AQUATIC ANGIOSPERMS OF INDIA

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ABSTRACT

Some of the salient features pertaining to the taxonomy of a few interesting aquatic angiosperms and their distribution, variability of fruits and seeds, their economic importance, floral biology, anatomy, embryology and cytology are presented here. The varied and diverse pattern of distribution of some Indian aquatic taxa is described with examples. Certain unique embryological features noticed in some aquatic plants are pointed out. Though the data on the cytology of Indian aquatic angiosperms is rather meagre, it is evident that from the evolutionary point of view, polyploidy has played an important role in the differentiation of races, varieties and species. The nomenclature of Nymphaees Hill and Nathamandra Planch., is discussed. Finally, the ample scope present for further work for a better understanding of these plants is emphasised.

INTRODUCTION

Commenting on the flora of India Hooker (1907), in the preface to the last volume of "Flora of British India", remarked that "it is perhaps the richest, and is certainly the most varied botanical area on the surface of the globe..." The alpine vegetation in the Himalayas, the evergreen rain forests in the Western Ghats, Eastern Ghats and parts of Assam, the deciduous forests and scrub jungles distributed all over the country, and the deserts, almost devoid of vegetation, in Rajasthan and Kutch bear witness to this statement. All these different types of vegetation are due to the influence of elevation, temperature, rainfall and biotic factors (including the human destructive activities by the axe, fire or overgrazing). Scattered through the length and breadth of the country, we also find ponds and lakes in which aquatic plants dwell. Aquatic angiosperms are interesting forms of plants showing remarkable adaptation to their aquatic habitat, and as they are much less affected than land plants to seasonal variations, it is possible to study them more or less throughout the year.

Because of the existence of numerous borderline species, it is rather difficult to define aquatic plants. Muenscher (1944) considered aquatic plants as "those species which normally stand in water and must grow for at least a part of their life cycle in water, either completely submersed or emersed." A similar view has recently been expressed by Reid (1951) who defines water plants as those "whose seeds germinate in either the water phase or the substrate of a body of water, and which must spend part of their life cycle in water. This ecological grouping includes plants which grow completely submerged (except when flowering) as well as a variety of emergent types."

We have in this country about 140 aquatic angiosperms and in the short space available it will not be possible to give a detailed account of all of them. Hence, only their salient features in a generalized manner, covering as many aspects as possible, are presented in the paper.

SOME INTERESTING AQUATIC TAXA

Euryale ferox Salisb., a member of the family Nymphaeaceae, is a perennial, densely prickly, aquatic herb with a thick, short rootstock. Leaves floating, orbicular, corrugate. Flowers blue, violet or red, epigynous, partially submersed: sepals 4, inserted on the edge of torus; petals numerous, shorter than the sepals; stamens numerous, grouped in fascicles of eight; ovary 8-celled, sunk in the dilated top of the torus; stigma discoid, depressed, concave; ovules few, borne on parietal placenta. Fruit is a spongy berry, crowned by the persistent sepals and covered by stout prickles; seeds 8-20 with pulpy aril; testa thick; endosperm mealy; embryo small.

It is found in fresh-water tanks and lakes in Kashmir, Uttar Pradesh, Bihar, West Bengal, Assam, Tripura, Manipur and Arunachal Pradesh. In Bengal it begins to flower from January to February and fruits in May to June.

Callitriche stagnalis Scop., which is a member of the family Callitrichaceae is a small, aquatic, perennual herb, rooting at nodes. Flowers minute, naked, axillary, usually monocious, solitary or sometimes one male and one female together in the same axil; bracteoles white, membranous, caducous; stamen 1, forming male flower; pistil in the female flower consists of a bicarpellary ovary; each cell of the ovary becomes divided by a false septum and there is a single pendulous, anatropous ovule in each of the four loculi; styles 2, long, subulate, placed transversely like the carpels. Fruit coriaceous, indehiscent, the four carpels combined into two pairs, separating at length, when ripe, into one-seeded sections; seeds pendentulous with fleshy endosperm; cotyledons short, radicle superior.

It occurs from the Himalayas to the Deccan and in the Western Ghats, Nilgiri and Pulney Hills in ponds and wet places at an altitude of 2100-3000 m. It flowers and fruits in the month of February.

Trapa bispinosa Roxb. (Water-chestnut) a member of Trapaceae is a very ancient plant, and fossil remains of the nut are known from the tertiary era.
It has long stems, bearing pectinate leaves beneath the surface of water and curious rhomboid rosulate leaves with swollen aereychymatous petioles on the surface. The stoloniferous stem has well developed lacunae both in the pith and cortex. There is very little mechanical tissue. The leaves are transversely heliotropic.

There is no primary root. The submerged stem bears two types of adventitious roots. Those near the base of the stem fix the plant to the muddy substrate. The rest are free-floating fibrous roots, below the leaf bases. They are branched and have a feathery appearance and are unusual in being green and photosynthetic. Cross sections of these show a tetrarch stele with an alternating xylem and phloem and an exarch protoxylem.

Flowers hermaphrodite, axillary, solitary, peduncled, projecting above the water surface; calyx tubular short, the limb 4-parted, adnate to the lower part of the ovary, calyx lobes 2, becoming spines on the fruit; petals 4, sessile, white, inserted on the margin of the epigynous, cup-shaped, sinuous coronal disc which has a dentate margin; stamens 4 with elongated, dorsifixed divergent anthers inserted with the full of starchy material; the ovary semi-inferior, 2-celled with a conical apex; ovules anatropous, pendulous, solitary in each cell, borne on axile placenta; style subulate, stigma capitulate. The 2-thorned fruit is one-seeded drupe and the stony endocarp has two upwardly enclosing the inner blade. The flowers are small, numerous, pedicelled, on a central stipe. They get detached just before anthesis and the mature buds rise to the level of the water. Sepals 3; petals 3, broadly elliptic; stamens 3. alternipetalous, anthers oblong, subsessile, 2-locular, latrrosely dehiscing; pollen grains large. The female inflorescence is much longer, 1-flowered, long peduncled, and the spathe consists of 2 nearly free blades, one enclosing the other with both margins and persistent; sepal 3, oblong, imbricate; petals 3, longer, linear, subvalvate. wrinkled: staminodes absent; ovary rostrate, composed of 6 carpels, 1-locular, the six parietal placentae far protruding and forming six cavities; styles 5, each forked from the base, arms slender, limbricate. Fruit ovate, acuminate, indescent, spaths persistent; seeds obconical, angular, containing starch. The embryo has a large suspensor cell. The integuments stretch so much during post fertilisation stages that they equal the growing embryo. When the fruit ripens and bursts, the cesta breaks off around the hypocotyl and remains as a ragged, easily loosened cap on the top of the cotyledon.

It is reported from South Andamans and South India along the seacoasts of Pamban, Krsusadi Island and Cape Comorin, particularly in the inter-tidal regions.

_Halophila ovalis_ (R. Br.) Hook. f. is another marine angiosperm of the Hydrocharitaceae, forming a common association with_ Enhalus acoroides_. It is a dioecious, slender, marine, submerged, creeping herb, usually rooting at nodes. At the nodes there are two scales, one embracing the stem, the other enclosing a lateral, often undeveloped shoot which bears the leaves which rarely have two scales below their base. Leaves opposite, petiolate, linear-oblong to ovate, penninerved, entire or serrulate, rarely hairy; between the leaves a new shoot appears.
which again bears scales and one or more pairs of leaves and the inflorescence. The sessile spathe is composed of the two membranous free bracts, one overlapping the other, elliptic, obvate or suborbicular, acute, rounded to or indented and keeled. Flowers unisexual, solitary, rarely one or more male and one female flower in a spathe. Male flower is pedicellate, with three imbricate perianth segments; the three stamens alternate with the sepal and nearly sessile, linear-oblong, the 2-celled anthers dehiscence extrorsely; the pollen grains are in the form of long chains or filaments; pistilode is absent. The female flower is sessile and the inferior ovary is elliptic or ovate, one-celled and bears many ovules on two parietal placenta; the apex of the ovary terminates in a long beak crowned with the three reduced sepals; the styles are linear, 2, 3, or 5, filiform and papilllose all over. The ovate, rostrate, one-celled fruit has a membranous pericarp and is included in the spathe. The few to many, globose or subglobose seeds have a membranous testa and the thick embryo has a spiral cotyledon in a cavity at the side.

It usually occurs in sheltered localities along the sandy coasts and in back-waters. The plants grow on coral reefs gregariously along the coasts in Kruasadi Island, Papuan, Cape Comorin, in the Ennore, Chilka and Calcutta Salt Lakes and Andaman and Nicobar Islands. It flowers during September and October.

FRUITS AND SEEDS

The fruits are very variable and they are of the nature of drupes, capsules (sometimes pyxidia), achenes, utricles and nuts. Kausik (1946) has made some interesting observations on the fruit and seeds of Enhalus acoroides. The fruit develops suspended in sea-water at varying levels below the surface. The outer surface of the fruit is densely clothed over by numerous stiff bristles and the tissue within is soft and fleshy. Embedded within the soft tissue are a few large seeds placed loosely inside the cavities. When the fruit bursts, the seeds are exposed and come in direct contact with the surrounding seawater. Since the outer integument has numerous air-filled cavities, the buoyancy of the seed increases and hence, it does not immediately sink in water. Later, however, the thin seed coat comes off as a loose cap by becoming ruptured at the base and the embryo thus becomes naked. The seed coat remains for some time as a ragged, easily loosening cap on the top of the cotyledon. The naked embryo is conical in shape with a large cotyledon containing plenty of starch filled cells. The radicle occupies the flat portion of the embryo and is nonfunctional. The plumule is well developed and shows a number of young leaves arising in quick succession. At the base of the plumule and a little to the side is formed a second root which later comes out during the germination of the embryo in the soil. In connection with young leaves of the plumule there are certain axillary scale-like structures called squamulae. The heavy embryos of Enhalus leave the seed coat and sink in the sea-water immediately. They become buried in the soil where they at once begin to grow further. Thus the embryo is liberated from the fruit and this represents a distinct form of vivipary.

Though the seeds in the three aquatic species of Utricularia are very small, yet they are different in their external morphology. The seeds in Utricularia stellaris are tabular, prismatic with 4-6 usually sharp angles; in U. flexuosa the seeds are prismatic with sharp angles and slightly winged margins; and finally in U. evoleta the seeds are lenticular with a broad, dentate, corky wing. It will thus he seen that these characteristic shapes of the minute seeds can safely be used for the identification of these taxa, even when the other vegetative parts and flowers are wanting.

DISTRIBUTION

The distribution patterns of some of the aquatic Indian taxa are varied and diversified, and a few cases are cited here as illustrations. While it should be emphasised that the data available is far from complete, an earnest effort has been made to search for information. In the Nymphaeaceae, Nymphaea nouchali, N. stellata and Nelumbo nucifera are common throughout the warmer parts of India; but Euryale ferox is confined only to the northern and north-eastern parts of India extending from Kashmir, Alwar in Rajasthan, Uttar Pradesh, Bihar, West Bengal to Assam, Tripura and Manipur. A similar pattern of distribution is also noticed in some fresh-water taxa of Hydrocharitaceae reported from India. While aquatic taxa like Hydrilla verticillata, Nechamandra alternifolia, Valisneria spiralis and Ottelia alismoides are found throughout India, the free-floating (sometimes rooting in shallow water) Hydrocharis dubia mainly occurs in northern regions of India extending from Kashmir, along the eastern regions of Uttar Pradesh and North Bihar to West Bengal. The pattern of distribution of four species of Nymphoides is noteworthy. Nymphoides cristatum and N. indicum are very common throughout India. N. parviflorum is rather scattered in its distribution, occurring in the states of Assam, Rajasthan, Western Deccan Peninsula (states of Mysore and Kerala) along the coasts. N. aurantiacum is reported to occur so far only in the Western Deccan Peninsula in the states of Mysore and Kerala and in the southern end of Madras state. Under the same plan of distribution mention may be made about two species of Dopatrium of the Scrophulariaceae. While Dopatrium juncum which is an erect, slender, fleshy herb with pink flowers is common throughout India. D. lobeloides a taller herb with comparatively longer flowers occurs in South Deccan and near Madras in tanks and wet places.
The six species of *Myriophyllum* of the family Haloragaceae exhibit an extremely varied pattern of distribution. *M. spicatum* occurs in northern portions of Uttar Pradesh and north-western parts of Kashmir and *M. verticillatum* has been reported only from Kashmir so far. *M. indicum* occurs in Kashmir, northern parts of Uttar Pradesh and Bihar, West Bengal, Assam, Agartala, Manipur and in the East Coast from Ganjam southwards. *M. spatulatum* is reported from Khandala, Mahabaleswar in Western Ghats and Mohili in Sanguar District of Madhya Pradesh. Among the two remaining species, while *M. tuberculatum* is reported from fresh-water lakes, tanks and puddles in West Bengal, eastern parts of Orissa and Myore, *M. intermedium* occurs at higher elevations in eastern regions of Madhya Pradesh along the Western Ghats, especially in Nilgiris and in the dry southern regions of Andhra Pradesh. The distribution patterns of *Hydrocera triflora* (Balsaminaceae) and *Cardanthera divaricata* (Acanthaceae) are interesting in that the former species is reported to occur in Uttar Pradesh, West Bengal, Naga Hills of Assam and certain parts of South India, and the latter is rather restricted mostly to West Bengal, perhaps extending up to Assam.

From the point of view of distribution and evolution, the Podostemaceae, in particular, are of great interest, and the classical works of Willis (1922, 1940) on this problem are well known. In India the Podostemaceae are well represented and as many as nine genera have been reported so far. Majority of the species, however, are mainly confined to Peninsular India and most of them occur in the hill streams and rivers of the Western Ghats extending from Bombay downwards to Trivandrum. The only species that has extended eastwards towards the Eastern Himalayas is *Zeylanidium lichenoides* which is reported from central parts of Assam. Some of the species are particularly interesting because they are confined to only certain localised regions. Thus, *Zeylanidium johnsonii* occurs in Western Ghats in mountain streams of Malabar; *Willisia selaginoides* and *Podostemon subulatus* in Western Ghats at Anamalais and *Farmeria indica* in the Tambraparni river in Tinnevelly. Similarly, the two varieties of *Zeylanidium lichenoides* viz., *khandalaense* and *bhoerense* are reported from the Thul Ghat near Igatpuri and Khandala, Western Ghats.

**Economic Uses**

- Quite a number of aquatic plants are economically important; some are edible or of medicinal importance (Chopra, et al., 1950), and others yield a variety of useful products. The seeds of *Euryale ferox* which are of the size of a pea or cherry are roasted and eaten. On roasting the seed coat swells and bursts and can be easily peeled off. The seed flour is used as arrowroot, as it is nutritious and easily digested. The seeds are also used as a tonic. The carpels of *Nelumbo nucifera*, popularly known as seeds, are eaten in various parts of the country and this has been one of the causes for the gradual disappearance of this plant. *Trapa bispinos*, called commonly “Singara”, is cultivated because the 2-thorned fruit, which is a one seeded drupe, is eaten either raw or cooked, the edible portion being the starchy cotyledons. According to Cooke (1958), a curious yellow cake called “Bir” is prepared out of the flowers of *Typha angustata* and is eaten by all classes of people living in Sind. In certain parts of India the rhizomes, petioles and pericarps of *Nymphaea nouchali* are eaten (Santapau, 1960). Except the roots all other parts of *Monochoria hastata* furnish a relished dish. The young leaves, shoots and roots of *Ipomoea aquatica* are edible. The tuberous rootstocks of *Aponogeton crispum* are also edible.

The powdered rhizomes of *Nymphaea nouchali* are used as a remedy for piles, dysentery and dyspepsia. The rootstock of *Typha angustata* is used as an astringent and diuretic, and the tuber of *Cyperus corymbosus* as a tonic and stimulant. The flowers of *Nelumbo nucifera* are recommended as a cardiac tonic and in fever and diseases of the liver; the seeds form a cooling medicine for skin diseases. Plants of *Fissuea repens* are used for curing ulcers and skin diseases and leaves of *Monochoria hastata* for curing boils. *Nymphoides indicum* is sometimes used as a substitute for chireta (*Sauria chirayita*) in fever and jaundice. The leaves of *Hydrolea zeylanica* are considered to possess antiseptic properties and are applied as a poultice for callous ulcers. The infusion of the leaves of *Limnophila rugosa* are used as a diuretic and tonic. There are many medicinal uses for the leaves of *Pista striatotes*. They are made into poultice and applied to haemorrhoids. The juice of the leaves is boiled in coconut oil and the preparation used externally in chronic skin diseases. The leaves are mixed with rose water and sugar and given for asthma and cough and with rice and coconut milk for dysentery. The ashes are applied to the ring worm of the scalp.

The juice of *Limnophila indica* is rubbed over the body in pestilent fevers; it is also given internally with ginger, cumin and other aromatics in dysentery. The leaves, roots and seeds of *Asieracantha longifolia* are used as a diuretic and employed for jaundice, dropsy, rheumatism and diseases of the urinogenital tract. The roots of *Monochoria vaginalis* are chewed for toothache.

The bulk of the stem of *Aeschynomene aspera* is made up of light soft pith which has good insulating properties. The pith is largely used in making toys, artificial flowers and models. In the laboratory the pith is used for embedding plant material for cutting free-hand sections. It also finds use in the manufacture of swimming jackets and life-belts. The stems of *Cyperus corymbosus* are used for making fine mats in the districts of Tinnevelly,
Tanjore, Madurai, Tiruchirapalli, South and North Arcot of Madras State and West Bengal. A durable fibre for fishing nets is produced from *Enhalus acoroides*. Some of the aquatic members of the Gramineae like *Coix aquatica*, *Paspalium geminatum*, and *Leersia hexandra* provide good fodder for cattle. *Eichhornia crassipes* is used for fattening pigs. Both *Hydrola verticillata* and *Vallisneria spiralis* are cultivated in aquaria, the former in particular is a good oxygenator. Some aquatics like *H. verticillata* and *Eichhornia crassipes* are used as manure. *Halophila ovalis* is also sometimes used as manure in coconut and other plantations.

**WATER HYACINTH, AN OBNOXIOUS WEED**

The water-hyacinth (*Eichhornia crassipes*), a native of Brazil, has become a serious pest in Bengal, Assam and has gradually spread throughout India. It inhabits stagnant or slow-moving fresh-water such as broad rivers near their banks, lakes, canals, railway ditches, pools and tanks. Because of its luxurient growth and extremely rapid multiplication, the plant becomes a troublesome weed, covering the entire surface of water, crowding all other plants, choking water courses and greatly hampering navigation and fishing. Various methods like removal of seedlings and entire plants have been suggested. Another view put forward is to effect a change in the edaphic factors of the plant's environment and poison the plant with suitable chemicals.

**FLORAL BIOLOGY**

Corresponding to the special environmental conditions in which these plants live they also exhibit some remarkable features in their floral biology, particularly with reference to their pollination. Kausik (1939) has made very interesting observations on pollination and its influence on the behaviour of the pistillate flower in *Vallisneria spiralis*. The staminate flower has two stamens with slender filaments spreading apart at right angles. Each stamen bears distally, when the anther has dehisced, a mass of large pollen grains. The two masses of pollen grains of a given flower project beyond the margins of the sepals so that the pollen grains may immediately come in contact with the stigmas of the pistillate flower. The pistillate flower has a slender, inferior ovary and three stigmas, each of which is bifid with two leaf-like fleshy expansions curling slightly outside. These stigmatic lobes lie between the sepals and expose their inner surfaces, which are densely clothed with stigmatic hairs.

The pistillate flower develops under water and is brought to the surface at the time of pollination by the elongated slender scape. The latter, because of its great length, places the pistillate flower in a planting position on the surface of water. The floral parts are exposed on the surface on account of their weight, the surface film forms a slight cup-like depression about each pistillate flower. At this time, staminate flowers floating on the surface are moved along by currents or wind and may reach these depressions, when they tumble down and strike against the stigmatic lobes of the pistillate flowers. In this act a quantity of pollen is immediately shed on the stigmatic lobes; the pollen grains are as large as 50 microns and are found sticking to the receptive stigmatic surfaces. Frequently, the water is distributed by the formation of strong waves; on such occasions the pistillate flowers may suffer a temporary submergence and the associate staminate flowers generally lose their contact with the stigma and drift away. But with the passing of the wave, the pistillate flowers are again exposed in the surface depressions. The transfer of pollen to the stigmatic lobes proceeds favourably during the short intervals when the surface of water is fairly quiet between successive waves.

The pistillate flower develops under water and when its ovules are in the megasporocyte stage, it is little more than 2 mm. long, with a very short stalk measuring about a millimetre. The stalk gradually increases in length until it brings the pistillate flower to the surface of the water. The increase in length is largely due to an elongation of the individual cells of the scape. When the pistillate flower has reached the surface of water it is nearly erect but later gradually assumes a more or less horizontal position by the further increase of the length of the scape. The stigmatic lobes spread out in about two to four hours and pollination is effected under favourable circumstances in about six hours. After pollination the scape of the pistillate flower undergoes a special torsion which is first evident at the base of the ovary. This is followed by the formation of a number of coils in the scape. These coils then draw closer and tighten and the pistillate flower retreats under water where the fruit develops.

Studies on the mode of pollination and seed formation in *Eichhornia crassipes*, the common water-hyacinth, have been carried out by Agharkar and Bauerji (1930). According to them, the flowers open as a rule in the morning, soon after sunrise; on cloudy and humid days, however, they open later. The stigma stands high above the stamens in the bud stage. After the opening of the flowers, the stigma occupies a position lower than the upper three anthers. The three lower anthers are situated at the mouth of the corolla tube. The flowers are mesostylous. The dry pollen grains which are ellipsoid imbibe water very rapidly and become ovoid. From the structure of the flower and the relative positions of the stamens and stigma the flower appears to be entomophilous. Under natural conditions only about 35% of the flowers are pollinated. Bagging experiments have shown that self-pollination also occurs in this plant to a consider-
able extent. Germination of the pollen grain on the stigma takes place within an hour after pollination. The style is traversed by three longitudinal canals and the pollen tube traverses the style through these canals. The axis of the inflorescence bends downwards considerably after flowering and brings the flowers under water wherever a free water surface is available. Seed formation takes place only in inflorescences which are submerged in water. Among external factors, humidity and temperature appear to have a great influence in seed formation.

Recently, flowering has been induced in Lemna paucicostata cultured in Heller’s medium by exposure to short days (unpublished observations of Dr. S. C. Maheshwari).

ANATOMY

In addition to the several exomorphic adaptive modifications noticed in water plants, like stems in the form of stolons and offsets, dissected roots, swollen spongy floating roots, large ovate to rotund floating leaves with a thick deposition of waxy coating on their surfaces, dissected submersed leaves, heterophyll, and leaves with swollen petioles, they also present a number of interesting endomorphic features, especially in their internal anatomy. Some of these are an epidermis with a thin cuticle, presence of stomata on upper epidermis of leaf and stem surface, development of chloroplasts in the epidermis and superficial tissues of the stem, a very characteristic broad aerenchymatous cortex with raphides in the air-spaces and finally a poorly developed vascular tissue and pith.

At the same time, developmental and descriptive studies on the anatomy of certain hydrophytes have also been very useful for a better understanding about the exact origin and morphology of a particular tissue or organ. In Nuphar lutea the zigzag branches of the stem bear fibrous roots at the nodes and spongy bladder-like swellings or floats on the internodes. The floats are composed of aerenchymatous tissue which helps the plant to float. The aerenchyma originates from a phellogen in the outer part of the cortex and consists of cells with cellulose walls and living contents.

Arora (1954) has recorded the presence of well-developed bacterial nodules on the roots as well as the stem of Aeschynomene indica. The nodules arise close to the place of emergence of the lateral roots, and the ruptured tissue in this region constitutes the path of infection. While the root nodules are endogenous and arise in the pericycle, the stem nodules originate in the cortex. The nodule is differentiated into an infected bacteroid region and an uninfected portion. A single vascular strand differentiates at the base of the nodule and gives off six to eight branches which taper unequally to the apex. The vascular tissues of the nodule mature from the base outwards. The xylem and phloem are arranged collaterally. An endodermis with caspary bands surrounds each vascular strand. Degeneration of the nodule is accompanied by the formation of a layer of suberized cells at its base which in turn forms a protective seal when the nodule is sloughed off.

Occurrence of polystyly has been reported in Nymphoides cristatum (Lemma cristatum) and Ottelia alismoides by Majumdar (1938). Polystyly occurs in the cortical region of the stolons and in the petioles of the leaves in the former species; in the latter taxon, polystyly is seen in the peduncle and leaf-stalk. The cortical steles of Nymphoides have each an endodermis surrounding it without a distinct pericycle, while the steles of Ottelia have both endodermis and pericycle surrounding each of them. The endodermal cells in Nymphoides have well-developed Casparian strips and in both cases they are characterized by the presence of starch grains.

Trapa shows an interesting type of stem anatomy in having intraxylary phloem and a pith with large intercellular spaces.

From the point of view of anatomy, the Podostemaceae are particularly interesting (McIntosh & Chalk, 1957). The vegetative body of the plants consists of a thallus which exomorphically can be differentiated into portions which roughly correspond to stems and leaves. The plants are attached by hair-like structures which originate as extensions of the epidermal cells. Intercellular air-spaces which is a characteristic feature of plants living in aquatic habitats are seldom noticed in plants of this family. This is correlated with the habitat of these plants which is in rapidly moving well aerated water. Mechanical tissue, when present, is in the form of collenchyma which is well developed around the vascular tissue. In larger taxa the collenchyma becomes converted into sclerenchyma consisting of lignified prosenchymatous elements with slit-like pits. In the scattered simple conducting bundles the xylem is much reduced, but the bast, on the other hand, contains broad sieve-tubes and companion cells. Another characteristic feature is the occurrence of silica bodies, especially in the superficial tissue of the thallus. In some taxa they are so numerous that they form a kind of protective cover which prevents the plants from collapsing in times of drought. Stomata are unknown and the epidermis which is not well differentiated and the hypodermal tissue contain chlorophyll. Secretory cells and cavities occur in certain species and fungal hyphae traverse in these cavities.

The presence of floats which is a characteristic feature of the inflorescence of Utricularia stellaris is not usually seen in U. flexuosa. In exceptional cases, however, they are seen in the latter taxon as well and Deva (1953) finds that when such floats are present, they are much larger in diameter than those of U. stellaris. They are branched at the tip.
and the branches are further divided into fine capillary segments. Their number may vary from one to half a dozen on an inflorescence and are irregular in arrangement.

The float in a transverse section is circular. Multicellular glandular hairs are scattered on the epidermis. The stalk of the hair is two celled and the gland consists of two elongated cells or several enlarged cells. The cortex consists of a ring of air chambers and constitutes the main bulk of the float. On the outer side they are limited by the epidermis. The partitions separating the air chambers are one cell thick. In the centre there is a narrow stele with a pith and only two layers intervene between the chambers and stele. The vascular bundles are arranged in a ring. A noteworthy feature of the bundles is the dissociation of xylem and phloem from each other at various levels. Consequently, a transverse section shows the two tissues forming separate bundles in addition to others showing the usual conjoint condition. The conducting elements are very much reduced and the cambium is absent. These features and the presence of air chambers are associated with aquatic habit. In the branches of the floats the vascular elements, pith and the air chambers of the cortex go on diminishing. Finally, the entire stele in the centre is represented by just a single xylem cell associated with a few phloem-like cells, of which the outer represents the epidermis.

There is some controversy regarding the morphological nature of the floats. Barnhart (1916) feels that they are modified leaves. Haines (1923), Kendall (1952) and Lloyd (1942) also regard them as leaves. Arber (1920), on the other hand, has regarded them as shoots. The anatomical study of Deva (L.L.) shows that the stele in the floats is like that of the stem and hence, the floats are the nature of modified shoots.

Mitra (1945) and Mitra and Majumdar (1952) by their anatomical studies have explained the exact morphology of the ocreaceous stipule in Polygonum orientale. According to them, the leaf primordium in this taxon receives one median and many lateral traces and the node is multilacunar. From the axis, the base becomes free as a tubular sheath and it continues its free upward growth till the laterals deviate from their vertical course and bend to follow a united horizontal course towards the central region of the sheathing base. During the united horizontal course the laterals give out branches and these branches maintain further upward growth of the sheath as the free upper tubular portion (stipule). The base, thus, forms a mantle enclosing the core in the internode. The ocrea is actually the sheath plus the stipule.

The frond of the Lemnaceae has been interpreted as a stem functioning as a leaf, as a modified leaf and as a structure partly foliar and partly axial. Arber (1919) compared the structure of Pisidia with Spirodela and considered the lemnaceous frond to be axial at the base and foliar at the distal region. She interpreted the distal part of the frond as a “petiole phylloide” and considered the pockets on the lower side of Spirodela as being formed by “wings of leaf-sheath, terminating into two minute ligular flaps” and on the upper side by the axis. Goebel’s (1921) interpretation of the frond is based on the idea that the main shoot never develops in the seedling—the distal portion represents a cotyledon, the proximal, a hypocotyl; the side members (daughters fronds) continue to repeat this pattern. Here the “tendency to asymmetry” is stressed as an important characteristic of the family. Brooks (1940) who expressed a somewhat different view, interpreted the plant body of Spirodela as a single sympodial branch bearing a prophyll, a leaf and a bract and terminating in an inflorescence, all somewhat reduced and fused to each other. Lawalrée (1943) considers the complexity of Lemnaceae as derived from the simple, embryo-like Wolfia. The resemblance of the young embryo of Lemma minor to an adult Wolfia frond (Lawalrée, 1952) is advanced as an evidence in support of this; but most workers derive the Wolfiae by further reduction from the Lemnaceae pattern. Recently, Hillman (1961) has stated; “that any hypothesis reading the Lemnaceae as a series advancing with increased complexity has to explain away the increasing vascularisation in the direction of Wolfia to Lemna, a trend of no evident selective value given the environment and the size of the plants.”

EMBRYOLOGY

Some of the aquatic plants are singular in their embryology; certain unique and interesting features are noticed in the entire family, or in certain genera of a particular family. The previous work on the Podostemaceae and the comparatively recent studies of Razi (1949) and Mukkada (1960) on the Indian species of these plants have revealed the following noteworthy features: the pollen grains are single or united in dyads; the separating wall between the pollen grains is pitted and only one of them produces a pollen tube, the other presumably serving as a source of food material (see Maheshwari, 1959, pp. 156, 157); embryo sac development follows the reduced Allium type; antipodals are usually lacking in the small embryo sac; there is a single polar nucleus (or cell); a pseudoembryo sac is formed; endospore is absent right from the beginning; the basal cell of the two-celled proembryo becomes vesicular, coenocytic and forms a haustorium. The loss of endospore, the formation of the pseudoembryo sac and the divergent type of embryo sac can be explained as derivative characters which are in all probability due to the special mode of life of these plants.

The male gametophyte of Halophila ovalis of the Hydrocharitaceae has been studied by Kausik &
Rao (1942) and their observations on the formation of the filamentous pollen grains are interesting. During the development of the anther, the walls of the tapetal cells break down and their contents form a periplasmodium which is much less intrusive than in other taxa of this family. The microsporocytes are rather long and narrow and form a number of regularly arranged linear rows in each anther lobe. This linear arrangement is seen later also in older anthers when meiotic divisions in the pollen mother cells are completed and still later when the pollen grains are maturing. The divisions take place transversely in each mother cell, so that the resulting microspores are found in a row, and not according to the tetrahedral or isobilateral types met with usually in angiosperms. Further, the linear tetrads of microspores formed by the mother cells in each row remain together without separating. In these filaments, clear spaces are seen at regular intervals and these indicate the limits of each individual tetrad of microspores formed by one mother cell. A number of such chains of microspores in the form of a bundle are found in each anther lobe and the whole bundle escapes as such when the thin anther wall dehisces. In the fully developed pollen grains the gametophyte consists of a tube nucleus and two small male cells. The bundle of pollen grains united together in chains floats on the surface of water, where it becomes caught and moves in the exposed stigmatic lobes of the pistillate flowers.

Very remarkable lateral endosperm haustoria are reported in Monochoria hastata, a member of the Pontederiaceae by Banerji and Halder (1942). The early stages of endosperm development follow the Helobial type. The chalazal endosperm chamber remains small and has only about half a dozen nuclei or even less. But the micropylar chamber shows active nuclear divisions and soon gives rise to two tubular outgrowths (one on each side of the chalazal chamber) which grow downward and invade the tissue of the chalaza. Subsequently, the main body of the chamber also elongates and fuses with the two haustoria to form a continuous mass of endosperm cells with the chalazal chamber still recognizable at the base.

The importance of comparative embryology as a tool for better understanding of the systematic position of a family or genus cannot be overestimated. Some excellent examples on this problem have been furnished by the detailed embryological studies on aquatic plants. A few such cases are discussed here.

The family Callitrichaceae includes a single genus, Callitriche with about 30 species of slender, semi-aquatic plants, extremely reduced in both vegetative and floral structures. The exact position of Callitriche has been a matter of dispute. According to Bentham and Hooker, Brown, De Candolle, Hegelmaier and Hutchinson, it is related to the Haloragaceae. Clarke (1865) felt that it should be placed under the Caryophyllaceae and Baillon (1858), owing to the reduction in floral structure, included Callitriche in the Euphorbiaceae. Pax and Hoffmann (1931) felt that it should be assigned to a separate family Callitrichaceae, close to the Euphorbiaceae.

The embryological characters in Callitriche make these assignments very unlikely. Jörgensen (1925, 1925) showed the existence of tenuinucellate ovule, a massive single integument and a cellular endosperm which forms well developed micropylar and chalazal haustoria. These features which are so characteristic of the Tubiflorae, together with the four-lobed nature of the ovary, have suggested a relationship with the Verbenaceae. The recent study of Nieuwes (1952) has fully confirmed this and has shown that even the embryo development in Callitriche and Verbena is essentially similar.

Subramanyam (1955) has shown that the Podostemaceae resemble the Crassulaceae in having a secretory type of anther tapetum, binucellate pollen grain, presence of starch grains in both pollen and embryo sac and in the haustorial behaviour of the basal cell of the embryo. In addition to these features, Crassula aquatica, a member of the Crassulaceae, has a mode of life somewhat similar to that of Podostemaceae. It has the most reduced endosperm in the Crassulaceae and this may well form a transitional stage leading to the complete suppression of this tissue in the Podostemaceae. It may also be pointed out here that on the basis of embryological features Maheshwari (1945) has concluded that it is "almost certain that the Podostemaceae are much reduced apetalous derivatives of the Crassulaceae".

The family Lemnaceae is considered by most botanists (Engler, 1871; Arber, 1910; Hegelmaier, 1886; Hutchinson, 1923b; Pule, 1938; Rendle, 1953; Wettstein, 1935) to be allied to the family Araceae and it is thought that the Lemnaceae have arisen as a result of regressive evolution in the following sequence (see Lawrence, 1931): Araceae (Pistia)—Spirodela—Lemna—Wolfia. According to Lawalrée (1943) the family does not show a close affinity with the Araceae, but has been derived from the Helobiales.

The investigations of Gupta (1933) and the detailed studies on the embryology of the Lemnaceae (Maheshwari, 1934, 1936, 1939) and Araceae (Maheshwari & Khanna, 1956) have shown that the Lemnaceae and Araceae resemble each other in the following features: successive divisions of the microspore mother cells, presence of a true periplasmodium, three-celled pollen grains (although in several aroids, mature pollen grains are two-celled), periclinal divisions in the nucellar epidermis, formation of a "nucellar cap", cellular endosperm, occurrence of an endosperm caecum at the chalazal end and the development of an operculum. The only major feature where the two families differ concerns the development of the embryo sac. In
the Lemnaceae the embryo sac is usually bisporic (Gupta, l.c. Lawáre'a, 1952; Maheshwari, 1954), while in the Araceae the development is generally monosporic. However, even in the Lemnaceae, Spirodela has a monosporic eight-nucleate embryo sac (Maheshwari, 1958). In the Araceae also it may be recalled that in certain cases, viz., Homalomena alba and H. rubra (Jüessen, 1928) bisporic embryo sacs have been reported.

The embryo sac in the Lemnaceae is bisporic, endosperm is cellular with a short chalazal haustorium and early divisions in embryogeny are irregular. None of these features is shared by the Helobiales. In all the families of this group, except the Alismataceae and Butomaceae, the embryo sac is monosporic. Even in Butomaceae, Butomus umbellatus has a monosporic embryo sac (Holmgren, 1913; Roper, 1952). The endosperm in the Helobiales is Helobial or Nucellar. The first division of the zygotic result in the formation of a terminal and a basal cell of which the latter remains undivided and becomes hypertrophied. On the other hand, in both Araceae and Lemnaceae the endosperm is cellular with a short chalazal endosperm caecum and the mode of embryo development is also similar.

The recent studies of Maheshwari (1951, 1956, 1958) and Maheshwari and Khanna (I.c.) indicate a close alliance between Araceae and Lemnaceae and have also shown that apart from the similarities between the two families in both megasporogenesis and endosperm development, the genus Spirodela constitutes a connecting link between the aroids and duck-weeds. These studies thus offer strong support to the assignment of Lemnaceae to Spathiflorae along with the Araceae as first suggested by Engler (I.c.).

The genus Trapa has been placed variously by different systematists. Bentham and Hooker (1883), Rendle (1952) and Hutchinson (1959a) placed it in the family Oenacraceae. However, as early as 1908, Raimann had erected a new family Hydrocaryaceae to accommodate the genus Trapa. Wettstein (I.c.) supported this view, while Pule (I.c.) stated that in the absence of any genus named Hydrocarya the family name should be changed to Trapaccaceae. The embryological features of Trapa (Ram, 1956) have provided very convincing data for its removal from Oenacraceae and assignment to the new family Trapaccaceae (Pule, I.c.). There are many pronounced dissimilarities between the embryological features of Trapa and Oenacraceae. In Trapa the ovary is semi-inferior, bilocular with a single pendulous ovule in each chamber; the pollen grains are pyramidal with three multifoil meridional crests; the chalazal megaspore invariably functions and the embryo sac is of the Polygonum type; endosperm is absent; the embryo conforms to the Solanaceae type, has two extremely unequal cotyledons and a well developed suspensor and a suspensor collar. On the other hand, in the Oenacraceae, the ovary is inferior, mostly tetraocular with many ovules in each chamber; pollen grains are basin-shaped, surrounded and bound together in long strings by 'tibris' (Beer, 1906); usually the micropylar megaspore develops and the embryo sac is of the Oenothera type; the endosperm is nuclear and the embryogeny corresponds to the Onagraceae type; the cotyledons are equal and the suspensor is short and inconspicuous.

Eames (1953) on anatomical evidence has expressed the view that Trapa does not belong to Oenacraceae and is not even closely related to it. Sphaerophyta occur commonly and the vascular bundle lacks a cambium.

Morphologically Trapa differs from the members of the Oenacraceae in having floating leaves with inflamed petioles; long, uniseriate, multicellular hairs on the petioles, pedicel and lower surface of the leaves; branched assimilatory roots; a single whorl of stamens; and two to four upwardly directed spines on the one-seeded fruits.

It is, therefore, evident that embryology, anatomy and morphology of Trapa fully justify its removal from the Oenacraceae and its inclusion in the newly erected family, the Trapaccacea.

CYTOLOGY

The data on the cytology of the Indian aquatic angiosperms is rather meagre and chromosome numbers for about 50% of the species are still not known. But with the information available, some points of interest are evident and they are briefly presented here. The chromosome numbers range from 2n = 10 as in Callitriche stagnalis (Löve & Löve, 1956) and Coix aquatica (Venkateswarlu, 1958) to 2n = 100 as in Nymphoides alternifolia (= Lagarosiphon roxburghii—Sharma & Bhattacharya, 1956). (The chromosome numbers in two European species of Callitriche, viz., C. hermaphroditica and C. truncata both with 2n = 6 is the lowest record and that in Nymphoides gigantea, an Australian species with 2n = 224 is the highest record for aquatic plants—see Darlington & Wylie, 1955; Löve & Löve, 1961).

From the evolutionary point of view polyploidy has played an important role in the evolution of races, varieties and species. Thus, in Hydrilla verticillata two races with 2n = 16 and 24 are known (Sinoto, 1929; Rao, 1950; Sharma & Bhattacharya, i.e.). While Jørgensen (1927) and Rao (l.c.) have reported 2n = 20 in Vallisneria spiralis, Sharma & Bhattacharya (l.c.) have recorded 30 and 40 somatic chromosomes in the races studied by them. Diploids with 2n = 14 (Harada, 1943) and tetraploids with 2n = 24 (Chase, 1947) have also been reported in Najas minor. (Najas guadalupensis, a species from West Indies, provides a classical example of polyploidy and six races with 2n = 12, 24, 36, 42, 48, 54 and 60 have been recorded by Chase,
Laggrospirnop \( \text{Roxb.} \) is a diploid \( 2n = 22 \) (Rao, I.c.), and the somatic numbers reported so far are 24 (Rao, I.c.), 44 (Islam, 1930), 66 (Rao, I.c.) and 72 (Narasimha Murthy, 1935). According to Rao (I.c.) the different races differ in their distribution, the diploids having a restricted range of distribution compared to the polyploids. *Polygonum orientale* (Doida, 1960) and *P. pulchrum* (Löve & Löve, 1942) are diploids with \( 2n = 22 \) while *P. glabrum* is a hexaploid with \( 2n = 66 \) (Sundara RagHAVAN & Arora, 1958). Compared to the somatic chromosome number in the diploid races of *Najas* minor \( (2n = 12) \), *Najas graminea* with \( 2n = 24 \) is a tetraploid (Harada I.c.). The diploid chromosome numbers reported in *Nymphaea* are \( 28 \) in *N. stellata* (Janaki Ammal, 1959), \( 84 \) in *N. stellata var. versicolor* (Sundara Raghavan & Arora, I.c.) \( 66 \) in *N. rubra* (Janaki Ammal, I.c.) and \( 56 \) and \( 84 \) in *N. lotus* (Langlet & Söderberg, 1927; Sundara Raghavan & Arora, I.c.). In the species from abroad, in addition to \( 2n = 28, 56 \) and \( 84 \), chromosome numbers as high as \( 112, 160 \) and \( 224 \) are also known (see Darlington & Wylicz, I.c.). The dominant role of polyploidy in the evolution of the different taxa is evident from the foregoing account.

### NOMENCLATURE

Nomenclature of plants has always been a headache to students of Botany and rather a very intriguing and difficult problem to researchers in Systematic Botany. The aquatic plants are no exception to this and careful studies have resulted in a clearer understanding of the identity of some of our plants. The nomenclature of two aquatic viz., *Limnanthemum* Gmel. and *Lagarosiphon* Harv. is briefly discussed.

Santapau (1962) has recently drawn attention to the nomenclature of *Nymphoides* versus *Limnanthemum*. According to him, O. Kunzte in Rev. Gen. Pl. 429, 1891, gives *Nymphoides* (oides) Ludw. 1737 in place of *Limnanthemun* Gmel. 1769. The name *Nymphoides* for this genus has been accepted among others by Merrill and Perry, who in Journ. Arn. Arbor. 30: 45, 1949 list two species under *Nymphoides* Hill. Some authors credit the name to Medikus 1789, apparently considering the publication of the name by Hill invalid. *Nymphodes* Ludw. 1737 must be left out of consideration, as being prior to 1753, in accordance with Art. 13 of the International Code of Botanical Nomenclature (1961). The question is whether John Hill, in British Herbal, 1736, may be accepted as the author of the name. The fact that Hill does not consistently follow the binomial system of nomenclature would invalidate all his specific names. If we consider Hill's generic names as invalid and accept only *Nymphoides* Medik. 1789 as valid, then *Limnanthemun* Gmel. 1769, has priority and should be retained. But Santapau (I.c.) points out that he cannot find anything in the code that would make generic names, properly described and published, invalid. The nomenclature of the two common Indian plants is as follows:


Subramanyam and Balakrishnan (1961) in their paper on "The genus *Nechamandra* in India" have pointed out that in all Indian floras a very problematic plant of the Hydrocharitaceae is described under the genus *Lagarosiphon*. Hooker (1888), Prain (1903), Cooke (1958) and Duthie (1960) describe it under the name *Lagarosiphon roxburghii*; Haines (1924) and Fischer (1947) place it under *Lagarosiphon alternifolia* and this name has been followed by a number of subsequent workers. Hutchinson (1950) differentiates *Nechamandra* from *Lagarosiphon* as follows:

- Male flowers with 3 fertile stamens, sometimes accompanied by staminodes; leaves alternate or veriscillate... *Lagarosiphon*
- Male flowers with 2 fertile stamens, unaccompanied by staminodes; leaves alternate... *... Nechamandra*

Further, Hutchinson (I.c.) states that the genus *Lagarosiphon* is confined to Tropical and S. Africa, whereas *Nechamandra* occurs in S. E. Asia and N. E. & Tropical Africa. A careful study of fresh specimens from various localities in India has revealed that the Indian specimens of this taxon show only 2 fertile stamens which are never accompanied by staminodes. Therefore this taxon must come under the genus *Nechamandra*.

The genus *Nechamandra* was first described by Planchnon in Ann. Sc. Nat. ser. 3: 11: 78, 1849, and under the genus he gave *Nechamandra roxburghii*, as the only species from India. Since the earliest specific epithet for this taxon is *alternifolia* (under the genus *Vallisneria* by Roxburgh), the correct name, according to Art. 55 of the code, is *Nechamandra alternifolia*. This combination has already been made by Thwaites in Enum. Pl. Zeyl. 332, 1864. The nomenclature of this taxon is given below:

CONCLUSIONS

It can be seen from the present account that the aquatic angiosperms are an extremely fascinating group of plants presenting an array of interesting features. These plants are well represented in our country, especially in the states of Kashmir, Uttar Pradesh, Madhya Pradesh, Bihar, Bengal, Assam and certain districts of Madras and Kerala. In comparison to the large number of aquatic angiosperms available, information on the structure and germination of seeds, floral biology with particular reference to pollination, distribution, embryology and cytology is rather scanty. Careful observations on these aspects will throw light not only on their life histories but also on their origin and patterns of distribution. Intensive explorations conducted in various localities are a necessary prerequisite for such studies. Particular mention must be made about the Chloronous numicus of many of the aquatic taxa. A detailed cytological study of these plants from different regions is likely to throw light on the evolutionary trends, particularly with reference to the role of polyploidy in the differentiation of races and species. Another fruitful line of work would be culturing these plants in suitable glass tanks or small artificial ponds to study their patterns of growth. There is thus ample scope for Taxonomists, Embryologists, Cytologists and Physiologists to tackle the different aspects of the problem relating to these plants and the data accrued, if pooled together, will help us a great deal in a better understanding of our aquatic plants.

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LITERATURE CITED


