Freshwater Animal Diversity Assessment

Developments in Hydrobiology 198

Series editor
K. Martens

Freshwater Animal Diversity Assessment

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Reprinted from Hydrobiologia, Volume 595 (2008)

Biodiversity.be

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BELGIAN SCIENCE POLICY

Springer

Library of Congress Cataloging-in-Publication Data

A C.I.P. Catalogue record for this book is available from the Library of Congress.

ISBN-13: 978-1-4020-8258-0

Published by Springer,
P.O. Box 17, 3300 AA Dordrecht, The Netherlands

Cite this publication as Hydrobiologia vol. 595 (2008).

Cover illustration: A few inhabitants of fresh water. (clockwise from top left): *Simulium arcticum* (larva) - photo by Michael Spironello; *Crangonyx richmondensis* - photo by Jonathan Witt; *Protorthemis coronata* - photo by Vincent J Kalkman; *Altolamprologus calvus* (Chisanse) - photo by Ad Konings

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Printed on acid-free paper

Printed in the Netherlands

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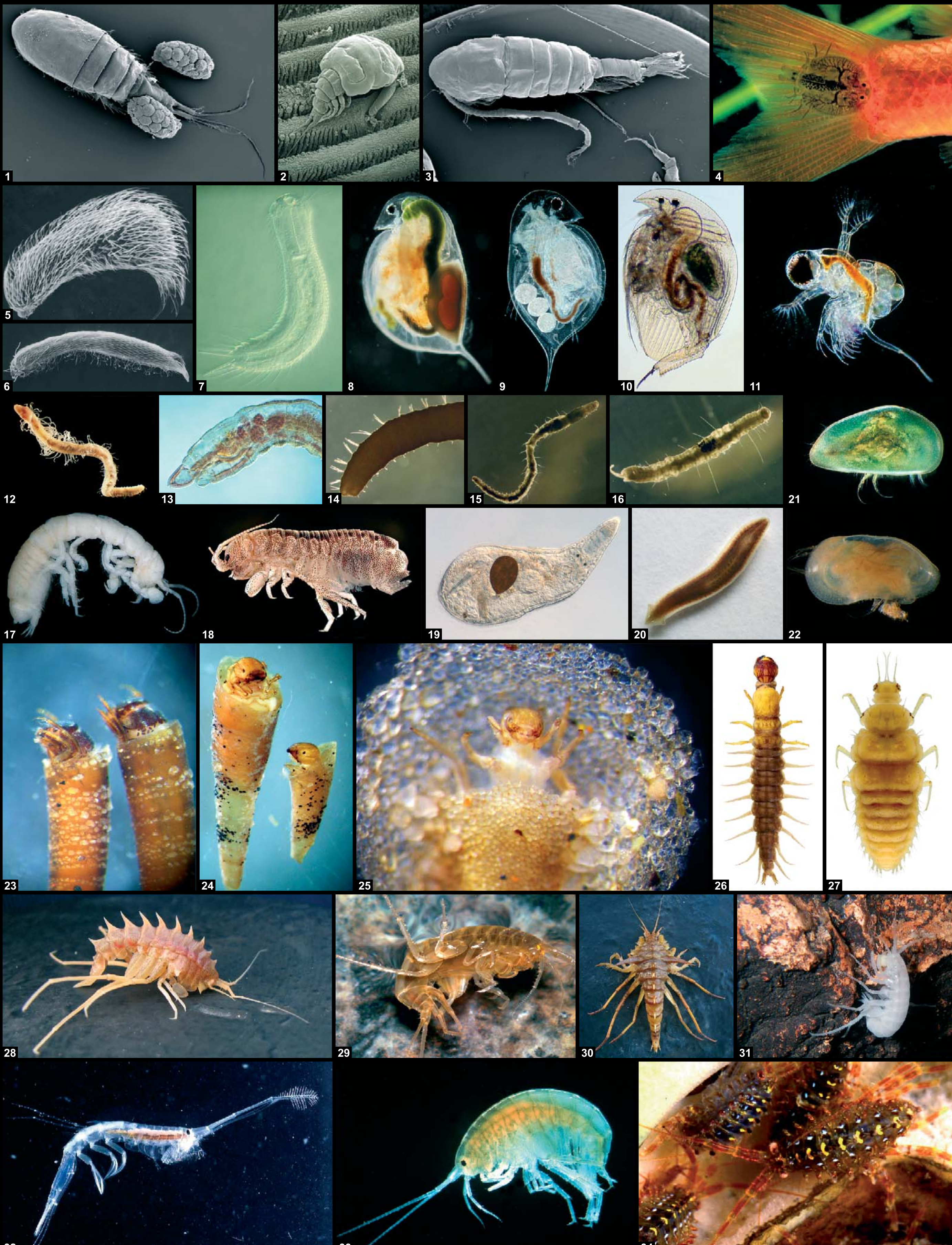
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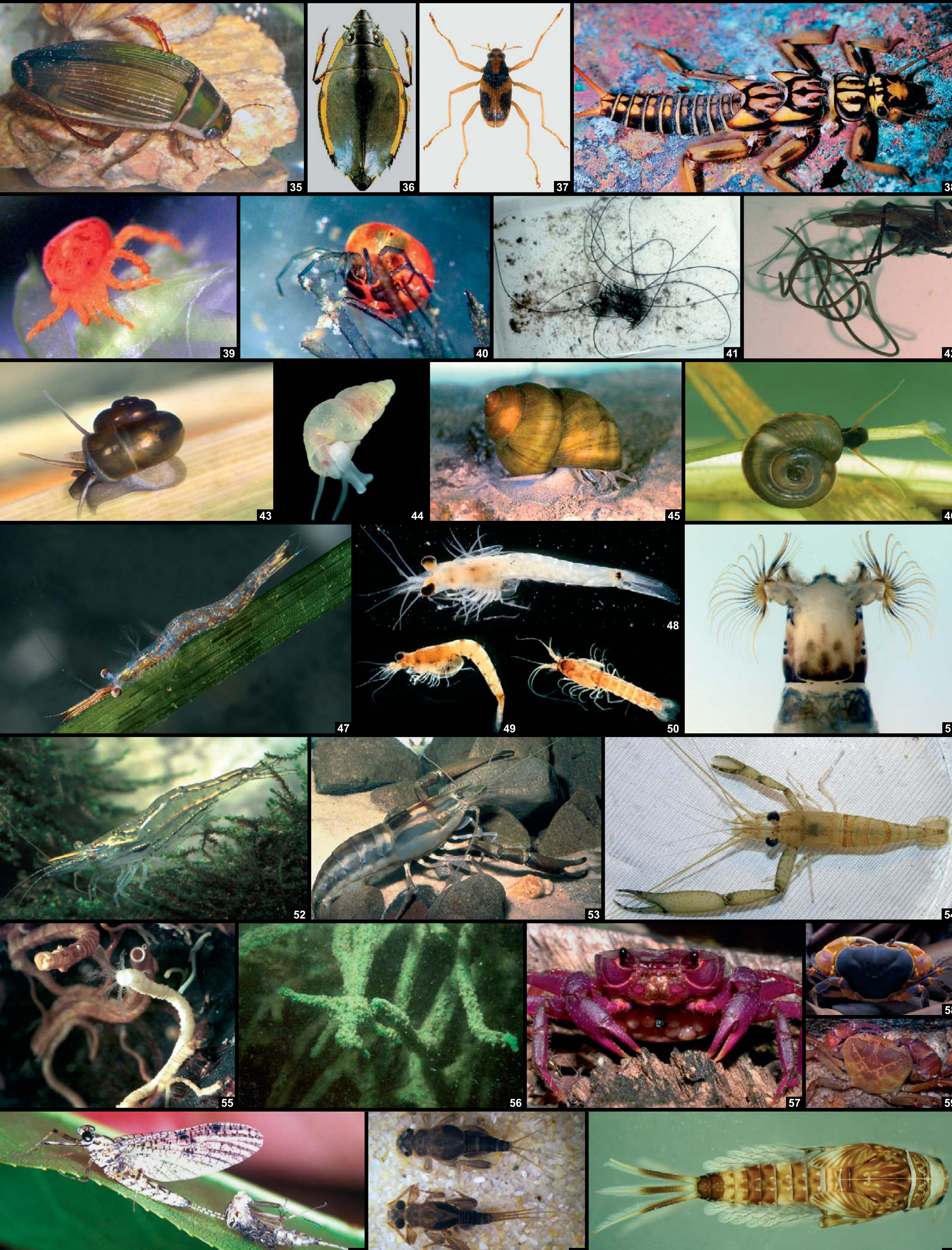
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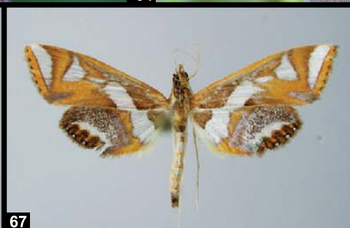
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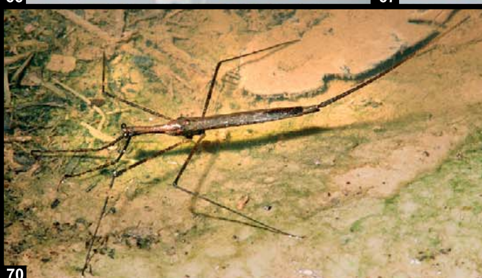
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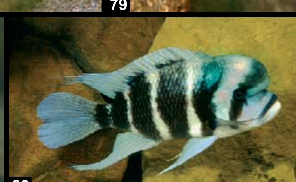
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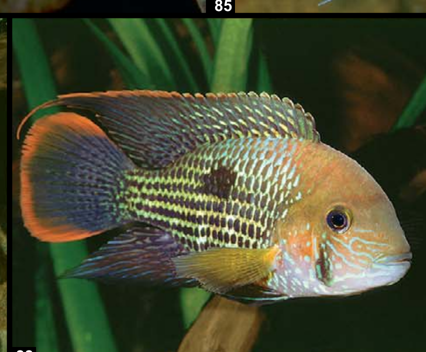
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DOI 10.1007/s10750-007-9168-0

FRESHWATER ANIMAL DIVERSITY ASSESSMENT

Foreword

Robert J. Naiman

This is a critical time for organisms living in continental waters. Quite literally, the hydrological regime of the Earth is being drastically altered to meet the needs of rapidly expanding societies or in response to alterations of the land and the atmosphere (Vörösmarty et al., 2004). Water regimes that helped shape the evolution of freshwater diversity and the life history adaptations of individual species will be different from now on. These major changes, to one of the Earth's most basic biophysical systems, is taking place with only a rudimentary understanding of the organisms being affected or the large-scale consequences of those changes (Dudgeon et al., 2006). Unfortunately, despite centuries of investigations of the Earth's biota, the taxonomy of freshwater organisms and their distributional patterns are just beginning to become clear—and therein lays the great value of this volume.

One of the most telling graphics about the state of fresh waters is from the recent Millennium Ecosystem Assessment (2005). Between 1970 and 2002—a mere 30 years, freshwater biodiversity declined $\sim$55%, while that of terrestrial systems and marine systems, each declined $\sim$32%. One must suspect that the actual value for continental waters was considerably higher considering the incompleteness of the taxonomic database on freshwater biodiversity. I find this to be a sobering statistic as well as a call to action for freshwater-related sciences and for conservation.

In reading the chapters I was struck by just how many described species were in some phyla—and even more, so by how many new species are described annually, how many are estimated to be awaiting description, and how little is known about distributional patterns. Clearly, the overall task is a daunting challenge for science and for science administration. Is enough emphasis being given to training a new generation of taxonomists? Are the most up-to-date techniques being widely used to assist with timely descriptions? Are existing and emerging data on species and distributions being compiled into databases where the broader research community has reasonable access? These and other key questions underpin deep concerns that freshwater taxonomy needs a 'fresh' start—and better coordination—if it is to fully contribute to global concerns about the condition and the management of continental waters.

Fortunately, there are a number of emerging global initiatives to assist the process of discovering the taxonomic richness of the Earth's fresh waters, and to understand the goods and services they provide to societies. The leadership by the editors in organizing

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the initial workshop and compiling this volume cannot be under-estimated. It not only summarizes a vast array of data on a large number of freshwater phyla but perhaps more importantly, it has also acted as a catalyst to garner the interest and support of international programs focused on understanding and conserving freshwater environments (e.g., UNESCO's International Hydrological Programme, DIVERSITAS International, The Nature Conservancy). The remaining tasks represent a grand scientific challenge but, with this volume as a starting point, the path forward seems much clearer.

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Hydrobiologia (2008) 595:3–8
DOI 10.1007/s10750-007-9235-6

FRESHWATER ANIMAL DIVERSITY ASSESSMENT

An introduction to the Freshwater Animal Diversity Assessment (FADA) project

E. V. Balian · H. Segers · C. Lévêque · K. Martens

Abstract The Freshwater Animal Diversity Assessment (FADA) project aims at compiling an overview of genus- and species-level diversity of animals in the continental, aquatic ecosystems of the world. It is a collective effort of 163 experts, and presents 59 articles treating the diversity and endemism of different animal taxa, ranging from microscopic worms to mammals, at global and regional scales. Given their structural importance, an article on macrophytes is also added. Here, we give an overview of the project's history, and outline the common framework of the various articles, as well as the conventions the experts agreed to adhere to in their treatises. Furthermore, we briefly introduce future prospects.

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Keywords Global biodiversity · Endemism · Metazoa · Aquatic · Non-marine · Freshwater · Review

Introduction

Notwithstanding decades, if not centuries, of taxonomic and faunistic work, it remains difficult to obtain a global overview of biodiversity of freshwater ecosystems. Available knowledge on the matter was never thoroughly compiled and is largely scattered, localised and focuses on a few well-studied groups. Consequently, answering the simple question: "How many species are there in the freshwaters of the world, on continents or in major biogeographic regions?" remained difficult. In addition to constituting relevant basic scientific knowledge on freshwater biodiversity, such an estimate would be a valuable tool for conservation purposes in the face of increasing pressure on freshwater ecosystems. Indeed, more and more evidence documents the major crises faced by biodiversity and biological resources of inland waters, and which are directly correlated to water resource integrity (Postel & Richter, 2003). In addition to their intrinsic value, freshwater ecosystems provide essential goods and services to humankind (Postel & Carpenter, 1997), especially in the third world communities that traditionally depend directly on the availability of natural resources.

Drawing a global picture of freshwater biodiversity has not raised much interest, mainly because of the peculiarities of freshwater habitats. Their island-like nature complicates a global approach, and most taxonomists are overwhelmed by local faunas, especially when studying the highly diverse communities inhabiting ancient lakes or the diversity of groundwater fauna. However, the recognition of changes at a global scale and their impact on freshwater ecosystems (Dudgeon et al., 2006) as well as the need to stop the loss of freshwater biodiversity, motivated the Convention on Biological Diversity (CBD) to support global assessments of status of and trends in freshwater biodiversity, for example Groombridge & Jenkins (1998, 2000) and Revenga & Kura (2003). However, till now, no exhaustive literature review had been performed across all taxonomic animal groups, and a more extensive approach was required to provide information on the diversity and distribution of freshwater species and genera of the world. The Freshwater Animal Diversity Assessment (FADA) project took up the challenge of compiling this information. At the same time, a global assessment was completed on macrophyte diversity, as vascular plants play a key role in structuring the habitat of, and providing food to, many freshwater animals.

In this article, we present a short history of the FADA project, describe its specific objectives, and the common standards and agreements the different FADA experts accepted in order to maintain coherence between the 59 articles of this special issue.

History of the FADA project

Previous assessments

In conjunction with the CBD, some prior attempts to estimate the number of freshwater organisms, and to identify priority areas for conservation, have been made, although these mostly focused on some better-known groups (Groombridge & Jenkins, 1998, 2000; Revenga & Kura, 2003). The latter paper not only compiled a wide range of information on water resources, water system characteristics, threats and conservation aspects, but also included a fairly detailed report of taxonomic diversity for many freshwater taxa. In addition, Revenga & Kura (2003) highlighted the need for additional work on species diversity and distribution in order to better define conservation priorities.

Toward a global assessment of freshwater animal diversity

A preliminary phase of the FADA project lasted from September 2002 to June 2003 and received support from DIVERSITAS and the "Centre National pour la Recherche Scientifique"—French National Research Institute (CNRS). The main objective was to produce a discussion document that identified gaps in our knowledge of freshwater biodiversity, and could be used to triggering experts reactions (Lévêque et al., 2005). This first study led to a gross estimate based on existing databases, published reviews and contacts with taxonomists. The study estimated that known freshwater animal species diversity worldwide was in the order of magnitude of 100,000, half of these being insects. Among other groups, some 20,000 vertebrates; 10,000 crustaceans and 5,000 mollusc species were reported as truly aquatic or water-dependent species.

The preliminary study highlighted gaps in the basic knowledge of species richness at continental and global scales:

1. Some groups such as freshwater nematodes or annelids are understudied and data on their diversity and distribution is scarce. Because current richness estimates for such groups are greatly biased by knowledge availability, we can expect real species numbers to be much higher;
2. Research intensity in the different zoogeographic regions is unbalanced: reliable regional estimates of diversity on the Neotropical and the Oriental regions are lacking for many groups, even for some usually well-known ones such as molluscs or insects.

In addition, the preliminary study of Lévêque et al. (2005) generated numerous comments from the taxonomic community, highlighting that certain key data had not been included. We welcomed these comments by inviting the concerned taxonomic experts to join efforts in the consecutive phase of the project.

Implementation of the FADA project

The Belgian Science Policy (BelSPO), the Belgium Biodiversity Platform and the Royal Belgium Institute of Natural Sciences (RBINS, Brussels, Belgium) provided the necessary support to launch the "Freshwater Animal Diversity Assessment" project in March 2005. Taxonomic experts were invited to join a team of authors to write an article on the diversity of each animal group. These coordinating authors participated in a workshop during which they presented the data on their taxonomic group, and together discussed standards of a common approach (October 13–16, 2005). The resulting reviews are included in the present special issue of *Hydrobiologia*.

As mentioned before, the main goal of FADA is to provide an expert assessment of animal species diversity in the continental (fresh) waters of the world, focusing on taxonomic and biogeographic diversity. The main three objectives for each group are:

1. to give an as accurate as possible estimate of global species and generic diversity;
2. to report on geographic distribution (by zoogeographic region, as described below), and to identify possible gaps;
3. to highlight the main areas of endemicity.

Because extant patterns are the results of historical processes, the project also emphasises phylogenetic aspects and processes of evolution and speciation. In addition, information on human-related issues, such as economical and medical uses, threats, conservation issues, is included when pertinent.

Characteristics of this special issue

Our assessment aims to cover the whole range of freshwater taxa from sponges and nematodes or bryozoans to mammals and birds, including a specific article on macrophytes, but excluding microbes, virus, protists, and algae. In addition, all groups, which are exclusively parasitic and not entirely aquatic are also excluded[1] (i.e., Acanthocephala, Monogenea, Digenea and others); a total of 59 groups/articles are included in this issue. Some articles address a whole Phylum (Rotifera, Porifera...), other papers address a class, an order or even a family, depending on factors like the number of species concerned, level of knowledge on the taxon, available expertise, or historical treatment of the taxon. For instance, an article addressing a relatively species-poor taxon (i.e., Halacaridae), has nevertheless been included, as little comprehensive information had previously been published. On the other hand, the insect order Diptera, is far too diverse, both in number of species and ecology, to be treated in a single article. Consequently, key freshwater families are treated in separate articles (Chironomidae, Culicidae, Simulidae, Tipulidae), and one article addresses the remaining Diptera families. Only the family Tabanidae is not included, as no global expertise appeared to be available.

[1] Micrognathozoa, a monotypic taxon of moss-dwelling microscopic organisms of which only two disjunct records exist (Disco Island, Greenland and the subantarctic Crozet Islands: De Smet, 2002), is not treated in a full article.

Article framework

Strict space limits, especially regarding references, were imposed on the authors in order to achieve a single-volume compilation: for each article, space was allocated according to an initial estimate of the diversity of the concerned taxon. A model article framework was imposed to ensure that all standard, required data and information be included, and to maintain coherence amongst reviews, as well as to allow analyses of the data across all taxa.

1. As the main focus of these compilations is not on biology or ecology, only a brief summary of these aspects and some key references are provided in the introduction of each article.
2. The first and main section of each contribution is the "*species and generic diversity section*", which provides information on the known number of species and genera, per relevant higher-level taxon (family, subfamily...). Depending on the group, optional material in this section includes diversity of higher taxa, diversity of groups in selected habitats, data on fossil diversity and estimates of unknown diversity. Only the Gastropoda and the Coleoptera sections do not provide data on generic diversity, but the respective authors provide their arguments for not submitting this information.

3. The second, optional, section deals with "*phylogeny and historical processes*". Most articles include a brief treatise on evolutionary origin, age, and history of the group. Supplementary information can be added on speciation and diversification processes over time in various areas of the world, and on morphological and molecular phylogenies. Some authors address the main drivers of change: natural and anthropogenic processes of selection and the factors influencing spatial and temporal changes in the genetic stock, in population size, and/or regarding habitat fragmentation.
4. The following, compulsory section on "*Present distribution and endemicity*" provides synthetic maps of species and generic diversity at the level of the main zoogeographical regions (Palaearctic, Nearctic...). The section can include reports on historical patterns and processes, e.g., how the break-up of Gondwana contributed to the present-day distribution. In addition, authors report on endemicity at the species and genus level, and identify hotspots of endemicity.
5. Finally, in a last optional section, "*Human-related issues*" are discussed. This deals with the (potential) economic or medical relevance of the taxon treated, its relevance to fundamental or applied research, or concern for conservation, e.g., IUCN's Red Data Book species, special reserves established or needed, and main threats.

Changes to this framework were allowed for short articles in which it was more logical to address species diversity and distribution together, especially if the optional section on phylogeny was not included.

Terminology

To ensure coherency and homogeneity between articles, the different experts agreed to adhere to common concepts and definitions. An overview of these is as follows.

1. Hotspot: This term is used in relation to richness or endemicity, however, not necessarily with reference to specific threats. In this we deviate from the definition by Myers et al. (2000), in which the term is used in relation with threats and conservation priorities.
2. Endemism/Endemicity: Use of these terms should always include a reference to the relevant geographical unit. In general, endemicity is discussed in relation to the main biogeographic units as defined below. In some cases, endemicity is treated regarding circumscribed local areas, such as Lake Baïkal, Lake Victoria, the Mississippi drainage, or others.
3. Cosmopolitan species: A taxon is considered cosmopolitan if it is present in all zoogeographical regions except Antarctica, unless stated otherwise.
4. Regarding terms related to conservation issues authors refer to the IUCN categories and the IUCN Red list (IUCN, 2006). For example, the term "extinct" is used only in the situation where no more living specimens exist on earth, versus "extirpated" indicating that a taxon or population has disappeared locally.
5. Aquatic and water-dependent species: Defining what exactly constitutes a freshwater species proved to be controversial. For practical reasons, we limited ourselves to non-marine species of inland waters in two categories:

   (1) The 'real aquatic species' accomplish all, or part of their lifecycle in, or on, water.

   (2) "Water-dependent" or "paraquatic" species show close/specific dependency upon aquatic habitats (e.g., for food or habitat).

   Limno-terrestrial species, i.e., species that require an aqueous matrix in strictly terrestrial habitats for active life, like the water film retained by some mosses, are not included in the total numbers. However, they can be discussed in the article when considered pertinent by the expert.

   For some groups, attributing taxa to these ecological categories (water-dependent, limno-terrestrial and terrestrial) turned out to be particularly difficult, mostly owing to a lack of information on life history or ecological requirements of the taxa concerned. Authors were asked to argument their decision on the inclusion or omission of taxa in the total count.

6. Fresh and brackish water species: While the present assessment focuses on diversity of non-marine taxa, a number of thalassic or athalassic

brackish water ecosystems are nevertheless considered. Regarding interface environments (estuaries, anchialine ponds), only the non-marine fauna is included from such habitats. Euryhaline species in estuaries are included in the record, if they show a genuine tolerance to freshwater (<3 g/l). Species that are restricted to such interface environments, and that are therefore absent from both purely marine or fresh waters are not normally included in the total count of freshwater taxa. These cases are specifically addressed in the separate articles, and they can be recorded separately, according to the relevant expert's judgement.

7. Geographical distribution: zoogeographical regions: Regarding the global distribution, reference is made to standard zoogeographic regions as defined in classic textbooks (e.g., Wallace 1876; Cox 2001). We acknowledge that it is impossible to strictly delineate the world's major biogeographic regions. Issues were raised regarding the transitional zone between the Palaearctic and Oriental regions in China and India, the limits between the Oriental and Australasian regions, and the Mexican plateau between the Nearctic and Palaearctic regions. For standardisation purposes, we use the following names and delineations for regions (Fig. 1):

- The *Palaearctic Region (PA)* consists of Europe and Russia, North Africa (not including the Sahara) and Northern and Central Arabian Peninsula, Asia to south edge of Himalayas.
- The *Nearctic Region (NA)* consists of North America, Greenland and the high-altitude regions of Mexico.
- The *Afrotropical Region (AT)* consists of Africa south of the Sahara, the Southern Arabian Peninsula and Madagascar.
- The *Neotropical Region (NT)* consists of Southern and coastal parts of Mexico, Central America, and the Caribbean islands together with South America.
- The *Oriental Region (OL)* consists of India and Southeast Asia south of Himalayas (including lowland southern China) to Indonesia down to the Wallace's Line. It extends

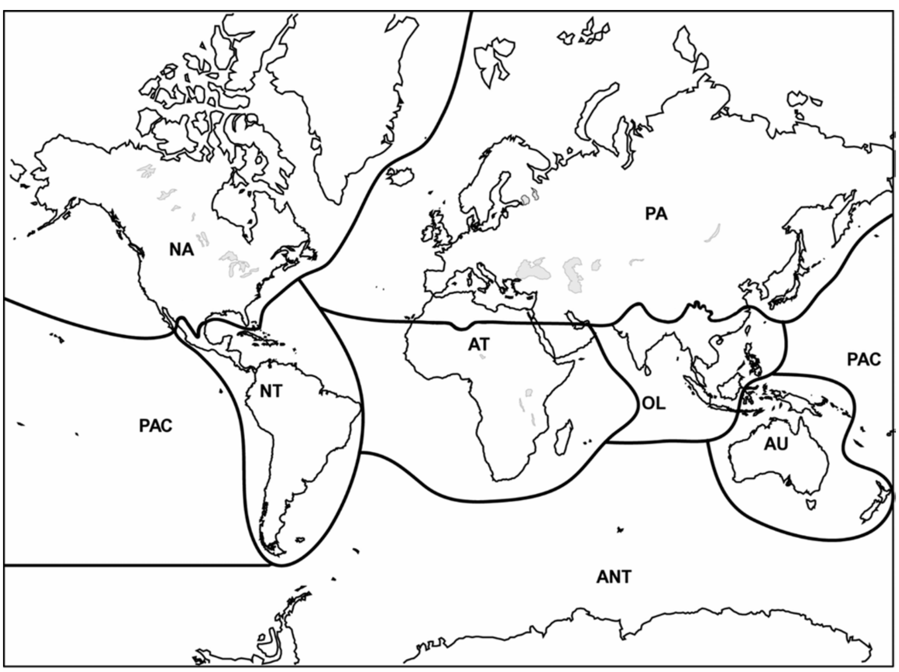

Fig. 1 Standard map of the zoogeographical regions. PA: Palaearctic Region, NA: Nearctic Region, AT: Afrotropical Region, NT: Neotropical Region, OL: Oriental Region, AU: Australasian Region, ANT: Antartic Region, PAC: Pacific Region and Oceanic Islands

through Indonesia as far as Java, Bali, and Borneo to Wallace's line, and includes the Philippines, lowland Taiwan and Japan's Ryukyu Islands.

- The *Australasian Region (AU)* consists of Australia and New Zealand, New Guinea including Papua New Guinea and the Indonesian province of Papua, and Indonesian Islands south and east of Wallace's Line. It includes the island of Sulawesi, the Moluccan islands (the Indonesian provinces of Maluku and North Maluku) and islands of Lombok, Sumbawa, Sumba, Flores, and Timor.
- The *Antarctic Region (ANT)* includes the Antarctic continent and the Antarctic and subantarctic islands south of the Antarctic convergence.
- *The Pacific Region and Oceanic Islands (PAC)*: includes the islands in the North and South Pacific ocean, with the Bismarck Archipelago, Vanuatu, the Solomon Islands, and New Caledonia.

In the few cases where experts were unable to clearly attribute a taxon to a specific region, arguments are listed in support of the final decision on the matter.

Conclusion

This is the first publication of the FADA project, and we are convinced that the information it contains will prove to be useful. In parallel to the production of this work, we are developing a database in which the taxonomic and distributional data on which the treatments presented here are based. This on-going task aims not only to provide access to the raw data the FADA experts have compiled, but we envisage developing a web portal containing additional functionalities like, for example, a repository for local distributional data (see Segers, 2007). These services and any supplementary information resulting from the project will be made accessible through http://fada.biodiversity.be (Balian et al., 2007).

Acknowledgements We are greatly indebted to all experts involved in the project, who contributed their expertise and passion to the daunting task of producing the present volume, and who always showed patience and enthusiasm despite the delays and difficulties encountered during the publishing process. Also, we gratefully acknowledge the numerous reviewers who offered their time and precious advice to improve the contributions.The project was supported by the Belgian Science Policy, the Belgian Biodiversity Platform, and the Royal Belgian Institute of Natural Sciences.

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Hydrobiologia (2008) 595:9–26
DOI 10.1007/s10750-007-9154-6

Global diversity of aquatic macrophytes in freshwater

P. A. Chambers · P. Lacoul · K. J. Murphy · S. M. Thomaz

Abstract Aquatic macrophytes are aquatic photosynthetic organisms, large enough to see with the naked eye, that actively grow permanently or periodically submerged below, floating on, or growing up through the water surface. Aquatic macrophytes are represented in seven plant divisions: Cyanobacteria, Chlorophyta, Rhodophyta, Xanthophyta, Bryophyta, Pteridophyta and Spermatophyta. Species composition and distribution of aquatic macrophytes in the more primitive divisions are less well known than for the vascular macrophytes (Pteridophyta and Spermatophyta), which are represented by 33 orders and 88 families with about 2,614 species in c. 412 genera. These c. 2,614 aquatic species of Pteridophyta and Spermatophyta evolved from land plants and represent only a small fraction ($\sim 1\%$) of the total number of vascular plants. Our analysis of the numbers and distribution of vascular macrophytes showed that whilst many species have broad ranges, species diversity is highest in the Neotropics, intermediate in the Oriental, Nearctic and Afrotropics, lower in the Palearctic and Australasia, lower again in the Pacific Oceanic Islands, and lowest in the Antarctic region. About 39% of the c. 412 genera containing aquatic vascular macrophytes are endemic to a single biogeographic region, with 61–64% of all aquatic vascular plant species found in the Afrotropics and Neotropics being endemic to those regions. Aquatic macrophytes play an important role in the structure and function of aquatic ecosystems and certain macrophyte species (e.g., rice) are cultivated for human consumption, yet several of the worst invasive weeds in the world are aquatic plants. Many of the threats to fresh waters (e.g., climate change, eutrophication) will result in reduced macrophyte diversity and will, in turn, threaten the faunal diversity of aquatic ecosystems and favour the establishment of exotic species, at the expense of native species.

Keywords Aquatic macrophyte · Aquatic weeds · Macroalgae · Diversity · Distribution · Composition · Lakes · Rivers

Guest editors: E. V. Balian, C. Lévêque, H. Segers & K. Martens
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Introduction

The term 'aquatic macrophytes' refers to a diverse group of aquatic photosynthetic organisms, all large enough to see with the naked eye. It includes macroalgae of the divisions Chlorophyta (green algae), Xanthophyta (yellow-green algae) and Rhodophyta (red algae) and the "blue-green algae" (more correctly known as Cyanobacteria), Bryophyta (mosses and liverworts), Pteridophyta (ferns) and Spermatophyta (seed-bearing plants), the vegetative parts of which actively grow either permanently or periodically (for at least several weeks each year) submerged below, floating on, or growing up through the water surface (Denny, 1985; Pieterse, 1990) (Table 1). Aquatic macrophytes range in size from *Victoria amazonica* with a leaf diameter up to 2.5 m, to the smallest angiosperms, tiny *Wolffia* spp. with a frond diameter less than 0.5 mm. Aquatic macrophytes include emergent macrophytes (plants that are rooted in submersed soils or soils that are periodically inundated, with foliage extending into the air), floating-leaved macrophytes (plants rooted to the lake or stream bottom with leaves that float on the surface of the water), submersed macrophytes (plants that grow completely submerged under the water, with roots or root-analogues in, attached to, or closely associated with the substrate) and free-floating macrophytes (plants that typically float on or under the water surface). Plant species which occur in ephemeral waterbodies (seasonally filled and refilled waters, such as floodplains and temporary ponds) challenge this definition. Our decision has been to include such species as "aquatic macrophytes", only if their environmental survival is clearly dependent upon regular refilling of their aquatic habitat with a source of fresh to brackish water.

The freshwater macroalgae are primarily represented by the green algae, especially the Charales, commonly known as the stoneworts or brittleworts (e.g., *Chara* and *Nitella* spp.). The Charales are often mistaken for higher plants because they have erect central stalks that are divided into short nodes and long internodes of elongated multinucleate cells, with a whorl of "branchlets" at each node (Fig. 1). Individual plants can vary greatly in size, from 5 cm to 1 m in length. This conspicuous stage is the haploid generation. Sexual reproduction commences with production by the haploid plant of complex oogonia and antheridia (often orange in colour and nested in the bases of the branchlets). Flagellated sperm produced in antheridia fertilize egg (oospheres) retained in oogonia, with the result being a diploid oospore. Germination commences with meiosis of the diploid oospore; a haploid protonemal stage develops from one product of meiosis and develops into the haploid plant. Only six genera and a few hundred species of Charales are extant, although a rich fossil record reveals far greater species diversity extending back to the Silurian (Tappan, 1980). The Charales are found in fresh and brackish waters on all continents except Antarctica, generally

Table 1 Freshwater macrophyte divisions and representative genera

Kingdom	Freshwater Macrophyte Divisions	Descriptive Term	Representative Freshwater Macrophyte Genera
Monera	Cyanobacteria	Blue-green algae	*Oscillatoria*, *Lyngbya*
Protista	Chlorophyta	Green algae	*Chara*, *Nitella*, *Cladophora*, *Enteromorpha*
	Rhodophyta	Red algae	*Lemanea*, *Batrachospermum*
	Xanthophyta	Yellow-green algae	*Vaucheria*
Plantae	Bryophyta	Mosses and liverworts	*Fontinalis, Riella*, *Ricciocarpus*
	Pteridophyta	Ferns and allies	*Azolla*, *Salvinia*, *Isoetes*
	Spermatophyta	Seed-bearing plants	*Sagittaria*, *Alisma*, *Butomus*, *Brasenia*, *Cabomba*, *Callitriche*, *Ceratophyllum*, *Scirpus*, *Carex*, *Myriophyllum*, *Elodea*, *Vallisneria, Juncus*, *Lemna*, *Utricularia*, *Nelumbo*, *Nymphaea*, *Nuphar, Spartina*, *Eichhornia, Potamogeton*, *Ranunculus*, *Sparganium*, *Typha*

in slow-flowing water or in lakes, where they can colonize down to great depths (100 m) in very clear water. In addition to the Charales, freshwater macroalgae include certain other genera of green algae (Chlorophyta: e.g., *Cladophora* and *Enteromorpha* spp.), yellow-green algae (Xanthophyta: e.g., *Vaucheria)* and red algae (Rhodophyta: e.g., *Lemanea* and *Batrachospermum* spp.). Multicellular filamentous "blue-green algae" (Cyanobacteria: e.g., *Oscillatoria* spp.) are also sometimes included in the "macroalgae", particularly species which form large tangled floating mats which can cause a nuisance in freshwater systems (Pieterse & Murphy, 1993). The brown algae (Phaeophyta), so characteristic of marine rocky shore systems, include seven periphytic species that occur in freshwaters but their inclusion in the "macroalgae" is debatable as filamentous forms are typically <10-mm long (Wehr, 2003).

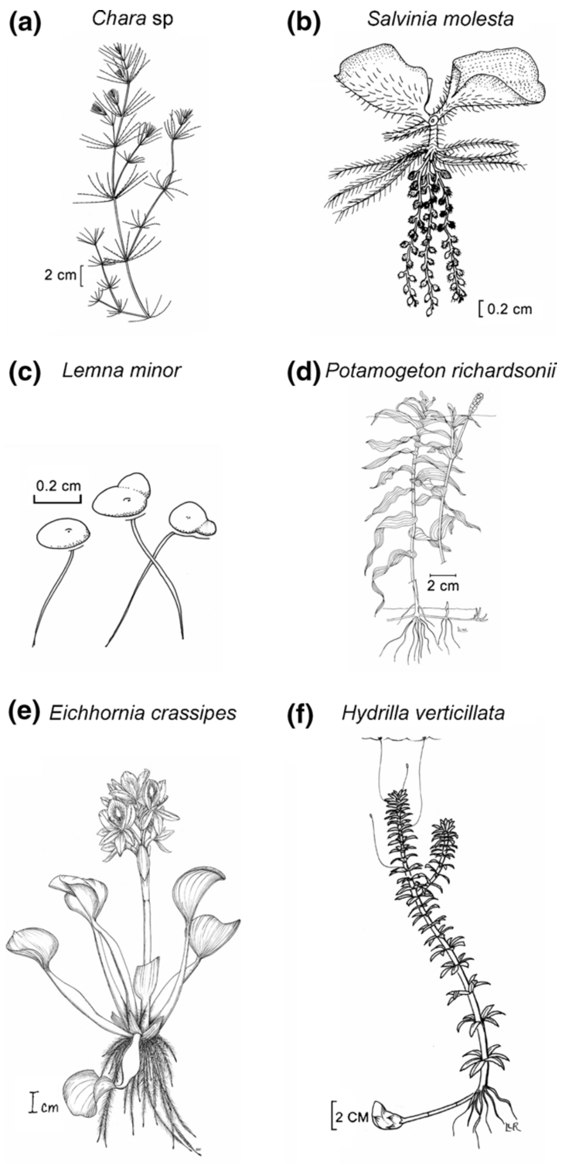

Fig. 1 Examples of aquatic macrophytes: (**a**) macroalgae *Chara* sp. (Order Charales), (**b**) *Salvinia molesta* (Division Pteridophyta), (**c**) *Lemna minor* (angiosperm), (**d**) *Potamogeton richardsonii* (angiosperm), (**e**) *Eichhornia crassipes* (angiosperm) and (f) *Hydrilla verticillata* (angiosperm). Line drawings are from the University of Florida, IFAS Center for Aquatic and Invasive Plants

The mosses, ferns and seed plants are all embryophytes, in that they have a common life cycle involving alternation of sporophyte and gametophyte generations**,** with the embryo sporophyte retained within the gametophyte at least initially. The bryophytes (mosses and liverworts) differ, however, from ferns and seed plants in that the haploid gametophyte generation, rather than the diploid sporophyte generation, is the most conspicuous. Thus the green moss, with its erect shoot bearing tiny leaf-like structures arranged in spirals, or the thin leathery liverwort are haploid gametophytes. The diploid generation arises after egg and sperm from male and female gametophytes fuse to produce a diploid zygote. The latter grows into a sporophyte, a stalked structure bearing a capsule that produces haploid spores (the future gametophyte generation). The sporophyte is never independent of the gametophyte, remaining attached for provision of water and nutrients. Also unlike ferns and seed plants, bryophytes lack true roots and vascular tissues for uptake and transport of water and organic and inorganic nutrients. About 0.5% of the 20,000 to 25,000 species of bryophytes are truly aquatic macrophytes, in that they require submergence in water to complete their life cycle (Cook, 1999). Other non-aquatic bryophyte species still require water for transfer of spermatozoids, but this can be accomplished simply by raindrops splashing sperm from male to female organs. Aquatic mosses and liverworts are often seen growing attached to rocks in mountain streams, but some (e.g., *Fontinalis antipyretica*) also grow in the shallow to moderately deep water of lakes and in slow-flowing lowland streams and canals. Bryophytes often dominate the macrophyte community found in polar lakes.

The Pteridophyta (ferns and allies) differ from the more primitive bryophytes in that the sporophyte is the dominant and more conspicuous generation, typified by the leafy frond of terrestrial ferns. However, unlike the more advanced seed plants, Pteridophyta lack seeds. Sporophyte plants develop sporangia that contain spores and for most ferns, the spores are identical (i.e., homosporous) and develop into a gametophyte with both antheridia and archegonia. However, some aquatic ferns (e.g., *Isoetes*) are heterosporous, producing separate male spores (microspores) that develop into male gametophytes with antheridia and female spores (megaspores) that develop into female gametophytes with archegonia. Unlike seed plants, the fern gametophyte is a free-living organism typically consisting of a small (<10-mm broad and long) green one-cell thick structure (the prothallus) with single greatly elongated cells (rhizoids) for absorption of water and minerals. The prothallus produces gametes (sperm and egg) that then fuse to form a zygote that grows by mitosis into the sporophyte. Of the 10,500–12,500 species of ferns and fern allies, there are about 171 species (1–2% of all species) that are truly aquatic macrophytes. Aquatic ferns and fern allies include horsetail or scouring rush (*Equisetum* spp.), quillwort (*Isoetes* spp.) and giant salvinia (*Salvinia molesta*), the latter being one of the world's worst aquatic pests (Fig. 1).

The Spermatophyta or seed-bearing plants, consist of two major groups: angiosperms, which have seeds enclosed in an ovary (which matures to become a fruit), and gymnosperms, in which the seeds are not so enclosed. Only the angiosperms, however, have aquatic species. Sporophytes are the dominant generation, and produce haploid microspores and megaspores that divide to form gametophytes. Haploid microspores develop by mitosis into haploid male gametophytes that contain a tube cell and two nonmotile sperm cells. Male gametophytes (pollen grains) are distributed by wind, rain, insects or other organisms. Haploid megaspores develop by mitosis into a haploid female gametophyte, which is composed of seven cells including a large central cell with two polar nuclei and an egg cell with one nucleus. The female gametophyte is retained in the megasporangium in the ovule. During a process that is unique to angiosperms and known as double fertilization, the nucleus of one sperm cell fuses with the nucleus of the haploid egg cell to produce a diploid zygote, and the nucleus of the other sperm cell fuses with the two polar nuclei of the large central cell to produce a triploid endosperm cell. Both the zygote and the endosperm cell divide by mitosis, producing a diploid embryo (the new immature sporophyte) and triploid endosperm (a food reserve for the embryo). Once this embryonic stage is reached, growth is temporarily halted. This stage is known as a seed and consists of the diploid embryo, triploid endosperm and diploid seed coat (from the female gametophyte). Of the 250,000–400,000 angiosperm species, there are only about 2,443 species (<1% of all species) that are aquatic. Aquatic angiosperms include the small free-floating duckweeds (e.g., *Lemna* and *Wolffia* spp.), the cosmopolitan submerged pondweeds (*Potamogeton* spp.) and invasive weeds such as water hyacinth (*Eichhornia crassipes*) and hydrilla (*Hydrilla verticillata*) (Fig. 1).

Species and generic diversity

Aquatic macrophytes are represented in seven plant divisions: Cyanobacteria, Chlorophyta, Rhodophyta, Xanthophyta, Bryophyta, Pteridophyta and Spermatophyta, consisting of at least 41 orders and 103 families. Including the filamentous green algae, the Chlorophyta contribute some 20 genera of aquatic macrophytes, comprising a few hundred species (mostly in the Orders Cladophorales and Charales). There are a few additional freshwater macrophyte species in the Rhodophyta and Xanthophyta, and probably fewer than 20 genera (though the taxonomy is confused) of Cyanobacteria which could be considered as macrophytes. The Bryophyta contribute 22 genera of aquatic macrophytes with about 110 freshwater species (Cook, 1999). Species composition and distribution of aquatic macrophytes in these more primitive divisions are less well known than for the vascular macrophytes (Pteridophyta and Spermatophyta); the remainder of this article focuses on the latter two plant divisions only.

Vascular aquatic macrophytes are represented by 33 orders and 88 families, with about 2,614 species (Table 2) in c. 412 genera (Table 3). Exact numbers are not possible to determine because it is not known whether many so-called 'wetland' species are truly

Table 2 Number of vascular aquatic macrophyte species currently known in the major biogeographic areas

Taxon	PA	NA	AT	NT	OL	AU	PAC	ANT	World
Pteridophyta									
Azollaceae	2	3	2	4	1	1			7
Blechnaceae	1		2		2	3	4		7
Equisetaceae	3	2	1		1		1		3
Isoetaceae	8	27	1	12	18	8			70
Marsileaceae	11	4	24	12	12	11	2		66
Polypodiaceae					1	1			1
Pteridaceae	1	3	2	3	3	2	2		5
Salviniaceae	1	2	2	8	2				10
Thelypteridaceae			2	1	2	2	2		2
Spermatophyta (Angiosperms)									
Acanthaceae	3	3	2	3	10	4	2		18
Acoraceae	1	1			2				2
Alismataceae	19	32	14	39	18	7	1		96
Amaranthaceae	1		1	5	2				7
Amaryllidaceae		1	1	2	1				4
Apiaceae	17	30	3	11	2	1			55
Apocynaceae	1				1				1
Aponogetonaceae			31		10	14			54
Araceae	15	22	19	31	90	19	7		139
Araliaceae		3	2	4		2			5
Asteraceae	1	12	16	29	18	3	1		56
Balsaminaceae	1				1				1
Boraginaceae	2		5	2	6	1			6
Brassicaceae	6	3	2	3	2				12
Burmanniaceae					3	1			3
Butomaceae	1				1		1		1
Cabombaceae	1	3	1	6	1	1			6
Campanulaceae	2	22	8	6	4	7			41
Cannaceae		1		1					1
Ceratophyllales	4	3	3	3	3	2	2		4
Commelinaceae	4	1	5	1	13	3	2		13
Convolvulaceae	2	1		2	1				3
Crassulaceae	2	1	2	3		1			8
Cyperaceae	73	123	78	149	87	67	35	3	276
Droseraceae	1		1		1	1			1
Elatinaceae	10	11	2	6	3	1			25
Eriocaulaceae	6	12	7	45	17	1	1		71
Euphorbiaceae		1		4					4
Fabaceae		6	1	13	2				17
Haloragaceae	10	15	4	11	7	41			65
Hanguanaceae					3	1	1		3

Table 2 continued

Taxon	PA	NA	AT	NT	OL	AU	PAC	ANT	World
Hydatellaceae					1	8			9
Hydrocharitaceae	20	12	43	15	40	23	5		108
Hydroleaceae	1	2		2	1	1			4
Hydrostachyaceae			29						29
Hypericaceae	1								1
Hypoxidaceae			1						1
Iridaceae	1	8	1	1					10
Juncaceae	7	9	4	3	4	2	2	1	14
Juncaginaceae	1	1	1	1		3			5
Lamiaceae	7	8	6	1	9	2	1		23
Lentibulariaceae	11	21	17	26	12	13			70
Limnocharitaceae		2	1	7	1	1			8
Linderniaceae	2	2	1	5	2	1			7
Lythraceae	13	8	13	33	26	6			78
Marantaceae		1	2	1	1	1	1		3
Mayacaceae		1	1	4					5
Melastomataceae				6					6
Menyanthaceae	8	5	16	8	15	36			73
Myrsinaceae	1	3	2						5
Nelumbonaceae	1	1		1	1	1			2
Nymphaeaceae	12	15	15	22	13	14			68
Onagraceae	2	7	4	11	5	4	1		17
Orobanchaceae			1						1
Oxalidaceae			2						2
Pedaliaceae	1								1
Philydraceae	1				1	1	1		1
Phrymaceae		1	1			7			8
Phyllanthaceae			1	1					2
Plantaginaceae	20	28	31	41	16	11	2	2	91
Poaceae	65	78	54	84	64	51	21	1	190
Podostemaceae	7	3	84	188	47	3			330
Polemoniaceae		3		1					4
Polygonaceae	7	9	3	9	3	2			20
Pontederiaceae	2	9	4	23	4	4			33
Portulacaeae	1	2	1	2	1	2		1	3
Potamogetonaceae	46	28	23	31	28	29	9	2	117
Primulaceae	1	1							2
Ranunculaceae	19	13		19	1	1		2	39
Rapateaceae				1					1
Rubiaceae			1	5					6
Saururaceae	1	1			2				3
Sparganiaceae	20	9		1	6	2			22
Sphenocleaceae			2		1				2
Tetrachonraceae				1		1			2