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# Water Beetles as Models in Ecology and Evolution

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## Abstract

Beetles have colonized water many times during their history, with some of these events involving extensive evolutionary radiations and multiple transitions between land and water. With over 13,000 described species, they are one of the most diverse macroinvertebrate groups in most nonmarine aquatic habitats and occur on all continents except Antarctica. A combination of wide geographical and ecological range and relatively accessible taxonomy makes these insects an excellent model system for addressing a variety of questions in ecology and evolution. Work on water beetles has recently made important contributions to fields as diverse as DNA taxonomy, macroecology, historical biogeography, sexual selection, and conservation biology, as well as predicting organismal responses to global change. Aquatic beetles have some of the best resolved phylogenies of any comparably diverse insect group, and this, coupled with recent advances in taxonomic and ecological knowledge, is likely to drive an expansion of studies in the future.

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## INTRODUCTION

Beetles are an evolutionary success story par excellence, being by far the most speciose order of animals on earth. The Coleoptera are an old radiation, whose evolutionary origins may date back to the Permian or even Carboniferous (147, 161). Of the features that underpin the evolutionary success of beetles, the presence of elytra is probably the single most important trait facilitating their colonization of aquatic habitats as adults, a lifestyle almost unknown in other holometabolous insects. As well as protecting the hindwings, the elytra enclose a subelytral air store, fundamental to gas exchange in almost all water beetle adults (30). At least 23 beetle families, from three of the four extant suborders, are predominantly aquatic as adults, larvae, or both (see **Figure 1**). Additionally, members of a number of other families are aquatic, or associated with water during at least one life-history stage, making the precise definition of a water beetle somewhat subjective (74, 130). What is clear is that water beetles are an ecological guild rather than a clade, with each aquatic colonization representing an independent transition between media, some giving rise to evolutionary radiations across the entire spectrum of inland waters. With more than 13,000 described species, water beetles are abundant and ecologically important in almost all nonmarine aquatic habitats, from the smallest phytotelmata to larger lakes and rivers, on all continents except Antarctica. Their wide geographical and ecological range together with a relatively stable and accessible taxonomy means that these insects are excellent models for addressing a variety of ecological and evolutionary questions. Here, we explore how water beetles have contributed to a range of disciplines, from macroecology to biogeography, sexual selection, and conservation biology.

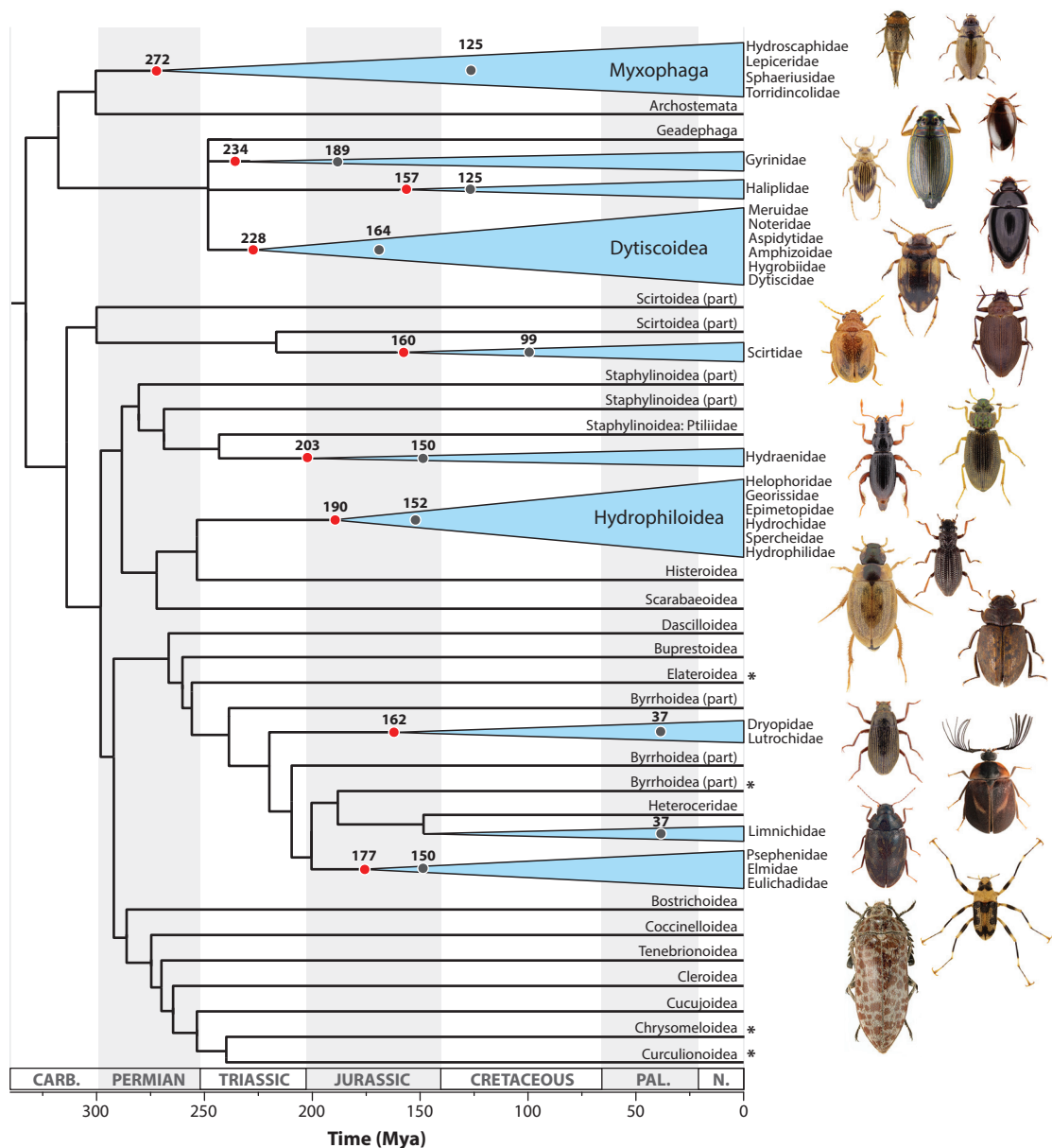
## EVOLUTION AND MACROECOLOGY

### Terrestrial–Aquatic Transitions

Among the insects, only Diptera have crossed the aquatic–terrestrial boundary as many times as Coleoptera (74). There are at least eight major transitions, and the actual number may be more than twice that (**Figure 1**) (130), with four of these resulting in radiations greater than 1,000 species. Not all aquatic beetles share the same ecology or evolutionary pathway to aquatic adaptation. In most, both the adult and larvae are aquatic. In others, only the larvae (Scirtidae) or adult (some Dryopidae and Helophoridae) live in water. Additionally, a number of water beetle lineages have experienced one or more secondary transitions back to terrestriality, particularly the Hydrophilidae and Hydraenidae (43, 102, 132, 143). The impact of these aquatic–terrestrial transitions on the evolutionary trajectories of lineages is not yet fully understood. In Hydrophilidae, habitat shifts were not themselves linked to changes in diversification rate, although increased habitat breadth may play a role (24). In other cases, transitions to terrestriality seem to be the result of unusual or idiosyncratic conditions, such as a rapid shift from streams to tree moss on Oceanic islands (134) or to forest litter (143). Hygropetric (or madicolous) habitats, where thin films of water flow over rock surfaces, have recently been revealed to support diverse water beetle assemblages (111, 133) and may be important stepping-stones between media.

### From Freshwater to Salt

Water beetles, together with some Diptera and Heteroptera, are among the few insects able to tolerate hypersaline waters, tolerating concentrations of more than 200 g/L of total solutes. This tolerance has developed independently—and recurrently—in several lineages, mostly Hydrophilidae (e.g., *Berosus*, *Enochrus*, *Paracymus*), Hydraenidae (*Ochthebius*), and Dytiscidae (some species of *Nebrioporus*, *Hygrotus*, and in the *Boreonectes* group of genera). Hypersaline habitats are usually



**Figure 1**

Representative time-calibrated phylogeny of Coleoptera showing the relative phylogenetic position and antiquity of each major water beetle lineage. The tree topology is simplified from McKenna et al. (84), with the exception that Adephaga is drawn as a polytomy between Geadephaga, Gyrinidae, Haliplidae, and Dytiscoidea. Divergence time estimates of crown lineages (red circles) are based on Toussaint et al. (147) (but see, e.g., 84 or 161 for an alternative dating), and the oldest known fossil taxa (black circles) are taken from Ponomarenko & Prokin (104). Primarily terrestrial lineages that contain some aquatic taxa are marked with an asterisk. See Supplemental Text for additional explanations and photograph details. Abbreviations: Carb., Carboniferous; N., Neogene; Pal., Paleogene.

**Supplemental Material** >

coastal, most commonly saltmarshes or rock pools, but they may also be found inland, with saline streams forming one of the most unusual aquatic environments (86). The evolution of salinity tolerance has been studied in detail in the *Enochrus* subgenus *Lumetus*, in which the evolutionary origin of salinity tolerance was associated with geological periods of increased aridification (10). There were also direct and relatively fast transitions between freshwater and hypersaline habitats, suggesting species may have evolved salinity tolerance before actually occupying saline habitats. Salinity tolerance may thus represent an exaptation from an adaptation to aridity, favored by a similar physiological mechanism. This hypothesis has been corroborated by further studies of physiological tolerance to salinity and desiccation (25, 95–99). Data on the evolution of salinity tolerance in other groups of Coleoptera are scant, but the association between the origin of salinity tolerance and periods of aridification seems to be recurrent (156). Another common pattern is the evolutionary conservation of habitat preferences. Despite multiple origins of salinity tolerance, species typical of saline habitats tend to cluster together in phylogenies more than expected, given their morphological differences (96, 120, 156).

### Going Underground

Given the global extent of subterranean waters (53), it is not surprising that aquatic beetles have colonized these systems multiple times, across five families in various parts of the world (61, 91, 137, 157, 158). Prior to 2000, most articles on subterranean water beetles were isolated species descriptions. Since then, it has been recognized that the subterranean dytiscid fauna of Australia is astoundingly rich, with around 100 species now known (36, 81). Australia's extensive subterranean environments, present for long periods of evolutionary time, may mean that this hypogean ecosystem is uniquely diverse. However, other areas with subterranean waters that share similar paleography, including parts of southern Africa and India, remain largely uninvestigated (57). Most Australian taxa are associated with calcrete aquifers, flooded natural concretions of soil cemented by limestone. In Western Australia, Miocene-Pliocene aridity (10–5 million years ago) drove the colonization of groundwaters by previously epigeal (surface-dwelling) beetles (81, 141). In all cases, described species are restricted to a single calcrete, these aquifers forming an archipelago of biologically isolated systems associated with paleodrainages (36, 81). Calcrete aquifers support one to three endemic dytiscid species, their colonization representing independent experiments in evolution (78). Coexisting species are always morphologically different from one another, with a relatively consistent average body-size ratio of 1.6 between them, despite marked differences in absolute beetle body sizes across calcretes—these insects provide one of the few empirical examples of self-organizing limiting similarity in nature (128, 155). In most aquifers, species derive from different ancestral lineages (81), suggesting that speciation occurred in allopatry. Eleven calcretes are currently known to contain sister species, however, which may have diverged locally (78). Whether the speciation of such taxa was truly sympatric remains unclear, as physicochemical conditions, including salinity, do vary across many individual calcretes (72) and population genetic structure has been observed in a number of taxa within aquifers (58). In at least one case, stable-isotope analysis has revealed differential prey specialization across a triplet of sister species (26), an observation consistent with sympatric divergence through resource partitioning.

Most subterranean Australian taxa were originally described in new, entirely hypogean genera on the basis of their derived morphologies, although subsequent molecular analyses have shown that they instead nest phylogenetically within genera with surface-dwelling representatives, mostly *Paroster* and *Limbodessus* (13, 80). As with the evolution of salinity tolerance, transitions to the subterranean environment are concentrated in a few lineages, for unknown reasons; in the Northern

Hemisphere, most stygobiont species are dytiscids of the subtribe Sietitiina (91, 92). The diversification dynamics of Australian *Paroster* suggest an early burst of speciation, which, together with the high degree of morphological diversity seen in the genus, is consistent with an adaptive radiation in groundwaters (141). However, the overall speciation and extinction rates do not appear to differ between surface and underground lineages (141).

The regressive evolution of features, particularly eyes, in subterranean taxa has long intrigued evolutionary biologists. There remains limited empirical evidence that eye regression is associated with the loss of protein-coding gene function, however. A comparison of Australian subterranean species with their fully eyed surface-dwelling relatives revealed that the eye pigment gene *cinnabar* behaves in a pseudogene-like manner in hypogean taxa (79). Two out of three species investigated further showed a complete absence of opsin transcription, consistent with a functional loss due to neutral mutations. The remaining species retained transcription of a long-wavelength opsin ortholog, despite living in an aphotic environment, which may indicate a novel pleiotropic role or an early stage of pseudogene development (138).

## Macroecology and Range Size

Understanding the drivers of geographical range size forms an important research focus in both macroecology (51) and its more recent offshoot macrophysiology (52). Most multicellular organisms have relatively limited geographical ranges, and relative range sizes typically vary considerably within clades, the majority of species being restricted while a few are much more widespread (51). Various explanations have been put forward to account for such observations, including differences in evolutionary age (51), dispersal ability (18), and fundamental niche breadth (27). Few empirical studies have explored these questions within a comparative framework, however. *Deronectes* diving beetles are one of the first and best-studied model systems in this regard; range sizes in these Palearctic stream dwellers vary from point endemics to species present throughout most of Europe. Multiple regression models show that thermal range—the absolute number of degrees centigrade between a species' mean upper and lower thermal limits—is a strong predictor of both latitudinal range extent and relative latitudinal position and is always more important than relative dispersal ability (34). This result remained when controlling for phylogeny, suggesting limited influence of evolutionary age—perhaps unsurprising in a clade in which species ranges have been shaped by Pleistocene climatic events that postdate their evolutionary origins (48). Differences in thermal performance may themselves be linked to metabolic plasticity (35) and setal tracheal gill densities (77, 154) in the genus, and in both *Deronectes* and *Ilybius*, diving performance has also been observed to differ between widespread and restricted taxa (33).

A strong association between thermal biology and range parameters is also seen in the *Agabus brunneus* group (Dytiscidae) (32, 66), where differences in the expression of proteins involved in energy metabolism and molecular chaperones (including heat shock proteins) have been observed between widespread and more restricted congeners (63, 64), pointing to a possible mechanistic basis behind differences in whole-organism performance. Whether physiological features of widespread species arose prior to (and therefore facilitated) their range expansions or appeared afterward as a result of local adaptation remains incompletely understood. The fact that broad physiological tolerances have been observed in single populations (32, 34) together with the genetic and ecological uniformity of many widespread taxa and their relatively recent origins (48) points toward the former explanation, however. In the temperate latitudes occupied by these beetles, widespread species are those that have been successful at expanding their geographical ranges in the Holocene, meaning that the location of a species' ice-age refugium may also influence its present range size and position (49, 50).

## Going with the Flow?

One of the most readily observable habitat preferences in aquatic Coleoptera (and macroinvertebrates in general) is whether they occupy running (lotic) or standing (lentic) waters. Species are usually found in one of these two broad types, and very few live in both. These contrasting preferences occur at all taxonomic levels, between families (e.g., Elmidae are almost exclusively lotic), genera, or even closely related species [e.g., *Ochthebius notabilis* (Hydraenidae) or *Nebrioporus ceresyi* (Dytiscidae) groups; see Reference 2]. Studies of Iberian aquatic Coleoptera first noted that lentic species had much larger geographical range sizes than their lotic relatives (115). These differences were related to the contrasting geological stability of the two habitat types: Species in more geologically ephemeral lentic waters are forced to disperse when the habitat disappears, while in more long-lived lotic systems, species can maintain local populations for longer. Consequently, lentic species were predicted to have higher dispersal abilities and interpopulation gene flow, resulting in larger, more dynamic geographical ranges and slower evolutionary turnover. Lotic species, in contrast, would tend to have lower dispersal abilities, with higher persistence of local populations and reduced interpopulation gene flow. Latitudinal diversity gradients of lentic and lotic species may also be expected to differ, as lotic species will be more dependent on historical factors and distance to glacial refugia, whereas lentic species will be closer to an equilibrium with current ecological and geographical conditions (108). It must be noted, however, that multiple factors influence dispersal ability in addition to habitat stability (18), so macroecological patterns related to habitat type will manifest as statistical trends, with exceptions always being possible (e.g., 131). It is also obvious that the lotic–lentic divide is a simplification of the complexity of freshwater habitats, which could be further subdivided (e.g., 73). Despite these limitations, most of the predictions (115) have proved accurate, mostly with data from aquatic Coleoptera but also other aquatic groups (e.g., 70, 83). Differences in geographical range between lotic and lentic species are not restricted to western Europe (37, 69) and can be associated with dispersal ability rather than ecological tolerance (11). The *Enochrus bicolor* complex includes eight Palearctic species, all of which occupy saline habitats (9). Widespread lentic species had significantly larger wings, relative to body size, than restricted lotic relatives, but running and standing water taxa differed little in thermal physiology (11).

The higher mobility of lentic species has apparently resulted in a faster recolonization of formerly glaciated areas in the Northern Hemisphere and a closer equilibrium with ecological conditions, while lotic species show a stronger dependence on latitude (114, 127). Differences in habitat stability are reflected in gene flow between populations (2, 83), although it is still not clear how these differences affect net diversification rates of lineages over longer evolutionary timescales (39, 40, 108, 110).

## BIOGEOGRAPHY AND DIVERSIFICATION

Because most water beetle lineages arose prior to the start of the breakup of Gondwana ca. 160 Mya (**Figure 1**), they have proven useful in providing a comparative model for the biogeographic consequences of Mesozoic vicariance events, as well as more recent episodes of Cenozoic colonization and diversification. Australia–Oceania and the Western Palearctic have been the primary foci for recent regional-scale biogeography and diversification studies, with Madagascar and the Neotropics having been studied to a lesser degree. The Nearctic and Oriental regions have been largely overlooked to date.

### Gondwanan Fragmentation

The separation of Africa and South America has been implicated in the diversification of several water beetle groups, including the dytiscid tribe Aciliini (28) and the hydrophilid tribe Hydrophilini

(140). The separation of Madagascar and India has been linked to the distributional pattern of hydrophilid cascade beetles in those regions (142). Gondwanan fragmentation may have played a role in the diversification of the Hydrobiusini (Hydrophilidae) (149), although the lineage likely originated in Laurasia. Additionally, there are a number of water beetle lineages that show a classical austral disjunction between southern South America, Australia/New Zealand, and/or South Africa, including the hydrophilid Cylominae (42) and Copelatinae (Dytiscidae) (22).

## Africa and Madagascar

No studies have focused on the internal biogeography of continental Africa, although several have examined the phylogenetic placement of newly discovered endemic lineages such as the South African *Aspidytes* (Aspidytidae) (111, 139) and *Capelatus* (Dytiscidae) (22). In contrast, Madagascar has been a particular focus for biogeographical and diversification studies. The current fauna has been shown to be a mix of ancient endemics (56) and Cenozoic colonizers and has perhaps served as a source of lineages back-dispersing to mainland Africa (29), a finding that should be tested with wider taxon sampling. A faunistic link between Madagascar and the South African Cape has been highlighted in dytiscids (109) and Hydraenidae (101).

## The Neotropics

Our knowledge of the Neotropical fauna, and particularly that of tropical South America, has grown substantially in the last 20 years. The region harbors substantial deep phylogenetic diversity, and recent studies have begun to unravel its distribution and origins. In Platynectinae diving beetles, the Andean and Guiana/Brazilian Shield faunas represent separate colonizations, which have diversified independently (144, 148). This phylogenetic separation between lineages found in the Andes and eastern Shield regions is implied in a number of other groups, including Hydrosaphidae (133). Additionally, the hypothesis that South America has served as a reservoir of diversity that has repeatedly dispersed northward into Central America, North America, and the Caribbean has been supported in a variety of water beetles (28, 38, 140).

## Australia and Oceania

The Cenozoic diversification of diving beetles across Australia and Oceania is one of the best-studied water beetle systems outside the Palearctic. Phylogenetic analyses of Australian Hydroporini reveal that eastern Australia was likely the ancestral source of the lineage when it began to diversify about 27 Mya and that the ongoing aridification of the continent has led to rampant extinction, as well as excursions underground (143–146). Recent radiations of Copelatinae (Dytiscidae) in New Guinea and New Caledonia are the result of repeated dispersal from Australian ancestors during the Miocene (12). There have been few incidents of back-dispersal or interisland mixing, with the notable exception of an incredible so-called supertramp species in the genus *Rhantus* (Dytiscidae), which originated in New Guinea and dispersed during the Pleistocene east to Australasia and New Zealand, and west as far as the Azores (14, 146).

## Western Palearctic

There has been substantial progress in recent years toward understanding the origins of the Mediterranean—and more widely, the Western Palearctic—water beetle fauna. Two general patterns emerge regarding the origin of Mediterranean endemics and the role of Pleistocene glacial cycles in shaping current faunas.

Virtually all Western Palearctic water beetles with restricted distributions are Mediterranean. The most ancient have been estimated to date from the Miocene, and these are mostly restricted to the Iberian and Anatolian peninsulas (48, 65, 113), in some cases forming two reciprocally monophyletic sister lineages [e.g., *Hydrochus* (Hydrochidae) and *Deronectes*]. There are no ancient endemics of such genera in mainland Italy or most of the Balkans, resulting in an east–west disjunction that has been long recognized biogeographically. The likely explanation for this disjunction is that most of the Italian and Balkan peninsulas remained submerged until the Pliocene (105), meaning that species of these genera endemic to mainland Italy south of the Alps and southern Greece are of Plio-Pleistocene origin. In these areas, there are, however, many endemics in taxa with an abundance of recent species, such as *Limnebius* and *Hydraena* (Hydraenidae) (117, 150, 151).

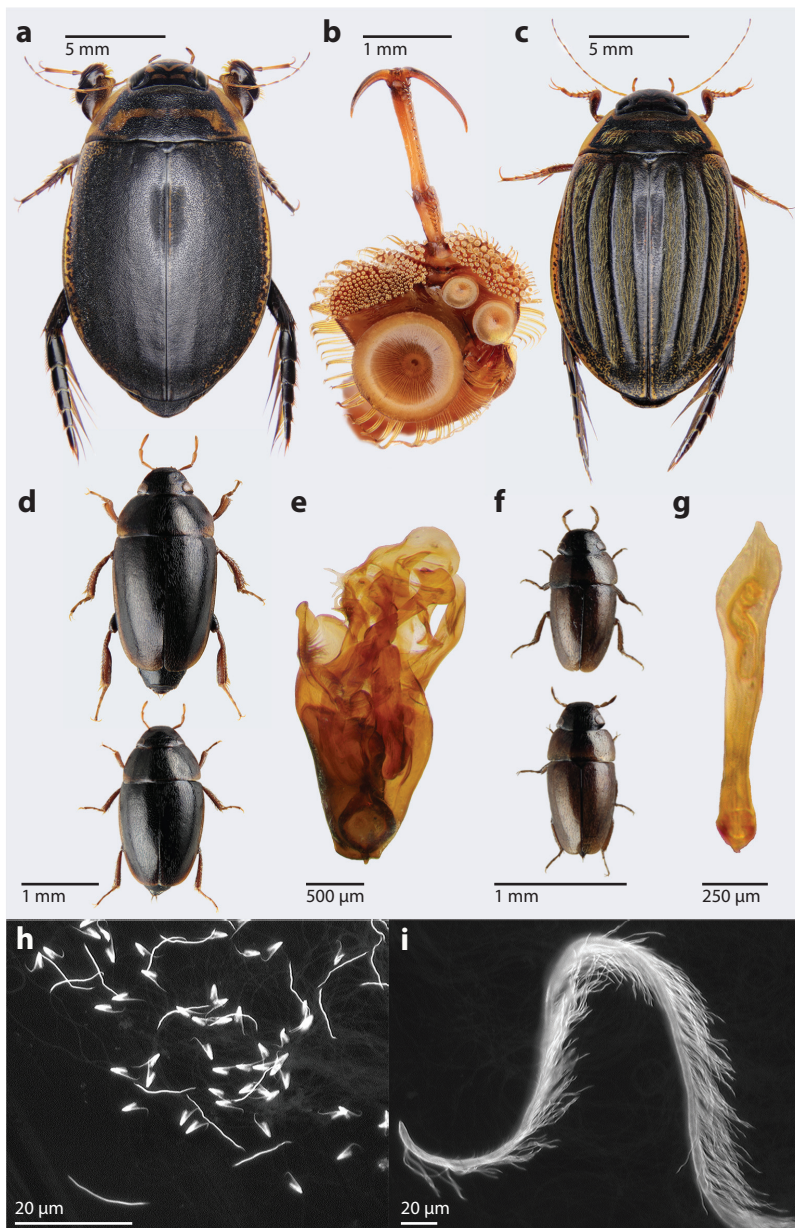
The availability of comprehensive phylogenies and phylogeographies of various groups of water beetles in western Europe and the Mediterranean region has revealed the complex role of Pleistocene glaciations in shaping current faunas. There are examples of the classic pattern of recolonization of recently deglaciated areas from the Mediterranean peninsulas (26, 62), mostly from populations at the northern edge of southern refugia. This implies that southern endemic species remained localized [e.g., *Deronectes* (48) and some *Hydraena* (112, 150)]. These southern endemics, in some cases of Pleistocene origin and sister to species with northern distributions (e.g., 116), may not have undergone significant range movements during their entire evolutionary histories, never colonizing areas directly affected by glaciations (1, 3, 112). In central and northern Europe, the fauna is dominated by widespread lentic species with good dispersal abilities (114, 127) or lotic species that expanded their ranges in a short temporal window with favorable conditions after the last glaciation (49, 112). These cycles of range expansion with subsequent fragmentation and speciation [similar to refuge speciation (94) or vicariance by niche conservatism (159)] may have acted as a so-called species pump, contributing substantially to current diversity.

## SEXUAL SELECTION IN WATER BEETLES

Sexual selection occurs when changes in trait frequency result from differential reproductive success between individuals. This includes intrasexual competition, as well as intersexual interactions such as mate choice (cryptic or otherwise) and forced matings (135). Sexual selection is implicated in the evolution of many complex traits, including insect genitalia (71, 136), and water beetle mating systems are complex and varied but best known to date in Dytiscidae. As with most insect groups, male genitalia often provide the primary means of differentiating closely related water beetle taxa (e.g., 91, 101, 102) and in some cases reach striking levels of complexity, particularly in the Hydraenidae (see **Figure 2**), where the precise homology of some structures remains unclear (117). In *Limnebius*, changes in body size appear to drive trends in genital evolution; reduced body size in the subgenus *Bilimnius* is accompanied by shrinkage and simplification of male genitalia, and several independent increases in body size in *Limnebius* s. str. are associated with larger, more complex genitalia (117, 118). There is also evidence for Rensch's rule in this genus, where male body size is more evolutionarily labile than female body size (119). The fact that greater sexual size dimorphism in *Limnebius* is not associated with more strongly developed secondary sexual characters suggests that the increased variation in male body size may have more to do with the lack of constraints associated with egg development and reproduction than with directional sexual selection (119).

Given differential gametic investment, the evolutionary interests of the two sexes often diverge, particularly when mating is relatively costly (135), leading to sexual conflict, which can drive evolutionary so-called arms races between males and females and result in extreme sexual dimorphism (100). Most male dytiscids have modified, sucker-like articulo-setae on the tarsi of their forelegs and middle legs (see **Figure 2**), which increases their ability to grasp females during

mating (7). In contrast, females of many species have enhanced dorsal sculpture, which reduces male grasping ability during pairing (75). Such female sculpture results from either a modification of existing surface reticulation (e.g., 19, 21) or the evolution of novel structures, including ridges and furrows or macroscopic granules on the elytra and irregular sculpture and hair-filled pits on the pronotum, in areas where male tarsi attach during mating initiation (**Figure 2**). Such traits are common in the larger Dytiscinae, where preinsemination sexual conflict dominates a sexual system characterized by long pairings, postinseminatory mate guarding (sometimes with



(Caption appears on following page)

**Figure 2** (Figure appears on preceding page)

Sexually selected characters in water beetles: *Acilius sulcatus* (Dytiscidae) (a) male habitus—note the expanded fore- and mid-tarsi; (b) ventral surface of male fore-tarsus—note the plunger-like articulo-setae, which function as attachment devices; (c) female habitus—note the furrowed elytra and hairs on the pronotum and elytra, which are resistance traits that make male attachment more difficult during pairing. *Limnebius* species (Hydraenidae): (d) *Limnebius truncatellus* male (top) and female (bottom) habitus—note the strong sexual dimorphism in body size and male leg modifications; (e) relatively complex male genitalia of *Limnebius truncatellus*; (f) *Limnebius evanescens* male (top) and female (bottom) habitus—note the limited sexual dimorphism in body size; (g) relatively simple male genitalia of *Limnebius evanescens*. (h,i) Sperm of *Hygrotus sayi* (Dytiscidae) imaged with epifluorescence microscopy, with only DNA-stained heads visible. (b) Isolated, dimorphic sperm, some with broad heads and basal spurs and others with filamentous heads. (i) Sperm conjugation—sperm with broad heads stack (like traffic cones), forming a scaffold that sperm with filamentous heads attach to. Panels b and i courtesy of Dawn Higginson.

the production of mating plugs), and vigorous attempts by females to dislodge males, particularly at the onset of pair formation (90). Although not quantified to date, such pairings are likely to impart a greater energetic cost to females than males, particularly since males restrict females' access to air when surfacing, in an apparent attempt to manipulate mating success (7, 90). Pairing duration and mating behavior in other water beetles are poorly known, but sexual dimorphism consistent with sexual conflict has been reported in a number of other dytiscid groups (19, 21) and Haliplidae (106). Male attachment devices seen in Gyrinidae and some Hydrophilidae may also indicate sexual conflict, although to date, these have not been investigated.

Some dytiscids are also intrasexually dimorphic, with two forms of female differing in their resistance traits—some being rough, while others are smooth, like males (89, 90). Differences in female resistance appear to drive the evolution of counter-modifications in male attachment devices, with nonrandom mating between male and female morphs leading to linkage disequilibrium between male and female traits and the coexistence of morphs through negative frequency-dependent selection (59, 60). In some species, there is marked geographical variation in the relative frequencies of rough and smooth female morphs, although the drivers of these distributions remain poorly understood (76). Sometimes, rough and smooth female populations are allo-/parapatric and associated with males differing in the extent of development of tarsal attachment suckers (17, 21). Differential mating success may drive observed changes in the geographical position of such contact zones (17).

In addition to preinsemination conflict, the Dytiscidae show great variation in female reproductive tract morphology (88), particularly in the subfamily Hydroporinae. Female hydroporine tracts frequently feature long, convoluted spermathecal and fertilization ducts, as well as other modifications (88), all of which point to the occurrence of sperm selection by females (23, 87). Dytiscid sperm morphology is varied and complex, again particularly in the Hydroporinae, where complex sperm conjugations and heteromorphisms have been reported (Figure 2) (67, 68). The evolution of sperm and female reproductive tract features are correlated across the family, consistent with strong sexual selection (67, 68). The role of morphologically complex spermatophores in this process (129) remains unknown, but these structures may play a role in sperm delivery and positioning and may function as mating plugs.

## BIODIVERSITY, CONSERVATION, AND GLOBAL CHANGE

Water beetles have great potential for biodiversity and conservation assessment of inland water habitats and have a number of features that make them an excellent indicator group. These include high species richness, wide ecological/habitat range, high functional diversity (reflecting multiple aquatic colonizations), relative ease of sampling (at least as adults), and the fact that they are

relatively well known taxonomically and biogeographically (46, 74, 107, 130). Being well known taxonomically, they have featured heavily in attempts to explore the effectiveness of DNA taxonomy and species delineation methods (e.g., 15, 93). In addition, taxa vary considerably in both their degree of ecological specialization and dispersal abilities, with some species being reliable indicators of water quality (47, 82, 85) or long-term habitat stability (e.g., 44, 45). To date, most detailed applications have been in Europe (46, 54, 55, 103, 122), and studies in other regions have been largely concerned with the diversity and conservation of the insects themselves. Beetles are also effective surrogates of wider macroinvertebrate diversity (20, 55, 121), reflecting patterns in both species richness and compositional similarity in the wider aquatic community. This surrogate effect has been widely used to address a range of conservation-related questions, particularly in southwest Europe. These include the setting of regional conservation priorities (5), area selection (122), the effectiveness of protected area networks (6, 55), sampling bias in environmental data sets (124, 125) and species distribution models (126), the influence of surrounding land cover on aquatic assemblages (41), and the importance of conserving the evolutionary history of a group (4).

Recent studies of ecophysiology and geographical range size in water beetles have provided insights into their relative vulnerability to global change, being examples of insect conservation physiology (8, 9). The distinction can be made between species more likely to persist in situ and those more likely to shift distribution, these two groups requiring different conservation approaches (8). *Deronectes* diving beetles are weak dispersers (16), whose occupied ranges bear little resemblance to those predicted by species distribution models based on macroclimate (123). In these beetles, geographically restricted Mediterranean endemics are more vulnerable to climate warming than their widespread congeners owing to limited heat tolerance and thermal plasticity (31, 34). Global change is reducing the extent of suitable habitat in the Mediterranean mountains (31), placing such taxa in double jeopardy. In reality, global change involves multiple stressors operating synergistically. In inland waters, these include increased temperatures and hypoxia (152), the latter resulting from both eutrophication and increased metabolic demand at high temperatures (153). Recent work suggests that the type of gas exchange mechanism and the degree to which individuals can regulate internal oxygen levels are good predictors of vulnerability to the combined effects of rising temperature and hypoxia, plastron-breathing elmids being much more strongly affected than surface exchanging dytiscids (152).

## FUTURE ISSUES

1. Water beetle families (particularly Dytiscidae, Hydrophilidae, and Hydraenidae) will be among the first diverse insect groups for which phylogenies with an almost complete taxon sampling could be available, allowing us to accurately explore the diversification processes that have shaped the biodiversity of lineages and regions.
2. Genomic/transcriptomic data will soon allow us to resolve difficult nodes in phylogenies (e.g., the status of Hydradephaga) and to explore the mechanistic bases of morphological and physiological adaptations. How are convergences between lineages at the phenotypic scale (e.g., complex antennal modifications used for gas exchange in Hydrophiloidea and Hydraenidae, similarities in thermal physiology or adaptations to extreme salinity and the subterranean environment) reflected at the genomic level? Such approaches could also explore convergences in the sensory apparatus associated with aquatic colonization and the level at which these changes have occurred—deep in the reception mechanism or only in the structures that receive the stimulus?

3. How general are the relationships between physiology and geographical range size revealed in Palearctic water beetles? There is an urgent need for similar comparative studies in tropical and southern temperate regions.
4. Most studies of water beetle sexual systems to date have focused on a limited number of diving beetle taxa. To understand the drivers of sexual conflict, further comparative studies are needed, both within the Dytiscidae and in other water beetle families. The emergence of larger, more robust phylogenies means that such studies can be conducted within a sound evolutionary framework.
5. Water beetles are excellent surrogates of aquatic biodiversity. To date, however, their use as indicator taxa has been largely restricted to Europe. Ongoing improvements to taxonomic, ecological, and biogeographical knowledge in other regions will make the wider development of water beetles in habitat assessment a realistic possibility in the near future.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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