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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, some of these events involving extensive evolutionary radiations and multiple transitions between media. With over 13,000 described species, they are one of the most diverse macroinvertebrate groups in most non-marine aquatic habitats, on all continents except Antarctica. A combination of wide geographical and ecological range, together with relatively accessible taxonomy make these insects an excellent model system for addressing a range 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 are likely to drive an expansion of studies in the future.

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 (148, 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 (75, 131). What is clear is that water beetles are an ecological guild rather than a clade, 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 non-marine 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 range 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

Amongst the insects, only Diptera have crossed the aquatic-terrestrial boundary as many times as Coleoptera (75). There are at least eight major transitions, and the actual number may be more than twice that (**Figure 1**) (131), 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 (44, 103, 133, 144). The impact of these aquatic-terrestrial transitions on the evolutionary trajectories of lineages are 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 (135) or to forest litter (144). Hygropetric habitats, recently revealed to support diverse water beetle assemblages (111, 134), may be important ‘stepping-stones’ between media.

From Freshwater to Salt

Water beetles, together with some Diptera and Heteroptera, are amongst the few insects able to tolerate hypersaline waters, with concentrations up to more than 200 gr/l. 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 *Boreonectes*). Hypersaline habitats are usually coastal, most commonly saltmarshes or rockpools, but they may also be found inland, with saline streams forming one of the most unusual aquatic environments (87). 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, 96–100). Data on the evolution of salinity tolerance in other groups of Coleoptera are scanty, but the association between the origin of salinity tolerance and periods of aridification seems to be recurrent (157). 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 similarities (97, 121, 157).

Going Underground

Given the global extent of subterranean waters (54) it is not surprising that aquatic beetles have colonized these systems multiple times, across five families in various parts of the world (62, 91, 138, 158, 159). Prior to 2000, most publications 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 (37, 82). Australia's extensive subterranean environments, present for long periods of evolutionary time, may mean that this hypogean is uniquely diverse. However, other areas with subterranean faunas that share similar paleography, including parts of southern Africa and India remain largely uninvestigated (58). Most Australian taxa are associated with calcrete aquifers in Western Australia, where Miocene-Pliocene aridity (10–5 million years ago) has driven the colonization of groundwaters by previously epigean beetles (82; 142). In all cases, described species are restricted to a single calcrete, these aquifers forming an archipelago of biologically isolated systems associated with paleodrainages (37, 82). Calcrete aquifers support one-three endemic dytiscids, their colonization representing independent experiments in evolution (79). Coexisting species are always morphologically different from each other, 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 providing one of the few empirical examples of self-organizing limiting similarity in nature (129, 156). In most aquifers, species derive from different ancestral lineages (82) suggesting that speciation occurred in allopatry. Eleven calcretes are so far known to contain sister species, however, which may have diverged locally (79). Whether the speciation of such taxa was truly sympatric, remains unclear, as physicochemical conditions, including salinity, do vary across many individual calcretes (73), and population genetic structure has been observed in a number of taxa within aquifers (59). 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 morphology, although subsequent molecular analyses have shown that they instead nest within genera with surface-dwelling representatives, mostly *Paroster* and *Limbodessus* (12, 81). 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 Siettitina (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 (142). However, the overall speciation and extinction rates do not appear to differ between surface and underground lineages (142).

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 (80). Two out of three species investigated further showed a complete loss of opsin transcription, consistent with neutral, regressive evolution. The remaining species retained transcription of a longwavelength opsin orthologue, despite living in an aphotic environment, which may indicate a novel pleiotropic role or an early stage of pseudogene development (139).

Macroecology and Range Size

Understanding the drivers of geographical range size forms an important research focus in both macroecology (52), and its more recent offshoot macrophysiology (53). Most multicellular organisms have relatively limited geographical ranges, and relative range sizes typically vary considerably within clades, the majority being restricted whilst a few are much more widespread (52). Various explanations have been put forward to account for such observations, including differences in evolutionary age (52) 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 varying 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 always more important than relative dispersal ability (33). This result remained when controlling for phylogeny, suggesting limited influence of evolutionary age – perhaps unsurprising in a clade whose ranges have been shaped by Pleistocene climatic events which post-date their evolutionary origin (49). Differences in thermal performance may themselves be linked to metabolic plasticity (35) and setal tracheal gill densities (78, 155) in the genus, and in both *Deronectes* and *Ilybius* diving performance has also been observed to differ between widespread and restricted taxa (34).

A strong association between thermal biology and range parameters is also seen in the *Agabus brunneus* group (Dytiscidae) (31, 67), 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 (64, 65); 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 expansion, or appeared afterwards, as a result of local adaptation, remains incompletely understood. The fact that broad physiological tolerances have been observed in single populations (31, 33) together with the genetic and ecological uniformity of many widespread taxa and their relatively recent origins (49) point toward the former explanation, however. In the temperate latitudes occupied by these beetles, widespread species are those which 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 (50, 51).

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, very few 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 2). Studies of Iberian aquatic Coleoptera first noted that lentic species had much larger geographical range sizes than their lotic relatives (116). 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, whilst in more long-lived lotic systems species can maintain local populations for longer. Consequently, lentic species were predicted to have higher dispersal abilities and inter-population 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 inter-population 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 (109). 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, exceptions always being possible (e.g. 132). 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. 74). Despite these limitations, most of the predictions of (116) have proved accurate, mostly with data from aquatic Coleoptera but also other aquatic groups (e.g. 71, 84). Differences in geographical range between lotic and lentic species are not restricted to Western Europe (38, 70) and can be associated with dispersal ability rather than ecological tolerance (8). The *Enochrus bicolor* complex includes eight Palearctic species, all of which occupy saline habitats (11). 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 (8).

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, whilst lotic species show a stronger dependence on latitude (115, 127). Differences in habitat stability are reflected in gene flow between populations (2, 84), although it is still not clear how these differences affect net diversification rates of lineages over longer evolutionary timescales (40, 41, 109, 112).

BIOGEOGRAPHY AND DIVERSIFICATION

Because most water beetle lineages arose prior to the breakup of Gondwana (**Figure 1**), they have been 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 (141). The separation of Madagascar and India has been linked to the distributional pattern of hydrophilid cascade beetles in those regions (143). Gondwanan fragmentation may have played a role in the diversification of the Hydrobiuisini (Hydrophilidae) (150) 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 (43), 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 South African *Aspidytes* (Aspidytidae) (111, 140) 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 (57), Cenozoic colonizers, as well as perhaps serving as a source of lineages back-dispersing to mainland Africa (29), a finding which should be tested with wider taxon sampling. A faunistic link between Madagascar and the South African Cape has been highlighted in dytiscids (110) and Hydraenidae (102).

The Neotropics

Our knowledge of the Neotropical fauna, and particularly that of tropical South America, has grown substantially in the last twenty 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 (145, 149). This phylogenetic separation between lineages found in the Andes and eastern Shield regions is implied in a number of other groups, including Hydroscaphidae (134). .Additionally, the hypothesis that South America has served as a reservoir of diversity which has repeatedly dispersed northwards into Central America, North America, and the Caribbean has been supported in a variety of water beetles (39, 141, 28).

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 (144, 146, 147). Recent radiations of Copelatinae (Dytiscidae) in New Guinea and New Caledonia are the result of repeated dispersal from Australian ancestors during the Miocene (14). There have been few incidents of back-dispersal or inter-island mixing, with the notable exception of an incredible “supertramp” species in the genus *Rhantus* (Dytiscidae), which originated in New Guinea and has dispersed as far as the Azores and New Zealand (13, 147).

Western Palearctic

There has been substantial progress in recent years towards understanding the origins of the Mediterranean – and more widely 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 (49, 66, 114), 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 and 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 (106), 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) (118, 151, 152).

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, 63), mostly from populations at the northern edge of southern refugia. This implies that southern endemic species remained localized (e.g. *Deronectes* (49) and some *Hydraena* (113, 151)). These southern endemics, in some cases of Pleistocene origin and sister to species with northern distributions (e.g. 117), may not have undergone significant range movements during their entire evolutionary histories, never colonizing areas directly affected by glaciations (1, 3, 113). In central and northern Europe the fauna is dominated by widespread lentic species with good dispersal abilities (115, 127), or lotic species that expanded their ranges in a short temporal window with favorable conditions after the last glaciation (50, 113). These cycles of range expansion with subsequent fragmentation and speciation (similar to refuge speciation (95) or vicariance by niche conservatism (160)) may have acted as a “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 (136). Sexual selection is implicated in the evolution of many complex traits, including insect genitalia (72, 137), 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, 102, 103), 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 (118). In *Limnebius*, changes in body size appear to driven trends in genital evolution; reduced body size in the subgenus *Bilimnius* being accompanied by shrinkage and simplification of male genitalia, and several independent increases in body size in *Limnebius* s. str. associated with larger, more complex genitalia (118, 119). There is also evidence for Rensch's rule in this genus, where male body size is more evolutionarily labile than female (120). 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 (120).

Given differential gametic investment, the evolutionary interests of the two sexes often diverge, particularly when mating is relatively costly (136), leading to sexual conflict, which can drive evolutionary "arms-races" between males and females and result in extreme sexual dimorphism (101). Most male dytiscids have modified, sucker-like articulo-setae on the tarsi of their fore and middle legs (see **Figure 2**), which increase 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 (76). 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 pre-insemination sexual conflict dominates a sexual system characterized by long pairings, post-inseminatory mate-guarding (sometimes with 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 (107). 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, others smooth, like males (89, 90). Differences in female resistance appear to drive the evolution of counter-modifications in male attachment devices, with non-random 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 (60, 61). 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 (77). 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 pre-insemination 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, 93). Dytiscid sperm morphology is varied and complex, again particularly in the Hydroporinae, where complex sperm conjugations and heteromorphisms have been reported (**Figure 2**)

(68, 69). The evolution of sperm and female reproductive tract features are correlated across the family, consistent with strong sexual selection (68, 69). The role of morphologically complex spermatophores in this process (130) remains unknown, but these structures may play a role in sperm delivery and positioning as well as functioning as mating plugs.

BIODIVERSITY, CONSERVATION, AND GLOBAL CHANGE

Water beetles have great potential for biodiversity and conservation assessment of inland water habitats, a number of features making 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 (47, 75, 108, 131). Being well known taxonomically, they have featured heavily in attempts to explore the effectiveness of DNA taxonomy and species delineation methods (e.g. 15, 94). In addition, taxa vary considerably in both their degree of ecological specialization, and dispersal abilities, with some species being reliable indicators of water quality (48, 86) or long-term habitat stability (e.g. 45, 46). To date, most detailed applications have been in Europe (47, 55, 56, 104, 123), studies in other regions largely concerned with the diversity and conservation of the insects themselves Beetles are also effective surrogates of wider macroinvertebrate diversity (20, 56, 122), 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 (4), area selection (123), the effectiveness of protected area networks (5, 56), sampling bias in environmental datasets (124, 125) and species distribution models (126), the influence of surrounding land cover on aquatic assemblages (42) and the importance of conserving the evolutionary history of a group (6).

Recent studies of ecophysiology and geographical range size in water beetles have provided insights into relative vulnerability to global change, being examples of insect conservation physiology (9, 11). The distinction can be made between species with high persistence ability, and those more likely to shift distribution, these two groups requiring different conservation approaches (9). *Deronectes* diving beetles are weak dispersers (16), whose occupied ranges bear little resemblance to those predicted by species distribution models based on macroclimate (128). In these beetles, geographically restricted southern endemics are more vulnerable to climate warming than their widespread congeners, due to limited heat tolerance and thermal plasticity (32, 33). Global change is reducing the extent of suitable habitat in Mediterranean mountains (32), placing such taxa in double jeopardy. In reality, global change involves multiple stressors operating synergistically. In inland waters, these include increased temperatures and hypoxia (154), the latter resulting both from eutrophication and increased metabolic demand at high temperatures (153). Recent work suggests that 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 (154).

FUTURE ISSUES AND DIRECTIONS

1. Water beetle families (particularly Dytiscidae, Hydrophilidae, Hydraenidae) will be amongst 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.

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Reference annotations

3. Development of a novel approach to infer speciation modes based on the phylogeny and current distributions of the species of a lineage.

10. Rationale for deriving conservation strategies from empirical biological/ecological data.

16. Extensive evaluation of how DNA barcoding performs at different spatial and evolutionary scales.

34. First study to compare the relative importance of different drivers of range size in a phylogenetically controlled framework.

58. Oldest known Malagasay animal lineage.

76. Overview of beetle diversity and biology, with discussion on what constitutes a water beetle.

92. Key review of generic diversity of major aquatic family.

98. On of the few insect studies on the origin of a trait (tolerance to salinity) combining both phylogenetic and experimental physiological data.

110. A review on the habitat stability hypothesis applied to differences in lotic-lentic habitats.

131. Up-to-date review of water beetle taxonomic diversity.

RELATED RESOURCES

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Figure legends

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. (85), with the exception that Adephaga is drawn as a polytomy between Geoadephaga, Grynidae, Haliplidae, and Dytiscoidea. Divergence time estimates of crown lineages (red circles) are based on Toussaint et al. (148) (but see e.g. 85 or 161 for an alternative dating), and the oldest known fossil taxa (black circles) are taken from Pomonorenko & Prokin (105). Primarily terrestrial lineages that contain some aquatic taxa are marked with an asterisk. See Supplementary File 1 for additional explanations.

Figure 2. Sexually selected characters in water beetles: (*a-c*) *Acilius sulcatus* (Dytiscidae) (*a*) male habitus – note expanded fore and mid tarsi; (*b*) ventral surface of male fore-tarsus – note plunger-like articulo-setae which function as attachment devices; (*c*) female habitus – note furrowed elytra and hairs on pronotum and elytra, resistance traits making male attachment more difficult during pairing. (*d-g*) *Limnebius* species (Hydraenidae) (*d*) *Limnebius truncatellus* male (above) and female (below) habitus – note strong sexual dimorphism in body size and leg modifications; (*e*) relatively complex male genitalia of *Limnebius truncatellus*; (*f*) *Limnebius evanescens* male (above) and female (below) habitus – note limited sexual dimorphism in body size; (*g*) relatively simple male genitalia of *Limnebius evanescens*. (*h-i*) sperm of *Hygrotus sayi* (Dytiscidae), epifluorescence microscopy with only DNA-stained heads visible (*h*) isolated, dimorphic sperm, some with broad heads and basal spurs, others with filamentous heads; (*i*) sperm conjugation –

sperm with broad heads stack (like traffic cones), forming a scaffold which sperm with filamentous heads attach to. Scale bars as follows: *a* & *c* = 5 mm, *b*, *d* & *f* = 1 mm, *e* & *g* = 500 µm, *h*-*l* = 20 µm.