TROPICAL AQUATIC PLANTS: MORPHOANATOMICAL ADAPTATIONS

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Summary

Tropical ecosystems have a high diversity of environments, many of them with high seasonal influence. Tropical regions are richer in quantity and diversity of wetlands. Aquatic plants are widely distributed in these areas, represented by rivers, lakes, swamps, coastal lagoons, and others. These environments also occur in non tropical regions, but aquatic plant species diversity is lower than tropical regions. Colonization of bodies of water and wetland areas by aquatic plants was only possible due to the acquisition of certain evolutionary characteristics that enable them to live and reproduce in water. Aquatic plants have several habits, known as life forms that vary from emergent, floating-leaves, submerged free, submerged fixed, amphibian and epiphyte. The habit of plants can reflect their requirement of water, expressed by their morphological and anatomical adaptations. Thus, amphibian species always inhabit littoral regions and the submerged fixed occur predominantly in deeper waters. In this

paper morphological and anatomical characteristics are presented, pointing out their adaptations to the environment.

1. Introduction and Definition

Aquatic plants are ecologically important due to their fundamental role in the aquatic system, contributing to the complexity of these habitats. They also constitute the basis of many food chains, being important in nutrient cycling and providing input of organic matter into the ecosystem.

Categorizing aquatic plants or their community is an issue raised for more then 2000 years, since Theophrastus (372-287 BC). For many authors the distribution pattern of these aquatic species in the environment and their categorization is not simple and may have several approaches. Some authors imply that aquatic plants live exclusively in the water column, but others also include species that inhabit wetlands with flooded periods. Through history aquatic plants have been categorized in many ways. Some scientists consider that essentially aquatic plants are those which develop and reproduce permanently in water, depending exclusively on what they obtain from this system. For these authors species that inhabit swamps should not be classified as aquatic plants. Another term commonly used was limnophyte in order to categorize the higher plants that inhabit fresh waters, thus excluding species that inhabit salt and salty waters. In order to identify aquatic plants, older botanists regularly used the terms “aquatic tracheophytes” or “aquatic cormophytes”, but they not included macroscopic seaweeds or mosses. The term “hydrophyte” had been extensively applied to categorize flooded aquatic plants and also to those with floating leaves, but excluded the emergent species. Many North American authors utilized this term to refer to all flooded aquatic higher plants, including those with floating leaves and also the emergent heliophytes. However, this misunderstanding indicates the difficulty of categorizing plants which have water as their habitat.

Vascular hydrophyte is a term widely used by many authors, and in this case, excludes seaweeds, bryophytes, and pteridophytes, which are important components of the aquatic systems. In this sense, the term “aquatic macrophyte” is generic and comprises any aquatic plant, independent of taxonomic group, and can be used to identify salt and salty water plants, or even those inhabiting wetland and continental aquatic environments. This term also includes the herbaceous species that develop in the water column, in the flooded and saturated soil. This term has been widely used to identify aquatic plants, and was adapted by the International Program of Biology (IPB). Aquatic macrophyte is the most adequate term for all plants that inhabit aquatic environments, and that share several morphological, anatomical and ecophysiological adaptations. Some authors consider aquatic macrophyte to be a distinct group from wetland plants, as they have a high water dependency, and do not resist dryness, whereas wetland plants can resist some dryness and soil with some aeration.

The aquatic plants considered here are those species which survive only in humid environments or even saturated with water, and those that have different moisture needs. Some develop in swamps, others in periodically flooded environments, and others in lakes, rivers and oceans. Aquatic plants show different life forms that are generally associated with different environmental conditions, since they are biologically modified (adapted) to the condition of water in excess. The aquatic plants distribution in lagoons systems is related to the adaptation developed by each species to survive in the humidity gradient (Figure 1). Therefore, the adaptive characteristics—morphological, anatomical, and some ecophysiological aspects—of each species (i.e. living exclusively in water, amphibious that support submerged, flooding and dry soil periods) are related to their habit, reflecting the morphological plasticity of their organs. It is important to remember that when aquatic plants are distributed in water, they only establish in the photic zone, which is that zone with enough light to allow photosynthesis.

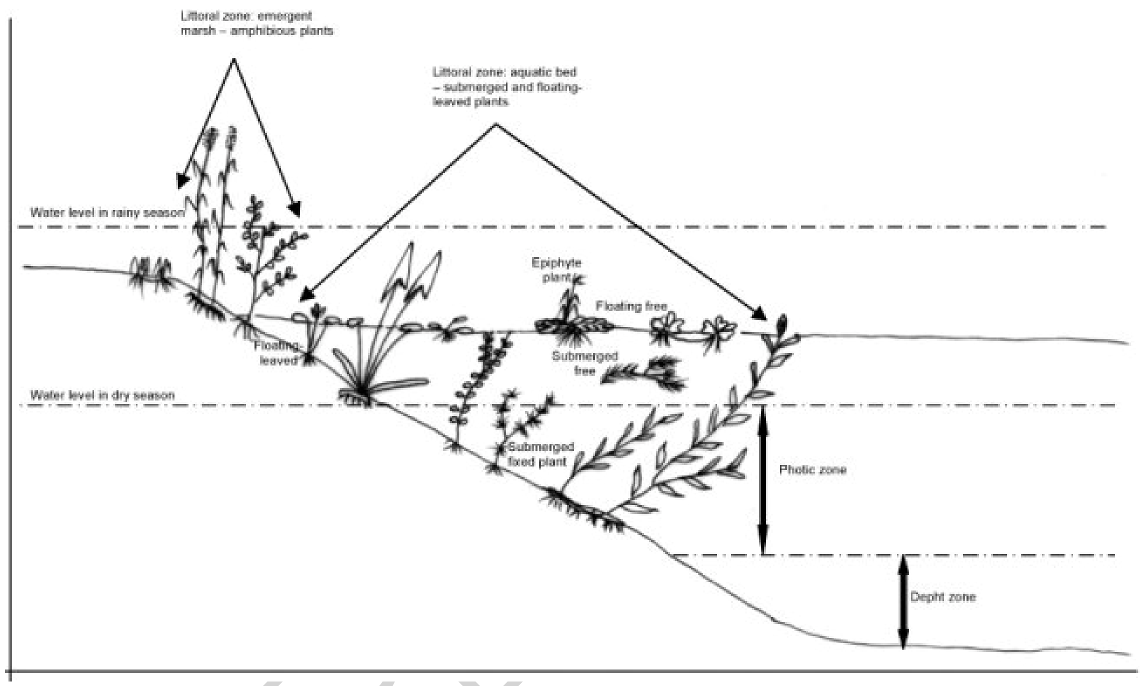

Figure 1: Diagram of a lacustrine system, showing all life forms of aquatic plants, with littoral aquatic bed dominated by submerged and floating-leaved plants and a littoral zone emergent marsh dominated by amphibious plants.

Water is the main abiotic factor that models the landscape, determining the occurrence of different types of aquatic plants. The existence of areas that accumulate water depends primarily on the local geology, geomorphology, soil type, topography and climate. The hydrologic pattern of wetland is the key to determine the composition, distribution, and diversity of aquatic plants inhabiting a region. Besides these factors, the water level variation during a seasonal cycle (rainy and dry) can also indicate all life forms that might occur in the water column (Figure 2).

Figure 2: Landscape of Pantanal Matogrossense, West-Central Brazil. This biome is seasonally flooded, favoring the development and propagation of many aquatic macrophyte species. (Photo: Paulo Robson de Souza – UFMS/Brazil).

2. Origin, Distribution and Diversity of Aquatic Plants

Undoubtedly, aquatic plants have originated from terrestrial plants. The evolutionary path of aquatic plants started and ended in the water. The first stage was the conquest of the aerial environment, resulting from the innovated capacity to achieve fertilization independently of water, and also from adaptations of vegetative organs to the dry environment. This allowed dispersion of plant into the terrestrial environment, especially for the angiosperms, which is the most abundant group of plants today. This transition from aquatic to terrestrial environment required an evolution of some structures to permit water transport (roots and vascular tissues), aiming, not only, to minimize the water loss to the external environment, but also to maintain hydric flow (cuticle and stomata), and to provide support to organs and tissues (cellulose and lignin).

Primitive plants irradiated to the terrestrial environment with the evolution of vascular plants and angiosperms, continuing the adaptive radiation that allowed the colonization of all environments distributed on the Earth surface. Eventually, a few species of bryophytes, pteridophytes, and angiosperms, especially herbaceous ones, returned to the aquatic environment, where they were able to survive and reproduce. Not only the fresh water but also the salt water environments were invaded by terrestrial plants. As the water excess limited growth and reproduction of these plants, the aquatic environment colonization by angiosperms resulted from the evolution of morphological, anatomical and ecophysiological characters. It is estimated that the amount of plant species that are adapted to the aquatic environment is no more then 1% of the angiosperms and 2% of the pteridophytes.

Among 250 000 species of angiosperms already described, only a small number is adapted to the aquatic environment, or even to soils saturated with water. Until recently the group of angiosperms was divided in two classes—monocotyledons and dicotyledons. According to genetic evidence from several molecular biology research studies, this classification needs to be revised, with the creation of a third group, the magnoliid, the characteristics of which are more primitives. Traditionally, this group was inserted in the dicotyledons, although there are some well distinguished characteristics. Inside the magnoliids two groups are recognised: 1) woody magnoliids; and 2) paleoherbs magnoliids, which is considered an isolated group according to the Actual Phylogenetic Group (APG II, 2003), widely used for angiosperms identification. Nowadays, the paleoherbs are considered ancestors of the monocotyledons, appearing some time before the end of the Cretaceous, more then 120 million years ago, and of the eudicotyledons, which are the dicotyledons with the exception of the magnoliids. Members of the Nymphaeales—Nymphaeaceae and Cabombaceae—and of the Ceratopyllales are the paleoherbs that occur today.

Many primitive families of monocotyledons are aquatic, indicating that the adaptive radiation to the aquatic environment occurred earlier in this group. Therefore, wetland and aquatic plants are more frequent among monocotyledons then eudicotyledons. It is estimated that among all aquatic plants occurring in the planet only 14% belong to the eudicotyledons, including submerged, free floating, fixed with floating leaves and emergent plants, while 52% belong to the monocotyledon families. Some authors suggested that the monocotyledons had their origin in the aquatic system, but this hypothesis is not well accepted. The use of DNA analysis to investigate phylogenetic correlation between aquatic and terrestrial plants may elucidate several questions not clarified yet. DNA analysis of families that have terrestrial and aquatic species indicate that the terrestrial group is evolutionarily more recent.

Several aquatic plants retain in the aquatic environment some reproductive mechanisms acquired in the terrestrial environment, and also depend on aerial pollinaters to favor sexual reproduction. A few species, however, developed a peculiar form of sexual reproduction, in which pollination depends exclusively on the aquatic environment. An example of this condition is the Ceratophyllaceae family, which has a single genus *Ceratophyllum* with a cosmopolitan dispersion. Species of this genus are entirely submerged, highly specialized to the aquatic habitat, with reduced leaves, without roots and stomata. Its pollination occurs in the water column, forming fruits with hooks that favor their fixation to the muddy substrate and to feathers and legs of aquatic birds. These characteristics are highly specialized and taxonomists have difficulties in recognizing phylogenetic correlations with other plant families. Species of *Ceratophyllum* do not possess xylem, petals or sepals, which are considered as primitive characteristics, but it is now understood that these adaptations are highly specialized to the aquatic environment. These plants have inhabited the aquatic environment for a long time, even longer than most other aquatic species. Recent molecular analysis indicated that species of this genus are located in the basis of the angiosperms.

Progresses in aquatic plant studies occurred mainly in the last decades of the twentieth century and are continuing, but most of these studies refer to systematics and ecology. Studies related to the phylogenetic correlation and evolution has received little attention until the present. Understanding the genetic structure of this group, its life history, the meaning of predominance of vegetative reproduction and high frequency of self-fertilization, when compared to terrestrial plants, is still incipient and requires a major advance in research in order to elucidate all the questions about this issue.

Aquatic plants inhabit swampy or humid environments, but the amount of water accumulated in the environment, and the distribution of the plants depends on topography, geology and climate. Wetland and essentially aquatic environments occur in coast regions, deltas, streamside zones, coast or continental lagoons, islands and flooded plains (where half of the wetlands in the planet are found) distributed along the tropical and sub-tropical regions. Aquatic plants display a wide geographic spread, over several continents, and many species are classified as cosmopolites. It is estimated that about 60% of all aquatic plants are in this category, in which the monocotyledons are the most widely distributed group. The wide distribution of many aquatic species indicates that they have efficient mechanisms to disperse their seeds or propagules, favoring colonization of other lands. Dispersion mechanisms found in this group are transport through water, migrating aquatic birds, wind and human activities such as navigation.

However, some aquatic plants species may be restricted to a small geographic area. The occurrence of endemism is very low, and generally it is a result of geographic barriers or specificity for climate or soil type. There are a few endemic species from swampy areas in Venezuela's mountains and California's seasonal lagoons, in addition to the tropical region of South America, which is particularly rich in endemic species, and the tropics and sub-tropics of Africa and Asia. Among the highly endemic genera are *Sagittaria* and *Echinodorus*, both belonging to Alismataceae family.

Table 1 lists all the families that have species inhabiting the aquatic environment or wetlands. It shows the most common groups which have hydrophytic individuals—including the truly aquatic and those that live in swamps with the exception of bryophytes. The morphological and anatomical characterization reported here refers exclusively to vascular plants. Table 1 also shows the geographic distribution, life form and pollination types available in the bibliography. All information listed here was based on the available bibliography, but pollination types might not be the same for all species from the related genus or family. This happens because the reproductive biology of most of species has not yet been studied.

Family	**Genera**	**Geographical distribution**	**Life form**	**Pollination form**
A. Hepaticae				
1. Ricciaceae	*Ricciocarpus*	Almost Cosmopolitam	Ff	-
B. Pteridophytes				
2. Adiantaceae	*Pityrogramma*	Africa, Tropical America	AM	-
3. Azollaceae	*Azolla*	Tropical; Fresh water	Ff	-
4. Ceratopteridaceae (Parkeriaceae)	*Ceratopteris*	Pan-tropical and subtropical; Fresh water	Ff	-
5. Isoëtaceae	*Isoetes; Stylites*	Cosmopolitan; Fresh water	AM; E; S	-
6. Marsileaceae	*Marsilea; Pilularia;Regnellidium*	Cosmopolitan; Fresh water	AM; E; S; Ff	-

7. Ricciaceae	*Ricciocarpus*	Some spp. in the world	Ff	-
8. Salviniaceae	*Salvinia*	Tropical; Fresh water	Ff	-
9. Thelypteridaceae	*Thelypteris*	Tropical and subtropical cosmopolitan	AM	-
C. Paleoherbs				
10. Cabombaceae	*Brasenia; Cabomba*	Cosmopolitan; Fresh water	Fl	Entomophilous and Anemophilus
11. Ceratophyllaceae	*Ceratophyllum*	Cosmopolitan; Fresh water	S; Fl	Hydrophilous
12. Nymphaeaceae	*Barclaya; Euryale; Nuphar; Nymphaea; Ondinea; Victoria*	Cosmopolitan; Fresh water	Fl; E; S	Entomophilous
D. Monocots				
13. Alismataceae	*Alisma; Baldellia; Burnatia; Caldesia; Damasonium; Echinodorus; Limnophyton; Luronium; Machaerocarpus; Ranalisma; Sagittaria; Wiesneria*	Cosmopolitan; Fresh water	E; Fl; S	Entomophilous
14. Aponogetonaceae	*Aponogeton*	Palaeotropical and southern Africa; Fresh water	Ff; S	Entomophilous or autogamous
15. Araceae (include Lemnaceae)	*Lemna; Pistia; Spirodela; Wolffia; Wolffiella; Acorus; Orontium; Calla; Cryptocoryne; Lagenandra; Aglaodorum; Typhonodorum; Montrichardia; Dracontioides; Lasia; Cyrtosperma; Colocasia; Peltandra; Dieffenbachia; Anubias; Xanthosoma; Urosphata*	Cosmopolitan (some spp.); Tropical, subtropical and temperate areas; Fresh water	Ff; E	Entomophilous (some species unknown)
16. Butomaceae	*Butomus; Ostenia; Tenagocharis*	Europe and temperate Asia	AM	-
17. Cannaceae	*Canna*	Tropical America; Subtropical; Fresh water	AM, E	Ornithophilous
18. Centrolepidaceae	*Hydatella; Trithuria; Aphelia; Centrolepis*	Asia; Temperate Australia; New Zealand	AM	Anemophilous
19. Commelinaceae	*Murdannia*	Pantropical	AM	-

20. Cymodoceaceae	*Amphibolis; Cymodocea; Halodule; Syringodium; Thalassodendron*	Tropical and subtropical; Salt water	S	Hydrophilous
21. Cyperaceae	*Ascolepis; Asterochaete; Baumea; Cyperus; Calyptocarya; Carex; Dulichium; Eleocharis; Eleogiton; Fimbristylis; Oxycaryum; Psilocarya; Rhynchospora; Scleria;*	Some spp. cosmopolitan	AM, E, EP	Anemophilous
22. Eriocaulaceae	*Eriocaulon; Leiothrix; Mesanthemum; Paepalanthus; Syngonanthus; Tonina*	Tropical and subtropical; Fresh water	E; S	Anemophilous ; Entomophilous
23. Hanguanaceae	*Hanguana*	Ásia; Malasya	S	-
24. Hydrocharitaceae (include Najadaceae)	Apalanche; Hydrocharis; Blyxa; Egeria; Elodea; Enhalus; Halophila; Hydrilla; Lagarosiphon; Limnobium; Najas; Ottelia; Stratiotes; Thalassia; Vallisneria	Cosmopolitan; Fresh and salt water. (*Vallisneria* introduced in several countries)	S; Fl	Anemophilous ; Entomophilous ; Hydrophilous
25. Hypoxidaceae	*Hypoxis*	South Africa	AM, E	Entomophilous
26. Iridaceae	*Iris*	Cosmopolitan	AM; E	Entomophilous
27. Juncaceae	*Juncus; Prionium*	Cosmopolitan	Fl; E	Anemophilous
28. Juncaginaceae	*Cycnogeton; Lilaea; Maundia; Tetroncium; Triglochin*	Tropical (few species); Fresh and brackish water	E	Anemophilous
29. Limnocharitaceae	*Hydrocleis; Limnocharis; Tenagocharis*	Tropical and temperate; Fresh water	E; Fl	Entomophilous ; some spp. probably autogamous
30. Lythraceae	*Ammannia; Cuphea; Decodon; Didiplis; Lythrum; Nesaea; Rotala; Trapa*	Some spp. tropical cosmopolitan; Tropical America	AM; E	-
31. Marantaceae	*Donax; Phrynium; Thalia*	América tropical, África	AM; E	-
32. Mayacaceae	*Mayaca*	Tropical; Fresh Water	E; S	Entomophilous
33. Orchidaceae	*Erythrodes; Habenaria*	Brazil, (with endemic specie of the Pantanal (*Habenaria aricaensis* Hoehne)	AM, E	Entomophilous

34. Philydraceae	*Philydrum*	Ásia; Australia	AM	-
35. Poaceae	*Arundo; Acroceras; Coix;Coleanthus; Echinochloa; Gynerium; Hemarthria; Hydrochloa; Hydrothauma; Hygroryza; Hymenachne; Imperata; Leersia; Luziola; Neostapfia; Orcuttia; Odontelytrum; Oryza; Panicum; Paspalidium; Paspalum; Pennisetum; Pseudoraphis;*	Cosmopolitan; Pantropical	AM; E; Fl	Anemophilous
36. Potamogetonaceae (include Zannichelliaceae)	*Althenia; Lepilaena; Groenlandia; Potamogeton; Pseudalthenia; Zannichellia; Zostera*	Cosmopolitan; Fresh (rarely brackish) water; marine and brackish genera tropical;	Fl; S	Anemophilous ; few hydro-anemophilous and hydrophilous (Zannchelliaceae)
37. Pontederiaceae	*Eichhornia; Eurystemon; Heteranthera; Hydrothrix; Monochoria; Pontederia; Reussia; Scholleropsis*	Pan-tropical and temperate American; Fresh water	E, S, Ff	Entomophilous
38. Ruppiaceae	*Ruppia*	Subtropical and Temperate; Salt and brackish water	S	Hydrophilous
39. Sparganiaceae	*Sparganium*	Temperate, Arctic, Malaysia and Australasia; Fresh Water	E; Ff	Anemophilous
40. Typhaceae	*Typha*	Cosmopolitan; Fresh water	E	Anemophilous
41. Xyridaceae (Abolbodaceae)	*Abolboda; Xyris*	Tropical South America; Fresh water	E	Anemophilous
E. Eudicots				
42. Ranunculaceae	*Caltha; Rununculus*	Temperates and frigid regions of the world	AM	Entomophilous
F. Core Eudicots				
43. Amaranthaceae	*Alternanthera*	South America	Ff or Fl	Entomophilous
44. Droseraceae	*Aldrovanda*	Europe; Asia	Ff	-

45. Haloragaceae	*Haloragis; Laurembergia; Loudonia; Meziella; Myriophyllum; Proserpinaca*	Cosmopolitan (but especially south temperate Some spp. Semi-terrestrial; all aquatic spp. in fresh water	E; S	-
46. Polygonaceae	*Polygonum*	Mexico; Wide distribution in South America	E	Entomophilous ; Hidrophilous
G. Rosids				
47. Melastomataceae	*Acisanthera; Nepsera; Rhynchanthera*	Central America and Brazil	AM, E	Entomophilous
48. Onagraceae	*Boisduvalia; Ludwigia*	Neoptropical; Wide in South America	AM, E	Entomophilous
H. Eurosids I				
49. Elatinaceae	*Bergia; Elatine*	Cosmopolitan (but *Elatine* mainly temperate, *Bergia* mainly tropical)	E; S	-
50. Euphorbiaceae	*Caperonia; Phyllanthus*	Tropical America	Ff	Entomophilous
51. Fabaceae	*Aeschynomene; Discolobium; Neptunia; Sesbania; Vigna*	Neotropical; Some countries in South America	E; Ff	Entomophilous
52. Podostemaceae	*Dicraea; Griffithella; Indotristicha; Mniopsis; Mourera; Podostemum; Tristicha; Terniola; Willisia*	Tropical (rarely subtropical). Flowing (often torrential). Fresh water	S	-
53. Polygalaceae	*Polygala*	Wide distribution in Brazil	AM; E	Anemophilous ; Entomophilous ; Hidrophilous
I. Eurosids II				
54. Brassicaceae	*Subularia; Cardamine; Rorippa*	Cosmopolitan (but chiefly from the temperate regions)	AM, E	Entomophilous
55. Clusiaceae	*Hypericum*	Temperate regions and tropical mountains	AM	Entomophilous
56. Malvaceae	*Byttneria; Hibiscus; Malachra; Melochia*; Pavonia	Some countries in South America	AM; E	Entomophilous
J. Asterids				
57. Balsaminaceae	*Hydrocera*	Eurasia; Africa and North America	Fl	Entomophilous

58. Hydrostachyaceae	*Hydrostachys*	Madagascar and Africa from the equator southwards	AM	-
59. Primulaceae	*Anagallis; Hottonia; Lysimachia; Samolus*	Some spp. cosmopolitan; West Africa; Asia	AM; E	-
K. Euasterids I				
60. Acanthaceae	*Justicia*	Tropical America	AM; E	Entomophilous
61. Convolvulaceae	*Ipomea*	Tropics of the world; South America	AM; E	Entomophilous
62. Gentianaceae	*Curtia*	Tropical South America	AM; E	Entomophilous
63. Hydroleaceae	*Hydrolea*	Tropical America	AM; E	-
64. Lamiaceae	*Dysophylla; Hyptis; Lycopus; Mentha; Pogogyne; Teucrium*	Wide distribution in Brazil	AM; E	Entomophilous
65. Lentibulariaceae	*Utricularia*	Pantropical; Central and South America	E; Sf	Entomophilous
66. Plantaginaceae	*Hippuris; Callitriche*	North temperate and cool South American. Fresh water; Cosmopolitan. Some spp. Semi-terrestrial; all aquatic spp. in fresh water	E; S	-
67. Scrophulariaceae	*Bacopa; Buchnera; Conobea; Craterostigma; Dopatrium; Hemianthus; Lindernia; Melasma;Micranthemum; Microcarpaea Monopera; Stemodia; Verônica*	Brazil; Some spp. in Tropical Africa and Australia	AM; E; Fl	Entomophilous
68. Solanaceae	*Schwenckia*	Perhaps restricted to the Center-West region of Brazil	E	Entomophilous
69. Sphenocleaceae	*Sphenoclea*	Pantropical; South America and United States of America	E	Entomophilous
L. Euasterids II				

70. Apiaceae	Berula; Carum; Centella; Cicuta;; Cynosciadium; Eryngium; Lilaeopsis; Limnosciadium; Hydrocotyle; Thorella; Oxypolis; Sium	Tropical and subtropical America	Ff	Entomophilous
71. Asteraceae	*Eclipta; Enydra; Eupatorium; Gymnocoronis; Pacourina*	Cosmopolitan; Tropical; Subtropical	AM	Entomophilous ; Some spp. ornithophilous and anemophilous
72. Campanulaceae	*Centropogon; Downingia; Grammatotheca; Howellia; Hypsela; Isotoma; Legenere, Lobelia; Mezleria; Poterella; Pratia*	Tropical; South America	AM, E	Entomophilous
73. Menyanthaceae	*Fauria; Liparophyllum; Menyanthes; Nymphoides;Villarsia*	Some ssp. cosmopolitan; Central and South America	E, Fl	Entomophilous
74. Rubiaceae	*Diodia; Pentodon*	Africa and American continent	AM, E	Entomophilous

Table 1. The main aquatic plants including bryophytes, pteridophytes and angiosperms with geographical distribution, pollination and life form. For angiosperms classification the APG II (2003) was used. Ff (Floating free); AM (Amphibiou plant); E (Emergent plant); S (Submerged); Fl (Floating-leaved plants); Epiphyte (EP).

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Biographical Sketch

Edna Scremin-Dias received her major in Biology from the Universidade Estadual de Maringá, Paraná, Brazil, in 1983, her M.Sc. in Botany from the Botany Department of the Universidade Federal do Paraná, in 1992, and her Ph.D. also in Botany, from the Biosciences Institute of the Universidade de São Paulo in

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