Utricularia emarginata, Benj.

BY

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With Plate XLIV.

THOUGH the genus *Utricularia* has received more attention than many others, owing to peculiarities of form, development, and to the possession of characteristic bladders, which features distinguish them from other plants, yet of the 150 or so species which are comprised in this interesting genus, only a very small fraction have been thoroughly examined, except from a systematic point of view. As early as 1848 Benjamin¹ gave his results of a minute examination of *Utricularia vulgaris*, *U. minor*, &c., only, however, from a morphological and physiological standpoint; and in this direction also are the recent investigations of Kamienski,² Pilger,³ Brown,⁴ Stapf,⁵ Small,⁶ Ostenfeld,⁷ Goebel.⁸ Other investigators such as Buchenau,⁹ Cohn,¹⁰ Darwin,¹¹ Pringsheim,¹² have greatly contributed to our knowledge of the structure and function of the various parts of the plant. From a comparative standpoint, however, the germination of the Utricularias is perhaps the most interesting and the most important; and among the first investigators in this direction was Kamienski,¹³ who took as his type the common bladderwort, *Utricularia vulgaris*. Goebel¹⁴ has described and figured other species, e. g. *U. oligosperma*, *U. reniformis*, &c., with a more detailed description of *U. vulgaris*. More recently,¹⁵ he has examined other species in greater detail, such as *U. flexuosa*,

¹ Botanische Zeitung, 1848.

² Supplement II, Ann. du Jard. Bot. de Buitenzorg, 1898. Botanische Jahrbücher. Engler, xxxiii, 1902.

³ Botanische Jahrbücher. Engler, xxx, 1901-2.

⁴ Trans. Linn. Soc., London (Ser. 2), vi, 1901.

⁵ Dyer: Flora Trop. Afric. 4, Sect. II, 1906. Dyer: Flora Cap. 4, Sect. II, 1904.

⁶ Flora of the United States. New York, 1903.

⁷ Repert. nov. sp. regni veget. Berlin., ii, 1906.

⁸ Gartenflora, 40, 42, 45.

⁹ Botanische Zeitung, 1865.

¹⁰ Über die Funktion der Blasen . . . Pflanzen, 3. Heft, 185.

¹¹ Insectivorous Plants.

¹² Monatsberichte der Berliner Akademie, 1869.

¹³ Botanische Zeitung, 1877.

¹⁴ Goebel: Pflanzenbiol. Schilderungen, 2, p. 127.

¹⁵ Ann. du Jard. Bot. de Buitenzorg, 9, 1890-1.

U. exoleta, *U. stellaris*, *U. coerulea*, &c., particularly from the standpoint of the relations of the various species one to another, and the homologies of the various parts, but also from the standpoint of germination. Glück,¹ in his comprehensive study of water and marsh plants, has classified the *Utricularias* that have been studied to some extent, according to their mode of germination, into three series.

1. Those having a number of primary leaves, for example :—*U. vulgaris*, *U. oligosperma*, *U. reniformis*.

2. Those having two primary leaves, for example :—*U. exoleta*.

3. Those having no primary leaves, for example :—*U. bifida*, *U. laterifolia*, *U. montana*.

Utricularia emarginata, a Mexican species, is one hitherto practically unmentioned by the various authorities on *Utricularia*. It is given as a distinct species in *Index Kewensis*; ² no mention is made of the species in Engler-Prantl, but being a true aquatic, it would fall under section B, in the classification of *Utricularias*, 'Wasserformen mit geteilten oder gefiederten Blättern.' The material used in the description was grown from seeds obtained in the Royal Botanic Garden, Edinburgh, from a specimen in Pringle's Mexican collection of 1904.

Conditions of germination. Mr. L. Stewart, foreman of the glass department of the Royal Botanic Garden, Edinburgh, has proved, as mentioned in a previous note,³ that the seeds flourish best in a shallow pan, having a thin layer of mud at the bottom with enough water to cover the mud. As the plant is insectivorous and the presence of Microcrustacea is essential for food, experience has shown that the best method of cultivation is to keep the plant in partial shade in still water. The water soon becomes alive with Microcrustacea, and the plant thrives and grows rapidly. The young seedlings from which some of the drawings were made at the different stages were kept merely in a small jar of water, maintained at a constant temperature by being placed on top of a jacketed embedding oven. The only difficulty here is the rapid evaporation of the water, and the danger of chilling when adding a fresh supply. Also, the water added must not be clean, as in that case the supply of Microcrustacea is soon reduced, and the plant dies for want of nourishment.

Seed and germination. The seeds of *Utricularia emarginata* are minute, about 0.5 mm., round, and covered with a dark brown, net-like testa, extending beyond the seed itself into a wing-like expansion with irregular edges (Pl. XLIV; Fig. 1, *a*). This outer covering is easily detached by means of a fine needle, revealing the round embryo in a light brown tegmen,

¹ Glück: Biologische und morphologische Untersuchungen über Wasser- und Sumpfgewächse. Teil ii, Jena, 1906.

² Linn., xx, 1847.

³ Ann. of Botany, vol. xxiii. Preliminary Note on *Utricularia emarginata*.

with a darker spot at the micropylar end, opposite to which all later development takes place. This dark spot indicates the place of attachment of the seed to the mother plant. When the tegmen is also removed, the naked embryo is seen to be not quite round in shape, but slightly flattened at the base, that is, at the micropylar end, where the primordium of the root would normally develop in other embryos. *Utricularia emarginata*, like *U. vulgaris*, is, however, rootless. In order to see the very early stages of germination, while the testa is not yet burst, the seeds must be carefully examined by dissecting off the outer coverings. Germination was regular in all the material examined: in this respect *Utricularia emarginata* differs from *U. exoleta* described by Goebel,¹ with which the present species would occupy a place in the second series of Glück's classification.²

The embryo, which is of a pale green colour, at first shows no differentiation, but very soon at the apex four primordia appear (Fig. 2, *a, b*). Of these, the two outer develop more rapidly than the two inner, thus showing the same order of development as in *U. vulgaris*, but to a more limited extent (Figs. 3-5, *a, a*). In that species, as Kamienski³ has pointed out, the organs appear in the following order: the oldest primary leaves are at the outside, the leaves gradually becoming younger as one proceeds inwards; the secondary shoot (*Adventivsprosse*) is formed from the youngest protuberance in the centre, the main stalk from the youngest but one, and the first bladder from the youngest but two. Though differing so much in the number of primary leaves, yet *U. emarginata* follows the same order of development. The outer two protuberances form the primary leaves, and develop most rapidly. Of the remaining two protuberances, one forms the main shoot (Figs. 3-5, *b*) and at first develops, not quite so rapidly as the two primary leaves, but more rapidly than the youngest outgrowth (Figs. 3-5, *c*), which forms another shoot—analogue to Kamienski's *Adventivsprosse*. Thus we have, although to a much more limited extent, the same order of development as in *U. vulgaris*.

From its earliest stages, the main shoot possesses circinate ptyxis (Figs. 4, 5, *b*), a feature noticeably lacking in the development of the two primary leaves (Figs. 3, 4, *a*). Though its growth is at first not so rapid as the two mentioned outgrowths, it soon outdistances them in length, and when the two primary leaves have ceased further development, the main shoot, having unlimited growth, still continues to increase at its rolled up apex (Figs. 6-9, *b*). By continued dichotomy of the growing point, as in other *Utricularias*, linear lateral appendages ('leaves' of authors) are given off (Figs. 6-9, *b*). The first bladder appears in a super-axillary position on the first formed of these appendages (Figs. 6, 7, 9, *e*). The younger shoot (*Adventivsprosse* of Kamienski) also elongates, but more slowly, and in its

¹ Ann. du Jard. Bot. de Buitenzorg, 9, 1890-1.

² p. 2.

³ Botanische Zeitung, 1877.

turn branches and produces lateral appendages and bladders. The two oldest outgrowths ('primary leaves') develop and increase in size until they attain a length of some two to three times that of the original seed, when further development, at least for a period, ceases. Investigation remains to prove whether these two primary outgrowths develop into ordinary water-shoots after the seed has fallen away. Of what physiological importance these so-called primary leaves are to the plant it is difficult to determine. That they are leaves and not cotyledons Goebel¹ affirms, and he asserts that if one be cut off, it will develop into an ordinary water-shoot. In his later paper,² however, he sees no reason why these two outgrowths should not be designated as 'cotyledons', though shoots can and do replace them.

The seedling with its growing points develops rapidly, the water-shoots reaching a great length, so that the plant covers a large area in a comparatively short space of time, always remaining submerged.

The general appearance of *Utricularia emarginata* therefore, which has been growing some time, is that of a matted mass of submerged water-shoots, with here and there flower-stalks arising out of the water.

The external appearance of the water-shoots have already been described.

The aerial flower-stalk does not develop for some time. In its origin it does not differ from that of *Utricularia vulgaris*, arising from a bud on the upper surface of the main stem. Only one example was seen, for it is difficult to discern the small bud on the water-shoot. At the base of every well-developed flower-stalk, however, is to be found a bud which in its turn gives rise to a flower-stalk, and it is from secondary flower-stalk buds that observations and figures were made. The bud arises at the base of the old flower-stalk in the axil of the youngest water-shoots formed, and is easily distinguishable to the naked eye, even in its young stages, by its solid appearance and reddish colour (Figs. 10, 11, *b*). It is early differentiated into stalk and flower-bud. It develops and in its turn bears a younger bud at its base. The old flower-stalk rises to a height of about 15–20 cm. and bears about 2–3 small flowers (Fig. 12). The flower (Fig. 13) does not differ very much markedly from that of *U. vulgaris*. The lower and upper lips of the corolla (Figs. 13, *a*, *b*) and the pouched petal (Fig. 13, *c*) are all yellow, while the tongue (Fig. 13, *d*) is white tipped with yellow.

The fruiting of *U. emarginata* is somewhat characteristic. While still young the fruit is green and opaque, and half-hidden under the persistent sepals. Later, however, it increases in size, becoming transparent, and the seeds show as dark spots through the ovary-wall. When the fruit is ripe, the flower-stalk bends over and lies flat on the surface of the water; the fruit, breaking away from the flower-stalk, opens, and floats on the surface of the water, the seeds in mucilage still adhering to the fruit wall. Finally

¹ Goebel: Schilderungen, 2.

² Ann. du Jard. Bot. de Buitenzorg, 1890–1.

the seeds, freed from the decaying mucilage, sink to the bottom of the water, and remain until ready to germinate.

Looking again at the base of the flower-stalk we find, as in *U. vulgaris*, limited shoots, usually about three in number, with small white protuberances (Fig. 11, *d*). These are rhizoids; though from the frequent transition at the tip into ordinary water-shoots, one might easily mistake their significance. The length of these rhizoids are from 5–15 mm. They possess circinate ptyxis and usually develop into normal water-shoots after the production of five or six rhizoid segments.

The rhizoid segments to the naked eye present the appearance of small whitish protuberances on the main shoot (Figs. 11, *d*, 15, *a*). Under the microscope they appear as divided into segments, six or nine segments being a very usual number (Fig. 16). These segments are caused by the dichotomizing of the main side branch of the rhizoid, one portion usually dichotomizing however, in advance of the other.

The rhizoid segments (Fig. 16) are in general shape not unlike those figured by Glück¹ for *Utricularia vulgaris*, but the individual segments are themselves more similar to those of *U. intermedia* or *U. neglecta*, for the ends of the segments are not pointed and bristle-tipped as in *U. vulgaris*.

The ends of the segments of the rhizoids of *U. emarginata*, also, do not broaden out, but preserve a uniform thickness, though they show a curling apex like those of other species (*U. intermedia*, &c.). The apices of the segments are thickly covered with glandular hairs (Fig. 16), but, as already remarked, there is no bristle present as in *U. vulgaris*.

The rhizoids of *U. emarginata*, as in *U. vulgaris*, are very reduced. They are metamorphosed water-shoots, and unlike *U. vulgaris* (according to Glück), the tip in *U. emarginata* is nearly always transformed into an ordinary water-shoot. Up till now, rhizoids have only been found on the two species, *U. flexuosa* and *U. exoleta* for the tropical submerged species, and the rhizoids of *U. emarginata* seem to differ in no marked way from the rhizoids of these two species.

Glück has worked out the function of rhizoids in land and water species of *Utricularia*, and has shown that in the case of submerged species, the rhizoids naturally lose their anchoring function to a great extent, and therefore become almost or entirely degenerate. The frequent metamorphosis of the rhizoids of *U. emarginata* into ordinary water-shoots should be noticed.

Examining the tip of even a very young rhizoid, bladders and leaf segments are to be seen formed in the usual way by the dichotomy of the growing point, one portion of the segment forming a roundish knob which will develop into a bladder, the other a more pointed portion which develops into a leaf segment ended by a sharp bristle (Figs. 15 *b*, 20 *a*, *b*). Sometimes the rhizoid segments have been changed into bladders and leaf

¹ Glück, loc. cit.

segments and the other half remain unchanged at the base. Various transitions are noticeable, all showing that the rhizoids are metamorphosed water-shoots (Figs. 17–20).

As fresh water-shoots are produced on the main stem, every well-developed flower-stalk is covered at its base by a cluster of water-shoots and rhizoids, possibly for the purpose of giving support and stability to a stem itself so much thicker and stronger than one of the frail water-shoots. The usual number of shoots at the base of a well-developed flower-stalk seems to be between twenty and thirty (Figs. 10, 11).

Bladders. The position of the first bladder has been observed. In its subsequent development it does not differ from that of *U. vulgaris*. The development of this organ is perhaps best watched in the region of the rolled-up apex of a water-shoot, where it appears in various stages. It arises as a roundish knob on a short stalk. Later, a slit is produced which gradually becomes larger until the whole becomes hollow. The bladders of *U. emarginata* only differ from those of *U. vulgaris* in the shape of the quadrifid processes (Fig. 22).

Morphology. The internal structure of the water-shoot is simple. A transverse section of the main stem (Fig. 21) or of one of the leaves shows a structure very similar to that of the floating leaf of *Salvinia natans*, and needs but little comment. The vascular system is weakly developed, and consists mainly of spiral vessels in the centre of the strand. These spiral vessels were very readily seen on treatment of the shoot with caustic potash, especially in the examination of the rhizoid segments, into which subsidiary vascular strands run (Fig. 16).

The internal structure of the flower-stalk (Fig. 14) is more complicated than that of the water-shoot. It differs mainly in the reduction of the aerenchyma, a feature which might be expected from its aerial nature. Though larger in its diameter (1–1.5 mm.) a transverse section of *U. emarginata* does not differ much in its essential features from that of the peduncal of *U. brachiata* recently described.¹

The epidermis is composed of regularly shaped cells slightly concave and thickened on their outside walls. Inside the epidermis is a small amount of aerenchyma. A ring of large cells forms the endodermis. In the ground-tissue the cells are small immediately behind the endodermis, but increase in size towards the centre, the cells of the pith being as large, if not larger than those of the endodermis. As in *U. brachiata*, five or six groups of vascular tissue are irregularly distributed, sometimes bordering on the pith and even in some cases occurring just behind the endodermis.

¹ New Phytologist, April, 1908. *U. brachiata*, R. H. Compton.

EXPLANATION OF PLATE XLIV.

Illustrating Miss Chandler's paper on *Utricularia emarginata*, Benj.

- Fig. 1. Seed of *Utricularia emarginata*. *a*, wing-like testa.
- Fig. 2. Naked seed showing four primordia. *a, a*, the two outer; *b, b*, the two inner.
- Figs. 3-9. Embryo in various stages of development. *a, a*, the two primary outgrowths; *b*, the main shoot; *c*, secondary shoot (*Adventivsprosse*); *d*, linear lateral appendage (leaf); *e*, first formed bladder.
- Fig. 10. Base of aerial flower-stalk showing development of—*a*, old flower-stalk; *b*, bud of new flower-stalk; *c*, water-shoot.
- Fig. 11. Same, later stage. *a*, old flower-stalk; *b*, bud of new flower-stalk; *c*, water-shoot; *d*, rhizoid segment.
- Fig. 12. Flower-stalk (nat. size) showing—*a*, flower; *b, b*, buds; *c*, bud of new flower-stalk; *d*, water-shoot.
- Fig. 13. Flower in detail. *a*, upper lip of corolla; *b*, lower lip; *c*, pouched petal; *d*, tongue.
- Fig. 14. T. S. of flower-stalk showing—*a*, epidermis; *b*, aerenchyma; *c*, endodermis; *d*, ground-tissue; *e*, vascular tissue.
- Fig. 15. Rhizoid showing—*a*, rhizoid segments; *b*, tip of rhizoid metamorphosed into ordinary water-shoot.
- Fig. 16. Rhizoid segments showing glandular tips and curled apices.
- Figs. 17-19. Development of bladders and leaf tips from rhizoid segments.
- Fig. 20. Segment of leaf dichotomizing. *a*, pointed apex which forms the leaf bristle; *b*, rounded apex which forms the bladder.
- Fig. 21. Transverse section of water-shoot.
- Fig. 22. Quadrifid processes inside the bladder of *U. emarginata*.

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