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STUDIES ON THE INDIAN *UTRICULARIA* LINN. —A REVIEW¹

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I am deeply conscious of the signal honour done to me by the Indian Botanical Society by awarding the Vishwambar Puri Medal for the year 1978. I consider myself lucky because I had the good fortune of knowing Professor V. Puri intimately for a little more than three decades from the time he started his career at the Meerut College, Meerut. His brilliant studies and authoritative knowledge on floral morphology of Angiosperms have brought international fame to our country. Before I present my address on this occasion, I will be failing in my duty if I do not express my deep sense of gratitude and respects to Professor M.A. Sampathkumaran and Professor L. Narayana Rao of Central College, Bangalore, and Professor P. Maheshwari of the Delhi University under whom I had the privilege of learning Botany, particularly in the disciplines

of Angiosperm morphology including Embryology and Taxonomy. These three Professors who are unfortunately no more with us, have left an indelible impression on me and they were a source of inspiration to many a Botanist of our country. Further, I would like to pay my respects to two more great teachers, Professor H.P. Banks and the late Professor A.J. Eames of the Cornell University, Ithaca, N.Y., under whom I had the good fortune of studying various disciplines of Botany. I have been brought up in a tradition where the Guru is accorded the highest place of honour.

INTRODUCTION

The genus *Utricularia* Linn., falls under the group of Carnivorous Plants called commonly Bladder Worts. About 400 species of angiosperms belonging to 5 families are known to be carnivorous (Heslop-Harrison, 1976) and *Utricularia*, one such carnivorous plant is included under the family Lentibulariaceae. These insectivorous plants depend for part of their mineral nutrition on the capture and digestion of small animals, mainly the Arthropods. Charles Darwin nearl a

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little more than a century ago (1875) was mainly responsible for the study of physiology of plant carnivory. Later, a very comprehensive work on all aspects of insectivorous plants is by Lloyd (1942). A fairly recent work on the genus *Utricularia* in Africa (south of the Sahara) and Madagascar is by Taylor (1964). Certain aspects of trap structure in *Utricularia* occurring in India are described in the classical work on Water Plants by Arber (1963), Aquatic Angiosperms by Subramanyam (1962) and in the recent treatise on the Biology of Aquatic Vascular Plants by Sculthorpe (1971). The twining, capturing and digesting mechanisms to devour insects have evolved in these carnivorous plants in such a way that they augment their supply of mineral nutrients thus enabling them to survive in habitats where few other plants can live (Heslop-Harrison, 1978). During the past ten years electron microscopy and high resolution cytochemical and biochemical methods have thrown new light on the structure and functions of these organs of the plant, that are involved to capture and digest the prey and the process of digestion itself (Heslop-Harrison, 1976).

With this as a brief introduction, I would like to confine myself to a general review of the studies on the genus *Utricularia* in India by me and others from various disciplines of botany. Incidentally, I have been interested in this genus for the past 20 years and all the species known from the sub-continent of India have been collected on a population basis and identified.

DISTRIBUTION AND TAXONOMY

About 150 species of *Utricularia* are reported with a world wide distribution (Heslop-Harrison, 1976). In India so far

30 species have been reported; of these, basing upon a tentative classification on their habits they can be classified into aquatic, epiphytic and terrestrial species; thus there are 5 aquatic species, 4 epiphytic species, and the remaining 21 terrestrial species inhabiting, marshy to semi-marshy regions or wet soils. Among these species not all of them are described by Clarke (1884) in the Flora of British India by Hooker et al., or in the Regional Floras of India because they are either new species or new records or imperfectly known species; the new species described by Blatter and McCann (1931) are *Utricularia equiseticaulis* Blatter and McCann and *U. ogmosperma* Blatter and McCann; the new records reported by Saxena during 1965, 1966 and 1970 respectively are *U. pubescens* Sm., *U. arenaria* A.DC., and *U. australis* R.Br.; Clarke (*l.c.*) has treated *U. minutissima* Vahl, as an imperfectly known species; it was reported to have been collected from only Malacca (*Koenig*), but this later turned out to be another new record for India (described as *U. liliput* Pellegrin (Subramanyam and Balakrishnan, 1960), a detailed description of which with illustrations was provided by Nair (1965).

In general, the plant body consists of ramifying system of slender stolons bearing traps for capturing small animalcules, leaves and small irregular-shaped root-like structures; traps are also borne on the linear to linear-spathulate leaves; the erect scapes arise on the stolons which arrange in rosettes and bear blue, purple or yellow flowers; the fruits enclose a number of minute seeds borne on a free central placenta. According to Heslop-Harrison (1976), the capturing device in *Utricularia* traps shows a trapping mechanism of the suction trap type; again according to her the digestive enzymes in

the bifid or quadrifid glands of *Utricularia* are hydrolases of the nature of esterase, acid phosphatase (non-specific) and protease.

Of the 5 aquatic species *U. aurea* Lour., *U. exoleta* R.Br., and *U. stellaris* Linn.f., show a wide range of distribution in the various states of the sub-continent of India. While *U. australis* R.Br., has a restricted distribution known only so far from Hassan District (Karnataka) and Indore District (Madhya Pradesh). *U. minor* Linn., has been reported so far from the high altitude ranges at Ladakh (3300 m), Spiti (4300 m) and Sikkim (3667 m). Among the 4 epiphytic species the most widely distributed in a number of states is *U. striatula* Sm.; it prefers higher altitudes, and is closely distributed all along the western ghats. The 21 terrestrial species show a varied distribution throughout the states of India. *U. equiseticaulis* and *U. ogmosperma* are more or less known from their type localities at Panchgani and Mahabaleshwar which are closely situated in the Maharashtra state and hence may be regarded as endemic to this region and according to Mahabale (1966) these are progressive endemics; *U. arenaria* is known from Pachmarhi (Madhya Pradesh), *U. pubescens* from Rajpur, near Dehra Dun (Uttar Pradesh) and Barapani, near Shillong (Meghalaya); while *U. albo-caerulea* Dalz. is restricted to south western Maharashtra, *U. roseo-purpurea* Dalz., is confined to the high altitude ranges of western ghats of only Kerala and Tamil Nadu respectively. The other terrestrial species show a fairly wide distribution and *U. caerulea* Linn., in particular shows a very wide distribution because it is reported in as many as twelve states. A comparison of these species with the closely situated Sri Lanka and the large land mass of south Africa

(Taylor, 1964) shows that while nine of these species occurring in India are common to India and Sri Lanka (Trimen, 1895), nine species are common to south Africa (Taylor, 1964, 1973).

Two interesting species are *U. reticulata* Sm., and *U. minutissima* Vahl because they represent the extremes in the relative size of these plants and other morphological features. *U. reticulata* represents a striking species because it is the tallest species of *Utricularia* occurring in India. It is usually found in rice-fields all along the west coast at low elevations; it produces erect interlacing scapes up to 25 cm or more long, twining on the stems of rice plants; the scapes bear large flowers with blue-violet corolla, the palate reticulated, with pale blue and white. At the other extreme the minutest species occurring in India is *U. minutissima* (Subramanyam, 1977). The plant body of these plants is visible outside only as a very short, simple, erect, filiform, brownish-purple scape 1.5–4 cm long with sparsely arranged basifixed bracts and bearing one to three very small light pink to pinkish-red flowers. Other unique features (Nair, 1965; Subramanyam, 1977) of these plants are the following: stolons mycelium-like, very much branched bearing numerous tiny traps and linear one-nerved leaves about 1 cm long; extraordinary minute traps borne on comparatively long stalks which are united with the wall of the trap along the posterior top corner so that the trap hangs from the stalks; latero-terminal narrow, circular mouth for the trap flanked on either side by an oblique fan-like wing consisting of paired vesicular cells one in each pair with a clavate gland at the tip; and the anterior end of the wall of the trap extending upwards into a flat, acute, slightly bent plate. It is because of the minute reddish-brown scapes simulating

the surrounding brown water-logged soil and mycelium-like stoloniferous underground plant body that this taxon had remained unnoticed and not collected since a long time in this country. While the majority of the utricularias are glabrous, two species *U. hirta* Klein ex Link (Joseph and Ramamurthy, 1961) and *U. pubescens* Sm. (Saxena, 1965; Rao and Joseph, 1967) have their scapes and floral parts finely hairy or setulose.

LEAVES

The leaves recently described by Taylor (1976 p. 565) as "plus or minus leaf-like photosynthetic organs" are variable in their shapes. They are regarded as modified stems. In the aquatic species the leaves are whorled, finely dichotomously divided into capillary segments, the ultimate segments sometimes finely setulose. In the case of *U. stellaris* at the base of these leaf-segments, leaf scales or auricles are present whose margins are deeply divided into linear ciliate segments; this distinct character serves in identifying this plant easily even in the vegetative condition. In the terrestrial species the leaves usually arise alternately or sometimes exhibit a rosette-like arrangement near the base of the scape. They are more or less linear or linear-spathulate, usually uninerved or trinerved sometimes connected by cross connections or even sparsely net-veined. In the case of *U. pubescens*, however, the numerous scattered leaves on the stolons are long petiolate, and peltate; the orbicular lamina is horizontal, fleshy, 1-5 mm in diameter; the margin is free and the venation is radiately forked or dichotomous; further the abaxial surface of the lamina is covered with numerous mucilaginous glands.

In the epiphytic species like *U. furcel-*

lata Oliver, *U. kumaonensis* Oliver, and *U. striatula* Sm., the leaves borne on long petioles are orbicular or reniform and persistent during anthesis and all of them characteristically exhibit an open dichotomous pattern of venation. The elaboration of this pattern of venation has been described in a detailed manner in *U. striatula* and its closely allied epiphytic species (Subramanyam and Yoganarasimhan, 1979). Along with this open dichotomous venation in the leaves, such interesting features as vein-approximation, isotomous branching, vein-anastomoses, blind vein-endings and very rarely cases of unconnected vascular strands were observed. An attempt has been made to explain the morphological significance of dichotomous venation which is regarded as may be due to reduction.

Very near the scape and borne on some of the stolons are root-like structures (called rhizoids by Taylor, 1964) with varied shape. They are short, stumpy and dichotomously branched in *U. aurea* and short and botryform in *U. exoleta*; in some of the terrestrial species like *U. baouleensis* and others they arise as clavate outgrowths arranged pinnately along the length of the stolons, particularly those arising from the base of the scape in a radiating manner. Since they are vascularised and endogenous they should be regarded as roots. In *U. roseo-purpurea* (Subramanyam and Banerjee, 1968) these short roots arise in a fasciculate manner from the base of the scape and externally they are beset with numerous short-stalked, button-shaped glands.

TRAPS

The traps are called bladders or utricles. They form a characteristic part of the underground stoloniferous system.

They are large in number, and usually borne on short delicate stalks on the stolons and sometimes on the petioles of the leaves and even on the abaxial surface of the delicate bifacial leaves. Exceptionally, in the epiphytic species the traps never occur on the leaves. The traps vary considerably between different species in shape, size, position of the mouth and the appendages to the mouth and their door. The chief function of these is trapping and later digestion of very minute animalcules. In general, the traps are more or less globose or ovoid and more or less laterally compressed. Details of the structure of the traps in certain Indian species of this genus have been provided (Nair, 1965; Subramanyam and Abraham, 1967; Subramanyam and Bannerjee, 1968). There are numerous, short stalked, small globular glands, distributed all over the surface of the traps. Since the outer epidermis of the traps is cutinised, the function of these glands or hydrpotes appear to be absorption. The mouth of the trap has a distinct rigid rim all round with reference to the stalk and it is lateral (*U. bifida*), latero-terminal (*U. minutissima*), terminal (*U. caerulea*, *U. kumaonensis*, *U. roseo-purpurea*) and basal in position (*U. baouleënsis*, *U. graminifolia*, *U. scandens* ssp. *scandens*, and *U. squamosa*). The upper side of the edge of the mouth which forms the dorsal lip is continued into branched multicellular processes called the antennae or appendages with or without glands. The antennae are unbranched as in *U. bifida*, *U. graminifolia* and others and branched into two to three branchlets in *U. baouleënsis*; in *U. kumaonensis* the appendages ramify further into four or five and in *U. striatula* they are numerous. Since most of these species occur in wet sandy or marshy habitats the branches of the

antennae help in the retention of capillary water, thus aiding an early entry of the prey into the mouth of the trap.

Each branch of the antenna ends in a uni- to multi-seriate filamentous hair which in turn bears an ellipsoid stalked gland at its tip as in *U. baouleënsis* or a spherical stalked gland as in *U. scandens*; the basal region of the two branches of the antennae in *U. kumaonensis* is expanded where numerous, three-celled spherical glands are present all along the inner surface which faces the upper rim of the mouth. In addition, three-celled glands are also present on the antennae. In a median longitudinal section, the wall of the trap surrounds a central cavity and consists of two layers, of which the inner bears digestive glands which are called bi- or quadrifids. The mouth of the bladder is associated with a complicated trap-door mechanism. The mouth is guarded by two valves of which the upper is larger, called the door, and the lower a small, membranous structure called the velum. Attached to the upper rim of the mouth is the door, curved on its outer surface; it hangs down and is continued backwards for some distance where it is free and lies on the threshold. The outer surface of the door is beset with a number of stalked multicellular glands. The parenchymatous cells of the door are arranged in a semi-circular, concentric rings and peculiar in having plicate margins which feature is conspicuously seen in *U. kumaonensis*. The lower semicircular rim of the mouth which consists of three to four layers of parenchymatous cells is continued into the cavity of the trap in the form of a cylindrical horseshoe-shaped, two-layered structure called the threshold whose two layers are appressed and fit into each other. The door closely fits into the threshold. Along the lower, or ventral basal

region of the mouth and projecting inwards freely is the tiny structure called the velum.

The trap mechanism is interesting. It is seen that the traps are usually found in two states; some with concave and others with convex sides. If an animalcule swims very near the mouth of the empty trap with concave walls and touches only the irritable hairs projecting into the apex of the valves it will be found that on touching the hairs the concave sides of the trap shoot out, becoming convex and at the same time, water with the animalcule is sucked into the trap. The entire process is extremely quick and it is impossible to observe directly anything more of what happens than the shooting of the walls and the filling up of the trap with water. According to Ekambaram (1916, 1918, 1926) who has studied the structure and mechanism of the traps in *U. aurea* (syn. *U. flexuosa*) the valve is made to assume a dome-shape by a differential change of dimensions in the cells of the two layers of the larger portion and that this dome is stretched out and made more rigid by the behaviour of the marginal tissue. Simultaneously with these changes, the walls shoot out and the water along with the animalcule is sucked in. With the immediate passing off of the effect of irritation the valve returns to its original position, assumes the dome shape and bars the exit of the organism entrapped. When once entrapped, the animalcules die and decay inside the trap and the decaying materials are absorbed by the quadrids on the wall of the trap and translocated into the plant for its nourishment.

SCAPES AND FLOWERS

Submerged aquatics like *U. stellaris* which produce erect inflorescences or

scapes peeping above the surface of the water develop four to six white spongy float-leaves in a verticillate manner near the base of the scape; these float leaves are inflated, ellipsoid or ovoid, reticulately-veined having a tuft of filiform external pinnules or reduced pinnae at their apices. They help in maintaining the scapes above the surface of the water in an erect position. Such buoyant floats are occasionally met with at the base of the scape *U. aurea* (syn. *U. flexuosa*). According to Deva (1953) who has studied their anatomy, the floats in this taxon are much larger than in *U. stellaris* and measure up to 20 mm in length and up to 4 mm in diameter. They are branched at the tips and the branches are further divided into fine capillary segments. The number of float leaves may vary from one to six on a scape and are irregular in arrangement. In a transverse section each such float shows a central ring of vascular bundles which all lack cambium; the conducting elements are reduced as in other vegetative organs; in some strands the xylem and phloem become dissociated. The great mass of tissue, between the epidermis and two cell layers surrounding the vascular bundles consists of a ring of air-filled cortical parenchyma separated by radial partitions, one cell in thickness. These lacunae persist reduced in size into the ultimate capillary branches of the float. Varied views are put forward to explain the morphological nature of floats. Barnhart (1916) feels they are modified leaves. Haines (1922), Rendle (1952), and Lloyd (*l. c.*) regard them as leaves. Arber (*l. c.*), on the other hand, has recognised them as shoots and the anatomical studies of Deva (*l. c.*) support Arber's views because the stele in the floats is like the stem and hence, the floats are of the nature of modified shoots.

Minute scales and bracts are present on the scape and their shape and chiefly their mode of attachment on the scape are of classificatory value. In the aquatic species they are obscure or absent; in the majority of the terrestrial taxa they are basifixed; in all the epiphytic species like *U. brachiata*, *U. furcellata*, *U. multicaulis* and *U. striatula* and in a few terrestrial species like *U. caerulea*, *U. nivea* and *U. roseo-purpurea* they are medifixed.

The flowers are yellow in colour in the aquatic species and in terrestrial taxa like *U. bifida* and *U. scandens* ssp. *scandens*; but in the remaining terrestrial and all the epiphytic taxa the flowers are chiefly blue or bluish-purple or purple or very rarely white (*U. caerulea*, *U. minutissima*).

Trichomes are present on the floral parts of *Utricularia* and their ontogeny has been studied in detail and a classification has been proposed (Farooq, 1966; Farooq and Siddiqui, 1966; Subramanyam and Narayana, 1969, 1978; Shamima and Siddiqui, 1974). They are epidermal in origin and of a varied nature; they are in the form of unicellular glandular hairs, long unicellular hairs with pointed apex, uniseriate multicellular hairs with a conical apical cell, uniseriate three-celled hairs, uniseriate three-celled hair with an apical cell large and glandular, hairs with four-celled glandular head multicellular or one-celled stalk and one-celled foot; peltate glandular hairs with multicellular head, one-two-celled and one-celled foot; many more variations of these hairs and trichomes are met with and they have been classified into various types from A to U; their position may be on the pedicel or on the abaxial surface of floral parts like bract, calyx, corolla, spur, filament of the stamen and even placenta and style; they are mostly present on the abaxial

and adaxial surface of the corolla in most of the species; they are rarely present on the filaments of stamens as in *U. bifida* (Shamima and Siddiqui, 1974), occasionally on the free central placenta in *U. scandens* (Farooq and Siddiqui, 1966) and rarely even on the style as in *U. reticulata* (Farooq and Siddiqui, 1966) and *U. nivea* (Shamima and Siddiqui, *l.c.*).

FLORAL ANATOMY

The floral anatomy of only six Indian species of *Utricularia* has been studied so far and they are *U. caerulea*, and *U. polygaloides* (syn. *U. stricticaulis*; Subramanyam and Narayana 1969), *U. aurea*, *U. exoleta*, *U. stellaris* and *U. striatula* (Subramanyam and Narayana, 1978). These studies have shown that the floral parts and their traces show connation, adnation and reduction. Anatomy shows the calyx to be pentamerous, although this is obscured grossly because it is two-lobed. The sepals show three vascular bundles, and a tendency towards suppression of the lateral bundles of the sepals is noticed. The corolla is gamopetalous, pentamerous and, like the calyx, is bilipped. The petals are traversed by a single vascular bundle which in turn branches further. There are only two stamens, antero-lateral in position and they are single-traced. The bicarpellary, syncarpous ovary is superior with numerous ovules borne on a free central placenta. In *U. caerulea* (Subramanyam and Narayana, 1969) and *U. aurea* (Subramanyam and Narayana, 1978) the dorsal carpellary trace of the posterior carpel is suppressed. There is no organisation of the ventral or common ventral bundles in the free central placenta. The stigma has two lobes only one of which, the anterior, is well developed and functional; it is recurved with radially

elongated, richly cytoplasmic cells on the abaxial side. A feature recorded in all the so far investigated species is the reduction of the posterior stigmatic lobe indicating that it is nonfunctional.

A unique feature in which *U. striatula* (Subramanyam and Narayana, 1978) differs from the other investigated species is the prolongation of the placenta towards the apex in the form of a narrow cylindrical structure. This is well developed and observed during fruiting stages and does not receive any vascular supply. Taylor (1964) reported such a prolongation not only in *U. striatula* but also in two other species of the genus like *U. appendiculata* and *U. bracteata*. According to him (Taylor, 1964) this prolongation is firmly attached inside the upper extremity of the capsule; he terms this type of placentation as free central—those attached only at the base being free-basal. The study on *U. striatula* (Subramanyam and Narayana, 1978) clearly shows that this cylindrical prolongation only extends into the base of the style with no histological fusion because the epidermal layers of the apical placental prolongation and the epidermal layers of the basal portions of the style and stigmatic lobes remain distinct.

Another interesting feature is that in all the species studied so far except *U. striatula* the pedicel, placenta and the stigmas are in the same line. But *U. striatula* differs from the other taxa, because in relation to the pedicel, the style and stigmas are lateral and anterior in position; the placenta which is also lateral appears to arise from the wall of the posterior carpel. This situation has been brought about by differential growth along the posterior side. This differential growth has affected the ovary as a whole and this is evident because the free central placenta arises from the base of the ovary,

and the style and stigmas are also in the same line as in other species. Hence, when viewed in relation to the pedicel, the placenta, style and the stigmas appear lateral. It may thus be concluded that the shift in position of the style and stigma and the placenta is only due to differential growth and not due to unequal development of one of the carpels.

PALYNOLOGY

The pollen morphology of 21 Indian species of *Utricularia* has been studied in great detail by Thanikaimoni (1966); these include four aquatic, five epiphytic and twelve terrestrial species. He has been able to conclude from his studies that there is correlation between the habit, seed and pollen characters in the Indian species of this genus. According to him (Thanikaimoni, *l. c.*) the aquatic habit is associated with winged seeds and the pollen grains are 11-13-colporate with the ectoaperture elongated; again here while the pollen grains in *U. aurea*, *U. exoleta*, (syn. *U. gibba* ssp. *exolata*) are 11-13-colporate, *U. minor* 14-15-colporate and *U. stellaris* (syn. *U. inflexa* var. *stellaris*) 15-18-colporate; the epiphytic species produce comose or glochidiate seeds and the pollen grains are 3-4-colporate and the ectoaperture is short; finally, in the terrestrial taxa where the seeds are scrobiculate or reticulate or striato-reticulate the pollen grains are 3-5-colporate, and the ectoaperture is elongated; further, while in *U. polygaloides* (syn. *U. stricticaulis*), *U. reticulata*, *U. albo-caerulea*, *U. arcuata*, *U. graminifolia* the pollen grain is 4-5-colporate, it is 3-4-colporate in *U. bifida*, *U. scandens* ssp. *scandens*, *U. uliginosa*, *U. caerulea*, *U. nivea* and 3-colporate in *U. roseo-purpurea* and *U. minutissima*.

CYTOLOGY

Comparatively, there is a dearth of information on the chromosome numbers of various Indian species of *Utricularia* and this with a review and a few more new reports have been provided (Subramanyam and Kamble, 1968). In general, meiosis in most of the species studied is normal and the chromosome numbers were determined at diakinesis and metaphase I; anaphase I shows clearly the distribution of equal number of chromosomes towards each pole. The tetrads of microspores are formed in the normal manner. Kausik (1938) reports $n=20$ for *U. caerulea* and Siddiqui (1959) $n=21$ for *U. aurea* (syn. *U. flexuosa*). Siddiqui (1959) found persistence of nuclei, nucleolar budding and fragmentation are normally present in *U. aurea*. He further finds that abnormal cytokinesis occurs in some cases in this plant and cleavage starts at the dyad stage. Other reports of haploid numbers are for *U. baouleensis* ($n=10$), *U. stellaris* ($n=21$), *U. minutissima* ($n=8$), *U. scandens* ($n=6, 7$) and *U. polygaloides* (syn. *U. stricticaulis*, $n=7$). Thus there are both aneuploids and polyploids. Further, in the case of *U. scandens* while in the population of plants collected at Elephant Falls, Shillong, East Khasia District, Meghalaya at an altitude of ca 1710 m the haploid number is 7, the population of the same species occurring in the Sanyasi Malai Hills, Yercaud, Salem District, Tamil Nadu, at an altitude of 1500 m, has a haploid number of 6 (Subramanyam and Kamble, *l. c.*).

EMBRYOLOGY

Quite a number of embryological studies on several Indian species of *Utricularia* have been carried out and two

centres, one at Bangalore (Kausik, 1935, 1938; Kausik and Raju, 1955, 1956; Shivaramaiah, 1964a,b, 1967; Shivaramaiah et al., 1975; Begum, 1965, 1969) and another at Aligarh (Khan, 1952, 1953, 1954, 1963a, b, 1964, 1970; Farooq, 1958, 1964a,b, 1965a,b, 1966; Farooq and Bilquis, 1966a,b; Farooq and Siddiqui, 1964; Siddiqui, 1965a,b,c, 1975; Siddiqui and Farooq, 1965, 1974) are chiefly responsible for these detailed embryological studies. Some of the remarkable and important embryological features are summarised below. The wall of the anther consists of an epidermis, a prominent fibrillar endothecium, an inconspicuous middle layer and a glandular tapetum of binucleate cells; cytokinesis is simultaneous and the microspore tetrads are usually tetrahedral; occasionally decussate or isobilateral tetrads are also met with. The microspores are free in most of the taxa except *U. aurea* and *U. arcuata* where they sometimes remain united in tetrads. The mature pollen grain at the shedding stage is three-celled, sometimes enclose starch grains and germinate in situ as in *U. scandens*. The ovules are unitegmic, tenuinucellate, usually anatropous and borne on a massive free central placenta; the vascular bundles branch in a tree-like manner in the placenta. At the base of each ovule some cells of the placenta have prominent nuclei and dense cytoplasm forming the placental nutritive tissue; further, this tissue is surrounded by a sheath of two or three layers of cells; it plays a significant role in the nutritional mechanism of the embryo sac. The hypodermal archesporium directly functions as the megaspore mother cell. The megaspore tetrad is linear, but T-shaped, isobilateral, inverted T-shaped, L-shaped and even irregular forms are met with. Usually the chalazal megaspore functions

and the development of the embryo sac conforms to the Polygonum type.

The behaviour of the embryo sac in relation to the nutritional mechanism of the ovule is interesting. When the developing embryo sac is at the two-nucleate stage, the nucellar epidermis and the remains of the degenerating megaspores disappear completely. The apex of the embryo sac is completely naked and after growing out of the ovule, becomes extra ovular and comes into contact with the placenta. At the 4-nucleate stage the embryo sac apex starts penetrating into the placental nutritive tissue, and at maturity, becomes buried in this tissue, thus serving a haustorial role. The embryo sac at this stage thus receives nutrition from the endothelium, the chalazal nutritive tissue and the placenta. This is significantly associated with the absence of a funicular vascular tissue, which is thus superfluous. In a large number of ovules of *U. aurea* (syn. *U. flexuosa*) and *U. stellaris* (syn. *U. inflexa* ssp. *stellaris*) which show degenerating embryo sacs, an unusual behaviour of the endothelium on the funicular side has been observed (Khan, 1963a; Farooq, 1964a). The walls of the endothelial cells break down and their nuclei come to lie in a common cavity. The longitudinal wall separating this cavity from the embryo sac bulges into the embryo sac more or less like a nodule. The nuclei located in this nodule-like protrusion are many in number, normal and healthy.

Since the apex of the embryo sac is extra ovular, there is no porogamy. The pollen tube meets the embryo sac in the ovary cavity and this is described as exogamy. Syngamy and triple fusion take place as normal processes during double fertilization and are observed in a number of species.

The endoeperm is ab initio cellular and the mode of development is according to the Scutellaria type (Schnarf, 1931). The two uppermost and two lowermost cells of the eight-celled endosperm differentiate into the micropylar and chalazal haustoria respectively. The two middle layers of cells by further divisions form the body of the endosperm. The nuclei of the haustorium become very much hypertrophied, later breaking into several separate lobes forming independent nuclei. Both the haustoria are quite aggressive. Variations have been reported in the planes of initial wall formation; the wall separating the cells of the haustoria may disappear so that the haustoria become two-nucleate as in *U. scandens*; as an abnormality the chalazal haustorium may extend into the funicle and show nuclear divisions as in *U. stellaris*. During later stages, a few layers of endosperm cells close to the micropylar haustorium become modified to form a plug, so that during the detachment of the seed from the placenta, the embryo is well protected.

It is rather difficult to assign the type of embryogeny to any particular type because of the great variation in the sequence of cell divisions during early stages; further, the mature embryo is undifferentiated. The cells of the embryo enclose starch and oil. A peculiar feature in *Utricularia* is the growth of the apex of the fertilised egg into a tubular structure. The zygotic tube penetrates into the endosperm proper and the nucleus after moving into the tube, divides near its apex. Thus the embryo is placed in a favourable position for its nutrition and safety. All the cells of the integument in the mature seed disappear except the outer epidermis which forms the seed coat. These embryological characters of *Utricularia* which belongs to Lentibulari-

aceae, strongly support that the closest allies of this family seem to be Scrophulariaceae.

FRUITS AND SEEDS

The fruits are small, globose or ovoid or rarely more elongated, sometimes dorsiventrally compressed capsules. The pericarp is membranous, firm and the style and stigma are persistent. Internally they are usually completely filled by the seeds and the swollen free central placenta. In the aquatic species the capsules are not dorsiventrally compressed; in the free floating submerged species *U. stellaris* the capsule is circumscissile, rupturing more or less completely along the equatorial line. In the epiphytic and terrestrial species dehiscence takes place in a number of ways. In the epiphytic *U. striatula* the more or less globose capsules are obliquely dorsiventrally compressed, keeled on their abaxial surfaces and dehisce by vertical slits.

The seeds exhibit a wide range in their form in the genus *Utricularia* than shown by any other genus. They are very small, in some cases minute, and their exomorphic characters vary from species to species. Thus the shape of seeds, pattern in the arrangement of epidermal cells of the seed coat, striations (if any) in these cells, epidermal projections and wings, and measurements of seeds are distinct from species to species. For a number of Indian taxa these exomorphic characters of seeds are so constant and stable that they serve as taxonomic characters of great importance for their identification (Abraham and Subramanyam, 1965). They vary in size and shape. While studying the seeds of various utricularias occurring in West Bengal it was observed that while the seeds of *U. exoleta* are

largest in size with a length/breadth measurement of 1427/1193 μm , they are comparatively the smallest in *U. nivea* with a length/breadth measurement of 223/108.3 μm . (Abraham and Subramanyam, *l. c.*). Further, wide variation occurs in the shape and size of the epidermal cells of the testa, and nature of testal outgrowths. Based on these characters a tentative key for the identification of the mature seeds has been proposed (Abraham and Subramanyam, *l. c.*). Thus while most of the seeds of aquatic species are slightly or distinctly winged, the seeds in the terrestrial and epiphytic species are not winged. In the aquatic species *U. aurea* and *U. stellaris* the seeds are slightly winged and tabular prismatic and polygonal in outline; in the other aquatic taxon *U. exoleta* the seeds show a prominent, crenulate, corky wing and lenticular in outline. In the terrestrial species the seeds are not winged. The seeds show variable outline being ellipsoid, ovoid, globose, subglobose and rhomboid. The epidermal cells of the seeds are usually reticulate or even scrobiculate as in *U. baouleensis*, *U. smithiana*, *U. squamosa* and *U. uliginosa*; the epidermal cells are finely striated in *U. ploygaloides* and prominently so in *U. baouleensis* and *U. bifida* (Abraham and Subramanyam, *l. c.*); in *U. nivea* the seed coat of the ovoid seeds shows minute clavate projections (Abraham and Subramanyam *l. c.*; Bhattacharya, 1976). The exomorphic characters of the seeds in the epiphytic species are particularly interesting. In *U. furcellata* and *U. striatula* the seeds are remarkable because they are glochidiate. In *U. furcellata* the seeds are obovoid or pearshaped and the glochidia are more or less restricted towards the broader end of the seeds; the glochidia arise from the outer surface of the epidermal cells which

have a wavy outline and they are slender, elongated, pyramidiform, capped with four nodular projections. The seeds in *U. striatula* are ellipsoid, cylindrical with glochidia, almost extending up to the base; the glochidia arise from epidermal cells with a wavy outline, which run parallel to the major axis of the seed and they are slender, elongated and each one of them is capped by recurving barbs which are pointed. According to Taylor (1964) the development of the glochidia on the seeds in *U. striatula* is an adaptation to environment. He regards that these remarkable glochidia probably become entangled with the 'leaves' of associated bryophytes thus preventing the seeds from dropping on unsuitable habitats on the ground beneath. In the other epiphytic species *U. kumaonensis* the ripe seeds have at their ends tufts of capillary hairs as long as the seeds. Thus from a single character of the seeds, the epiphytic species of *Utricularia* can be easily identified from the rest.

In a recent study on the germination of seeds and seedlings which includes certain Indian taxa like *U. bifida* and *U. striatula* it has been shown (Kondo, Segawa and Nibara, 1978) that in contrast to the aquatic species, terrestrial and terrestrial-epiphytic species of *Utricularia* show different seed germination patterns and seedlings.

EXPERIMENTAL STUDIES

Interesting experimental studies have been carried out on certain utricularias (Doreswamy and Mohan Ram, 1969, 1971; Mohan Ram 1978; Mohan Ram and Doreswamy, 1966; Mohan Ram and Dutta, 1966; Mohan Ram et al., 1972). The studies of Doreswamy and Mohan Ram (1971) have shown in *U. stellaris* (syn. *U.*

inflexa var. *stellaris*) that when portions of the stolon were raised in axenic cultures, flowering could be induced on BM to short day regimes of 16 hours dark/8 hours light or 14 hours dark/10 hours light; further, the flowers undergo cleistogamy and fruit and seed set were formed only when 20 or more inductive cycles were given. In this taxon the inflorescence is held erect by a circlet of floats. The stamens in an open flower are seen closely appressed to the funnel-shaped stigma. The pollen grains germinate *in situ* and the germinated grains are deposited in the form of a mass by the inward bending of the stamens and the dehiscence of the anthers. As stated already under *in vitro* a good seed set has been recorded, thus showing that the plants are self-compatible. Kausik and Raju (1955) while describing the mode of pollination in *U. reticulata* from observations in the field have shown a similar mechanism of pollination. Taylor (1964) has pointed out that there is extreme variability in the stature and in the size, shape and number of flowers in the epiphytic species *U. striatula*; in this taxon there is a transition in the showey forms with the lower lip of the corolla 1 cm wide to the minute cleistogamous forms which are never showey. In a careful study, Killian (1953) under field conditions has observed in *U. striatula* that plants exposed to direct sunlight for a period of just one hour per day produced chasmogamous flowers which were pollinated by Diptera whereas plants in the constantly shaded habitats produced cleistogamous flowers only. Thus in the reproductive biology of the utricularias special pollination is of great significance.

A curious device of an insectivore like *Utricularia* is its capacity to trap insects. It is regarded that the nitrogen derived from the insect prey is an obligate require-

ment of these insectivorous plants (Lloyd, 1942; Pringsheim and Pringsheim, 1962, 1967; Harder, 1963). According to Pringsheim and Pringsheim (1967) peptone or beef extract is essential for cultured plants of *U. minor* and *U. ochroleuca*. These substances enhance vegetative growth in *U. exoleta* and were essential for flowering (Harder, 1963). In axenic cultures of *U. exoleta* (syn. *U. gibba*) it has been observed by Mohan Ram and Dutta (1966) that beef extract and tryptone supported maximum vegetative growth and abscission of traps was delayed. In *U. stellaris* (syn. *U. inflexa* var. *stellaris*), growth occurs even on a medium containing nitrate, thus showing that the requirement of organic nitrogen or protein is not an absolute requirement (Doreswamy and Mohan Ram, 1969). It must be pointed out at the same time that the presence of organic nitrogen sources like casein hydrolysate and yeast extract stimulated higher rates of growth. Questioning what then is the function of traps Mohan Ram (1978 p. 4) states "It appears that their development must have been a morphological mutation, which during evolution, must have become secondarily

useful in an environment deficient in nitrogen. This view is strengthened by the fact that under the same ecological conditions, numerous other flowering plants exist without any special contrivances for deriving extra sources of nitrogen".

CONCLUSION

Lastly, it has to be stated that while the utricularias are biologically an extremely interesting group of insectivorous plants, because they have the trapping mechanism for catching insects in their traps, there is a report that they can be usefully employed for biological control. There is a press report (Deccan Herald 25th October, 1976 29 (291):7, 1976) that the scientists working in the National Environmental Engineering Research institute, Nagpur have observed that the traps of *U. aurea*, an aquatic carnivorous plant growing in quite waters, have been found to trap and kill mosquito larvae. The larvae are mostly caught by tail ends, and rarely at the other parts of the body. These insectivorous plants can grow in abundance in small ponds and tanks where mosquitoes breed and control the larval population by trapping.

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