Structural and Developmental Diversity of *Utricularia* Traps

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This paper presents a collection of scanning electron micrographs showing architecture, function, and development of the traps of various species not or only partially described by Lloyd (1931, 1932, 1942), Thurston & Seabury (1975), Meyers (1982), Fineran (1985), Sasago & Sibaoka (1985), Juniper et al.(1989), Taylor (1989), and Richter (1989,1990).

Trap features common to most *Utricularia* species

There are about 214 bladderwort species (Taylor 1989). All of them produce traps (bladders) to catch small animals, algae, or soil particles in the water or mud.

The traps are stalked,lens-shaped bladders. Their wall is about two cell layers thick. The inner lumen is sealed by a valve-like elastic door (D in Fig. l) that is in tight contact with a multicellular threshold (T) preserving the shape of the opening. The primordial trap shows a slit as the first sign of bladder formation (Figs. 9, 12). The upper lip becomes the trap door while the lower lip forms the massive threshold.

The side walls of the trap are flexible. In the set phase the side walls are bowing inwards due to a negative hydrostatic pressure inside (Fig.10). Opening and closing of the door during firing may happen extremely rapidly, within 30 milliseconds or so (Sydenham & Findlay 1973, Fineran 1985). After firing, the bladder is filled, and the side walls are convex (Fig.ll). Resetting (by pumping out up to 40% of the water inside) requires 15-30 minutes (Sydenham & Findlay 1975, Sasago & Sibaoka 1985, and own observations).

There are various types of trichomes (hairs) along the internal and external trap surface (Thurston & Seabury 1975, Fineran 1985, Juniper et al.1989):

• Quadrifid and bifid trichomes (Fig. l) act as internal glands; they mainly absorb water during the resetting phase. Afterwards, they may secrete digestive enzymes and absorb digested products of the victims (Fineran 1985, Juniper et al.1989). Quadrifid trichomes are evenly scattered along the inner side of the trap, whereas bifid trichomes are restricted to the inner face (underside) of the threshold. The shape of the quadrifid trichomes can be used to distinguish some *Utricularia* species (see Taylor 1989).

• Densely packed glandular cells (called pavement epithelium) are found on the outer face of the threshold on which the door lies when the trap is closed (Fig. l:pe). The pavement epithelium prevents leakage of water into the trap when it is set (Juniper et al.1989). Sydenham & Findlay (1975) and Sasago & Sibaoka (1985) observed in traps resetting under paraffin oil that water is extruded at the door and not elsewhere. From this observation they concluded that pavement epithelium is functioning as water extrusion area (see also Juniper et al.1989:68,124).

• Club-shaped or long-stalked mucilaginous glands are located around the interior of the trap entrance (Figs.15,17). These glands produce a starch-containing mucilage (Thurston & Seabury 1975). This mucilage seals the door after firing and may also attract prey (Fineran 1985, Juniper et al.1989).

• The trap entrance is often ornamented with about four nonglandular hairs (Figs.1,8,15). They are called trigger hairs because they are believed to function in tripping the trap door (Sasago & Sibaoka 1985, Juniper et al.1989).

• Many species are provided with antennae (A) and bristle hairs (B) guarding the trap entrance (Figs. 7, 14, 17). Sometimes, mere touching of these antennae triggers firing. These appendages may serve to direct potential prey to the door (Juniper et al.1989:66).

• The external trap surface (apart from the entrance area) may or may not be covered with globular glands (Figs. 1, 6, 13, 19). These external glands may help in water extrusion from the trap although this commonly held opinion was questioned by Sasago & Sibaoka (1985) (see also Juniper et al.1989:70).

Trap features distinguishing *Utricularia* species

The range of trap variation was already intensively studied by Lloyd (1931,1932). The shape and size of the traps, as well as the position of the mouth, appendages and door, differ considerably between species and are often used for species identification (Juniper et al.1989, Taylor 1989). Regarding the genus *Utricularia* in general, the traps range in size from 0.2 to 6 (or even up to 10) mm.

Trap Position: The traps may arise from the stolons (e.g., *U. humboldtii*, Fig.2). Or they may arise from the leaves (e.g., *U. foliosa*, Fig.12).

Degree of trap coiling: Trap development may happen without coiling at all, e.g., in *U. livida* (terrestrial, Figs. 9-11), and *U. foliosa* (aquatic, Figs.12-14), both species with terminal position of the mouth. In *U.alpina* (which is terrestrial or epiphytic) the trap primordium starts to coil soon after its formation from the stolon surface (Figs. 3-5, see also Brugger & Rutishauser 1989). The mouth of the maturing trap is basal, i.e., situated next to the bladder stalk (Figs. 6-7). Similarly, various aquatic and terrestrial species show obvious trap coiling during development (*U. gibba, U. tricolor, U. dichotoma*, Figs. 16-21).

Shape and number of appendages around the trap entrance: Some epiphytic species like *U. alpina* possess two unbranched antennae covering the lateral areas of the trap mouth (Fig . 7). *Utricularia humboldtii* may or may not show two antennae on the traps. Especially mature large traps are devoid of antennae at all (Fig. 8). A pair of branched antennae is observable on the traps of *U. foliosa*. The antennae of this species are entire during early trap development (Figs. 12-13). Later, each primordial antenna divides up into three long bristle hairs (Figs. 14-15). In *U. gibba* (including *U. biflora)* there are a few bristle hairs in addition to the two prominent branched antennae (Fig. 17, see also Thurston & Seabury 1975). The trap entrances of *U. tricolor* and *U. dichotoma* are covered by wing- or sail-like appendages, with or without marginal teeth (Figs. 19, 21). In *U. dichotoma* there is in addition a long spine forming a beak (Fig. 21). Several radial rows of prominent glandular hairs around the trap entrance are typical for*U. livida* (Figs. 10-11) and other closely related terrestrial species like *U. sandersonii* and *U. bisquamata* (see Taylor 1989, Brugger & Rutishauser 1989). In other species as *U. humboldtii* positionally equivalent glandular hairs around the trap entrance are quite inconspicuous (Fig. 8).

Besides the trap features mentioned above there are other vegetative characters useful to distinguishing the sections and species of *Utricularia* (see Brugger & Rutishauser 1989, Juniper et al.1989, Rutishauser & Sattler 1989, Taylor 1989).

Concluding remarks

Since Charles Darwin, several botanists and other plant lovers were intrigued by the unique trap mechanism and bladder morphology in the genus *Utricularia*. However, the mechanism causing the traps to fire is not yet fully understood (Fineran 1985, Juniper et al.1989). We can only speculate about the functional significance (adaptive value) of certain trap features, e.g., the position of the trap entrance and the varying appendages (antennae, papillate hairs, wings) protecting the entrance. Terrestrial and epiphytic species with their traps in mud or wet soil normally show less prominent antennae and bristles than aquatic (i.e., submerged) species. Some of the trap features, however, may not even have an adaptive value at all.

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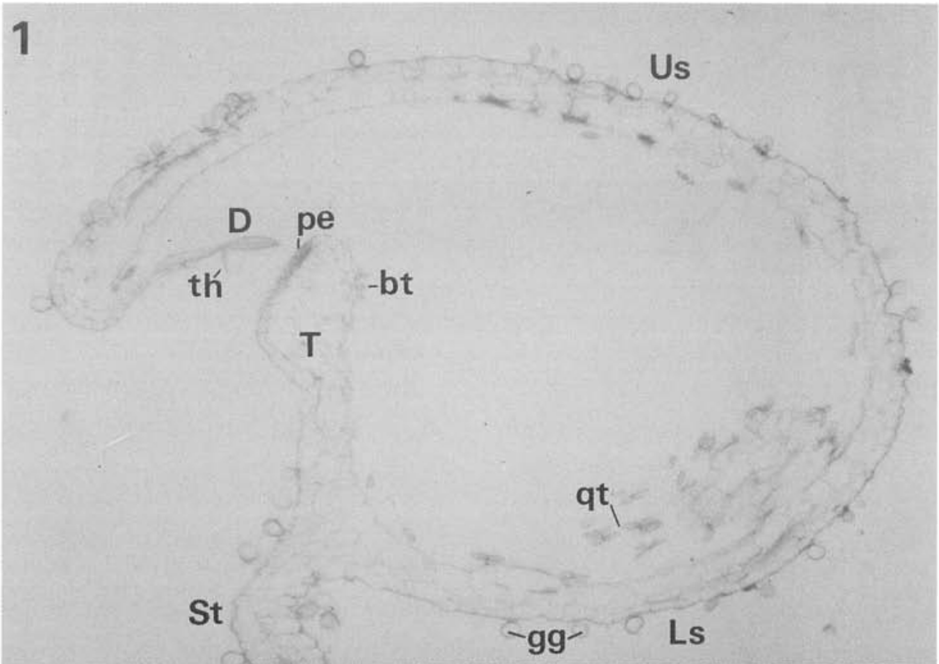
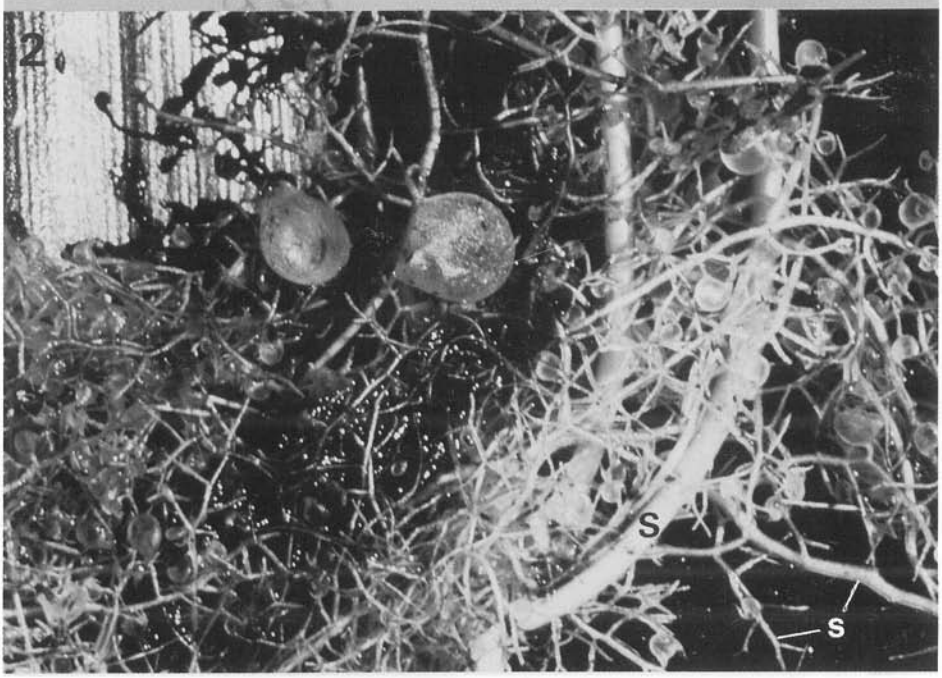
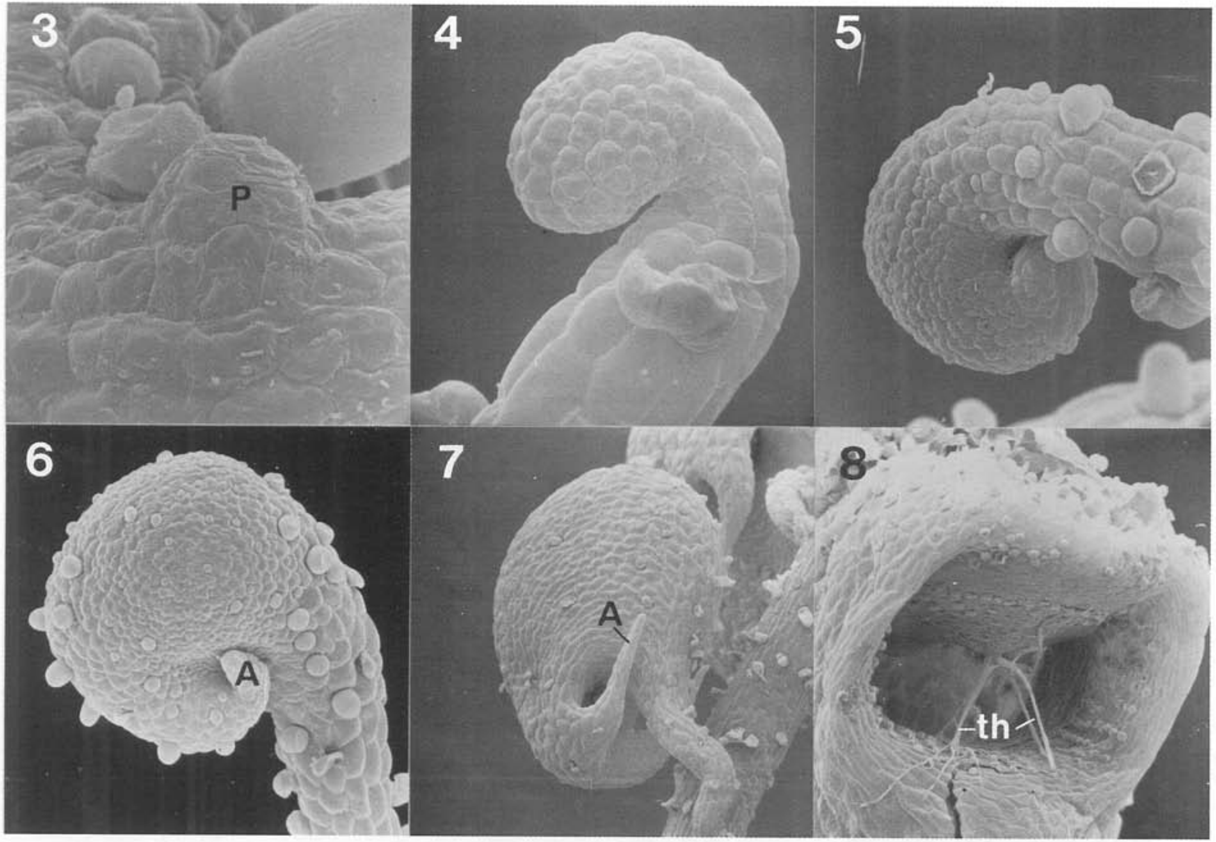
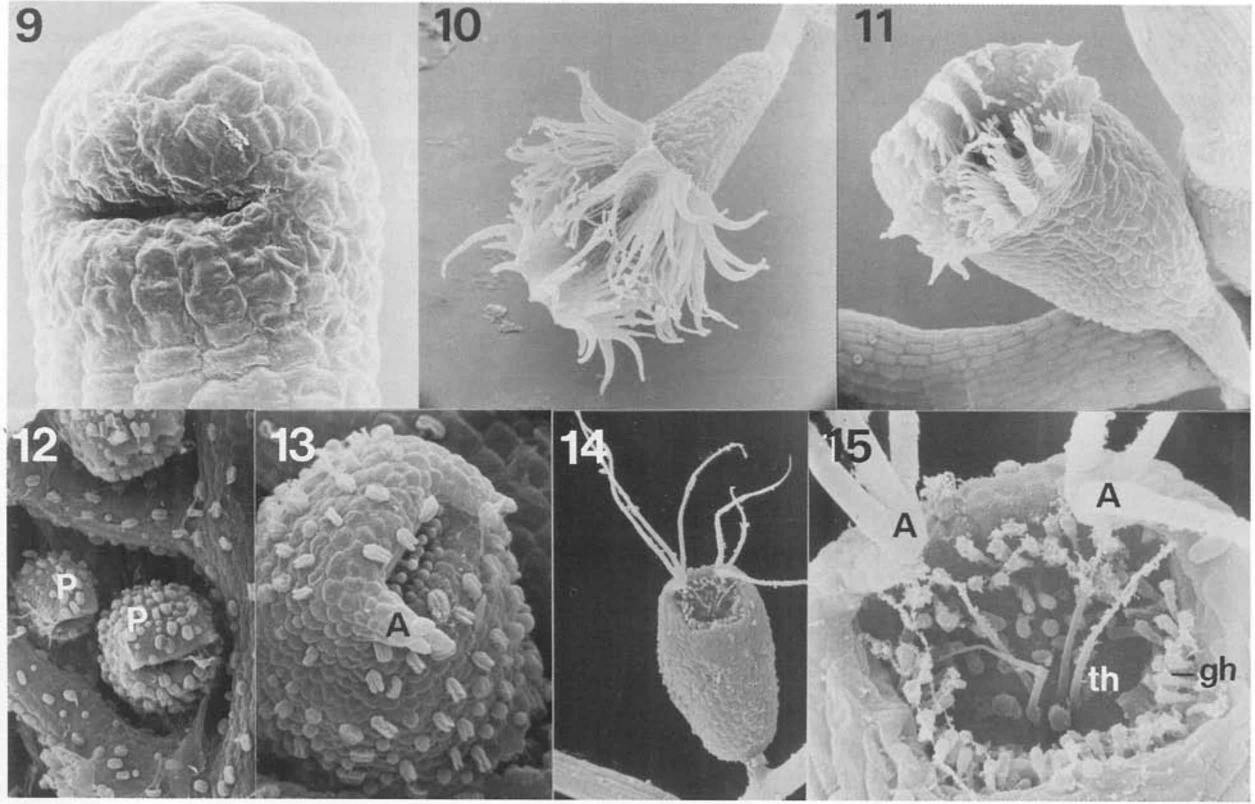




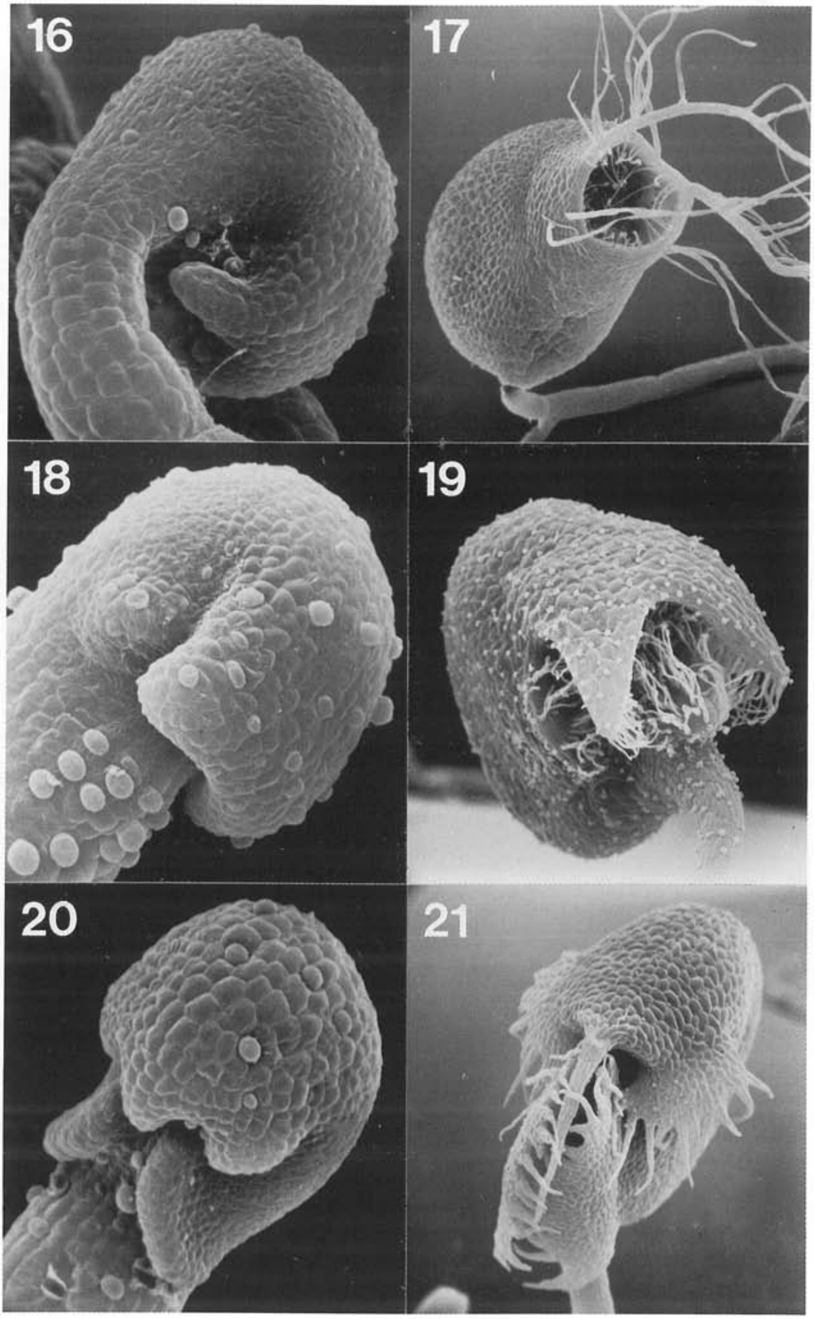
Figs.1-2. *Utricularia humboldtii* (epiphytic, from Venezuela, cultivated by L. Bütschi, Sundew Farm, Bern). - 1. Longisection of mature trap. Us = upper side, Ls = lower side, St = stalk, T = threshold with the pavement epithelium (pe) on the outer side and bifid trichomes (bt) on the inner side, D = valve-like door, qt = quadrifid trichomes, gg = globular glands. - 2. Dense network formed by thick stolons (S) and thin stolons (s), large and small traps. 60x / 1.8x



Figs. 3-8. *Utricularia alpina* (terrestrial or epiphytic, cultivated at Zurich Botanical Garden). Trap development.—3. Trap primordium (P) arising from a stolon.—4-5. Two consecutive stages of trap development. Notice coiling of the primordial trap.—6. Young trap with antenna initials (A).—7. Mature trap with two antennae (A).—8. *Utricularia humboldtii*. Entrance area of 4 mm big trap, th = trigger hairs. 1260x / 690x / 330x / 170x / 65x



Figs. 9-15. *Utricularia livida* (terrestrial, cultivated at Zürich Botanical Garden).—9. Trap primordium with initial stage of mouth formation.—10-11. Mature traps.—12-15. *Utricularia foliosa* (submerged aquatic, from S. Florida: R. Rutishauser 9/1988—12. Detail of young pinnate leaf, with trap primordia (P).—13. Young trap, with antenna initials (A).—14. Mature trap with two trifid antennae.—15. Entrance of trap shown in fig.14, A = antennae, interior of entrance with glandular hairs (gh) and trigger hairs (th). 850x / 55x / 75x / 130x / 265x / 48x / 240x



Figs. 16-21. Young and mature traps, respectively, of three additional species.—16-17. *Utricularia gibba* (submerged aquatic, fixed specimen from North Carolina: R. Rutishauser 10/1988).—18-19, *Utricularia tricolor* (terrestrial, cultivated by L. Butschi, Sundew Farm, Bern).—20-21. *Utricularia dichotoma* (terrestrial, cultivated at Zürich Botanical Garden). 375x / 50x / 320x / 45x / 260x / 55x