opposite size classes of prey (reviewed by Wellborn et al. 1996). Most larval dragonflies are omnivorous ambush predators, whereas large active dragonfly larvae, such as species of *Anax* and *Aeshna*, often show a more active foraging mode than other odonates (Larson 1990). Because fish are capable of swimming at much higher speeds than most macroinvertebrates, larval dragonflies are less successful in prey capture if the prey performs evasive behaviors (McPeek 1990). Correspondingly, communities with invertebrate top predators, such as large predaceous dragonfly larvae, are associated with prevalence of larger sized and more actively foraging prey organisms compared to communities dominated by predaceous fish (Wellborn et al. 1996). Analyses of gut contents confirm that large *Aeshna* dragonfly larvae successfully and regularly prey on small sized (total body length: <5 mm) dytiscid adults (Larson 1990). In the same study, Larson (1990) demonstrated an interesting negative correlation between larval dragonfly density and dytiscid beetle density along a surface area gradient in bog pools, with dragonfly densities increasing with bog pool size. Bog pools were lumped into only four size classes, making this a tantalizing association that bears further investigation.

Effective antipredator adaptations not only reduce the prey's vulnerability to predation, but may also involve costs in terms of time or energy expenses (Clark and Harvell 1992). In the absence of predators, prey organisms have to trade-off the risk of predation against the cost of expressing antipredator adaptations. For example, the most common behavioral antipredator adaptation is a change in activity, because reduced activity levels may result in reduced probability of predator encounters (Sih 1987). Because an animal is more likely to encounter food items when it searches actively (Gerritsen and Strickler 1977), reducing activity levels also results in decreased feeding, growth, and development rate (McNamara and Houston 1994; Stoks et al. 2003). Although many studies have investigated activity levels of prey under various combinations of predator presence, ontogenetic stage, and food level (e.g., Wohlfahrt et al. 2007), we are unaware of such studies using larval dytiscids as focal prey.

In the presence of visually hunting predators, differences in the prey species coloration can influence their vulnerability to predation (Brodie 1992) (information on the biological bases of color can be found in Chap. 6 in this book). For example, counter shading has been shown to optically flatten the three dimensional shape of prey animals due to displaying darker dorsal regions contrasting to the ventral region of the body (Ruxton et al. 2004). Prey may also adapt to the background color of their environment using background matching (Endler 1984) or disruptive color patterns (Sherrat et al. 2005). Larson (1990) suggested that longitudinal stripes in larval *Ilybius pleuriticus* act as an antipredator adaptation against visually hunting dragonfly larvae. Because the success of each type of crypsis depends upon the habitat specific background color (Endler 1984), dytiscid species occurring in similar habitats may tend to possess similar color patterns on their bodies. Larson (1996) suggested that bright color patterns conferred crypsis to dytiscids occurring in habitats with low structure and, therefore, provided protection against visual predators. Conversely, predaceous diving beetles occurring in densely vegetated or shaded habitats with dark substrates are more likely to display dark color patterns (Balke et al. 1997). Species found in multiple habitat types or in different communities across their range may accordingly be expected to experience antagonistic selection on their color patterns.

An experimental test on dytiscids with contrasting body size and color patterns has confirmed antagonistic selection on coloration patterns under conditions of contrasting water clarity (Wohlfahrt and Vamosi 2009) (Fig. 10.4). Small prey species often experience higher vulnerability to predation compared to species with larger body size (e.g., Stein 1977; Richardson and Anholt 1995; Eklöv and Werner 2000). In an environment with clear water, dytiscids with coloration patterns had equally low mortality rates in presence of predaceous aeshnid dragonfly larvae, independent of body size. In contrast, in an environment with dark water conditions, small sized dytiscids (<5 mm) had higher mortality rates compared to larger sized dytiscid species (5–10 mm), and larger sized dytiscids that displayed coloration patterns also experienced increased mortality rates (Wohlfahrt and Vamosi 2009). Thus, whereas

Fig. 10.4 Adult *Coelambus* (*Hygrotus) marklini* (*left*) and *H. sellatus* (*right*) collected from ponds in Alberta, Canada. These species show drastically different marking patterns on the elytra that may reflect antagonistic selection like that examined in Wohlfahrt and Vamosi (2009) (Photo courtesy of Don Yee 2013)

dytiscids that possess coloration patterns may compensate for an increased predation risk due to small size under clear water conditions, larger sized dytiscids may experience antagonistic selection on coloration patterns in habitats with contrasting water clarity. These results illustrate that interactions among predation regime and environment can result in multiple outcomes of predator induced selection, and may likely be one factor leading to increased species diversity at the metapopulation and metacommunity scales.

10.4 Dispersal

Thus far we have largely focused on the influences of "within-site" abiotic and biotic factors on variation in community composition among sites. Various abiotic properties of water bodies and the surrounding shoreline have been shown to be important in influencing the presence or absence and relative abundance of dytiscids. From the studies conducted to date, predation appears to be the dominant species interaction, although additional work with larvae may eventually reveal a role for resource competition. Before moving on to consider the influence of phylogenetic relatedness on community structure, there is one outstanding issue we need to consider: the presence and abundance of species at a site will be correlated with the rate at which individuals of that species disperse from other locations and successfully colonize the focal site, with reliance on dispersal appearing to be negatively correlated with water permanence (Larson et al. 2000) (for more details on dispersal in dytiscids see Chap. 9 in this book). That is to say, a consideration of the factors structuring local communities is incomplete without a consideration of the role of dispersal. Unfortunately, but unsurprisingly given the relative paucity of community studies in general, the literature on factors affecting dispersal in dytiscids specifically with a view to determining their community consequences is relatively sparse. Larson et al. (2000: pg. 9) noted that "*dispersal strategie*s [in dytiscids] *are not well understood*" – our literature surveys suggest that this state of affairs has not dramatically changed (but see Yee et al. 2009 for an investigation of factors promoting dispersal in two dytiscid species). Indeed, even the three studies that we review here were largely concerned with factors affecting dispersal and colonization of sites by dytiscids, rather than with the explicit effects that dispersal had on community structure of focal water bodies.

Wilcox (2001) investigated the role of colonization properties on the abundance of predators in seasonal wetlands. In an interesting design, Wilcox (2001) created 27 artificial ponds in a wildlife refuge, resulting in three replicates for each combination of pond size (three levels) and distance from semi-permanent seep (three levels), which served as the source for predators. Unfortunately, because "*identification of dytiscids to genus and species requires examination under a microscope*", all dytiscids were "*aggregated … for analysis*" (Wilcox 2001; pg. 466). Pond size had no effect, whereas there was a significant negative effect of distance from source on dytiscid abundance. Furthermore, there was a significant interaction between pond size and distance from source, with a stronger negative effect of distance on colonization rates in smaller ponds. The effect of distance quickly decreased with time, with all pond sizes having comparable abundances after only 3 weeks. Although these data suggest that dytiscids can quickly colonize newly available habitats, it is worth noting that the farthest block of ponds was only 180 m from the source, which is relatively short compared to the distance individual dytiscids may fly (Lundkvist et al. 2002).

Lundkvist et al. (2002) compared the beetles caught in traps in water and air in an agricultural landscape within two urban landscapes. Although community patterns were not investigated, their flight trapping data revealed that dispersal by dytiscids can be quite significant: two seasons of effort flight trapped 42 species and 1,653 individuals. Much of the variation in species distribution among flight traps was explained by three environmental variables: landscape type, distance from water, and vegetation complexity near traps. With regard to possible influences on community structure, their data suggested that flight activity levels are not constant over the season, although the pattern of variation among time periods may vary among years. In the first year of their study, dispersal levels were highest in May and generally decreased with time, although there was a suggestion of a brief increase in August. In the second year of their study, flight activity was low for 4 months (April, May, August and October), and high in June, July, and September. Because anthropogenic impacts on aquatic communities are only likely to grow with time, we hope more studies similar to this one will be carried out in future.

Finally, Schäfer et al. (2006) examined the relationship between dytiscid community patterns in nine wetlands and several landscape variables at five spatial scales.

Although they did not formally measure flight patterns (all of their traps were located under water), they "*sampled only adult … dytiscids since* [they] *were mainly interested in the dispersing life-stages*" (Schäfer et al. 2006, pg. 60). Species richness and diversity of dytiscids were positively associated with water permanence, whereas abundance was negatively correlated with amount of forest cover. A positive association with open areas was interpreted as possibly supporting the notion that wetlands were more visible from the air in open than forested environments. The influence of visibility, however, could not be distinguished from the tendency of ponds in forested areas to have reduced levels of aquatic vegetation, likely due to increased shading compared to those in more open areas.

10.5 Phylogenetic Community Composition

In a previous section, we considered how phenotypic traits can be important in structuring natural communities and showed that contrasting combinations of phenotypic traits may lead to differences in prey survival depending on the environment (e.g., Wohlfahrt and Vamosi 2009). The influence of environmental factors on the phenotypes of prey species has been elucidated in several systems, although none perhaps as thoroughly as in the case of the Trinidadian guppy (e.g., Endler 1980, 1995; Reznick 1982; Gordon et al. 2012). Guppy populations have been categorized as belonging to one of two ecotypes: low-predation vs. high-predation populations. Populations of the two ecotypes predictably differ in many traits, with individuals from low-predation populations tending to be more colorful, maturing later, investing more resources into reproduction and having fewer but larger offspring. These and other differences between the two ecotypes have been shown to have a genetic basis (Reznick 1982; Gordon et al. 2012). An important challenge in community ecology remains the investigation of interactions between species traits and community composition, and the influence of evolutionary processes on the species traits (Cavender-Bares et al. 2004). Phylogenies are increasingly being used in investigations of the influence of evolutionary, ecological, and stochastic processes on community assembly (reviewed by Webb et al. 2002; Cavender-Bares et al. 2009; Vamosi et al. 2009).

The results of an investigation of the interactions among phylogenetic relatedness, habitat-use, and phenotype in anuran species (Richardson 2001) revealed that phenotypic traits could not be predicted by habitat nor taxonomy alone, because many combinations of traits may result in successful adaptation to a certain habitat. Regardless, phenotypic traits are not taxonomically independent. Closely related species share a common history, and with this, may share many phenotypic characteristics (Stearns and Hoekstra 2001). Thus, closely related species are expected to be ecologically more similar than distantly related species (Webb 2000). Because the development of phenotypic traits may be restricted by the evolutionary history of a lineage, our understanding of the mechanisms that shape communities may be improved by the consideration of phylogenetic relationships among coexisting species (Cavender-Bares et al. 2004; Vamosi et al. 2009; Fig. 10.5). We are aware of

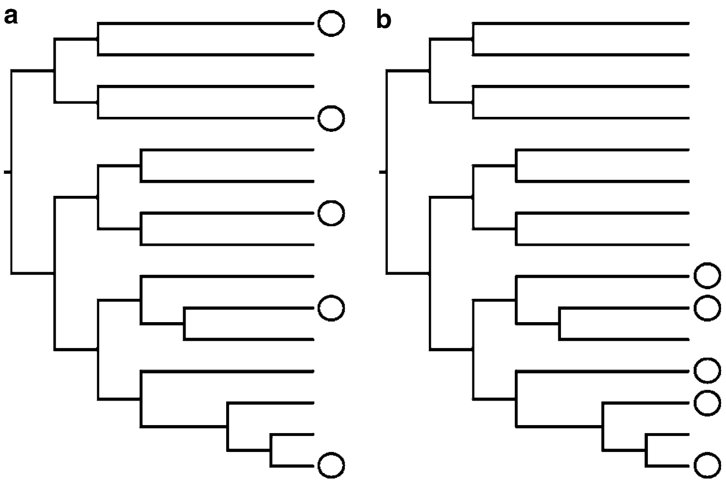

Fig. 10.5 Two hypothetical communities drawn from a regional pool of 15 species. Community A consists of five relatively distantly related species (*open circles*), which would be considered phylogenetically even, whereas Community B consists of five closely related species, which would be considered phylogenetically clustered. Dytiscid communities tend to more closely resemble the scenario represented in B than that in A, although there is a continuum of patterns observed and relatively few are as clustered as that shown (see Vamosi and Vamosi 2007; Vamosi et al. 2009)

concerns raised in the literature about potential flaws in the classic coexistence theory underlying studies of phylogenetic community structure (Mayfield and Levine 2010). In brief, there is growing evidence that interspecific competition is not necessarily strongest between closely related species, even if there is a significant phylogenetic signal to phenotypic traits. Because a full consideration of these issues is beyond the scope of this chapter, we focus on the patterns observed to date in dytiscid communities and largely refrain from definitive statements about possible mechanisms underlying these community patterns.

As mentioned earlier, coexistence of similar species may be facilitated by environmental variables acting as filters, and thereby they may restrict the community to species with certain sets of phenotypic traits (e.g., Webb 2000; Vamosi and Vamosi 2007; Silver et al. 2012). Phenotypic similarity is often a result of trait conservatism in the evolution of species that share a common history (Zimmermann 1931; Ackerly et al. 2006). However, phenotypic similarity can also arise in distantly related species due to convergent evolution, when species evolved under similar environmental conditions (e.g., Webb et al. 2002; Vamosi et al. 2009). Thus, environmental filtering can either increase the relatedness of coexisting species that share conserved phenotypic traits, or decrease relatedness due to the retention of species that share convergent traits (Webb et al. 2002).

In general, the phylogenetic composition of communities is expected to depend on the degree of phylogenetic conservatism in traits that are important for the persistence of species in certain habitats. Coexistence of closely related species and, with this, a high degree of phenotypic clustering is expected only if important

Fig. 10.6 Elytra coloration patterns of coexisting *Laccophilus proximus* (*top*) and *L. fasciatus rufus* (*bottom*) (Photo courtesy of Kristopher Pitcher 2010)

phenotypic traits are conserved (Webb et al. 2002; Kraft et al. 2007). For example, a study on Caribbean lizards (Losos et al. 2003) showed that a long history affected by competitive interactions resulted in niche divergence and reduced relatedness (i.e., led to phylogenetic evenness) in lizard communities.

A combination of phenotypic traits, as opposed to a single trait, may affect the likelihood of persistence of species in certain environments (Williams and Hero 1998). Multiple phenotypic traits need to be considered in phylogenetic analyses, because natural selection is known to affect phenotypes as a whole (Endler 1995). Investigations of potential patterns in community composition can thus be complicated by the necessity to simultaneously consider the phylogenetic relatedness of coexisting species, and the degree of conservatism or convergence in multiple phenotypic traits (Kraft et al. 2007). In dytiscids, body size and coloration pattern both are important phenotypic traits influencing survival rates in predator presence depending on the environment (Wohlfahrt and Vamosi 2009). Body size is a phenotypic trait in dytiscids that exhibits strong phylogenetic conservatism (Larson et al. 2000; Vamosi and Vamosi 2007). Closely related dytiscid species are similar enough in body length that they may be grouped into different body size classes (small: <5 mm, medium sized: 5–10 mm, large: 10–15 mm, very large: >15 mm, Vamosi and Vamosi 2007). In contrast, closely related dytiscid species may vary distinctly in their elytra coloration patterns, especially within the smaller sized species (Larson et al. 2000; Pitcher and Yee 2014, Fig. 10.6). In a recent study of potential mechanisms promoting the coexistence of congeners, Pitcher and Yee (2014) found few phenotypic differences between two *Laccophilus* species, except for elytra coloration patterns, and also little evidence for strong competitive interactions that would explain their slight habitat differences in the wild.

For statistical analyses of phylogenetic community composition in dytiscids, a dated phylogenetic tree (e.g., Ribera et al. 2004; Vamosi and Vamosi 2007; Ribera et al. 2008) can be used to investigate whether coexisting dytiscid species are more closely or more distantly related than expected by chance. Null models are used to determine whether the phylogenetic distances of the coexisting species significantly differ from random (Webb 2000). Therefore, phylogenetic distances (i.e., mean phylogenetic distance [MPD] and mean nearest taxon distance [MNTD] values) need to be calculated and compared to the phylogenetic distances of 1,000 randomly generated communities, the so-called null communities (Cavender-Bares et al. 2006). These null communities can then be used to compute null distributions of MPD and MNTD values. Finally, null distributions are compared to the observed distributions from natural communities. In dytiscid communities, phylogenetic clustering appears to be the prevalent pattern (Fig. 10.5), with closely related species with similar body size coexisting in the same habitat more often than expected by chance (e.g., Vamosi and Vamosi 2007; see also Larson 1985). These results suggest that phenotypic traits allowing the species to persist in a habitat show strong phylogenetic niche conservatism. Phylogenetic structure was also negatively correlated with mean body size of the community, with a tendency towards weak phylogenetic evenness with increasing mean body size. A possible explanation for this pattern might be that larger sized dytiscids may compete more strongly with each other for resources than do smaller sized dytiscids, leading to the exclusion of similarly large dytiscid species. Alternatively, large dytiscid species may be most likely to be found in communities with a diversity of smaller species, which would be prey for larger species, leading to evenness at the community level (Vamosi and Vamosi 2007).

The results of a community analysis in dytiscids confirmed that gradients in morphology parameters were associated with environmental filters. An important biotic factor that influenced phenotypic community composition was the presence or absence of the regional top predators, small fish or aeshnid dragonfly larvae (Wohlfahrt 2010). Predation by small bodied, gape-limited fish may lead to increased body size in coexisting prey organisms (Wellborn et al. 1996). Thus, increased abundance of similar large sized dytiscid species in fish-dominated habitats may be associated with increased predation risk for small dytiscid species. Correspondingly, abundance of small dytiscid species were increased in habitats with fish absent and in habitats with dense submerged vegetation, which may lead to reduced predation risk (Dionne and Folt 1991). Prevalence of species with plain and blotched elytra patterns coexisting in habitats with increased vegetation density and/or absence of predaceous aeshnids, whereas species with more distinct elytra patterns coexisted more often in habitats with aeshnids present (Wohlfahrt 2010). Therefore, not only conserved phenotypic traits, such as body size, may play a role in shaping dytiscid communities. Traits with weaker phylogenetic signal, such as coloration pattern, may also influence species composition and phylogenetic community structure.

The scale of the community analysis may also influence the results of phylogenetic investigations. For example, investigations of the community composition in oak trees have revealed that on the local scale, important phenotypic traits for the passage through environmental filters may derive from convergent evolution, resulting in phylogenetically even communities (Cavender-Bares et al. 2006). In contrast, on the regional scale, important phenotypic traits may be conserved, resulting in phylogenetic clustering. The phylogenetic composition of communities may depend on the degree of phylogenetic conservatism in traits associated with the persistence of species in certain habitats, with a higher degree of clustering expected when important traits are conserved (Webb et al. 2002; Kraft et al. 2007). Species may coexist in local communities because they possess phenotypic traits that allow them to pass through environmental filters, or because they are abundant in the regional species pool. However, the importance of phenotypic traits for local or regional coexistence cannot be explained without consideration of the species evolutionary history (Webb et al. 2006). In the only analysis of dytiscids that we are aware of, changing the regional scale from one that encompassed only species that were present at the local scale to one that included most species found across the province of Alberta had little qualitative effect on the resulting community patterns (Vamosi et al. 2009). Because this was only a pilot investigation of the possible effects of regional pool identity on local patterns, we advocate that more systematic analyses be conducted with other datasets, possibly starting with those readily available in older papers (e.g., Nilsson et al. 1994).

10.6 Summary and Future Directions

Community ecology has been a very active sub-discipline of ecology from its inception when Charles Elton documented the feeding relationships among the inhabitants of Bear Island in the Barents Sea (e.g., Summerhayes and Elton 1923). Given the high local species richness and abundance that is often attained by dytiscids in a variety of temperate water bodies, we find it somewhat curious that studying them from a community perspective does not have a longer and richer history. Indeed, querying the search phrase "topic = (communit* AND dytiscid*)" in Web of Science returned a very modest ~100 hits at the time of writing, with the earliest such publications being from the mid-1990s (e.g., Larson 1985). A pair of related impediments is almost certainly responsible for this relative paucity of studies: (1) the considerable effort it can take to confidently distinguish members of some of the smaller, locally abundant and species rich genera (e.g., *Hydroporus*), and (2) the general inability to identify larvae, which often represent the largest component of samples for much of the field season, below the genus rank with morphological characters alone. Yee (2010), for example, studied predation rates in three dytiscid taxa, which were referred to only as *Graphoderus*, *Rhantus*, and *Dytiscus*; based on relative abundances of adults in the sampled ponds, these were surmised to represent *G. occidentalis*, *R. sericans* and *D. alaskanus* and/or *D. dauricus*, respectively. Coupled with a solid grounding in the ecology and natural history of dytiscids, it would appear that the best way forward for the next generation of community analyses will be the adoption of DNA barcoding techniques for identifying individuals in large samples (see Forward to this book). Although there are currently insufficient numbers of sequences available for North American species (A. Banwell and S.M. Vamosi, unpublished observations), efforts underway by the Barcode of Life System (BOLD; Ratnasingham and Hebert 2007) hold considerable promise. Recently, Baselga et al. (2013) demonstrated the potential of this approach, examining beta diversity at three levels of organization (haplotype, nested clade, and species) in 23 local assemblages, using a total of 5,066 sequences estimated to represent 274 species of water beetles. Curiously, they sequenced a 825-bp region at the 3′ end of the cytochrome c oxidase I (COI) gene whereas BOLD, which launched the DNA barcording enterprise a decade ago, focuses on a 684-bp region at the 5′ end of COI. Once sufficient sequences have been generated, it will be fruitful to investigate whether the patterns described earlier for adults, such as apparent lack of interspecific competition and a general trend for phylogenetic clustering in local communities, will hold for larvae. Such data may also encourage researchers to test more modern views of communities, such as that advanced by Chase (2005), and attempt to better understand the role of dispersal in linking and shaping local assemblages across landscapes.

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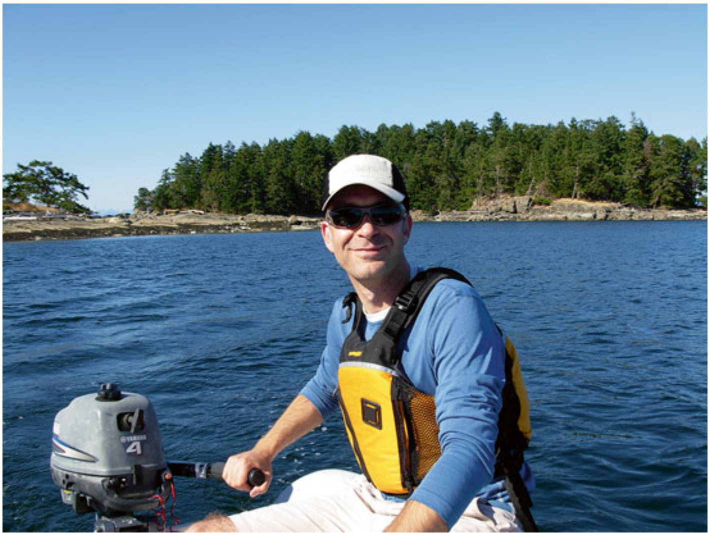

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Chapter 11
The Conservation of Predaceous Diving Beetles: Knowns, Unknowns and Anecdotes

Garth N. Foster and David T. Bilton

> *This is a critical time for organisms living in continental waters.*
>
> Naiman (2008)

Abstract Aspects of the conservation of Dytiscidae are discussed with particular reference to the benefits, potential and realized, associated with the listing of individual species as threatened internationally and nationally. Examples are drawn on a global basis, but inevitably with some bias to the predaceous diving beetles of western Europe endangered by a history of intensification of agriculture, industrialization, and urbanization.

Keywords Conservation • Dytiscid • Europe • Extinction • Red list

11.1 Introduction

Few readers of this book will need reminding that the freshwaters of the world are undergoing an unprecedented level of transformation as a result of expanding human populations, and that this impact is intensifying. Freshwaters represent a tiny fraction of the global habitat occupied by organisms, yet hold a disproportionately

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large percentage of all known species (Dudgeon et al. 2006). In the case of macroinvertebrates, beetles are second only to flies in terms of the number of species occurring in inland waters, and amongst the beetles, the Dytiscidae represent one of the major aquatic radiations, being found in practically every form of inland waterbody on Earth, where they are often the most ecologically important, or indeed the only, predators.

With over 4,000 species worldwide (Jäch and Balke 2008; Nilsson (2013) counted 4,223 species) predaceous diving beetles oblige us to pose the perennial ecological question "How can so many species occupy the same habitat?" Until we understand the precise ecological requirements of individual taxa it is risky to provide detailed guidelines for species-level conservation, but at least we have many Red List treatments, mainly national (e.g., Norway by Kålås et al. 2010), occasionally transnational, e.g., Ireland by Foster et al. (2009), and often regional, e.g., Flanders by Scheers (2012) and Schleswig-Holstein by Gürlich et al. (2011). Many case studies and reviews have identified particular species under threat, those cited here being intended to exemplify different aspects of the conservation problem across the world but inevitably drawing heavily on the European experience. Do we have any way of knowing why one species is at risk of extinction and another is doing rather well? Could the answer be related to that question about why so many species can live together? The only certainty is that we do not know this answer or these answers. Investigations of interrelationships between co-existing predaceous diving beetle species are often frustrated by the complexity of responses, e.g., the variation in assemblages of seven *Hydroporus* species co-occurring along a pH gradient could not be explained by pH (Juliano 1991).

Conservation effort focused on predaceous diving beetles has been most active in the western Palaearctic, an area that has borne the brunt of urbanization, intensive agriculture, and industrialization in the past but also, at least in the north, an area with relatively few of the narrowly endemic species, the global loss of which must be an overriding conservation concern. Much has been found out in this European struggle, the degree to which the lessons learnt have wider relevance to conservation globally remaining to be seen. As more and more of the globe shifts from wilderness to development (sensu Sutherland 2004) the European experience may become all too applicable.

11.2 Dytiscidae as a Group Worthy of Conservation

Predaceous diving beetles are diverse and yet uniform (see Chap. 4 in this book). Their ground plan is instantly recognizable, whether the largest (the Amazonian *Megadytes ducalis* Sharp – 47.5 mm long – Fig. 11.1) or what is possibly the smallest (the Australian outback and subterranean *Limbodessus atypicalis* Watts and Humphreys 2006 – 0.9 mm long – Fig. 11.2). All are non-marine aquatic insects with the exceptions of a few species living in leaf litter (e.g., Brancucci and Hendrich 2010) and some of Sharp's (1882) Group 1 of *Agabus*, the species with discontinuous outlines, that

Fig. 11.1 The sole known specimen of *Megadytes ducalis* Sharp. There is a rumour (Jones 2010) that this specimen was found in the bottom of a dugout canoe by the Amazon. The coin is 22 mm in diameter (Photograph by Garth Foster)

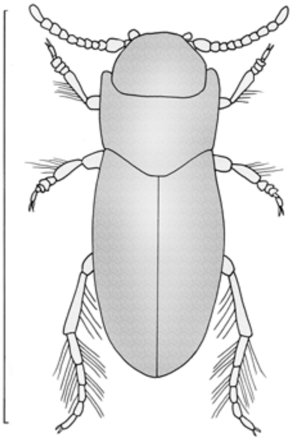

Fig. 11.2 The smallest known dytiscid beetle in the world, *Limbodessus atypicalis* Watts and Humphreys, found in a borehole in the Northern Territory, Australia. The scale is 1 mm (Redrawn from Howard Hamon in Watts and Humphreys (2006))

live in wet areas beside rather than in streams on mountains, extreme forms of which are known as “tropicoalpine super specialists” (Nilsson 1992). Predaceous diving beetles vary in distribution from the almost cosmopolitan *Rhantus suturalis*

(Macleay), the so-called “supertramp” (Balke et al. 2009), which ranges from Ireland to New Zealand, to many flightless subterranean species confined to single aquifers, as noted in a review by Spangler (1986), with the most numerous examples now known from Australia (e.g., the *Limbodessus* and *Nirripirti* described by Watts and Humphreys (2006)).

Dytiscidae occur in practically all inland aquatic environments on Earth, from wet rock faces on mountains (e.g., *Hydroporus pilosus* group and *Africophilus* species) to fast flowing streams and rivers (e.g., many of the *Deronectes* group of Hydroporinae), ponds, wetlands, groundwaters and even bromeliad tanks (Balke et al. 2008) (see Chap. 7 in this book). In many habitats they are abundant and speciose, and may constitute the top predators, having both high ecological importance, and reflecting processes occurring, and assemblage composition, at lower trophic levels. In addition, compared to many other aquatic insects, in particular the Diptera, they are relatively well-known from systematic and biogeographic perspectives (see Chaps. 2 and 3 in this book), particularly so in Europe and North America. For these reasons, and others, such as the relative longevity of many species as adults (enabling them to be sampled over an extended season), such beetles provide an excellent surrogate taxon for wider freshwater biodiversity, an approach that has been applied in a number of different regions, across a wide range of inland water habitats (e.g., Bilton et al. 2006; Picazo et al. 2012). In addition to their application as surrogate taxa, many predaceous diving beetles have narrow ecological niches, and so are excellent indicators of ecological quality and the conservation status of sites (e.g., Foster et al. 1990, 1992). Some of the poorly dispersing taxa are claimed as indicators of ecological continuity, such as those associated with pool systems in the remains of ice eruptions formed in periglacial, near-permafrost conditions, now named as lithalsas by Pissart (2003) and formerly referred to as pingos (Foster 1993; Bameul 1994).

11.3 Naturalness and the Causes of Loss

As with any work on biodiversity loss, the usual litany of human-inspired disasters is difficult to avoid, but it may be better to focus on a few aspects in detail where there is some detailed appraisal or a promise of recovery. With both habitat and species recovery it is important to consider what one is attempting to recreate. Perceptions of what is ‘natural’ are clearly prone to generational amnesia, particularly in areas of the globe which have been severely impacted for centuries, and for which historical accounts are scant (Papworth et al. 2009; Rick and Lockwood 2013).

11.3.1 Drainage

When Charles Darwin was collecting water beetles in the Fens to the north of Cambridge in the 1820s, he would have had access to Whittlesea Mere, the largest lake in southern England (Fig. 11.3). It and the surrounding fenlands supported

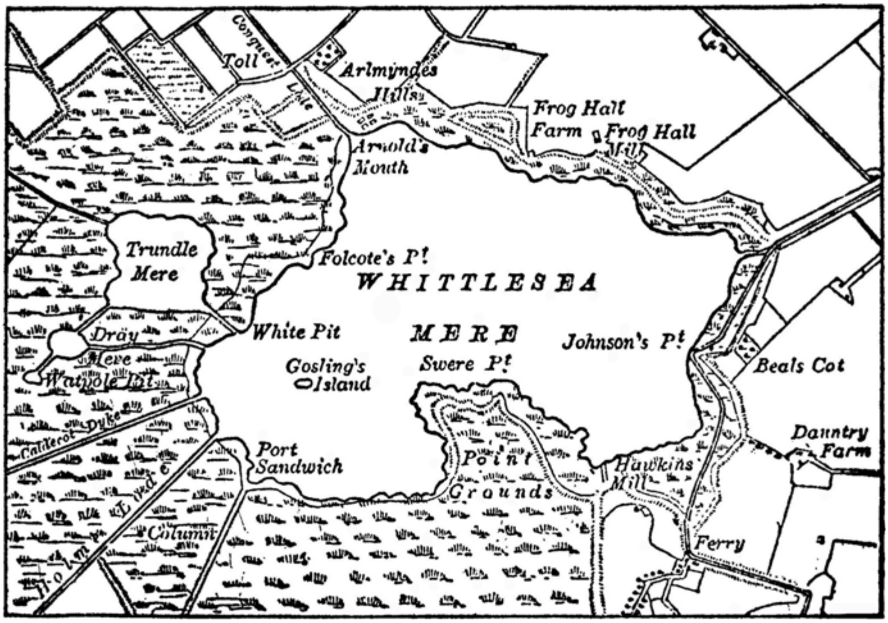

Fig. 11.3 Whittlesea Mere in 1850 immediately prior to its drainage. This was one of the earliest collecting sites for dytiscid beetles in England (As reproduced by Wentworth-Day (1954) from Miller and Skertchly (1878))

aquatic animals now extinct in Britain, including *Rhantus bistriatus* (Bergsträsser) and *Graphoderus bilineatus* (De Geer) (Fig. 11.4). The lake's destruction in the 1850s was the inevitable consequence of drainage begun during the Roman occupation (Rotherham 2013). The lake, becoming ever higher than the shrinking peat of the surrounding land, supposedly posed a tsunami-like threat to the surrounding area, and was easily drained by the newly available steam-driven pumps. Its floor subsequently produced some of the most fertile land in Britain. Some surviving peatland in the area became the first nature reserves in the world. Wicken Fen was set up as a reserve in 1899 by the National Trust and Woodwalton Fen was acquired as a private reserve in 1910 (Friday 1997; Godwin 1978). These reserves retained some, but not all, of the predaceous diving beetle rarities. The Norfolk Broads' fenland 50 miles to the east continued to provide mere-like habitat complexes in former mediaeval peat-diggings, with *R. bistriatus* and *G. bilineatus* known until the early twentieth century. These beetles probably disappeared because of a loss of water quality and the resultant change in vegetation. In practice the networks of drains in the Cambridgeshire Fens continue to support part of the original predaceous diving beetle fauna plus many species of temporary and slow-running fens, the assemblage being artificial and seen at its best in drains fed by clean water upwelling from the gravels beneath the peat (Foster et al. 1990; Foster and Eyre 1992). A very similar story of drainage, loss and faunal change has been played out, or is in active progress, in wetland areas throughout the world.

Fig. 11.4 *Graphoderus bilineatus* (De Geer) – one of the two dytiscid species listed under the European Union Habitats Directive and the Bern Convention (Photograph courtesy of Claus Wurst)

11.3.2 Pollution

The European Union's Common Agricultural Policy (CAP) was directed at increased food production, so driving agricultural intensification, and this has resulted in widespread water contamination with farm fertilizers and pesticides, a multinational approach to pollution that is often suggested as the cause of loss of predaceous diving beetle species from western Europe. The partial extinctions of the two species listed in the Habitats Directive, *Dytiscus latissimus* L. (Fig. 11.5) and *Graphoderus bilineatus*, are possible examples, though their decline certainly began before the initiation of the CAP. Land use change must be important, many aspects of it being cited by Hendrich and Balke (2000) and Hendrich (2011) in the case of *D. latissimus*. Cuppen et al. (2006b) note the potential importance of wet and dry acid deposition in moorland pools for damage to populations of *G. bilineatus* but identify the importance of moorland systems receiving high quality seepage water as essential for survival. In the United Kingdom the extensive and ongoing decline of some taxa appears to follow agricultural intensification. *Hydroporus rufifrons* (Müller) is a species of temporary and fluctuating wetlands, particularly in floodplains, and has been lost from most of the UK in the course of the twentieth century, this decline apparently following the northwestern spread of intensive agriculture from the lowlands of the southeast (Balfour-Browne 1940; Foster et al. 2008). Such data are correlatory, however, and in most cases we have no clear understanding of how such species are impacted by the intensification process, and whether agricultural chemicals have a direct or indirect effect. Perhaps the best example suggesting that nutrients are a key factor is the recovery or re-colonization of the Naardermeer, Weerribben, Wieden, and Nieuwkoopse Plassen by *G. bilineatus* in the Netherlands following phosphate removal from the Ijmeer water supply (Cuppen et al. 2006b).

Fig. 11.5 *Dytiscus latissimus* L. – the largest European dytiscid and the other species listed under the European Union Habitats Directive and the Bern Convention (Photograph courtesy of Lars Hendrich)

11.3.3 Encroachment

Over and above drainage, habitat loss can come about by many other forms of human interference – urbanization, industrialization, afforestation, and deforestation. It is unfortunate that humans position so many of their cities on estuaries and navigable rivers, as huge swathes of habitat have been lost through such encroachments across the world. David Sharp (1917) decried the Hammersmith Marshes, in the heart of London, as, "*portions and parcels of the dreadful past*", being among, "*the very best spots in Britain for Entomology*". Sharp noted that "*in London last year* [1916] *I went to Hammersmith to try and identify the old collecting ground. I quite failed, and what a falling off I found! What people call the advance of civilisation produces a very depressing effect on those of us who recollect the beauty of suburban London 60 or 70 years ago.*" Now, of course, there is not the remotest portion of this marshland, which Sharp described as running a mile and a half north-west from Holland House to Notting Hill. Sharp might find some consolation in the area, however, in that it houses large reservoirs, now abandoned as water supplies, which support a suite of pioneer predaceous diving beetles including *Hygrotus nigrolineatus* (von Steven) not found in Britain until 1983 (Carr 1984) and certainly not a beetle that Sharp could have found in his time.

Urbanization's impact may be even more marked in areas of higher biodiversity, such as many tropical regions. Balke et al. (1997) and Hendrich et al. (2004) highlight the pressures on predaceous diving beetles and other water beetles in the urban area of Singapore and its surroundings, where a number of species are considered locally extinct, or threatened.

11.3.4 Climate Change

It is easy to prophesy losses to predaceous diving beetles associated with climate change but difficult to identify examples of such losses to date. We have, however, a good understanding of changes in the water beetle fauna over the course of the

Pleistocene glaciations, with an appreciation of the ability of that fauna to respond to rapid changes in temperature regime, built on the pioneering work of Russell Coope (see Elias 1994 for a detailed review): for example the Mongolian and Canadian *Hygrotus unguicularis* (Crotch) occurred on the Isle of Man (between Ireland and Britain) in the last interglacial period 12,000 years ago (Joachim 1978). In the northern hemisphere at least, shifts in geographical range over the course of the Pleistocene appear to be the norm for many high latitude predaceous diving beetles. Any assumption that these insects are able to cope with current climatic shifts is dangerous on many counts, however. As well as questions regarding the rapidity and direction of current climate change in comparison to that experienced in the Pleistocene, there is the added complication that modern habitats are so highly fragmented that most species will be unable to track their climate envelopes in the future (Hoegh-Guldberg et al. 2008). In contrast to the story at high latitudes, Abellán et al. (2011) found that for Europe Pleistocene range movements do not appear to have been the norm for narrow-range endemic species distributed around the Mediterranean. Such species may be restricted to individual mountain systems as a consequence of poor heat tolerance (Calosi et al. 2008), and so be in double jeopardy in the face of climatic warming, which compromises them physiologically, and reduces the extent of their available habitat.

In addition to rarity, gas exchange mechanism may shape species' responses to ongoing climate change. As shown by Verberk and Bilton (2013), species with greater ability to control their oxygen uptake are likely to be more able to cope with increasing temperatures and anoxia in freshwater. Being surface exchangers, this means most predaceous diving beetles are likely to be less sensitive than similar taxa that obtain oxygen directly from the water, but it also points to the possible sensitivity of stream and (semi) subterranean taxa relying on plastrons and/or physical gills (Kehl and Dettner 2009; Madsen 2012).

11.3.5 Globalization, and the Fourth Horsemen of the Apocalypse

Invasive species offer a fundamental threat to biodiversity throughout the globe, and have a major role in diminishing the diversity of predaceous diving beetles, fish in particular having often displaced them as the top predators. Larson et al. (2000) identified the predator hierarchy in Canadian latitudes whereby fish dominate in the deep, permanent waters that allow survival beneath ice, odonates dominate in shallower water that does not dry up in summer, and beetles dominate in fluctuating or temporary wetland habitats. This model appears to be more widely applicable, but, in terms of conservation, habitat isolation also needs to be taken into account. Upland pools without significant outflows and streams above sills or discharging straight to the sea rather than into rivers provide refuges for predaceous diving beetles unless, as has been so often the case, man intervenes by introducing game fish. Predatory fish such as salmonids, pumpkinseed (*Lepomis gibbosus* (L.)) and the western mosquito fish (*Gambusia affinis* (Baird & Girard)) are generally regarded as being the most detrimental to insects, but it has been proposed (Kloskowski 2011) that bottom-feeding coarse fish such as the common carp (*Cyprinus carpio* L.) may do more damage by rendering the habitat permanently turbid. Fish can be lost from unbuffered waters by acid deposition, resulting in increases in some predaceous diving beetle populations (Foster 1991a), but this can hardly be claimed as a victory for conservation!

Invasive wildfowl, turtles, and crayfish are also important. Pederzani and Fabbri (2006) characterized the Louisiana Crayfish *Procambarus clarkii* (Girard) as the Fourth Horseman of the Apocalypse, fourth that is to "Conquista" (eutrophication associated with agriculture), "Guerra" (chemical warfare) and "Carestia" (famine). They listed eight rare species of predaceous diving beetle under threat from it around Rome. Possibly our most dramatic example of its devastation to date is the Les Marais de la Perge in Médoc, France where *Graphoderus bilineatus* was discovered in 1990. Bameul (1994) recorded 109 species of water beetle at la Perge but found only two in 2009 (Bameul 2013). It appears that *P. clarkii* colonized large parts of the area following a hurricane in December 1999 that caused extensive flooding in Gironde. Similar instances of the impact of *Procambarus* have been observed in a number of sites in Spain, where endorheic lagoons, with diverse water beetle faunas have been stocked with crayfish (Andres Millán, pers. comm.). In southern Spanish streams *Procambarus* appears to affect both the population density and ecology of rheophilic dytiscids; *Agabus brunneus* (Fab.) and *Deronectes hispanicus* (Rosenhauer), typical river pool species, apparently become restricted to riffle sections in the presence of crayfish, presumably because riffles provide refugia (DTB, personal observations).

Alien plants can also threaten aquatic invertebrate communities though there do not appear to be any examples specific to the Dytiscidae. New Zealand Pigmyweed, *Crassula helmsii* (Kirk), was originally introduced to Britain by aquarists and was first recorded as an escape there in 1956 (Leach and Dawson 1999), subsequently spreading to some of the most remote islands. Although the habitat structure of this plant appears superficially suitable for predaceous diving beetles, *Crassula* beds hold few species or individuals (GNF, personal observations on Alderney, Arran, Guernsey, the Isle of Man and Tiree; DTB personal observations in Devon and Hampshire). Denton (2001) noted that some predaceous diving beetles survived in the presence of *C. helmsii* but swards of this plant are known to eliminate native wetland plants. Whether *Crassula*'s apparent impact on predaceous diving beetles is direct or indirect is, however, unclear.

11.4 Types of Conservation

Conservation efforts in general can be divided into *ex-situ* and *in-situ* (see e.g., Hambler 2004), those concerning predaceous diving beetles to date, with the possible exception of Vahruševs (2011) falling into the former category. For what some might misguidedly regard as an obscure group of insects it is also important to differentiate between **active** and **passive** conservation. "Active" in the sense that predaceous diving beetles, perhaps just one species, might be the primary focus of the conservation activity – and "passive" in that the survival of the beetles relies on what is being done for another target group or habitat. Whilst some predaceous diving beetles are large enough to have appeal to the general public, and perhaps also to policy-makers, e.g., *Dytiscus latissimus*, or *Megadytes ducalis* – the largest predaceous diving beetle on Earth, which is also claimed to be the rarest insect (Jones 2010). Sadly most Dytiscidae will always depend on "passive" conservation for their survival.

Vahruševs's (2011) work on *Dytiscus latissimus* is concerned with laboratory rearing (Fig. 11.7), to which a corollary must be attempts at introduction or, as put by IUCN (2012), "assisted colonisation". There is very little published experience of translocations of predaceous diving beetles. Balfour-Browne (1962) recounted what is almost certainly the first attempt, in August 1906, when he took *Agabus undulatus* (Schrank) from Yorkshire to the Norfolk Broads: this introduction failed. Recent experience of translocating *Hydroporus rufifrons* within England has been instructive but the long-term outcome of the project remains to be seen (GNF, personal observations, and see Bray et al. 2012 concerning a trematode parasite detected in the donor population).

Thomas (2011) has noted that the species at greatest risk of extinction caused by man-mediated climate change are often narrow range endemics, something which has been demonstrated to apply to at least some dytiscids (Calosi et al. 2008). Thomas has argued that it would be better to move such taxa to places with appropriate climate, rather than to try to improve on their current habitats – an approach termed "assisted translocation" by Dawson et al. (2011). In a European context he notes that Britain is an ideal recipient for translocated species as there are already 2,000 introduced species there that are claimed not to have affected indigenous species. A last gasp attempt to build up a population of Iberian Lynx (*Lynx pardinus* (Temminck)) in an alien land might find favor amongst conservationists, but could we seriously contemplate harvesting and releasing any of the Iberian or island endemic dytiscids in the same way?

11.5 European Conventions: Including a Case-Study in Conservation Legislation and Its Consequences

International initiatives to protect individual species of predaceous diving beetle began in the 1980s. The Bern Convention (....on the Conservation of European Wildlife and Natural Habitats) was signed in 1979 and has to date been signed up to by 44 countries. Its Appendix II for "Strictly Protected Fauna Species" lists 710 animal species including 10 beetles. The two predaceous diving beetles, *Dytiscus latissimus* and *Graphoderus bilineatus*, were chosen from a shortlist of 117 species selected by 10 specialists from 10 countries (Anonymous 1986; Foster 1991b). Signatory nations were expected to enforce protection of these species by preventing them from being disturbed, captured, killed, or traded. Here we discuss the selection process, and its consequences for dytiscid conservation, based partly on first-hand experience.

The Bern Convention provided the model for the European Union (EU) Habitats Directive (92/43/EEC) of 1992, which required the recognition of "sites of Community importance" and Special Areas of Conservation (SACs), thus setting up an international network of "Natura 2000" sites based on scarce or threatened habitat types and species. Its Annex II lists the same two predaceous diving beetles among 38 beetle taxa. Member countries of the EU are required to maintain or, where appropriate, restore sites to favorable conservation status in the natural range of some important habitats listed in Annex I and the species in Annex II. This "passive" approach to the conservation of beetles has produced a good range of dytiscid sites but with some anomalies, for example the absence of inland saline water bodies (Sánchez-Fernández et al. 2008). Gutowski and Przewożny (2013) emphasize the importance of *Dytiscus latissimus* and *Graphoderus bilineatus* as the only beetles to represent aquatic habitats, thus having the potential as umbrella species.

What criteria might be applied to select one species over another (Hambler 2004)? Some predaceous diving beetles may qualify as flagship or umbrella species, such as the more conspicuous indicators of high quality wetlands. In other cases a species may be recognized as having conservation priority owing to its phylogenetic uniqueness (sensu Vane-Wright et al. 1991). A dytiscid example is *Acilius duvergeri* Gobert, formerly distributed from SW France to Morocco, which has declined severely because of loss of Mediterranean wetlands, and is today recorded certainly only from one site in Sardinia (Dettner 1981; Millán and Castro 2008). As well as apparently being the rarest large diving beetle in the western Palaearctic, and one of the most endangered dytiscids on earth, *A. duvergeri* is sister to all other members of the genus (Bergsten and Miller 2006). In biogeographical terms, should one concentrate on a species endemic to a particular mountain range, which may be quite common there (e.g., many southern European *Stictonectes* and *Deronectes*), or to a widely distributed species that is in decline over much of its range, a fate which has befallen many northern European fen dwellers? This dichotomy is particularly apparent in western Europe where intensification of most human activities in the northern lowlands might be contrasted with the climate change associated with some of those activities impacting on the isolated montane and island faunas of the south, which are richer in endemic species. Going back to the original selection process it is worth noting that we were obliged to select species for the Bern Convention on the basis that their distribution lay mainly within Europe, that the species should be reasonably easy to identify, and that the species should be under serious threat in Europe as a whole, but not necessarily in every place (Foster 1991b). Thus, we were guided towards species that might benefit from an international approach. Whether by design or by chance, such criteria may serve to relegate the conservation of a species confined to a particular mountain range or Mediterranean island to being a national issue. All else being equal, such species are generally of greater importance than taxa that are rare in one country but common elsewhere. The latter often form the basis of national Red Lists (see Hunter and Hutchinson 1994).

Settling for widely distributed species under serious threat, the third criterion "reasonably easy to identify" comes into play. What did this really mean? It seemed to rule out the smaller species, despite the fact that many large Dytiscidae can be just as easily misidentified as smaller ones. Was it just because such large beetles might be more easily detected in illegal transit? Or were they more capable of being viewed as flagship species (Hambler 2004)? A customs official might have some difficulty deciding the species of *Graphoderus* intercepted. He or she would be in good company as an English specimen of *G. bilineatus* was originally chosen as the neotype for *G. cinereus* (L.) by Jack Balfour-Browne (1960) before it was appreciated (Angus 1976) that *G. bilineatus* had at one time lived in England. That neotype selection was later suppressed (International Commission of Zoological Nomenclature 1989). Little wonder then that a common name proposed for *G. bilineatus* is The Chequered History Beetle! Adding further to the confusion was *G. zonatus* Hoppe, discovered in England in 1953 but passed over as *G. cinereus* until Angus's review (1976).

The selection of *Dytiscus latissimus* and *Graphoderus bilineatus* was greeted with indifference by most coleopterists initially. Fears about bureaucratic restrictions on survey work have been little more than restrictions imposed by individual nations before the Bern Convention. Most EU member states have enacted legislation to license the collection, transport, and possession of these beetles as among European Protected Species (EPS). They are not, however, covered by CITES, the Convention on International Trade in Endangered Species of Wild Fauna & Flora. More importantly, the requirement placed upon governments to protect these species by the Habitats Directive has proved to be highly beneficial to our understanding not just of their current distributions, with associated site protection, but also for clarification of their basic biology. Such reviews support the idea that both species have been lost over much of the western lowlands of Europe, but are surviving well in the east and to the north, so much so, for example, that *D. latissimus* is listed as of Least Concern in the latest Norwegian Red List (Kålås et al. 2010). Work in the Netherlands has been concerned mainly on analysis of modern survey data for both species (*D. latissimus* – Cuppen et al. 2006a; *G. bilineatus* – Cuppen et al. 2006b). A model for *G. bilineatus* was particularly useful in relating its distribution to moderate conductivity and to the presence of a rich mixture of emergent and submerged vegetation with some floating-leaved plants such as water-lilies (with duckweed never dominant). Vahruševs and Kalninš (2013) reviewed data for *D. latissimus* for 26 sites in Estonia, 42 in Latvia, and 37 in Lithuania. The array of ecological data demonstrated a wide tolerance, for example occupied sites ranging in pH from 3.5 to 9.8 and in conductivity from 0.05 to 0.46 mS/cm. Water depth proved of interest with deeper waters (more than 1 m) being needed in the colder part of the range of *D. latissimus*, presumably so that it can survive in winter, and echoing the model previously used to explain fish dominance in a northern climate. Intensive research on *D. latissimus* and *G. bilineatus* has emphasized their similarities, often being found in the same area, but also fine differences in their habitat requirements. For example, *G. bilineatus* is more or less confined in canals and ditches on peat areas in the Netherlands whilst *D. latissimus* is found in acid boggy ponds (Jan Cuppen, pers. comm.), and that these distributions were narrower than in the past. In Germany, Hendrich (2011) has noted that the former association of *D. latissimus* with carp ponds is no longer possible because of their present day management, with liming,

Fig. 11.6 Large traps have had to be developed to study *Dytiscus latissimus*, which is too big to be caught in the usual kind of bottle trap. In practice the fisherman's keepnet, suitably baited, has been found most effective. The one illustrated here in fact belongs to a Byelorussian angler – and it was occupied by *latissimus*! The trap illustrated here was found to be baited with beecomb, but many studies (e.g., Volkova et al. 2013) have proved the worth of the use of a bait of red meat or liver (Photograph by Garth Foster)

removal of vegetation, steep banks and artificial lining, emphasizing a narrowing in habitat requirement in a different way.

Non-destructive traps have been developed that have recently been used for mark-and-recapture, demonstrating for example the longevity of *D. latissimus* in the wild (Hendrich et al. 2013; Schmidt and Hendrich 2013). Traps can, however, prove highly destructive if left untended (Fig. 11.6). Attempts to rear both Bern Convention species in captivity have proved difficult, the most progress being made by Vahruševs (2011) with *D. latissimus* at Latgale Municipal Zoo, Latvia (Figs. 11.7 and 11.8).

A major feature of current European Union conservation activity is implementation of the Water Framework Directive (WFD or, in full, "Directive 2000/60/EC of the European Parliament and of the Council establishing a framework for the Community action in the field of water policy"). A principal requirement of this directive is to return water bodies to "good ecological status" by 2015. Governments of member states have developed catchment management plans. It remains to be seen whether this directive will achieve long-term sustainable water management, and whether "good ecological status" really equates to high water quality, but at least the WFD has obliged government agencies to look beyond the major rivers and lakes of each catchment, and perhaps to devote less attention to fish and more to macroinvertebrates as indicators of ecological status. Predaceous diving beetles have not achieved

Fig. 11.7 A complete breeding system. Vahruševs (2011) gave a complete guide to building equipment suitable for observing the development of *D. latissimus.* “Aqua-terrariums” had a ventilated aerial part suitable for pupation and an aquatic part holding ca 100 US gallons (400 l) and supporting up to 60 individuals. Particular attention was paid to temperature control, water filtration and simulating seasonal variations (Photograph courtesy of Valery Vahruševs)

a high profile in this re-evaluation of aquatic ecology but their conservation must benefit “passively” (see types of conservation above). In particular, measures to restore near-natural river structure and flow will be of value as well as reductions in diffuse and point source pollution.

11.6 Popularity, Biodiversity and Ecosystem Services

Dytiscids cannot be expected to achieve the popularity among the public or in scientific circles enjoyed by showy insect groups such as butterflies (e.g., Pollard and Yates 1993; Kudrna et al. 2011) and bumblebees (e.g., Goulson 2010). Apart from providing a demonstrably imperfect control of mosquitoes (Larson et al. 2000) and the occasional delicacy in a Cantonese restaurant (Jäch 2003), Dytiscidae are unlikely to feature highly in delivering the “ecosystem services” elaborated by the Millennium Ecosystem Assessment (2005). An indication of the importance of predaceous diving

Fig. 11.8 Seen here is a larva of *D. latissimus* hatching from its egg in captivity. Unusually amongst dytiscids, the larvae do not appear to be cannibalistic, but separate rearing is still considered necessary to avoid larvae being affected by the external digestion secretions of others (Vahruševs 2009) (Photograph courtesy of Valery Vahruševs)

beetles in ecosystem function has, however, recently been demonstrated through the mesocosm studies of Rudolf and Rasmussen (2013). Manipulating the numbers of adults and larvae of *Cybister fimbriolatus* (Say) resulted in significant shifts in animal biomass, phytoplankton, periphyton and decomposition rates, and, as measured via diurnal oxygen cycles, different rates of respiration and net primary productivity. In addition, as discussed above, they can play a role as surrogates of wider aquatic diversity and indicators of ecosystem health. The biodiversity of Dytiscidae results in an array of potentially exploitable corticosteroids in their prothoracic defensive glands (Dettner 1987) associated with a huge diversity of endosymbiotic bacteria implicated in the transformation of these substances (Gebhardt et al. 2002).

Recognition of the value of predaceous diving beetles is more likely to be associated with their species richness, and therefore their conservation should have benefited most when the paradigm of biodiversity (Convention on Biological Diversity 1992) held sway post-Rio. A possible example is provided by the UK Biodiversity Action Plan (UKBAP – UK Biodiversity Group 1999), a non-government (mainly Royal Society for the Protection of Birds) initiative that for a while ran in parallel with government initiatives based largely on UK conservation-based legislation concerned with site protection. The UKBAP listed six dytiscid species for which species action plans drew down funding to research species status, mainly in England. So far as dytiscids are concerned the UKBAP lived on when these species were placed on the lists in the Natural Environment and Rural Communities Act

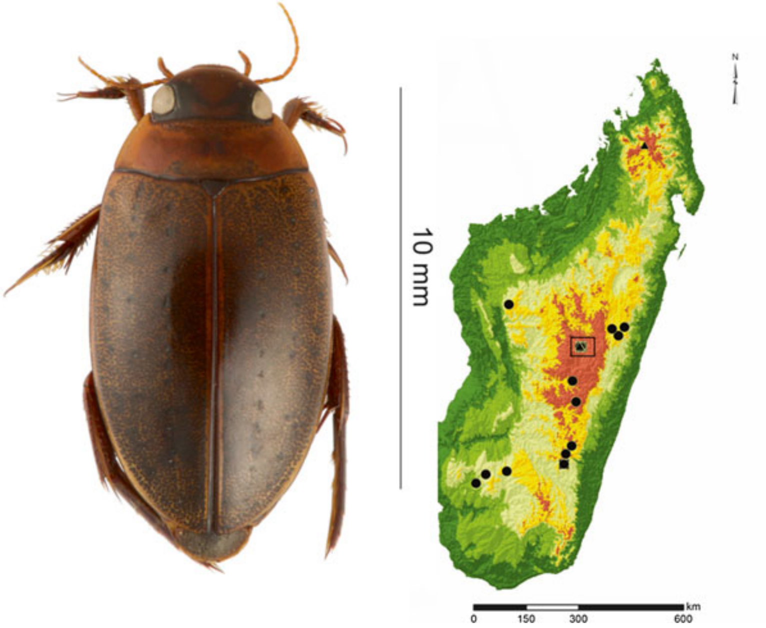

Fig. 11.9 *Rhantus manjakatompo* Pederzani and Rocchi is one of three Madagascan *Rhantus* confined to the high plateaux and all found together only at Manjakatompo (in the *rectangle*) (Hjalmarsson et al. 2013). Photograph Johannes Bergsten; map adapted from FTM, 1995. *Foiben Taosarintanin'i Madagasikra*. Institut Géographique et Hydrographique National 27/95

2006 (NERC Act) (Section 41 in England and Section 42 in Wales). The extent to which the prospects of the species themselves "living on" remain to be seen. Certainly, the UKBAP has facilitated useful research on the distribution and genetic diversity of dytiscids in Britain (e.g., Foster and Carr 2008; Foster et al. 2008; Lott 2005), but with one of the species (*Laccophilus poecilus* Klug) having last been seen in England in 2002. Any study of species richness must ultimately focus on the individual species involved.

The study of Madagascar's water beetles (Isambert et al. 2011, drawing on work by Monaghan et al. 2009), takes the study of predaceous diving beetle biodiversity to a new level by comparing species richness, phylogenetic diversity, and endemism in ten national parks. This work demonstrates that our understanding of species-level taxa is high, i.e., molecular and morphological designations were largely (91 %) in agreement. The concern is that phylogenetic diversity and endemism are negatively correlated, presumably because many of the endemic species are the result of relatively recent radiations *in situ*. Consequently, ranking sites on the basis of the phylogenetic diversity they support, an approach frequently used in conservation, may mean that globally rare, endemic species are ignored – i.e., just the ones one often wishes to target! This is surely a powerful conservation message with wide application "serviced" by predaceous diving beetles. The detailed work in Madagascar can also be used in a more orthodox way to identify biodiversity hotspots (see Fig. 11.9 concerning endemic *Rhantus* species – Hjalmarsson et al. 2013).

11.7 Global Lists

If numbers are important then world lists ought to provide important tools for conservation of predaceous diving beetles. Unfortunately the task of listing the entirety, or anything like it, of Dytiscidae fitting the criteria for threat status has proved impossible to date. The first attempt (IUCN 1990) listed 15 species in the United States, all rated "Indeterminate" apart from one possibly Extinct species, plus the two Bern Convention species, rated as Endangered. Later IUCN Red Lists were based on detailed criteria. The IUCN 1996 List (Baillie and Groombridge 1996), the last to be published as a hard copy, had eight predaceous diving beetles listed as Endangered and four as Vulnerable, the American species having disappeared because no-one could be found to re-evaluate them. Six species were listed as Extinct and 55 were listed as having been listed in 1994, but "now Not Evaluated". The present IUCN Red List is web-based, version 2013.1 simply indicating the previous listings of predaceous diving beetles, usually with the remark "needs updating".

Has appearing on a world list had any benefits? The fact that the list has not been updated recently by water beetle specialists could suggest not, but this may be the result of a lack of appropriate funding. One of the potentially embarrassing problems associated with such lists is that supposedly extinct species regularly turn up unharmed. It is so much easier to prove the existence of a previously unknown species than it is to prove the extinction of a known one! Many criteria applied by IUCN to categorize species are difficult to apply to most invertebrates, being based on population density, for example, or are simply unmeasurable with any confidence in taxa such as dytiscids. The often-quoted "extent of occurrence", defined by a convex polygon encompassing all points of occupation, may also be spurious as a way of defining occupancy, potentially encompassing a lot of empty space between isolated populations and affected by the extent to which an occupied feature such as a river or a coastal strip is linear. However, these problems can be circumvented and a species consigned to the Red List without the need for large amounts of data.

Appearance on a world list ought to provide leverage for funding to research on individual species. This has certainly been effective where it is possible to cite treaty or other legal obligations, as discussed above.

11.8 Dumbing-Down

Great play is currently being made of the benefits of "Citizen Science", involving amateurs in research projects. For those of us with a longer view this supposed recent discovery of the benefits of engaging with the public makes little sense as coleopterists have from the very first come from many walks of life. Professional scientists may well lead in the interpretation of results but the study of biodiversity was regarded as a respectable hobby for gentlemen and the occasional lady in Victorian times, often associated with professional collectors (Salmon 2000). Certainly, specialist knowledge is not a barrier to finding water beetles (Fig. 11.10), and

Fig. 11.10 Specialist knowledge and lack of sampling technique are not a barrier to generating useful conservation knowledge. One of the rarest of the large diving beetles is *Acilius sinensis* Peschet, originally described from southwest China. No specimens could be found – and not for the want of trying – for 82 years until a taxi driver found two specimens in a water-filled rut by a forest track in 2007 near the Myanmar border (Hendrich 2008). The taxi driver had neither collecting equipment nor, indeed, experience (Photograph courtesy of Lars Hendrich)

harnessing the drive of children to go pond-dipping is probably a prerequisite to a life of hunting for predaceous diving beetles (Fig. 11.11).

When the first IUCN Red List was put together (IUCN 1990) European coleopterists, if they noticed at all, were intrigued to find that North American candidates had common names; e.g., the Mono Lake Diving Beetle, *Hygrotus artus* (Fall). Since then common names have become more frequent, but are still often greeted with hostility. That hostility is justified when the common name is used without the Latin one, or when the name is misleading (in the IUCN Red List "Perrin's Cave Beetle" was coined for *Siettitia balsetensis* Abeille de Perrin, when the species almost certainly lived in gravels under the Var in France). Common names were contrived for all of the species in the Irish list (Foster et al. 2009), though this was resisted for the British list (Foster 2010) save for a few choicer ones. Reaching out to the average conservationist should not really require a dumbed-down common name but the experience is that if the expert does not contrive a name then someone less knowledgeable will come up with one instead. A great advantage of common names is that there is no Law of Priority: the best one will win. Learned societies attempting to control the choice of name (see Ferro 2013) will have no more luck than self-appointed publicists. Scientists might, however, be better employed contriving common names for habitats: for example, stating that a species is "madicolous" means nothing to most people – and it is misleading anyway as "living on rock" is not the

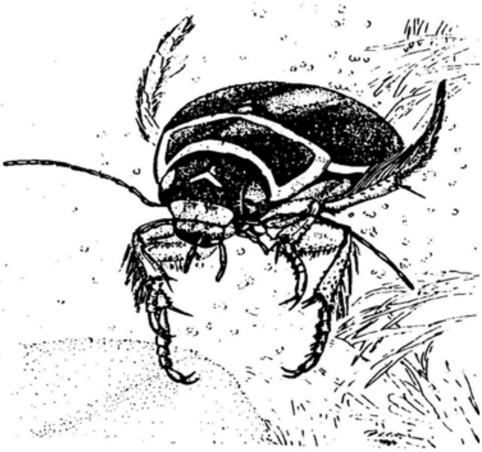

Fig. 11.11 Wirdiena ta' l-Ilma, the Maltese name for *Dytiscus circumflexus* Fabricius, was rated as Vulnerable in the Maltese Red Data Book (Cilia 1989). It was considered "large enough to encourage irresponsible collecting by parties of children on frog-hunts" and was the only beetle illustrated. More recently it might, as a flagship species, be considered a legitimate target by the next generation of children (Drawing by Joseph L. Cilia)

same as "living on wet rock", which it is usually intended to mean. "Hygropetalous" is more accurate but what is wrong with "living on wet rock" in the first place? One does not have to invoke "film stars" to make the habitat perceivable!

IUCN could perhaps learn a similar lesson. In their Red List coupling the statement that *Meladema imbricata* (Wollaston) is Critically Endangered on the basis of "A1c" whereas *M. lanio* (Fab.) is Vulnerable and "B1+2b" is not particularly illuminating to most readers. "One-liners" – such as *imbricata* being endemic and confined to four permanent high altitude streams on the three western Canary Islands whereas *lanio*, although confined to Madeira, is still relatively abundant (Ribera et al. 2003) – make so much more sense. Knowing that *M. imbricata* shares "A1c" with, for example, the Taiwan Cypress (*Chamaecyparis formosensis* (Matsum)) may of course ultimately prove useful for meta-analysis but means little otherwise.

11.9 The Way Ahead: "Passive Conservation" and the Possible Pitfalls of Connectivity

A recent study by Iversen et al. (2013) has challenged some basic ideas about conserving rare and endangered species. They demonstrate that *Graphoderus bilineatus* could be found in many "unsuitable" habitats in the core area of its distribution, in Estonia, Poland, and Sweden. This is unlike experience in Germany (Hendrich and Balke 2000) and in the Netherlands (Cuppen et al. 2006b), where the habitat could be more closely defined. Iversen et al. (2013) emphasize the value of a "dynamic landscape", such as is provided by the large floodplains of Poland, the morainic landscape of Estonia, and the myriad of lakes, mires, and bogs on the exposed bedrock of Sweden. They also mention the benefits associated with beaver activity and even the provision of artificial sauna- and fishponds. Such “passive” conservation measures, i.e., those not directed at a particular beetle but perhaps associated with a more populist target (e.g., amphibians in Estonia, Rannap et al. 2009) must provide the principal method of conserving Dytiscidae. Extensification of conservation effort is a natural corollary of metapopulation theory as applied in conservation (Hanski 1998), demanding connectivity of localized populations. In some areas, new wetland landscapes are being created in the hope that they emulate ancient ones; the Great Fen Project in the UK (Bowley 2007) is targeted to reflood 9,000 acres of land associated with one of Britain’s earliest wetland reserve, Woodwalton Fen (Rothschild and Marren 1997). The isolated fragments of habitat doomed by metapopulation theory may hold the key to survival of endangered species, at least in the short term, and those species may be lost following attempts to reconnect them (see Verberk et al. 2010 for an example in Dutch bog systems). If poor quality water pervades the new system, previously isolated refugia will be lost. Water quality is often a more important issue here than connectivity, and should be borne in mind when attempts are made to connect sites or to increase aquatic habitat density. Also, in a time of rapid climate change, it may be alien and invasive species that benefit most from improved connections (Vila and Ibanez 2011). Theory and fashion must not be allowed to triumph over practice.

11.10 Future Directions

Our knowledge of dytiscid systematics and biogeography has improved since the IUCN list was last revised, and the global Red List for Dytiscidae could probably be extended to cover perhaps a quarter of the known species, i.e., about a thousand taxa. In conducting such a revision, at least we might have something authoritative to quote about the extent to which various groups are under threat – tropical rainforest streams, subterranean systems in the Australian outback, species affected by agricultural intensification in western Europe or by industrialization and urbanization in China, mountain endemics affected by climate change, island endemics being lost through tourist development, and so on. Additionally this would raise the profile of these important and, for us at least, most charismatic insects.

Given the successes associated with listing two dytiscid species in the Bern Convention and under the European Habitats Directive it also appears desirable to produce Red Lists at continental scales. If formalized through IUCN these would fill the gaps for those countries lacking national Red Lists, as well as gaining an overview of the extent of the problems that predaceous diving beetles face at the regional level. Such approaches should, if possible, focus on regions that make sense biogeographically, rather than sticking to political boundaries.

As discussed by Sutherland (2004) the most effective conservation approach at a landscape scale is largely determined by the extent of anthropogenic habitat modification: largely intact ecosystems require less conservation management than highly modified landscapes. Such ideas obviously apply to dytiscids, even if their conservation is largely passive, falling under the umbrella of other taxa or ecosystems. In areas where the extent of wetland habitat has been severely reduced in recent years by human agency, habitat (re)creation may benefit dytiscid assemblages by increasing the density of suitable patches, something which has been demonstrated to be vital for the survival of some threatened taxa at least (e.g., Iversen et al. 2013). Such schemes should always bear water quality in mind, and aim to increase the density of high quality habitat, rather than just aquatic habitats *per se*. What works for larger vertebrates may not always work for invertebrates with more exacting requirements at the microhabitat scale. Schemes such as the Million Ponds Project in the UK (Pond Conservation 2013) which aim to do just this may benefit a suite of dytiscids in the future.

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In 2004 **Garth Foster** retired from the Scottish Agricultural College (now part of SRUC), where he was amongst other things head of the Environment Division. He was at last able to devote himself fulltime to the study of water beetles, having first taken an interest in them in 1961. He is secretary to the Balfour-Browne Club, an international study group for water beetlers started in 1976, and he chairs the Aquatic Coleoptera Conservation Trust, a charity devoted to work on British species under threat. Photograph by Annie Ross.

David Bilton has worked on water beetles one way or another for approximately 30 years. He has a particular interest in understanding biogeographical patterns, including the role of dispersal, and never tires of finding new beetles. After studying Zoology at the University of Oxford he obtained his Ph.D. on *Hydroporus* population genetics and phylogeography from the University of London and is currently a Reader in Aquatic Biology at Plymouth University in the southwest of England.

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