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FRESHWATER ANIMAL DIVERSITY ASSESSMENT

Global diversity of water beetles (Coleoptera) in freshwater

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Abstract The global diversity of True Water Beetles, False Water Beetles and Phytophilous Water Beetles (sensu Jäch, 1998a. In Jäch & Ji (eds), Water Beetles of China, Vol. II. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien: 25–42.) is assessed. Facultative Water Beetles, Parasitic Water Beetles and Shore Beetles (sensu Jäch, 1998a. In Jäch & Ji (eds), Water Beetles of China, Vol. II. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien: 25–42.) are here classified as "paraquatic" and are thus not included in the assessment. It is estimated that about 18,000 species of aquatic Coleoptera are roaming the earth at present. About 12,600 (70%) of these are already described (deadline: October 2005). About 30 beetle families have aquatic representatives, and in 25 of these families at least 50% of the species are to be considered as aquatic. Six families are supposed to include 1,000 or more aquatic species: Dytiscidae (3,908 described species/5,000 estimated), Hydraenidae (1,380/2,500), Hydrophilidae (1,800/2,320), Elmidae (1,330/1,850), Scirtidae (900/1,700) and Gyrinidae (750/1,000). Scirtidae and Hydraenidae are regarded as the least explored families, the number of described species in each of these two families probably will be almost doubled in the future. The Palearctic (ca. 3,350 described species/ca. 3,900 estimated), the Neotropical (2,510/3,900) and the Afrotropical Region (2,700/3,750) harbour almost the same number of water beetle species, followed by the Oriental (2,200/3,580) and the Australian/Pacific Realm (1,340/2,100). The Nearctic (1,420/1,550) is by far the poorest region in terms of water beetle diversity.

Keywords Insecta · Coleoptera · Water beetles · Global diversity

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Freshwater Animal Diversity Assessment

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Introduction

Beetles are holometabolous insects, normally with adecticous, exarate pupae. Adults are characterized by a strongly sclerotized body with the forewings hardened into elytra, which serve to protect the more delicate hind wings, as well as the dorsal surface of the hind two thoracic segments (pterothorax) and abdomen. Other derived characteristics of adult beetles are: presence of a gula; antenna primarily with 11 articles; hind wings folded under elytra;

thorax broadly connected with abdomen, so that the primary functional units of body are head, prothorax, pterothorax-abdomen, rather than the more typical head, thorax, abdomen of many other insect orders; genitalia retracted into abdomen.

Beetles represent the world's most speciose animal order. Although about 400,000 species have been described until today, some biodiversity experts estimate that millions of species may actually roam the earth. Beetles occur on all continents[1] except on Antarctica itself, although many species live on the Subantarctic Islands (e.g., Kerguelen, Campbell).

Beetles represent one of the largest orders of "aquatic" animals. However, the majority of Coleoptera is terrestrial, only a minor percentage can be regarded as "aquatic" (definition given below). According to Crowson (1981: 429) water has been "invaded" at least 10 times independently during the evolution of Coleoptera, but this process in fact seems to have happened more than 20 times, and the water's edge has been "approached" even more often. Water beetles do therefore not represent a single monophyletic clade. Accordingly, their behavioural and morphological adaptations to the aquatic environment are exceptionally diverse. The smallest water beetles are less than 1 mm, the largest ones are about 5 cm long.

In the "great three" aquatic insect orders (Ephemeroptera, Plecoptera and Trichoptera) there is usually a fully submerged, long-lived larval stage and a shorter-lived, fully terrestrial adult stage. This type of life cycle is comparatively scarce in beetles (e.g., Scirtidae, Psephenidae). The life histories of water-associated beetles are in fact extremely manyfold, differing greatly between families. In contrast to most representatives of other higher taxa the ecology of many species of beetles cannot be simply defined as "aquatic" or "terrestrial". In Coleoptera aquatic and terrestrial behaviour very often grade almost imperceptibly into each other at the water's edge. The difficulties in the ecological classification are related mainly to the following factors: (1) amount of time spent in contact with water, (2) degree of submergence, (3) degree of water dependance, (4) motivation for getting into contact with water (food, refuge, etc.). These factors tend to be most variable and they are displayed in various combinations, differing greatly between, and often within beetle families. Even some of the most typical aquatic families have fully terrestrial representatives (e.g., three genera of Dytiscidae) and many of the typical terrestrial families (e.g., Lampyridae) have at least some representatives that spend much time under water. The habitat preference of a beetle may not only differ between the stages (larva, pupa, adult) but it may even be different from one larval instar to another, as in Hydraenidae (Jäch et al., 2005a) or Lampyridae (Ho et al., 1998; Jeng et al., 2003), where a gradual change from aquatic to riparian behaviour is not exceptional in the larval stage. In certain cases behaviour may even deviate between populations of the same species, depending on habitat availability; in *Ochthebius haberfelneri* Reitter (Hydraenidae), *Aphodius alternatus* Horn, *Dyscinetus morator* F. (Scarabaeidae) or *Dryops nitidulus* (Heer) (Dryopidae), aquatic and fully terrestrial populations/specimens have been recorded. Furthermore, many beetle species are very small (>2 mm), being therefore able to live more or less exactly at the land-water margin. It is often not possible to decide whether a certain species is to be regarded as "aquatic" or "terrestrial" unless the biology of adults, pupae and all larval instars has been studied very carefully, which is usually very difficult in most of the tiny representatives. First instars of some riparian beetles (e.g., Sphaeriusidae) are so small that even a very thin film of water is sufficient to keep them partly submerged. The larval instars of most species of tiny beetles are still undescribed today! Of the 1,420 species of Hydraenidae, larvae are known from only about a dozen species, which is about 1%!

In order to overcome these classificatory difficulties, Jäch (1998a) defined six ecological groups based on more than 40 families of beetles more or less strongly associated with aquatic habitats: (1) "True Water Beetles" (at least partly submerged for most of the time of their adult stage), (2) "False Water Beetles" (submerged for most of the time of their larval stage, adults always predominantly terrestrial), (3) "Phytophilous Water Beetles" (living and feeding on water plants (mono- or oligophagous), submerged for at least some time in any developmental stage), (4) "Parasitic Water Beetles" (like Phytophilous Water Beetles, but their hosts are aquatic mammals), (5) "Facultative Water Beetles" (actively submerged

[1] In this chapter "all continents" refers to North America, South America, Europe, Africa, Asia and Australia.

(occasionally or regularly) or actively dwelling on the water surface (occasionally or regularly) for a limited period of time, e.g., while hunting, feeding, seeking refuge, etc., during any of their developmental stages in at least one population) and (6) "Shore Beetles" (riparian, living close to the water's edge during all their developmental stages, not entering water voluntarily). With a few exceptions, the amount of time spent in contact with water is gradually decreasing from category 1–6.

True Water Beetles and False Water Beetles are generally regarded as "aquatic" because they are fully submerged at least in the larval stage. However, in Phytophilous Water Beetles, Parasitic Water Beetles and Facultative Water Beetles the amount of time spent in contact with water and the degree of submergence and/or water dependance are most variable. It is often impossible to decide whether a certain species is to be regarded as "aquatic" or "riparian/terrestrial" unless the biology of adults and all larval instars of all populations has been studied very carefully. The delimitation of Facultative Water Beetles from Shore Beetles and strictly terrestrial ones poses a major problem in connection with the global assessment of the number of freshwater species. River margins, stream banks and lake shores are home to thousands of beetle species. However, the life histories of Facultative Water Beetles, Shore Beetles and truly terrestrial beetles intergrade smoothly and so far no attempt has ever been made to provide exact definitions to distinguish between "aquatic", "paraquatic" (Facultative Water Beetles, Parasitic Water Beetles, Phytophilous Shore Beetles, Shore Beetles) and "purely terrestrial" species. No global assessment of Shore Beetles has ever been carried out. This is most regrettable from the conservation point of view, because river banks are greatly suffering from destruction world-wide. River margins are among the most vulnerable habitats in Europe. Their fauna is thus severely threatened (Jäch et al., 2005b). A global assessment of riparian arthropods (especially Araneae, Orthoptera, Blattodea, Dermaptera, Hemiptera, Hymenoptera, Coleoptera, Diptera) is dearly needed.

It should be noted here that there is no species of Coleoptera (except maybe some stygobiontic ones) that does not voluntarily leave water for at least some hours (e.g., for pupation and/or dispersal flight) during its life. No water beetle has so far been confirmed to be ecologically 100% "aquatic" as, for example, are whales or most fishes.

The terms "amphibious", "amphibiotic", "semi-aquatic" and "semi-terrestrial" were often used in connection with water beetles and other animals. However, it should be stressed that these terms have been variously defined. According to Schaefer & Tischler (1983) amphibious is the same as semi-terrestrial: "denoting an animal, which due to its organisation has to spend certain phases of its life under water and others on land, like dragonflies, mayflies, caddisflies or amphibia". According to Webster's Encyclopedic Unabridged Dictionary of the English Language there is a difference between amphibiotic: "living on land during the adult stage and in water during a larval stage", and amphibious: "living or able to live both on land and in water". Jäch et al. (2005a) defined amphibious as "being able to live below and above the water surface in the same developmental stage". The term semi-aquatic (not found in Schaefer & Tischler, 1983) is defined in Webster's as "partly aquatic; growing or living close to water and sometimes found in water". According to Torre Bueno (1989) semi-aquatic species are "living in wet places or partially in water (Borror et al.)"! It is recommended to avoid all these four special terms or to provide unambiguous definitions when using them.

Aquatic beetles are found to live in almost all kinds of aquatic habitats, such as rivers, springs, lakes, ditches, puddles, phytotelmata, seepages, ground water. They are known to survive trapped in ice. Salinity is also not a limiting factor for some species of water beetles—according to Gerdes et al. (1985) *Ochthebius corrugatus* Rosenhauer can cope with a salinity up to 250‰. However, beetles do not inhabit the oceans[2], although numerous species live at their shores, where they can be found in hypersaline rock pools of the supralittoral, i.e., the spray (or splash) zone slightly above the intertidal zone. In contrast to other insects, water beetles prefer small, richly vegetated ditches. In larger lakes, they prefer the swampy margins, as for instance the reed belt of the Central European Neusiedler See, where water beetle biomass is probably higher than anywhere on earth.

[2] The margins of the Baltic Sea, where some species of water beetles (e.g., *Macroplea mutica*) may regularly be encountered, are rather brackish than truly marine.

Most water beetles are benthic organisms, Gyrinidae adults (and some Staphylinidae) are neuston dwellers, which can glide on the water surface; other species (e.g., some Hydraenidae, Hydrophilidae and Lampyridae) can be found "walking" upside-down on the underside of the surface film, and some are living exclusively on water plants or on their mammal hosts. A considerable number of water beetles are able to swim and dive. Many species, especially those which live in well-oxygenated running waters (Elmidae, Hydraenidae adults) stay submerged for most of their life and breathe by means of a microplastron (a very thin layer of air, held by a dense coating of hydrofuge setae). Some Elmidae were encountered down to a depth of more than 10 m below the water surface.

Apart from typical aquatic biotopes containing water of atmospheric origin, beetles can also live in watery liquids of biogenic origin, e.g., in flowing tree sap (hygroarboreal habitat), which is the preferred choriotope of many Diptera, Nitidulidae (Tree Sap Beetles) and Nosodendridae (Wounded Tree Beetles), where they quite often can get totally submerged. Flowing tree sap and rain water may gather in a natural cavity to form a phytotelma, and accordingly, the habitat distinction between flowing tree sap and phytotelmata is gradual. Other liquid substances, like fresh cow dung, are generally not classified as aquatic habitats, although they are practically nothing else but a watery fluid of biogenic origin containing a high percentage of organic particles and it is therefore not surprising that hydrophilids are a major component of the cow dung fauna. However, coprophilous beetles shall not be included in this survey. Also not included are beetles living on snow (e.g., Cantharidae larvae). Especially in early spring, when the surface of the snow melts, nivicolous insects are indeed walking in a very thin layer of water. Finally, it should be mentioned that cave beetles often need 100% humidity and therefore also strongly depend on H_2O, at least in its gaseous phase.

Comprehensive up-to-date regional country-level information on water beetle species has for instance been published for the Netherlands (Drost et al., 1992), Scandinavia (Nilsson, 1996), China (Jäch & Ji, 1995, 1998, 2003), Malaysia (Balke et al., 2004a), Singapore (Hendrich et al., 2004), and South Carolina (Ciegler, 2003).

A key as well as colour illustrations for many families of water beetles was provided by Jäch & Balke (2003) and Balke et al. (2004a); detailed accounts on the morphology of most water beetle families can be found in the Handbook of Zoology (Beutel & Leschen, 2005a).

Species diversity

For practical reasons, the term "aquatic" is herein used strictly in connection with True Water Beetles, False Water Beetles and Phytophilous Water Beetles (sensu Jäch, 1998a), even if they spend much of their individual life on land.

Facultative Water Beetles, Parasitic Water Beetles and Shore Beetles (sensu Jäch, 1998a) are here considered as paraquatic. Their ecology is inseparably connected with aquatic biotopes although they spend most part of their life on the shores. Paraquatic beetles are just briefly treated herein; they are not included in the assessment. Also not included in this assessment are the few water beetles that occur in hypersaline marine rock pools (e.g., some specialized ochthebiine hydraenids) and Shore Beetles living at sea coasts.

Chelonariidae were repeatedly regarded as aquatic (e.g., Ciegler, 2003). However, numerous authors (e.g., Brown, 1972; Spangler, 1980a; Ivie, 2002; Beutel & Leschen, 2005b) have pointed out that this family is not associated with water.

The order Coleoptera is comprised of four suborders, three of which have aquatic representatives: Myxophaga (77 described species, ca. 90% aquatic), Adephaga (ca. 30,000 described species, ca. 18% aquatic), and Polyphaga (ca. 370,000 described species, ca. 1.25% aquatic). While truly terrestrial species are an exception in the Myxophaga, eight of the 11 extant families of Adephaga are regarded as predominantly aquatic (Gyrinidae, Haliplidae, Meruidae, Noteridae, Amphizoidae, Aspidytidae, Hygrobiidae, Dytiscidae), and only 13 of the ca. 150 recognized families of the large suborder Polyphaga are regarded as "predominantly aquatic" (Helophoridae, Epimetopidae, Hydrochidae, Spercheidae, Hydrophilidae, Hydraenidae, Scirtidae, Elmidae, Dryopidae, Lutrochidae, Psephenidae, Cneoglossidae, Eulichadidae). Larvae of the scirtoid family Decliniidae are still unknown and it cannot be excluded that they are aquatic like scirtid larvae.

In addition to these 25 typically aquatic families, another 12 families (1 adephagan and 11 polyphagan) have at least one representative living in (or in very close association with) a freshwater habitat, but the majority of their members is exclusively terrestrial: Carabidae (Adephaga), Leiodidae, Staphylinidae, Scarabaeidae, Ptilodactylidae, Lampyridae, Nitidulidae, Monotomidae, Chrysomelidae, Nanophyidae, Erirhinidae, Curculionidae (Polyphaga). Larvae of some species of Limnichidae are probably also aquatic (W. D. Shepard, pers. comm.) but detailed ecological studies are still lacking.

Nosodendridae, a small family known to occur in tree sap, are not included in this assessment. However, it should be kept in mind, that further research might reveal, that some nosodendrids are well able to live in phytotelmata like the nitidulid *Amphicrossus japonicus* Reitter (see below).

Typical Shore Beetles (sensu Jäch, 1998a) are found in numerous families, e.g., Carabidae (Adephaga), Lepiceridae (Myxophaga), Helophoridae, Hydrophilidae, Georissidae, Histeridae, Ptiliidae, Leiodidae (Cholevinae), Staphylinidae, Micropeplidae, Scarabaeidae, Elateridae, Limnichidae, Heteroceridae, Lampyridae, Latridiidae, etc. (Polyphaga).

Species described after 2005 are not included in this assessment.

Predominantly aquatic families

At least 50% of the species of each of the 25 families in this group are aquatic. All the typical water beetle families are included here. Ecologically, they are mostly True Water Beetles, like Predaceous Diving Beetles (Dytiscidae), Whirligig Beetles (Gyrinidae), Water Scavenger Beetles (Hydrophilidae) and Riffle Beetles (Elmidae), or, to a lesser percentage, False Water Beetles, e.g., Water Penny Beetles (Psephenidae).

Adephaga

1. Gyrinidae. About 750 described species in 13 genera. Gyrinids occur on all continents. Adults and larvae of all species are strictly aquatic. The majority of the species lives in running water. – Literature: Beutel & Roughley (2005), Mazzoldi (1995).

2. Haliplidae. About 200 described species in five genera are found on all continents, but they are more diverse in the northern temperate regions. Larvae and adults of all species are truly aquatic. They live mainly in stagnant water, some species prefer lotic habitats. This family is remarkably well explored; new discoveries are rather exceptional. – Literature: Vondel (2005).

3. Meruidae. Monogeneric family described from Venezuela in 2005. The single known species lives at the gravelly margins (interstitial) of mountain streams. – Literature: Beutel et al. (2006), Spangler & Steiner (2005).

4. Noteridae. About 250 species in three subfamilies and 14 genera have been described so far. The family occurs on all continents. Adults and larvae are aquatic; *Noterus* pupates under water in air-filled cocoons. Noteridae are commonly found in stagnant water between roots of water plants. The monogeneric Phreatodytinae (six species, all restricted to Japanese groundwater habitats) are considered as distinct family by certain authors. – Literature: Nilsson (2005a).

5. Amphizoidae. Monogeneric family with five described species, known only from North America and China. Larvae and adults of all species are aquatic living in rather fast flowing rivers. – Literature: Nilsson (2005b).

6. Aspidytidae. Monogeneric family with two species from South Africa and China. Larvae and adults live in seepages; pupae unknown. – Literature: Balke et al. (2003, 2005), Nilsson (2005c).

7. Hygrobiidae (Paelobiidae). Monogeneric family with six described species, occurring in Europe, China and Australia. Larvae and adults of all species are aquatic (stagnant water). The discovery of new species is not to be expected. – Literature: Nilsson (2005d).

8. Dytiscidae. With almost 4,000 described species in 175 genera, this is the most speciose water beetle family; it occurs on all continents. A total of 10 subfamilies (Agabinae: 388 spp., Colymbetinae: 130 spp., Copelatinae: 568 spp., Coptotominae: 5 spp., Dytiscinae: 377 spp., Hydrodytinae: 4 spp., Hydroporinae: 2,012 spp., Laccophilinae: 400 spp., Lancetinae: 8 spp., Matinae: 8 spp.) are presently recognized. Larvae and adults of almost all species are aquatic; they live in a wide variety of freshwater habitats: stagnant water, running water, groundwater (as deep as 30 m underground), seepages, phytotelmata; only five species are known to be fully

terrestrial (humicolous). – Literature: Larson et al. (2000), Nilsson (2001).

Myxophaga

1. Lepiceridae. Monogeneric family with two New World species. Adults of *Lepicerus inaequalis* are usually found on sand banks very close to streams. Adults have never been found in the water, but assuming that the still undescribed larvae live in sand well saturated with water (interstitial), they might get submerged regularly and should thus be able to breathe under water (Shepard, pers. comm.). The second species, *L. bufo*, is also found in sandy habitats along stream courses, but often well away from the water and is thus classified as paraquatic. Photographs of lepicerid habitats are found at http://www.amatl.net/lepi.html. – Literature: Arce-Pérez (1997), Reichardt (1976).

2. Torridincolidae. About 31 tiny species in seven genera occurring in South America (three genera), Africa (incl. Madagascar) (three genera) and Palearctic Asia (one genus). An undescribed species is known from the Philippines. The species are found in mountain streams; many of them have a preference for hygropetric habitats. So far known, all Torridincolidae are aquatic in all three developmental stages and thus they are the most strongly water-associated beetle family. Undescribed species are known from Paraguay, Venezuela, China and the Philippines. – Literature: Endrödy-Younga (1997a), Jäch (1998b), Spangler (1980b).

3. Hydroscaphidae. About 21 tiny species in three genera occurring on all continents except Australia. One species, *Hydroscapha natans*, is recorded from two biogeographical regions. Adults and larvae of all species are aquatic preferring seepages (hygropetric habitats), hot springs, or the interstitial of gravel banks of streams and rivers. – Literature: Jäch (1995a), Löbl (1994, 2003a).

4. Sphaeriusidae. Monogeneric family with 23 tiny species occurring on all continents. Several species are reportedly terrestrial (humicolous); other species (e.g., the type species *Sphaerius acaroides* Waltl) occur at the margins of running and/or stagnant water, often in wet sand very close to the water surface. As it can be assumed that they get submerged regularly, they are here classified as True Water Beetles. Numerous undescribed species are deposited in various museums. A precise evaluation of the percentage of aquatic, riparian and fully terrestrial species is currently not possible, because the ecology of most species is still unknown. However, it is assumed that the majority of the species is aquatic. – Literature: Arce-Pérez (1997), Beutel & Raffaini (2003), Endrödy-Younga (1997b), Hall (2003), Löbl (1995, 2003b).

Polyphaga

1. Helophoridae[3]. Monogeneric family with about 185 species, more or less confined to the Holarctic Realm. Adults of most species are considered truly aquatic (about 75% living in stagnant water, R. Angus, pers. comm.); several species are usually encountered slightly above the water line and therefore seem to be facultatively aquatic or riparian; only few species are strictly terrestrial. Larvae of *Helophorus* are riparian or strictly terrestrial (humicolous). This family is remarkably well explored; new discoveries are not common, but molecular studies might yield new siblings. – Literature: Angus (1992), Hansen (1999).

2. Epimetopidae[3]. About 29 species in three genera occurring in the New World (*Epimetopus*), Africa (*Eupotemus*) and Asia (*Eumetopus*). Adults of all species are probably aquatic (sandy margins of lentic habitats), ecology of larvae unknown. – Literature: Hansen (1999), Jäch (2002), Ji & Jäch (1998), Skale & Jäch (2003).

3. Hydrochidae[3]. Monogeneric family with about 180 species; hydrochids occur on all continents. All species are truly aquatic, living in well-vegetated stagnant water and/or at the edges of very slowly flowing water. Unfortunately, taxonomic research in this family has been badly corrupted by a single unqualified author, and it is therefore most difficult to keep track with the number of ill-defined new taxa and resulting synonymies being published each year, a thorough revision is dearly needed. – Literature: Hansen (1999), Short & Hebauer (2005).

4. Spercheidae[3]. Monogeneric family with 18 species. The genus occurs on all continents. Larvae

[3] Helophoridae, Epimetopidae, Hydrochidae and Spercheidae are treated as subfamilies of Hydrophilidae in Lawrence & Newton (1995), but they are generally accepted as valid families by most water beetle specialists (see Hansen, 1999).

and adults generally live in stagnant water. – Literature: Hansen (1999), Short & Hebauer (2005).

5. Hydrophilidae. About 2,652 species in 174 genera. Hydrophilids occur on all continents. They comprise four subfamilies: (1) Horelophinae: monotypical, New Zealand, adults obviously riparian or hygropetric; (2) Horelophopsinae: monogeneric, two species, New Guinea (Yapen Island) and Japan (Ryukyu Archipelago), the Japanese species is obviously aquatic, the ecology of the Yapen species is not exactly known; (3) Hydrophilinae: 1,740 species in 66 genera, on all continents, adults and larvae of most species are living in stagnant water, running water, in phytotelmata or seepages, numerous species are reportedly riparian or terrestrial (humicolous); (4) Sphaeridiinae: 909 species in 106 genera, most of which are terrestrial; only seven genera include aquatic representatives. In total, about 70% of Hydrophilidae are aquatic. – Literature: Hansen (1991, 1997, 1999), Short & Hebauer (2005).

6. Hydraenidae. About 1,420 species in about 40 genera. Hydraenids are encountered on all continents and inhabit even some Subantarctic Islands, where only few insects are able to cope with the hostile climatic conditions. While adults of most species are aquatic (stagnant water, running water, seepages), many are riparian or strictly terrestrial and a few species are known to live exclusively in hypersaline marine rock pools. Hydraenid larvae are usually riparian or terrestrial, only the first instar of some species is aquatic. The Subantarctic species are poorly studied. They are, however, not associated with freshwater. This family probably contains the largest number of undescribed species, and it is the only family in which more than 1,000 species are expected to be still undescribed. Two new genera and 95 new species of Hydraenidae have been described between January 2004 and September 2005. Even in the comparatively well explored Europe, about 40 (!) new species of Hydraenidae were described in the last 10 years (1995–2005). Several hundred new species are housed in the collection of the Vienna Natural History Museum. – Literature: Hansen (1998), Jäch et al. (2000).

7. Scirtidae. About 900 species in 30 genera. Scirtids occur on all continents. Larvae are usually aquatic, although there are reports about scirtid larvae found in wet soil and on rotten logs. Imagos are generally terrestrial, but adults of *Hydrocyphon* are occasionally collected under water; pupae of *Hydrocyphon* are also reported to be aquatic. Scirtid larvae are found in running water (about 20%), in stagnant water, phytotelmata, and in groundwater. The ecology of scirtids is most poorly studied. Since there is no detailed information on the presumably terrestrial species, all Scirtidae are here provisionally classified as aquatic (False Water Beetles). – Literature: Klausnitzer (2004), Lawrence (2005), Yoshitomi & Satô (2005).

8. Elmidae. About 1,330 species in 146 genera. Elmids occur on all continents. Two subfamilies are presently recognized: Larainae (26 genera, 130 species), and Elminae (120 genera, 1,200 species). However, the phylogeny of elmids has never been carefully studied, therefore major changes concerning the generic and tribal concept are to be expected. At present, there is a proportionally high amount of genera (seven times as many as in Hydraenidae, a family with a comparable number of described species). Adults and larvae of all species are considered to be aquatic, however, adults of many Larainae species often can be encountered below or a little above the water line or in spray zones of water falls and cascades. Members of this family are generally living in lotic habitats, very few species are encountered at lake shores or in ponds. Dozens of undescribed species are deposited in various museum collections. – Literature: Brown (1981a, 1981b), Kodada & Jäch (2005a).

9. Dryopidae. About 300 species in 33 genera. Dryopids occur in all biogeographical regions, but they are absent from the Australian continent. Larvae are generally riparian or terrestrial; adults of about 75% of the species are regarded as aquatic (lotic and lentic habitats), the remaining ones are riparian or terrestrial (humicolous, arboricolous). The ecology of numerous species living close to the water margins has never been studied thoroughly, and some species of the genus *Dryops* classified here as aquatic may in fact turn out to be riparian. Dozens of undescribed species are deposited in the Vienna Natural History Museum. – Literature: Brown (1981a), Kodada & Jäch (2005b).

10. Lutrochidae. About 15 species, all confined to the New World. Larvae and adults are reported to be aquatic in lotic habitats (riparian gravel, emergent rocks or submerged wood). Lutrochidae are generally

regarded as True Water Beetles; however, like in dryopids, thorough ecological studies are still wanting and it cannot be excluded that some species are in fact facultatively aquatic or riparian. Adults occasionally leave the water. So far only one genus is recognized; several undescribed species and at least one new genus are deposited in various museum collections. The family is in need of a taxonomic revision. – Literature: Brown & Murvosh (1970), Ide et al. (2005).

11. Psephenidae. About 272 species in 35 genera. Psephenids occur on all continents. They are comprised of four subfamilies: Eubrianacinae, Eubriinae, Psepheninae, Psephenoidinae. Larvae are always aquatic, almost exclusively occurring in running water; with few exceptions, adults and pupae are strictly terrestrial. – Literature: Arce-Pérez & Shepard (2001), Brown (1981a), Lee et al. (2005).

12. Cneoglossidae. Monogeneric family with eight Neotropical species. Adults are terrestrial. The larva of *Cneoglossa edsoni* was found "inside submerged rotting brushwood, in small shallow streams with moderate to fast running water". Nothing is known about the larval behaviour of the remaining species, which are herein tentatively classified as aquatic. – Literature: Costa et al. (2005).

13. Eulichadidae. About 21 species in two genera occurring in North America and Asia. Larvae live in streams, but adults are strictly terrestrial. A revision of the genus *Eulichas* with description of several new species is in preparation (J. Hájek, pers. comm.). – Literature: Ivie (2005), Jäch (1995b).

Not predominantly aquatic families

The 12 families listed in this group are primarily terrestrial. Most of these families are very well-known and speciose (e.g., Ground Beetles (Carabidae), Rove Beetles (Staphylinidae), Leaf Beetles (Chrysomelidae), Snout Beetles (Curculionidae)). However, they contain a small percentage of aquatic members. The aquatic representatives of these families probably do not include True Water Beetles, only few can be regarded as False Water Beetles (e.g., some Lampyridae and some Ptilodactylidae) and Parasitic Water Beetles. Most species are to be classified as Phytophilous Water Beetles or Facultative Water Beetles; some Phytophilous Water Beetles can dive very well and may spend most of their life under water. However, the degree of submergence and/or water dependance is extremely variable in Phytophilous Beetles.

Adephaga

1. Carabidae. More than 20,000 species. A few of the many riparian members in this family can be classified as Facultative Water Beetles: Adults and larvae of *Carabus clathratus* L., *C. variolosus* F., *C. menetriesi* Hummel (Carabinae) are reported to hunt for snails, crustaceans, insect larvae, tadpoles and small fish under water, thus getting fully submerged; other species, e.g., *Oodes helopioides* (F.) (Oodinae) and *Chlaenius* spp. (Chlaeniinae) are reported to stay under water for some time to seek refuge; specimens of *Brachygnathus* sp. (Panagaeinae[4]) from Paraguay were collected between submerged roots, ca. 15 cm below the water surface; some riparian species of Cicindelinae are known to snatch tadpoles from the shallow water, but they do not get fully submerged. *Hydrotrechus cantabricus* Carabajal et al., a subterranean Trechinae from Spain, is described as being permanently in contact with a layer of water and it may therefore represent a True Water Beetle, however, more ecological research is necessary to confirm this assumption. – Literature: Carabajal et al. (2000), Jäch (1998a), Klausnitzer (1996), Wachmann et al. (1995).

Polyphaga

1. Leiodidae. About 3,000 species and about 250 genera in six subfamilies: Camiarinae, Catopocerinae, Leiodinae, Coloninae, Cholevinae (=Catopinae, incl. Bathysciinae), Platypsyllinae (=Leptininae) (classification acc. to Lawrence & Newton, 1995); at least two of these subfamilies have paraquatic representatives. The platypsylline *Platypsyllus castoris* Ritsema is regarded as a Parasitic Water Beetle. It lives in the fur of beavers (*Castor fiber* L.) and thus gets submerged frequently. A similar ecology is recorded from *Silphopsyllus desmanae* Olsufiew which is known to live on the water mole (*Desmana moschata* L.). The Bosnian cave beetle *Hadesia*

[4] Panagaeinae are included in Harpalinae in Lawrence & Newton (1995).

vaseceki (Cholevinae) was regarded as strictly aquatic by early authors. However, Remy (1940) pointed out that *Hadesia* never gets submerged voluntarily, although it is "extremely hygrophilous", which was confirmed by M.E. Schmid (pers. comm.), who observed several specimens in their natural environment. However, *Hadesia vaseceki* is evidently brushing subterranean seepages for food and therefore it can be classified at least as facultatively aquatic. Another closely related European cave beetle genus, *Antroherpon* Reitter, was reported to live close to subterranean streams. – Literature: Absolon (1915), Chappuis (1927), Jäch (1998a).

2. Staphylinidae. More than 30,000 species in ca. 30 subfamilies (classification acc. to Lawrence & Newton, 1995). Although this family contains hundreds of riparian and intertidal species, hardly any of these can be classified as aquatic in the strict sense, although members of the subfamily Steninae can glide ("skim") over the water surface at an enormous speed and are therefore probably the fastest "swimming" beetles!

Lesteva spp. (Omaliinae) are often found on the underside of stones in streams, being thus fully submerged. It is not known for how long they enter the water and whether they do it to search for food or to take refuge. About 100 species have been described in this genus. The subfamily Steninae includes two genera: *Stenus* (ca. 2,100 species), and *Dianous* (ca. 200 species). All species of *Dianous* and hundreds of species of *Stenus* live very close to the edges of freshwater habitats (lentic and lotic). At least one species, *Stenus fornicatus* Stephens, was reported to stay submerged voluntarily. Many *Dianous* and *Stenus* have especially water repellent tarsal ventral surfaces and are able to move very skillfully on the surface film of the water, for which they can use three different modes of locomotion, of which "expansion skating" (releasing an abdominal secretion) is by far the most effective one. No comprehensive field research on the behaviour of Steninae has been carried out and we know very little about the amount of time spent on the water and the motivation to do so (refuge, hunting). Therefore at present it cannot be determined how many of the stenines can be classified as "aquatic" (True Water Beetles) or as "paraquatic" (Facultative Water Beetles, Shore Beetles). Without doubt, there are several hundreds of paraquatic species in this subfamily. A few species of Staphylininae (*Hesperus kovaci* Schillhammer, *Odontolinus* sp.) feed on aquatic dipterous larvae in phytotelmata. Specimens of *Trichocosmetes norae* Schillhammer reportedly sit on leaves above the water surface, and then drop onto the water surface in order to escape enemies. – Literature: Betz (2002), Schillhammer (2002).

3. Scarabaeidae. About 28,000 species in 13 subfamilies (classification acc. to Lawrence & Newton, 1995). The facultatively aquatic Rice Beetle, *Dyscinetus morator* (Dynastinae), can spend several hours under water while escaping disturbances or while feeding on water plants (e.g., *Eichhornia crassipes*). The Rice Beetle obviously is not monophagous, it also feeds on terrestrial plants, such as carrots and radishes. Therefore it cannot be classified as Phytophilous Water Beetle. *Aphodius alternatus* (Aphodiinae) usually lives in moist habitats along freshwater margins in North America; however, several populations evidently have adopted truly aquatic habits in grassland vernal pools; hence, this species has to classified as facultatively aquatic. – Literature: Buckingham & Bennet (1989), Rogers (1997).

4. Ptilodactylidae. About 500 species in more than 30 genera and five subfamilies (acc. to Lawrence & Newton, 1995). Ptilodactylids occur on all continents, but only introduced synanthropic terrestrial species have been reported from Europe. Larvae of the subfamily Anchytarsinae (on all continents), Areopidinae (one species from North America) and some Cladotominae (e.g., *Drupeus hygropetricus* Lee et al.) are known to be aquatic (or at least facultatively aquatic). They are found between gravel or on submerged wood in lotic habitats or in seepages. Adults are strictly terrestrial. Since the aquatic behaviour has not been confirmed for all species of Anchytarsinae and comprehensive taxonomic revisions have not been carried out, the numbers given in the assessment are rather arbitrary. – Literature: Aberlenc & Allemand (1997), Lawrence & Stribling (1992), Lucht (1998), Stribling (1986).

5. Lampyridae. Almost 2,000 species in over 90 genera and eight subfamilies. Larvae of comparatively few species are truly aquatic or facultatively aquatic, living in running or stagnant water. Adults are generally terrestrial. Truly aquatic larval stages were confirmed for six species of the genus *Luciola*. Facultatively aquatic species (e.g., *Pyractomena*

lucifera Melsheimer, *Pristolycus kanoi* Nakane) are found near seepages, creeks, swamps, marine rock pools, etc. – Literature: Buschman (1984), Downie & Arnett (1996), Jeng et al. (2003).

6. Nitidulidae. About 3,000 species in seven subfamilies (classification acc. to Lawrence & Newton, 1995). Nitidulids occur on all continents. Numerous species live in tree sap. Adults of one species, *Amphicrossus japonicus*, are here classified as facultatively aquatic. They are found in "bamboo sap" in Malaysian rainforests and also in phytotelmata, where they can stay submerged for a long time (D. Kovac, pers. comm.).

7. Monotomidae. More than 200 species in two subfamilies, occurring on all continents. Monotomids usually live under bark. *Cyanostolus aeneus* (Richter) was reported to be aquatic, living on submerged wood in streams and rivers. However, no detailed studies have been carried out to determine the amount of time spent in contact with water and the degree of submergence and/or water dependance. Specimens collected recently in Austria were found under the bark of a submerged piece of wood, about 10 cm above the water line (R. Schuh, pers. comm.). *Cyanostolus aeneus* is hence classified as facultatively aquatic (paraquatic). – Literature: Peacock (1978).

8. Chrysomelidae. About 46,000 species in 20 subfamilies (classification acc. to Jolivet & Verma, 2002). Numerous species are regarded as Phytophilous Water Beetles. At least one subfamily, Donaciinae, is obligatorily associated with aquatic plants, with larvae and pupae generally submerged; adults of two genera, *Macroplea* and *Neohaemonia*, are often found under water. Several members of Alticinae[5], Chrysomelinae, Galerucinae and Hispinae live on emergent aquatic plants, usually above the water surface; many of them are capable of walking on the water surface and may survive under water for a long time. Several Central American hispines are found in phytotelmata (water-filled floral bracts). – Literature: Konstantinov (2003), Mohr (1960), Seifert (1982).

9. Nanophyidae[6]. About 300 species in 29 genera (classification acc. to Alonso-Zarazaga & Lyal, 1999). Several species of the genus *Nanophyes* Schönherr are regarded as Phytophilous Water Beetles; they are feeding in the stems of aquatic plants (*Alternanthera*, *Ludwigia*). – Literature: Lawrence & Britton (1994), Sankaran (1972).

10. Erirhinidae[7]. About 300 species in numerous genera and two subfamilies (classification acc. to Alonso-Zarazaga & Lyal, 1999). About 10 genera are known to include Phytophilous Water Beetles. – Literature: Anderson (2002).

11. Curculionidae. The world's most speciose animal family with probably more than 60,000 described species in 16 subfamilies (classification acc. to Alonso-Zarazaga & Lyal, 1999). About seven genera in two subfamilies (Bagoinae, Ceutorhynchinae) are known to include Phytophilous Water Beetles. Most species of Bagoinae are exclusively aquatic, but some were captured on land (M. Alonso-Zarazaga, pers. comm.). Many aquatic weevils can dive very well and spend most of their live under water. – Literature: Angus (1966), Caldara & O'Brien (1998), Colonnelli (2004), Klausnitzer (1996).

Shore beetles/phytophilous shore beetles

When talking about freshwater beetles one must not ignore all those many species that live at the margins of aquatic habitats. They are strongly depending on the microclimate, substrate and the food web of their aquatic environment. Any environmental influence (e.g., water pollution, power plants, drought) effecting the truly aquatic species will have more or less the same effect on the Shore Beetles, although they hardly get into contact with water actively! Their ecology is inseparably connected with the aquatic biotope although they are not part of it physically. In contrast to Facultative Water Beetles they do not enter water voluntarily.

Shore Beetles are often difficult to distinguish from truly terrestrial beetles (especially humicolous ones—living in damp places).

About 22 families containing Shore Beetles (from freshwater shores and sea shores) were listed by Jäch (1998a): Sphaeriusidae, Carabidae, Helophoridae,

[5] Alticinae are included in Galerucinae in Lawrence & Newton (1995).

[6] Nanophyidae are regarded as a subfamily of Brentidae in Lawrence & Newton (1995).

[7] Erirhinidae are regarded as a subfamily of Curculioninae in Lawrence & Newton (1995).

Georissidae, Hydrophilidae, Histeridae, Hydraenidae, Ptiliidae, Leiodidae (Cholevinae), Staphylinidae, Scarabaeidae, Dryopidae, Limnichidae, Heteroceridae, Elateridae, Lampyridae, Phycosecidae, Melyridae, Monotomidae, Tenebrionidae, Salpingidae, Anthicidae. Several additional families, e.g., Lepiceridae, Agyrtidae, Micropeplidae, Ptilodactylidae, Byrrhidae, Lampyridae and Latridiidae must be added to that list.

Altogether, there are certainly several thousand species of Shore Beetles world-wide. For reasons explained above (see Introduction), exact numbers cannot be provided at this point. In Carabidae and Staphylinidae there is a rather high number of riparian representatives, but no detailed assessments were carried out in these two families so far. Georissidae (monogeneric, about 70 species) are generally humicolous (wet sand banks, wet meadows). Heteroceridae (five genera, more than 200 species) are noteworthy because they are exclusively riparian living at muddy margins of running as well as stagnant waters.

Limnichidae (about 40 genera and almost 400 species) are here tentatively listed as a Shore Beetle family. All species are living at wet places. Most representatives are found at the shores of freshwater habitats, often very close to the water's edge and it seems that quite a number of species of Limnichidae (e.g., *Caccothryptus*, *Pseudeucinetus*) might in fact be at least facultatively aquatic. Almost nothing is known about larval behaviour.

Numerous Phytophilous Beetles (numerous Chrysomelidae; numerous Curculinoidea; *Telmatophilus* spp. (Cryptophagidae); *Phalacrus caricis* (Phalacridae)) live on aquatic or riparian plants (e.g., *Carex*, *Typha*, *Phragmites*) but hardly ever get in contact with water. They are therefore classified as paraquatic (Phytophilous Shore Beetles).

Conclusions

Only six of the "aquatic" families treated herein are supposed to include at least 1,000 species of water beetles: Dytiscidae, Hydraenidae, Hydrophilidae, Elmidae, Scirtidae and Gyrinidae (Table 1, Fig. 4).

Without any doubt the Predacious Diving Beetles or Dytiscidae are the world's most speciose water beetle family. With an estimated total of 4,800 species, there are about as many dytiscids as in the next two families (Hydraenidae and Hydrophilidae) taken together. Hydrophilidae are presently regarded as the second most speciose family. However, with the inclusion of the estimated undescribed species, hydraenids will soon overtake hydrophilids in the diversity ranking (Fig. 4). Each of these two families probably comprises distinctly more than 2,000 species. Elmidae and Scirtidae follow next with somewhat less than 2,000 species. Gyrinidae represent a family of medium diversity, with an estimated 1,000 species. All the following families have less than 1,000 aquatic representatives.

With an estimated 1,120 undescribed species (45% of the total number of species estimated), Hydraenidae are definitely one of the least explored families. This is mainly due to their small size (the largest species is only 3.3 mm long), their cryptic habits (many species live in tiny rain forest puddles, where they are difficult to detect) and the enormous degree of local endemism (see below). With an estimate of 800 undescribed species scirtids represent even a higher percentage of undiscovered species: ca. 47%. This can be credited to the lack of specialists (at present there are not more than three scientists contributing to scirtid taxonomy regularly), and to the fact, that the short-lived adults of this family are rarely collected. With about 18% undescribed species, Dytiscidae are comparatively well studied. With approximately 520 undescribed species, elmids (28% undescribed) and hydrophilids (22% undescribed) will also contribute considerably to the increase of the global water beetle fauna. Among the less speciose water beetle families, Dryopidae, with an estimated 43% undescribed species, are noteworthy.

About 12,600 (ca. 3%) of the known species of Coleoptera are regarded as "aquatic". Adding estimations of undescribed aquatic species it can be assumed, that actually about 18,000 water beetle species roam the earth.

Phylogeny and historical process

Coleoptera first occur in fossil records of the Lower Permian of Moravia and the Ural. These beetle ancestors were certainly terrestrial.

Water beetles do not form a monophyletic group but rather occur in three of the four different suborders of the Coleoptera where they have adopted aquatic

lifestyles independently. A comprehensive account of the general biology and evolutionary trends of water beetles was published by Crowson (1981: Chap. 13). The sturdy exoskeleton of adults, in connection with a rather well sealed subelytral space that may contain an air reservoir, was most likely functioning as major preadaptation of Coleoptera for the invasion of water. It is obviously this subelytral space that allows even many terrestrial beetles to survive under water for some time. Several aquatic lineages gave rise to secondarily terrestrial forms, such as the hydraenid *Edaphobates puetzi* Jäch & Díaz living in Chinese *Rhododendron*-forests or the blind and wingless dytiscid *Typhlodessus monteithi* Brancucci, which was collected from leaf litter on a New Caledonian mountain top.

Based on morphological analyses and according to recent DNA sequence data (Hughes et al., 2006) Myxophaga are the sister group of Polyphaga. Their age could be mid Triassic.

Molecular data suggest that the typically aquatic adephagan beetle families have entered the aquatic environment only once (e.g., Shull et al., 2001), while morphological data rather suggest two or three independent invasions (Beutel et al., 2006). In any case, Gyrinidae (known from Lower Permian deposits) take a basal position within Hydradephaga. Beutel (1997) suggested that the Adephagan ancestor was carnivorous as both adult and larva, and the aquatic medium was invaded by terrestrial species dwelling at river and/or pond margins. Dated molecular phylogenies remain to be presented, but the wider distribution of several genera and multiple subfamilies in different families suggest that diversification cannot be pinned down to only one tectonic event such as the breakup of Gondwana. Major driving forces in the diversification of the larger families include the adaptation to adult surface dwelling, which led to a speciose group (Gyrinidae) after a new habitat has been conquered, as well as evolution of the simultaneous stroke of adult middle and hind legs in Noteridae and Dytiscidae for advanced swimming behaviour (Ribera et al., 2002; Balke et al., 2005).

The major aquatic groups in the large suborder Polyphaga belong to the Staphyliniformia/Scarabaeiformia (e.g., Hydraenidae, Hydrophilidae) and the Elateriformia (e.g., Elmidae, Psephenidae). Hydraenidae are the sister of the terrestrial Ptiliidae, as proven by morphological and molecular data (Beutel & Leschen, 2005c; Caterino et al., 2005). Hydrophiloidea are very probably the sister of a terrestrial clade as well, probably Histeroidea or Scarabaeidae (Beutel & Leschen, 2005c; Vogler, 2005). The enormous diversity of hydraenids (probably the second largest water beetle family on earth) can obviously be explained by their minute body size enabling them to inhabit even very small aquatic biotopes (e.g., tiny puddles, interstitial of gravel banks), and by the development of an antimicrobial "exocrine secretion delivery system" (ESDS), being composed of exocrine glands interacting with various cuticular structures (especially on underside of head and prothorax). Polyphaga probably have originated in the mid Triassic. Considering the high number of families with single aquatic representatives in different genera (see above under "Not predominantly aquatic families") we can assume that the invasion of the aquatic medium has occurred about 20 times in Polyphaga. Curculionoidea, for instance, must have invaded water independantly at least four times, and in Lampyridae aquatic (or paraquatic) behaviour might be a separate evolutionary process in almost every second of the aquatic species.

The biogeographic history of the different groups largely remains to be investigated. However, it more and more emerges that dispersal must have played an important role in the evolution of dytiscid diversity. For example, many Australian and Pacific species, even morphologically highly modified ones, appear to be of comparably recent origin as inferred from DNA sequence divergences (Balke et al., in prep.). As another example, the diving beetle subfamily Copelatinae, with 568 known species, has a pantropical core range, which might have been formed by dispersal rather than ancient plate tectonic events (Balke et al., 2004b).

Distributions, main areas of endemism

The delimitations of the biogeographic regions in this chapter mainly follow the World Catalogue of Insects, Vols. 1–3, 7 (Adephaga, Hydrophiloidea, Hydraenidae) and the Catalogue of Palaearctic Coleoptera, Vol. 3 (Dryopoidea). However, it should be noted, that the biogeographical limits in the World Catalogue of Insects, Vols. 1–2 (Hydraenidae, Hydrophilidae) differ from Vols. 3, 7 (Adephaga). Weber's Line is here chosen as border between the Oriental and the Australian/Pacific Region. At least

for the predominantly aquatic families, Mexico is here entirely regarded as Neotropical.

Subantarctic species are included in the geographically closest realm in this assessment (species from South Georgia have for instance been included in the Neotropical Region).

Water beetles are found in all biogeographic regions, from Ellesmere Island in the north to Tierra del Fuego in the south, and they are encountered even on many of the remotest Pacific Islands. And although, on average, diversity is greater in humid climates, some of the desert regions are quite rich in water beetles (see below).

Water beetles display their greatest diversity in the tropics. Haliplidae, Amphizoidae and Helophoridae are the only exception to this rule. Haliplidae are distinctly more diverse in the Holarctic Realm than in any of the tropical regions, and although most tropical countries are still rather poorly examined we do not expect a significant increase of species in this family. Helophoridae are even more strongly confined to the northern temperate regions; a mere 0.7% of the species are found outside the Holarctic Region! All five known species of Amphizoidae are Holarctic.

In contrast to the statement by Lévêque et al. (2005), most aquatic beetles are not "cosmopolitan, or widespread". Although there is quite a number of wide-spread Holarctic species, only very few species are distributed in more than two realms, e.g., *Rhantus suturalis*. In fact, the diversity and the degree of local endemism is extremely high in almost all water beetle families, especially among those living in running waters in warmer climates.

Dytiscidae. In Europe, the Iberian Peninsula must be regarded as a hot spot of endemism, with 34 out of about 164 Iberian species (ca. 20%) only occurring in Spain and Portugal (Ribera, 2000), but levels of endemism are even higher on the Macaronesian Islands, Madeira (50%) and the Canary Islands (30–40%, depending on taxonomy) (Balke & Hendrich, 1989; Balke et al., 2002). The larger tropical Islands such as Borneo (endemism: 63%) and especially New Guinea (>70%) feature most remarkable diving beetle radiations with very high levels of regional endemism (Balke et al., 2002) where, as far as currently known, species turnover might be high even between neighbouring valleys. In that respect, New Guinea might prove one of the most important global water beetle hot spots where total species numbers remain hard to estimate even at the beginning of the 21st century. Australia, with ca. 90% endemic species, is home to the world's largest assemblage of groundwater beetles, with most of the more than 50 known groundwater dytiscid species occurring in calcrete aquifers in the desert (Leys et al., 2003; Pain, 2005). New Caledonia and Fiji were recently screened for diving beetles, and both islands revealed an unexpectedly diverse fauna, with levels of endemism around 90%.

Hydraenidae (Fig. 1). The presumably second largest water beetle family is unchallenged with regard to endemism. Most of the hydraenid species from warmer climates (arid or tropical) are to be regarded as SORD (species of restricted distribution). The highest species diversities are probably found in tropical/subtropical montane forests. The Hydraenidae of some presumptive biodiversity hot spots, such as Borneo and New Guinea, are still very poorly studied. Only two species of *Hydraena* have been described so far from New Guinea and none from Borneo, although at least 100 undescribed species collected in these two islands during a few water beetle expeditions are deposited in the Vienna Natural History Museum. More than 100 species of *Hydraena* have been described from Turkey and about 60 species from Greece, many of them restricted to a single island, a single mountain range or even to a single streamlet (e.g., *Hydraena pangaei*, *H. gynaephila*). The exceptional diversity of hydraenids can very probably be credited to their small size and their limited dispersal abilities. Paradoxically, even larger rivers have been confirmed as potent dispersal barriers for hydraenids: *Hydraena alpicola* and *H. saga*, two very closely related mountain stream dwelling species, are for instance effectively separated from each other by the Danube River in Lower Austria. Very little is known about the species diversity of hydraenids in montane areas of tropical Africa and tropical South America.

Hydrophilidae. The main areas of endemism are obviously in the tropics but accurate data are still lacking. As in dytiscids and hydraenids, hydrophilids from tropical Africa and tropical South America are very poorly known.

Elmidae. Among the larger water beetle families, only elmids are more or less exclusively confined to running water. Due to their flight abilities, they are less diverse than Hydraenidae, especially in arid

Fig. 1 Habitus of *Hydraena* s.str. (Hydraenidae), undescribed species from China. With a total of about 570 described species *Hydraena* represents the most speciose water beetle genus of the world. With more than a thousand species still awaiting description it may well be the most successful aquatic genus on earth. The antimicrobial "exocrine secretion delivery system" (ESDS), being composed of exocrine glands interacting with various cuticular structures (especially on underside of head and prothorax) is nowhere as specialized as in this genus, which is obviously the key to its "success"

climates. Their greatest diversity is found in montane areas of tropical and subtropical rainforests. In Southeast Asia, Borneo seems to be a biodiversity hot spot. Tropical Africa and tropical South America are still very inadequately explored. Even North America, which has been quite thoroughly studied with regard to most water beetles, is in need of a modern elmid revision. Some of the wide-spread West-Palearctic elmids might in fact represent complexes of closely related species, which should be tested by molecular analyses.

Scirtidae. Very little can at present be said about the main areas of endemism of this very poorly studied family. Without doubt, they are most diverse in tropical countries (lowland as well as montane areas).

Gyrinidae. In the Oriental Realm, Borneo obviously must be regarded as a biodiversity hot spot for this typically tropical family. Africa is comparatively well explored, but tropical South America and New Guinea may still harbour notable numbers of undescribed species.

Counting the presently described species, the Palearctic Region houses the highest number of water beetles species (Table 2, Fig. 2). Although comprehensive water beetle surveys are still lacking for large parts of the Neotropical and Afrotropical Realms, it is estimated (after including the undescribed species) that the Palearctic (ca. 3,350 described species/ca. 3,900 estimated total), the Neotropical (2,510/3,900), and the Afrotropical Region (2,700/3,750) harbour more or less the same number of water beetle species, followed by the Oriental (2,200/3,580) and the Australian/Pacific Realm (1,340/2,100). Undoubtedly, the Nearctic (1,420/1,550) is by far the poorest region in terms of water beetle diversity (Fig. 3).

Within the Palearctic Region, the Mediterranean countries and Anatolia are to be regarded as biodiversity hot spots, at least for certain families. In the comparatively well-explored Oriental Region, Borneo was found to be a hot spot of paramount significance for many water beetle families.

One of the world's most comprehensive biodiversity projects was aimed at the exploration of the water beetle fauna of China, which was virtually unknown before this survey (CWBS)[8] got started in 1993. More than 500 sampling stations have been investigated since then and several hundred new species have been detected, many of which were described in a comprehensive three-volume monograph (Jäch & Ji, 1995, 1998, 2003), compiled by 50 authors from 18 countries. The southeastern parts of China (attributed to the Oriental Region or to the Palearctic Region acc. to different specialists) were found to be extremely diverse with a very high degree of local endemism. Even in the Special Adminstrative Region of Hongkong, where stagnant water habitats have been drained (growing rice is not allowed) and where numerous streams are frequently sprayed to kill mosquitos, about 70 species of water beetles are known meanwhile, some of which seem to be endemic to the former British crown colony (see Jäch, 2004).

[8] See http://www.nhm-wien.ac.at/nhm/2Zoo/coleoptera/publications/chinaindex.html

Table 1 Global assessment of water beetle species; AE = estimated number of aquatic species; + = plus 1–10. Estimations include assumed number of undescribed species and possible new faunal records. PA: Palearctic, NA: Nearctic, AT: Afrotropical, NT: Neotropical, OL: Oriental, AU: Australian, PAC: Pacific

Family/Regions	PA	NA	NT	AT	OL	AU + PAC	Total (all regions)
	AE	AE	AE	AE	AE	AE	AE
Carabidae	?1+	0	0	0	0	0	?1+
Gyrinidae	50+	50+	280	250	300	70	1,000
Haliplidae	61	65+	39+	26+	20+	15	220
Meruidae	0	0	1+	0	0	0	1+
Noteridae	30+	16	93+	95+	30+	8+	270
Amphizoidae	2	3	0	0	0	0	5
Aspidytidae	1+	0	0	1+	0	0	2+
Hygrobiidae	1	0	0	0	1	4	6
Dytiscidae	1,050	500	1,200	1,200	600	600	4,800
Lepiceridae	0	0	1+	0	0	0	1+
Torridincolidae	1+	0	40	6+	1+	0	60
Hydroscaphidae	9+	1	6+	1+	5+	0	40
Sphaeriusidae	20	3+	20	2+	40	2+	100
Helophoridae	155+	40+	4+	3+	6+	0	200
Epimetopidae	0	4	19+	2+	8+	0	50
Hydrochidae	30	30+	60	60	25	50	250
Spercheidae	5+	0	2+	9+	6+	2+	25
Hydrophilidae	400	220	700	550	630	300	2,320
Hydraenidae	800	100	300	450	500	350	2,500
Scirtidae	250	130	250	250	500	300	1,700
Elmidae	340	120	360	400	350	220	1,850
Dryopidae	90	20+	100	70	70	1+	350
Lutrochidae	0	3+	30	0	0	0	30
Ptilodactylidae	7+	3+	8+	30+	4+	5+	?100
Psephenidae	92+	15+	70	50	130	14+	370
Cneoglossidae	0	0	?8+	0	0	0	?8+
Eulichadidae	11+	1	0	0	30	0	30
Lampyridae	6+	0	0	0	1+	0	6+
Chrysomelidae (Donaciinae)	70+	60+	5+	12+	27+	2+	180
Chrysomelidae (other subfamilies)	70	10+	200	20	100	40	440
Nanophyidae	0	1+	0	0	1+	1	3+
Erirhinidae	120	73+	50	120	50	50	470
Curculionidae (Bagoinae)	140	45	0	100	90	40	415
Curculionidae (Ceutorhynchinae)	50	30	1+	10	1+	1+	100
Total	3,900	1,550	3,900	3,750	3,580	2,100	18,000

Human related issues and conservation

Relationships between water beetles and mankind are more diverse than usually expected.

Due to their ability to produce an audible sound, Squeak Beetles, *Hygrobia hermanni* (F.) (Hygrobiidae), were sold as childrens pets on British markets in the past (Wesenberg-Lund, 1943). Still today *Cybister* spp. (Dytiscidae) are sold in Hong Kong pet shops for use in the aquarium (Jäch & Easton, 1998), a formerly common practice in Europe as well (Wesenberg-Lund, 1943), which has unfortunately been forgotten.

Table 2 Global assessment of water beetle species; A = number of described species of True Water Beetles, False Water Beetles and Phytophilous Water Beetles (sensu Jäch, 1998a); T = total number of species (aquatic, paraquatic and terrestrial). Total number of not predominantly aquatic families not provided for biogeographical regions. PA: Palearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australian, PAC: Pacific

Family/Regions	PA		NA		NT		AT		OL		AU + PAC		Total (all regions)	
	T	A	T	A	T	A	T	A	T	A	T	A	T	A
Carabidae		?1		0		0		0		0		0	20,000	?1
Gyrinidae	50	50	50	50	200	200	220	220	210	210	40	40	750	750
Haliplidae	61	61	65	65	39	39	26	26	20	20	15	15	204	204
Meruidae	0	0	0	0	1	1	0	0	0	0	0	0	1	1
Noteridae	30	30	16	16	93	93	95	95	29	29	8	8	250	250
Amphizoidae	2	2	3	3	0	0	0	0	0	0	0	0	5	5
Aspidytidae	1	1	0	0	0	0	1	1	0	0	0	0	2	2
Hygrobiidae	1	1	0	0	0	0	0	0	1	1	4	4	6	6
Dytiscidae	953	953	488	488	743	743	1,060	1,060	534	532	449	446	3,913	3,908
Lepiceridae	0	0	0	0	2	1	0	0	0	0	0	0	2	1
Torridincolidae	1	1	0	0	24	24	6	6	0	0	0	0	31	31
Hydroscaphidae	9	9	1	1	6	6	1	1	5	5	0	0	21	21
Sphaeriusidae	8	4	3	3	1	1	2	2	7	?7	2	2	23	?19
Helophoridae	150	155	42	40	4	4	3	3	6	6	0	0	185	178
Epimetopidae	0	0	4	4	19	19	2	2	8	8	0	0	29	29
Hydrochidae	22	22	30	30	42	42	40	40	13	13	36	36	180	180
Spercheidae	5	5	0	0	2	2	9	9	6	6	2	2	18	18
Hydrophilidae	510	380	243	200	639	570	593	450	687	460	362	210	2,652	1,800
Hydraenidae	700	692	85	85	140	138	230	215	125	120	140	130	1,420	1,380
Scirtidae	200	200	100	100	100	100	50	50	250	250	200	200	900	900
Elmidae	240	240	100	100	260	260	320	320	200	200	150	150	1,330	1,330
Dryopidae	70	69	20	20	70	60	40	35	80	30	4	1	280	200
Lutrochidae	0	0	3	3	12	12	0	0	0	0	0	0	15	15
Ptilodactylidae		?7		?3		?8		?30		?4		?5	500	?56
Psephenidae	92	92	15	15	36	36	14	14	105	105	14	14	272	272
Cneoglossidae	0	0	0	0	8	?8	0	0	0	0	0	0	8	?8
Eulichadidae	11	11	1	1	0	0	0	0	19	19	0	0	19	19
Lampyridae		6		0		0		0		1		0	2,000	6
Chrysomelidae (Donaciinae)		70		60		5		12		27		2	166	166
Chrysomelidae (other subfamilies)		50		10		100		10		70		20	46,000	260
Nanophyidae		0		?1		0		0		?1		1	300	3+
Erirhinidae		90		73		35		50		15		20	300	283
Curculionidae (Bagoinae)		115		35		0		40		50		27	267	260
Curculionidae (Ceutorhynchinae)		29		13		1		2		0		1	1,316	42
Total		3,346		1,419		2,508		2,693		2,189		1,334		12,604

Pemberton (1990) reports about the use of *Cybister* sp. for a kind of lottery in Korea.

Dytiscids were often blamed for causing considerable harm to fish fry (Wesenberg-Lund, 1943), but there are few actual studies on that subject, and more research is needed to assess potential harm (as well as benefits) of water beetles to aquaculture (Vazirani, 1972). Dytiscids are predators of mosquitos and may play an important role in controlling them. Their actual importance is not yet understood, but at least

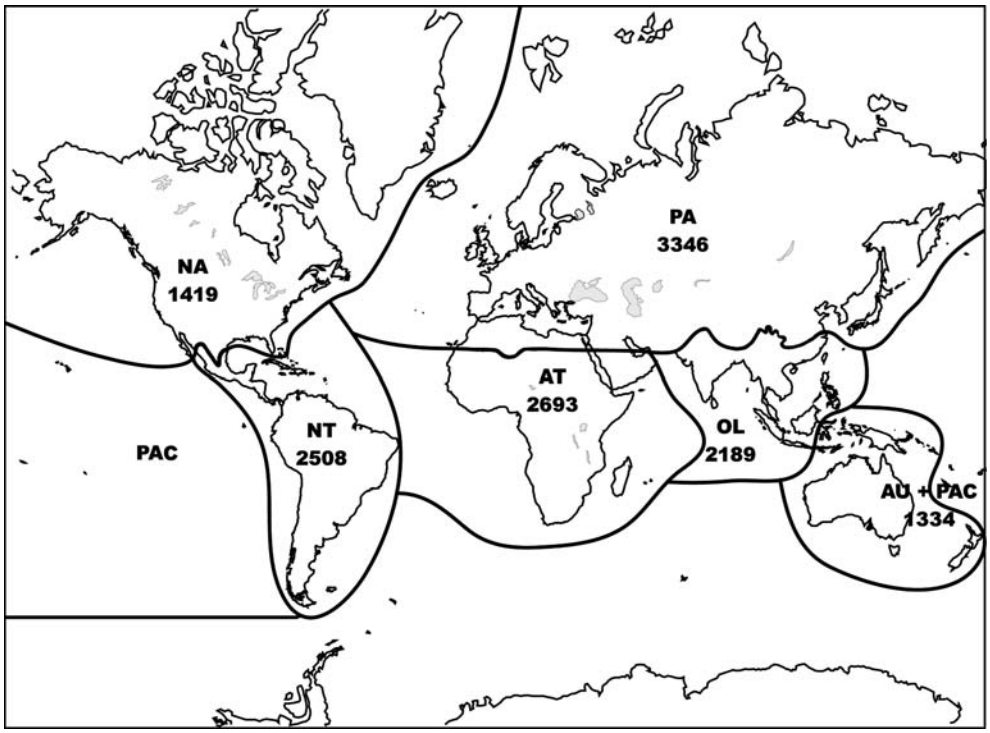

Fig. 2 Global diversity of water beetles by zoogeographic regions. Borders between realms arbitrary. Species from the Antarctic Region (ANT) and the Pacific Region (PAC) have been included to adjacent realms. AU: Australia, AT: Afrotropical, NA: Nearctic, NT: Neotropic, OL: Oriental, PA: Palearctic, PAC: Pacific

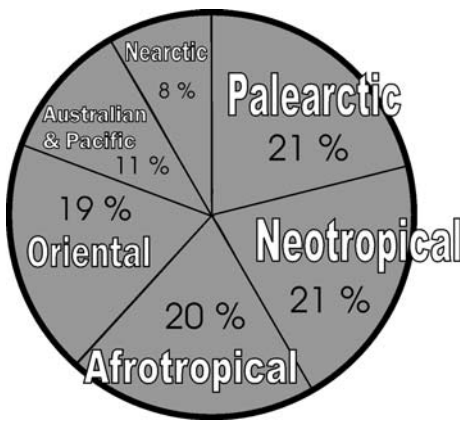

Fig. 3 Estimation of global diversity of water beetles by biogeographic regions

some attention is nowadays paid to that problem (Mogi et al., 1999).

Apart from these marginal relationships between manhood and water beetles, the applied relevance of aquatic Coleoptera can be summarized in three main groups.

Environmental indication

Water beetles, especially Elmidae, are increasingly gaining recognition as biological indicators for (1) water quality (saprobial index), (2) habitat types, (3) biological functionality and (4) species and habitat conservation (red lists) (see Moog, 2003; Jäch et al., 2005b). A comprehensive list of saprobic valencies of the Austrian elmids was published by Moog & Jäch (2003).

The IUCN Red List of Threatened Species (see http://www.redlist.org/) contains also a number of water beetles. However, this list has obviously not been compiled by water beetle experts and it is therefore dearly in need of revision. Two New Caledonian dytiscids, *Rhantus alutaceus* and *R. novaecaledoniae*, both listed as extinct in the 2004 IUCN Red List of Threatened Species, definitely suffer from ongoing habitat loss, but were otherwise still collected during expert fieldwork recently. On the other hand, some species, which have repeatedly been recorded as being probably extinct, e.g.,

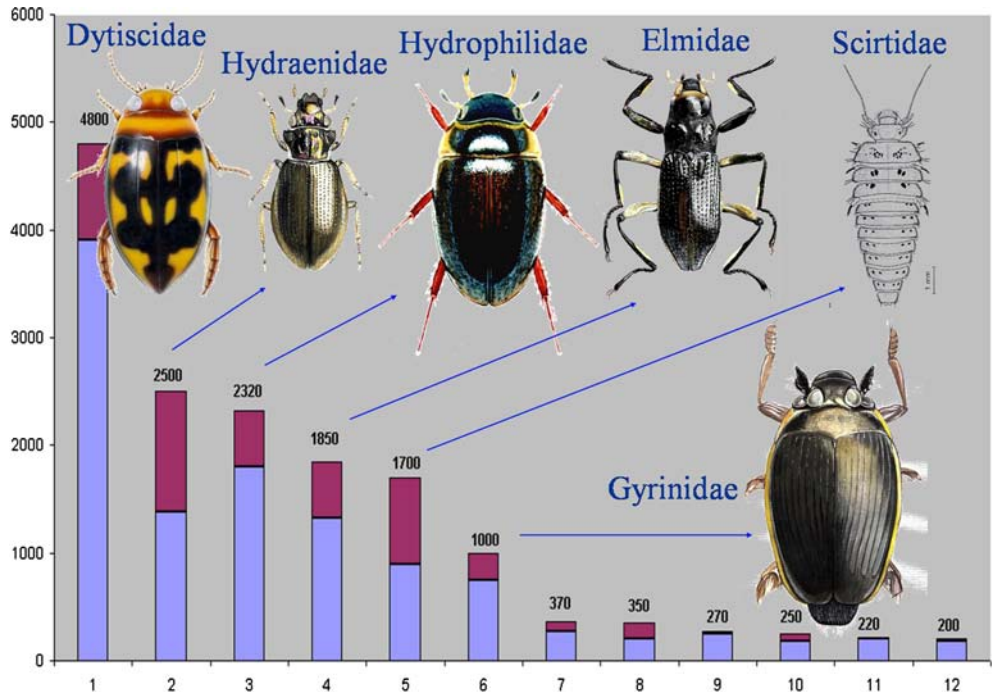

Fig. 4 Global diversity of water beetle families; number of described species (pale grey/blue) and estimation of undescribed (dark grey/purple) species in 12 beetle families; paraquatic and terrestrial members not included; 1—Dytiscidae, 2—Hydraenidae, 3—Hydrophilidae, 4—Elmidae, 5—Scirtidae, 6—Gyrinidae, 7—Psephenidae, 8—Dryopidae, 9—Noteridae, 10—Hydrochidae, 11—Haliplidae, 12—Helophoridae

Hygrobia davidi from China and *Hydraena sappho* from Greece (see Audisio et al., 1996), have not been included in the IUCN Red List so far. Numerous coleopterists (e.g., P. Audisio, M. Hess, U. Heckes, M.A. Jäch, A. Komarek, H. Schillhammer, H. Schönmann) have vainly searched for the latter species in the last two decades.

In general, water beetle communities all around the world suffer from desertification, irrigation, eutrophication induced by lifestock, man, and agriculture, as well as overall loss of primary habitats. Species living in aquatic habitats surrounded by tropical rain forests seem to be especially vulnerable to deforestation, which is devastatingly effecting chemical and physical characters of freshwater biotopes. Furthermore, in numerous water beetles at least one stage of the life cycle is spent outside the water. Therefore, any disturbance of the immediate surroundings of an aquatic habitat must be considered a major threat for its water beetle communities.

Pest and pest control

Several species of Phytophilous Water Beetles are used to control water plants that are regarded as pests while others are destructive to plants of economic importance.

The South American *Agasicles hygrophila* Selman & Vogt (Chrysomelidae: Alticinae) was introduced to several countries on various continents to control Alligatorweed (*Alternanthera*). The Neotropical *Cyrtobagous salviniae* (Erirhinidae) is used as control agent for the Water Fern (*Salvinia*) and has been introduced, for instance, to India, Thailand and Australia. Two species of *Neochetina*, *N. eichhorniae* and *N. bruchi* (Erirhinidae), natives of South America, were released in the USA and Asia where they are most effective in reducing the flowering and potential growth of waterhyacinth (*Eichhornia crassipes*), the world's most important aquatic weed spreading at an alarming rate. The Waterlettuce Weevil, *Neohydronomus affinis* (Erirhinidae), from South America was released in Florida and Australia for biological control

of *Pistia stratiotes*. Species of *Nanophyes* (Nanophyidae) are feeding in the stems of invasive plant pests, such as the Water Primrose (*Ludwigia*).

The Rice Water Weevil, *Lissorhoptrus oryzophilus* Kuschel (Erirhinidae), is a most destructive pest of rice (*Oryza sativa*). It originates from America, where it is a particularly severe pest in Louisiana. Larvae of *L. oryzophilus* are responsible for the main damage as they feed on leafs for a short period and then crawl down to the roots; they have paired dorsal hooks to pierce the roots for obtaining oxygen. The fourth larval instar forms a mud-coated cocoon attached to the roots. Serious crop losses are reported in all countries where this species occurs (up to 60% in Japan). *Lissorhoptrus oryzophilus* has been spread accidentally to all continents except Africa and Australia. To Europe (Italy) it was introduced rather recently (Caldara et al., 2004). *Lissorhoptrus oryzophilus* is not only a pest of rice, but it also attacks many other wild grasses and sedges (Poaceae and Cyperaceae) which serve as alternative hosts for adults in or near rice fields, rendering pest management most difficult. Furthermore, resistance to some insecticides has also been reported. In Asia and in California only parthenogenetic females are known. Other Erirhinidae, e.g., *Lissorhoptrus simplex* (Say) and *Afroryzophilus djibai* Lyal, are causing heavy damages too.

Cuisine and medicine

The medical/nutritive relationships between water beetles and mankind have obviously been more diverse in the past, but they have survived to some extent. Even today, various species are used for human consumption (both as medicine and as confection). Eating water beetles is still practised in Madagascar, New Guinea and Asia, for instance in China, where two genera, *Hydrophilus* Geoffroy (Hydrophilidae) and *Cybister* Curtis (Dytiscidae) are offered for sale in Guangdong markets and restaurants. Remarkably, *Cybister* is more expensive than *Hydrophilus* (Jäch, 2003). Ding et al. (1997) published a list of medicinal insects in China and mentioned that *Cybister* was consumed in order to improve blood circulation. According to Hoffmann (1947) water beetles are considered as an anti-diuretic.

More than a century ago, *Austrelmis condimentarius* (Philippi) (Elmidae), was used as seasoning for food in South America, and it was reported to have considerable commercial value (Philippi, 1864; Netolizky, 1916).

In the early 19th century, *Aulonogyrus strigosus* F. (Gyrinidae), was roasted and eaten by Australian aborigines (Mjöberg, 1916; Ochs, 1924) and approximately at the same time, gyrinids were used in Europe as an aphrodisiac for cows and mares (Netolizky, 1916, 1919; Ochs, 1966).

Rubbing Gyrinidae (*Dineutus*, *Gyrinus*, etc.) and Dytiscidae (*Hydaticus*, *Rhantus*) onto young girls breasts for stimulating their growth is a unique traditional practice still alive and wide-spread in East Africa (Kutalek & Kassa, 2005). In their prothoracic defence glands dytiscids produce steroids resembling human hormones! However, there is insufficient evidence to conclude that the chemical defence mechanism of the water beetles is in fact responsible for a possible growth of the breasts.

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