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Utricularia multifida (previously *Polypompholyx multifida*) has suction traps like all the other *Utricularia* species (Lloyd 1942)

Abstract: The hypothesis of Reifenrath et al. (2006) that the traps of *Utricularia multifida* (formerly *Polypompholyx multifida*) “might not function with a low pressure-suction movement” was first proposed by Lloyd in 1932 and disproved by the same author by his meticulous studies on living material in the following years and published in his book on *The Carnivorous Plants* in 1942. The fact that trap morphology in *Polypompholyx* basically displays the same design as all the other subgenera and species of *Utricularia* properly belongs to Taylor’s reasons to argue for the status of a subgenus of *Polypompholyx* in 1986 and 1989/1994. The trap of *Polypompholyx* is not a “missing link” to the different design of that of the protozoa-trapping genus *Genlisea*.

Peter Taylor argues for the status of a subgenus of *Polypompholyx* in his taxonomic monograph on the genus *Utricularia* (1989/1994, p. 78) as follows (emphasis added here as well as in the ensuing quotations):

“This subgenus [*Polypompholyx*] has been traditionally treated as a distinct genus by all authors since 1844, although the species were originally described by Robert Brown as *Utricularia*. When treated as a separate genus the name *Polypompholyx* has been conserved against *Cosmiza*. **The principal, or perhaps the only, difference is the presence of four, rather than two, calyx lobes.** Also, however, before the discovery of *U. westonii*, only one type of external trap morphology was known in the group, and this differed somewhat from the known traps of *Utricularia*. Nevertheless, the range of diversity in these organs throughout the genus is so great that were the calyx not different, **I feel that generic segregation would never have been proposed on the basis of the trap morphology alone. The internal organization of the traps is not different from that found in the rest of *Utricularia*.** Now that another type of trap, which is in some ways intermediate, is known to occur on a species with four calyx lobes the case for retaining *Polypompholyx* as a distinct genus is considerably weakened. Lang (1901) in a long paper on the morphology, anatomy and seed development of *Polypompholyx* has demonstrated that five sepal primordia are to be found in the developing bud (as they are in *Utricularia* – see e.g. Subramanyam & Narayana 1978), the lower calyx lobe being the result of the fusion of two sepals. The obvious conclusion is that the four-lobed condition in *Polypompholyx* is either of an ancestral type, intermediate between a presumed primitive *Utricularia* calyx with five sepals and the present calyx with two lobes, or it is a reversion towards an ancestral type. While examining material of *U. flaccida* some calyces were seen to have two well developed small lobes at the base of the upper (i.e. three-sepal) calyx lobes. It is tempting to think that this is a partial reversion to the ancestral calyx (see Fig. 169/6). Certainly *Polypompholyx* is very much closer to *Utricularia* than it is to the rest of the family, (Lloyd for instance (1942) treated the two ‘genera’ in the same chapter), and I feel that subgenus is the correct rank for this group.”

Thus, Taylor had no doubt that the investigations and descriptions of one of the most ingenious and most meticulously working pioneers of carnivorous plant research,

Francis Ernest Lloyd, on the trap mechanism of *Polypompholyx* (1942, and republished 2007) were essentially correct, so that he was able to base his revision of the status of the (previous) genus *Polypompholyx* on the fact that, among others, **“The internal organization of the traps is not different from that found in the rest of *Utricularia*”** (see above). Lloyd had, in fact, carefully studied the trap mechanism in *Polypompholyx* and presented his observations in his book *The Carnivorous Plants*.

He mentioned (p. 257) that “the whole trap to be described (p. 262) is extremely curious. Because of the thickness of the walls and other parts and the masses of glandular hairs on the door and on the floor of the antechamber, **it was difficult to study the trap in action, and especially to photograph it. Nevertheless the attempt succeeded (24 — 8)**”. And he continues: “When the trap is set, the door shows a simple curve, along the sagittal line from the upper hinge, which is very thick and does little bending, to the edge which lies just within the ridge of the pavement. When relaxed, just after discharge, the lower two-thirds of the door is convex, the upper hinge showing little movement — a slight bending in its distal zone only. It is evident that the very deep cells of the outer course of this tissue exert a strong tangential pressure on the lower parts of the door, ensuring a tight application of the selvage to the pavement when the door is relaxed and a still tighter application when the trap is set.”

Of *Polypompholyx* and *Utricularia monanthos* he states (p. 256):

“Both *U. monanthos* (24 — 3) and *Polypompholyx* (24 — 8) act in the same way, and they also have been studied in the living condition. *U. monanthos* was grown for me in Edinburgh in 1934 (1936a) and *Polypompholyx* could be examined in 1936 at the University of Western Australia at Perth near which it grows. The structures involved are, however, to be considered separately.”

As for *Utricularia monanthes*, see the appendix*. On pp. 262 and 263 he presents his analysis of the *Polypompholyx* trap:

“Lastly the genus *Polypompholyx* (36 — 1-9), the trap of which was described with respect to the entrance mechanism on p. 257. It has a very special form in this genus (**there is little variety**), in which the stalk plays a special part of the approach to the door.

The form of the trap and a number of anatomical details were described by F. X. LANG in 1901 from material in the GOEBEL collection, which I examined later.

The traps are of various sizes, the largest measuring 4 mm. in length. For the most part they are smaller, about 1.5-2 mm. In one species (possibly *P. latifolia*, though BENTHAM did not admit this species [it was probably *Utricularia (Polypompholyx) multifida*] the traps are dimorphic both in size and structure (36 — 8, 9). **In all the species** (probably four [three according to Taylor 1989/1994, pp. 77-86, *U. tenella*, *U. multifida* and *U. westonii*, the latter belonging to section 2, *Tridentaria*, of the subgenus *Polypompholyx*]) **they present the following characters.** Viewed from above, the body of the trap is seen to be roundly triangular with a forked rostrum in front and a broad wing on either side. The margins are entire but carry stiff hairs. The fork of the rostrum is seen to clasp the stalk, over which the whole forward part of the trap is inclined. The top of the trap body is almost flat — this is the upper side of the three sided body. Seen from below the trap body evidently has two lateral faces, from the upper angles of which the wings extend. The

stalk, which now hides the rostrum, gradually swells on its approach to the trap, and is molded into two low ridges, one on each side, just before the insertion is reached. These ridges are strongly ciliated, forming guiding fences directing prey to the entrance of the trap, which is approached only laterally because of the contact of the rostrum on the stalk. The wings complete two funnel effects, one on each side. Viewed now from the side the stalk is seen to be increasingly massive as it approaches the trap, and this is due to a large intercellular space which inflates the lower moiety below the rostrum. The upper half is expanded into a ridge which becomes deeper under the rostrum, then to be reduced. The loss of height is, however, compensated for by a comb of stiff hairs with long, tapering capitals, and their ends curiously distorted (LANG) as if bent during development by impinging against the rostrum. This ridge being tightly pressed against the rostrum divides the approach to the door into two lateral vestibules, so that the prey must advance under the wings from behind, to be diverted by the combs of bristles on the sides of the stalk toward a space beneath the rostrum. This space has the wall of the trap for its floor and the rostrum and door for its roof, and is an antechamber leading to the entrance proper. Its floor is clothed with mucilaginous hairs with long whip-lash capitals, lying pointed toward the entrance. The roof, which is chiefly the door, bears similar hairs, longer toward the door insertion, shorter toward its free edge. **The entrance is a small semi-circular hole in the trap wall, which stands at a steep angle with the floor of the antechamber.** The semicircular edge of the entrance is clothed with pavement epithelium, the middle zone of which lies just within this edge. The outer zone, which carries the **velum**, faces outwardly (36 — 8, 9). The inner region bears glandular hairs of various forms, at first with conical capitals, then with **bifids**. **Quadrifids** of large size occupy the interior wall surface. The door lies almost at right angles to the plane of the threshold, result of the forward bending of the rostrum. **The action of the door has been already described (p. 257)[see above].** Histologically the door presents a unique feature in the very great depth of the inner course cells in the upper hinge region, the door gradually tapering in thickness toward the edge. Of this we may say that **these thick cells can exert a strong tangential thrust so as to press the door selvage firmly against the pavement, the outer zone of which bears the velum, seen in living material at Perth, W. Australia.** The door selvage is not thickened. Its cells are of equal thickness in both courses, and there is no obvious middle piece. This means that the door selvage must bend over the pavement, not impinge edgewise on it. The tripping mechanism consists of short, bent, glandular hairs, 30-40 in number, scattered on the surface of the door below the middle point (36 — 5).

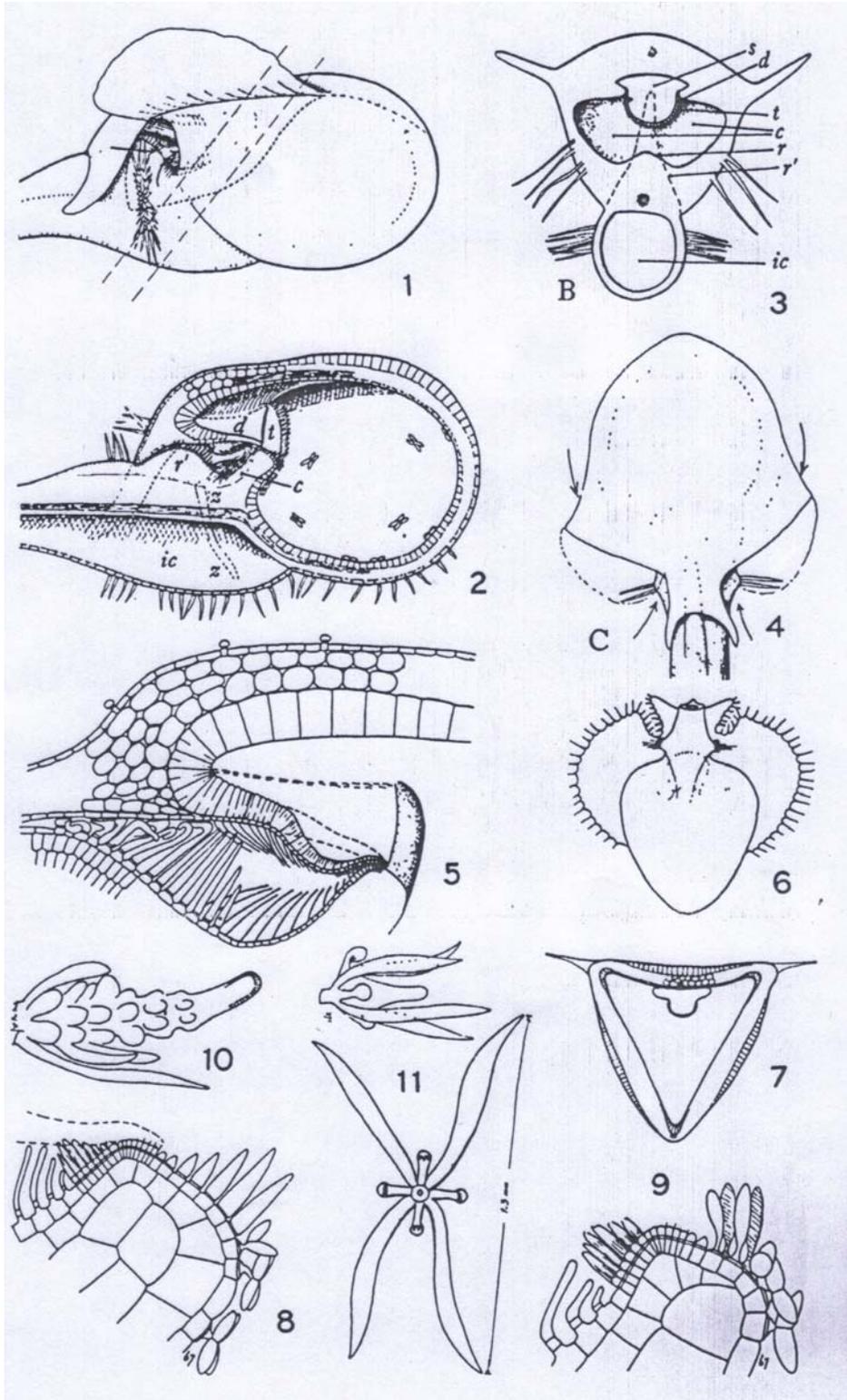
The dimorphism in the traps of *P. latifolia* has been indicated. There are two sizes of traps. In the larger, the threshold behind the pavement bristles with a dense fringe of conical glands of graduated sizes, described by LANG. Inside this pale stand some bifid glands. In the small sized trap there are no conical glands. In their place there are glands with single-celled capitals of the form of the bifids and quadrifids. Inside the traps are bifids (36 — 8, 9).

The walls consist of four courses of cells, the two epiderms and two courses of parenchyma. The epiderms vary in thickness. The outer is thickest in the middle of the sides, and the inner thickest at the angles, here forming a hinge structure.

The total thickness of the three walls, which have four courses of cells throughout, is always greatest at the middle of their faces, producing a hinge effect at the angles. Further, the outer epidermis is always thin at the angles and progressively thicker toward the middle of the faces, while the inner is thick at the angles and thin elsewhere, the more readily allowing compression on the inside of the angles and on the outside of the faces. **It is evident from mere inspection that these massive walls must exert a big pull when the trap is exhausted of water** (36 — 7).

In closing this account one cannot but wonder at the astonishing variety of trap structure. It is not less astonishing that **there is no evidence that one form of trap is superior to another in action.**"

For *Utricularia multifida* (*Polypompholyx multifida*) Lloyd shows many of the details graphically in Plate 36, pp. 342/343 as follows (as for the photographs of Plate 24, Fig. 8 see, please, the original work of 1942):



— Plate 36. —

- FIGS. 1-9, *Polypompholyx*; FIGS. 10-11, *U. tubulata*.
FIG. 1. — Trap (side view) of *P. multifida* F. Muell
FIG. 2. — Same, sagittal section: *c*, antechamber; *d*, door; *ic*, large intercellular space in the stalk; *r'*, ridge along ventral surface of the stalk; *z*, a zone of hairs seen in FIG. 1.
FIG. 3. — Transverse section, embracing part indicated by the parallel broken lines in FIG. 1, looking inwardly; *s*, space above door; *d*, door; *c*, back wall of antechamber; *r*, *r*₁, ridge along the stalk; *ic*, intercellular space in the stalk.
FIG. 4. — Trap, view from above. Arrows indicate directions of approach of prey, as also in FIG. 1.
FIG. 5. — Entrance, showing the door in the relaxed posture. The broken lines indicate the set posture (*cf.* 24 — 8).
FIG. 6. — Trap of *P. tenella*, from below.
FIG. 7. — Transverse section through body of trap of *P. multifida*, showing the occurrence of deep compression cells.
FIG. 8. — Transverse section of the threshold of the large traps of *P. latifolia*.
FIG. 9. — Same, of the small traps.
FIG. 10. — Growing point of *Utricularia tubulata*.
FIG. 11. — A whorl of very young leaves and traps alternating at the same level. Lateral view with growth apex above the numeral, axial view below.

However, in 1932 the same author, Francis E. Lloyd, had published a paper on *The range of structural and functional variety in the traps of Utricularia and Polypompholyx* (Flora 126: 303-328) – at a time when he had not yet access to study living *Polypompholyx* material – in which he proposed the hypothesis (p. 325) “that in *Polypompholyx* **the door acts as a simple valve** and is incapable of contributing to the sustention of a low pressure of water within the trap”.

The author cautiously added: “Whether the **walls** of the trap act as they do in *Utricularia*, producing a low pressure of water in the interior, or not, we cannot, in the absense of the study of living material by experimental methods, say; **nor indeed can we be certain that the foregoing interpretation is correct**. We can at the moment go only so far as the structural evidence seems to indicate.”

Thus – on the foundation of his careful studies of living material – ten years later *the author had clearly revised his earlier hypotheses* (see the details above), although (to quote again the author’s words) “**it was difficult to study the trap in action, and especially to photograph it. Nevertheless the attempt succeeded** (24 — 8).”

Interestingly in 2006 Kerstin Reifenrath, Inge Theisen, Jan Schnitzler, Stefan Porembski and Wilhelm Barthlott published a paper on the *Trap architecture in carnivorous Utricularia (Lentibulariaceae)* (Flora 201 : 597-605), based on

scanning and transmission electron microscopy, in which they corroborate the earlier investigations – in full agreement with Lloyd and further authors – that “some characteristics of the traps of terrestrial *Utricularia multifida* (subgenus *Polypompholyx*) differ remarkably from traps of other species, e.g. trap door anatomy and trap walls” (p. 597).

However, in clear contrast to the studies of Lloyd in living *Polypompholyx* material, the authors develop the hypothesis (as Lloyd in 1932) “that these traps might not function with a low pressure-suction movement. We suggest regarding these traps as channel traps with a permanent open door, resembling the traps of related genus *Genlisea* (Barthlott et al., 1998)” (p. 603). Their reasons? “The sidewalls consist of three or four cell layers instead of two in the other terrestrial species, together with a multi-celled door making the whole trap very robust. Additionally, the entrance is more or less covered by dichotomously divided appendages fixed in dorsal position of the door, forming two lateral tubular channels densely covered with hairs (Fig. 2d)” (also p. 603).

Yet the authors do not mention that Lloyd had suggested virtually the same hypothesis in 1932 due to his studies of non-living *Polypompholyx* material (Karl Goebel’s “entire collection, preserved in fluid” – Lloyd 1932, p. 303) and that he later revised his hypothesis by his research on living *Polypompholyx* plants in Australia as shown in detail above (although Reifenrath et al. cite Lloyd’s book of 1942).

If Reifenrath et al. were correct, Taylor’s revision would have been based on a basically wrong assumption (“The internal organization of the traps is not different from that found in the rest of *Utricularia*” – see above) and the subgenus *Polypompholyx* should regain its status of a genus. However, on 18 January 2007, I wrote the following e-mail to the first author (this was more than a year before I checked the original literature as referred to above; the ensuing page and figure numbers refer to the paper of Reifenrath et al. 2006): “... A question concerning *Utricularia multifida*: Why [or, what for] has it “two-armed glands” (function: “the transport of water out of the trap after the suction process”, p. 598), a door with a *threshold* including a *pavement epithelium* (Fig. 4b), “larger diameters of the rear walls (180%)” (p. 603) etc., when the traps don’t function as a suction mechanism?”** (I could as well have mentioned the *velum* – function: to guarantee a watertight door.) The query was not answered.

On the basis of Lloyd’s meticulous investigations on living material I conclude that *Utricularia multifida* (subgenus *Polypompholyx*) has suction traps like all the other *Utricularia* subgenera and species and that Taylor’s revision was correct.

In our paper on carnivorous plants (Lönnig and Becker 2004/2007) as well as in earlier discussions (Lönnig 1998/2001 and 2000/2001), we mentioned some

of the evolutionary problems, which are presented by the trap mechanisms of *Utricularia* and some other genera. The trap of *Utricularia multifida*, subgenus *Polypompholyx*, is – closely investigated – certainly not something akin to a “missing link” between the trap mechanism of the remaining ca. 220 *Utricularia* species and that of the protozoa-trapping genus *Genlisea*, which displays a very different trap mechanism (for the details, see Juniper, Robins and Joel 1989, Barthlott et al. 1998, Barthlott et al. 2004, Fischer et al. 2004, Lönnig and Becker 2004/2007, Plachno et al. 2007), so much so that Taylor, after noting that *Genlisea*’s trap “is relatively simple when compared with that of *Utricularia*”, comments on the *Utricularia* trap (1989/1994, p. 40):

“It does not seem possible to me to say, of the *Utricularia* trap, which of the many types could be judged primitive or advanced. An apparently simple or complex exterior gives us, or at least me, no inkling as to how this evolved or perhaps more importantly, why the extraordinary diversity we see was necessary. However I cannot, unlike Charles Kingsley (1872, p. 314), dismiss the idea of evolution and accept that, in all their complexity, they were simultaneously created.”***

In a similar vein, Lloyd comments (1942/2007, p. 7):

“It is not without interest to note that among the *Lentibulariaceae* we find examples of the simplest traps (*Pinguicula*), the most complex of the pitfall type, (in the lobster pot of *Genlisea*), and **the incomparable trap of *Utricularia***, whose only rival is that of *Dionaea*. Which of the two is the more “wonderful” (I refer now to Darwin’s statement that he thought *Dionaea* the “most wonderful plant in the world”) will perhaps be a matter of opinion, but the evidence seems to favor *Utricularia*.

...About the origin and evolution of the carnivorous plants, however much these questions may intrigue the mind, little can be said, nor have I attempted to discuss them.

...The fact that they have originated at two or more distinct points in the phylogenetic tree is of major importance. How the highly specialized organs of capture could have evolved seems to defy our present knowledge.”

(As to the topic of convergence in carnivorous plants, see Lönnig and Becker 2004/2007). Nevertheless, the theory of intelligent design – as being clearly different from creationism – may be an option for the origin of the genus *Utricularia* and other genera of carnivorous plants.****

Appendix

*“*U. monanthos* (34—I-5). — In this and allied species, the threshold is very broad, front to back, and near its inner limit is bent, curving downwards. Beyond the bend lies the dense pavement which receives the middle piece, which is therefore applied on the inside of the bend. This looks like a pretty poor arrangement, yet it works. The major zone in front of the bend is occupied by an ample velum which arises also from the walls projecting in front of the door. Here is formed a complete massive ring resting against the bulge of the upper part of the door when in the relaxed posture. When in the set posture, the inner portion of the velum arising from the pavement alone continues to block the entrance of water. The door is still longer than in *U. capensis* etc., but the middle piece is relatively smaller, and the middle area is correspondingly large, occupying about four-fifths of the door length. When in the set

posture, the whole of this large area is concave, so that the sagittal curve is now continuous with that of the middle piece, which by virtue of the thrust of the lateral hinges is impressed against the dense pavement just inside the bend of the threshold. The trigger consists of a group of sessile hairs just above the bend of the door. The action when the trap is fired is like that in *U. capensis*“ (Lloyd 1942/2007, p. 256).

**Original in German: “... Eine Frage zu *Utricularia multifida*: Wozu hat sie “two-armed glands” (Funktion: “the transport of water out of the trap after the suction process”, p. 598), eine Tür mit *threshold* including a *pavement epithelium* (Fig. 4b), “larger diameters of the rear walls (180%)” (p. 603) etc., wenn die Fallen nicht doch als *suction mechanism* funktionieren?”

***Here is Charles Kingsley’s comment on the origin of *Utricularia* after mentioning some of his observations on the bladderworts of Trinidad and other parts of South America:

“In the face of such strange facts, **is it very absurd to guess that these *Utricularias***, so like each other in their singular and highly specialised flowers, so unlike each other in the habit of the rest of the plant, have **started from some one original type** perhaps long since extinct; and that, carried by birds into quite new situations, they have adapted themselves, by natural selection, to new circumstances, changing the parts which required change—the leaves and stalks; but keeping comparatively unchanged those which needed no change—the flowers?”

On the other hand, Kingsley seems to have accepted natural selection in the sense of Darwin’s friend, the botanist Asa Gray. On *Calycophyllum* (a tree), Kingsley writes (<http://www.gutenberg.org/files/10669/10669.txt>):

“But it is not the flowers themselves which make the glory of the tree. As the flower opens, one calyx-lobe, by a rich vagary of nature, grows into a leaf three inches long, of a splendid scarlet; and the whole end of each branch, for two feet or more in length, blazes among the green foliage till you can see it and wonder at it a quarter of a mile away. This is ‘the resplendent *Calycophyllum*,’ elaborated, most probably, by long physical processes of variation and natural selection into a form equally monstrous and beautiful. There are those who will smile at my superstition, if I state my belief that He who makes all things make themselves may have used those very processes of variation and natural selection for a final cause; and that the final cause was, that He might delight Himself in the beauty of one more strange and new creation. Be it so. I can only assume that their minds are, for the present at least, differently constituted from mine.”

He also defends natural selection against some theological objections elsewhere. Besides, in his book there is a quotation of Elias Fries (1794-1878, one of the fathers of mycology), which seems to be of topical interest for the current *ecological* situation in many parts of the world (considering the time it was written, I like to add it here in the appendix, although it may only be indirectly related to our topic):

“A broad belt of waste land follows gradually in the steps of cultivation. If it expands, its centre and its cradle dies, and on the outer borders only do we find green shoots. But it is not impossible, only difficult, for man, without renouncing the advantage of culture itself, one day to make reparation for the injury which he has inflicted; he is the appointed lord of creation. True it is that thorns and thistles, ill-favoured and poisonous plants, well named by botanists “rubbish-plants,” mark the track which man has proudly traversed through the earth. Before him lay original Nature in her wild but sublime beauty. Behind him he leaves the desert, a deformed and ruined land; for childish desire of destruction or thoughtless squandering of vegetable treasures has destroyed the character of Nature; and, terrified, man himself flies from the arena of his actions, leaving the impoverished earth to barbarous races or to animals, so long as yet another spot in virgin beauty smiles before him. Here, again, in selfish pursuit of profit, and, consciously or unconsciously, following the abominable principle of the great moral vileness which one man has expressed - “Apres nous le deluge” - he begins anew the work of destruction. Thus did cultivation, driven out, leave the East, and perhaps the Deserts formerly robbed of their coverings: like the wild hordes of old over beautiful Greece,

thus rolls the conquest with fearful rapidity from east to west through America; and the planter now often leaves the already exhausted land, the eastern climate becomes infertile through the demolition of the forests, to introduce a similar revolution into the far West.”

****As for an introduction to the theory of intelligent design, see please <http://www.weloennig.de/DynamicGenomes.html>

In contrast to this theory, the Darwinian theory of additive typogenesis (G. Heberer) necessarily postulates innumerable small steps of adaptive character by, as Mayr says, mutations with “*slight or even invisible effects on the phenotype*”. Thus, enormous numbers of often improbable intermediate forms must have been involved in the origin of any of the present trap mechanisms of the different genera of carnivorous plants. To repeat some further quotations from earlier papers: "Macroevolution (evolution between species) is composed of numerous small microevolutionary steps (additive typogenesis)" – Kutschera 2001, p. 250. Or: "Uncountable successive small microevolutionary steps have led to large changes in the body forms of organisms in the course of millions of years (macroevolution, concept of additive typogenesis)" – Kutschera 2006, p. 204.

Darwin had already postulated "infinitesimally small variations", "steps not greater than those separating fine varieties" and "insensibly fine steps" for evolution, "for natural selection can act only by taking advantage of slight successive variations; **she can never take a leap**, but must advance by the shortest and slowest steps".

Regarding the origin of the trap mechanism of *Utricularia vulgaris*, Nachtwey asked the following questions (1959, pp. 99/100): “Which nondirectional mutation should have occurred first in a normal leaf tip and subsequently displayed any selective advantage? Without an advantage it would have been lost as trivial. The modern synthesis strongly emphasizes that mutation and selection have to cooperate to generate new structures. So, by which blind mutations should the suction trap have originated?” And regarding the problem of further evolutionary stages the writer continues: “Even a perfect suction trap displaying the astonishing ability to rapidly catch animals would have no advantage in the struggle for life because the prey would not be digested. Conversely, the production of highly effective digestive juices would be of no avail for the tip of a leaf as long as it could not capture the prey, which is absolutely necessary. But even if suction trap and digestive juices cooperated, nothing would be gained in the struggle for life. The dissolved proteins must also be absorbed and metabolized to species-specific proteins. *The formation of the suction trap requires the perfect cooperation of many different genes and developmental factors. Only in the end a benefit is reached in the struggle for life, but not by any evolutionary stage.*” (Italics by Nachtwey.) Nachtwey concluded that none of the contemporary evolutionary theories was able to answer these questions, proposing that the answer might lie outside the present scientific paradigms.

“Although other scenarios could possibly be envisioned and some objections raised against Nachtwey’s reflections (perhaps unknown functions of nascent structures, perhaps minor uptake of organic compounds by leaves without digestive and absorbent glands), the problem appears to have been aggravated by the recent discoveries that the well-being of *Utricularia purpurea* appears to be largely independent of its prey [Richards 2001](see details under nutrition and digestion above).” For this and further points, see Lönning and Becker 2004/2007.

However, for any problems of the synthetic theory (neo-Darwinism) Richard Dawkins comes to the rescue by the following suggestions on the origin of the eye – proposals, which he thinks are principally valid for the genesis of any complex organ. Thus, we may apply his ideas as well to the origin of *Utricularia's* trap.

As to the question, “Is there a continuous series of Xs [gradations/links] connecting the modern human eye [or the trap of *Utricularia*] to a state with no eye [or no trap mechanism] at all?” – Dawkins’ answer is: “It seems to me clear that the answer has to be yes, provided only that we allow ourselves a *sufficiently large* series of Xs.” And he continues (1986, p. 78, and paperback edition 1996, italics in the former quotation by Dawkins, but now emphasis added):

"You might feel that 1,000 Xs is ample, but if you need more steps to make the total transition plausible *in your mind, simply allow yourself to assume 10,000 Xs*. And if 10,000 is not enough for you, *allow yourself 100,000*, and so on."..."Given, say, a hundred million Xs, we should be able to construct a plausible series of tiny gradations linking a human eye [or the trap of *Utricularia*] *to just about anything!*"

I am especially fond of Dawkins' conclusion that by the neo-Darwinian method the human eye (or the trap of *Utricularia*) could thus be linked "**to just about anything**" (or, more precisely, that "we should be able to construct a *plausible series of tiny gradations* linking a human eye [or the trap of *Utricularia*] **to just about anything**"). And yes, concerning the possibilities and potentials of his method, I suppose that Dawkins is almost literally correct.

The problem only is that his method essentially consists of pure phantasy, not science ("...*if you need* more steps to make the total transition *plausible in your mind, simply allow yourself...*" etc.). In contrast, in science we need *testable* hypotheses, which in the most convincing case means that the hypothetical steps should be reproducible, at least in principle. "The principle of science, the definition almost, is the following: The test of all knowledge is experiment. Experiment is the single judge of "truth."" – Richard Feynman, nobel laureate (physics). Yet a method which allows us to link *Utricularia* *to just about anything in our mind*, is hardly more than an instruction or direction how to persuade oneself in accord with some unproven basic assumptions or – in a worse case – deceive oneself in agreement with an ideology.

Moreover, for any real scientific theory, criteria should be given concerning the question under which circumstances the theory is proven wrong, – constituting a category of testable criteria usually also missing in the line of the Darwinian argumentation (for further points, see, please, the topic *Inwieweit gelten Poppers Falsifikationskriterien auch für die Evolutionstheorie?* <http://www.weloennig.de/Popper.html> and Klaus Wittlich: <http://www.weloennig.de/NeoVorKl.html>).

Concerning additional points of Dawkins arguments on the origin of the eye, see please <http://www.weloennig.de/AuIIDaw.html>, on the questions what mutations really can do, see Lönnig 2004: <http://www.weloennig.de/Loennig-Long-Version-of-Law-of-Recurrent-Variation.pdf>, and what selection can achieve: <http://www.weloennig.de/NaturalSelection.html>

Further related papers can be found under <http://www.weloennig.de/internetlibrary.html> and <http://www.weloennig.de/literatur1a.html>

References

Except appendix. The references of the papers and books mentioned in the appendix can be found in Lönnig 2007 <http://www.weloennig.de/GiraffaSecondPartEnglish.pdf> and/or Lönnig and Becker 2004/2007 (see below) and the links given.

Barthlott, W., Porembski, S., Fischer, E. and B. Gemmel (1998): First protozoa-trapping plant found. *Nature* **392**: 447 [On *Genlisea*].

Barthlott, W., Porembski, S., Seine, R., and I. Theisen (2004): Karnivoren. Biologie und Kultur fleischfressender Pflanzen. Verlag Eugen Ulmer, Stuttgart.

(Hervorragende Übersicht, viele sehr gute farbige Abbildungen, auch rasterelektronenmikroskopischen Details der Reusenfalle von *Genlisea* p. 131.)

Fischer, E., Barthlott, W., Seine, R. and I. Theisen (2004): Lentibulariaceae. In: The Families and Genera of Vascular Plants. Edited by K. Kubitzki, Vol. VII, Flowering Plants, Dicotyledons, Lamiales (except Acanthaceae including Avicenniaceae), pp. 276282. Springer-Verlag, Berlin. (P. 281 concerning *Utricularia*: "...traps occasionally absent (*U. neottioides*).") – Excellent figure of the trap of *Genlisea margaretae* by I. Theisen.)

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Lönnig, W.-E. (1998/2001): Gregor Mendel, der Wasserschlauch (*Utricularia*) und die Evolution. <http://www.weloennig.de/Utricularia.html>

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Plachno, B. J., Koziaradzka-Kiszkurno, M. and P. Swiatek (2007): Functional ultrastructure of *Genlisea* (Lentibulariaceae) digestive hairs. *Annals of Botany* **100**: 195-203. ("In spite of their similar architecture, the digestive-absorptive hairs of Lentibulariaceae feature differences in morphology and ultrastructure" (p. 195). "Taking together previously published work on Lentibulariaceae hairs (Fineran and Lee, 1975; Heslop-Harrison and Heslop-Harrison, 1981; Fineran, 1985) and the present results, it is clear that the most complicated terminal cell in the digestive hairs of this family has evolved in *Utricularia*. In contrast to the sessile hairs in *Pinguicula* and *Genlisea*, in *Utricularia* the quadrifid and bifid terminal cells not only play a role in secretion and absorption but also partially take over the function of the middle cell" (p. 201) "In mature traps of *Genlisea*, digestive hairs are stimulated continuously, because prey enter opened traps all the time. Enzyme secretion occurs in the absence of prey in plants from *in vitro*

sterile culture (Plachno, 2006; Plachno *et al.*, 2006). For these reasons, we suggest that digestive enzymes are continuously secreted to the trap interior (continuous digestive activity). Mucilage has been observed inside *Genlisea* traps (Studnicka, 2003a; Plachno *et al.*, 2005b). Thus, digestive pools of viscous fluid occur in *Genlisea*. However, unlike in the secretory cells of mucilage glands of *Drosophyllum*, *Drosera*, *Utricularia* and *Pinguicula* (Schnepf, 1961, 1963; Vintéjoux and Shoar-Ghafari, 1997, 2005) hypertrophy of dictyosomes and large vesicles containing mucilage were not observed in *Genlisea*" (p. 201.).

Porembski, S. and W. Barthlott (2006): Advances in carnivorous plants research (Editorial). *Plant Biology* **8**: 737-739.

Reifenrath, K., Theisen, I., Schnitzler J., Porembski, S. and W. Barthlott (2006): Trap architecture in carnivorous *Utricularia* (Lentibulariaceae). *Flora* **201**: 597-605.

Abstract: "Within carnivorous plants, the bladderworts (*Utricularia*) possess the most complicated traps whose mechanisms are not yet completely understood. For the first time, a representative survey of different traps from both subgenera (*Utricularia* and *Polypompholyx*) is presented. Based on scanning- and transmission electron microscopy, traps of 14 species of *Utricularia* (out of 215 species) representing 11 sections (out of 35 sections) and including all life forms (aquatic, epiphytic, and terrestrial) were investigated. Additionally, it was tested whether life forms correlate with trapping mechanisms. Most morphological and anatomical features of the traps vary considerably between the different life forms, e.g. position of trap and trap entrance as well as form and position of trap appendages. Morphological data support the basal position of subgenus *Polypompholyx* within the genus. Some characteristics of the traps of terrestrial *Utricularia multifida* (subgenus *Polypompholyx*) differ remarkably from traps of the other species, e.g. trap-door anatomy and trap walls. This might be an indication for a primordial (non-suction) trapping mechanism in the former species, similar to that of the eel-traps of the closely related genus *Genlisea*."

As documented above, according to the investigations of Lloyd (1942/2007) on living material, the latter hypothesis is not correct in the otherwise informative paper (many SEM, LM and TEM pictures).

Richards J. H. (2001): Bladder function in *Utricularia purpurea* (Lentibulariaceae): Is carnivory important? *American Journal of Botany* **88**: 170–176.

Taylor, P. (1986): New taxa in *Utricularia* (Lentibulariaceae). *Kew Bulletin* **41**: 1-18. In this paper Taylor first proposed the state of a subgenus for *Polypompholyx* (p. 2: "...as the traps especially and all other parts of the plant [except the 4 rather than 2-lobed calyx] differ in no significant way from those of the rest of the genus it is now proposed to include them in *Utricularia*. Within the genus they appear to be most closely allied to the section *Pleiochasia*.")) and described *U. westonii* belonging to a new section, *Tridentaria*, displaying different traps. The species was first discovered by Weston in 1971. Moreover, on the basis of molecular data – chloroplast *trnK* intron and *matK* –, Müller and Borsch (2005 in: *Plant Syst. Evol.* **250**: 39-67) suggest to add the section *Pleiochasia* with 33 species to *Polypompholyx*. "However, **the combined *trnL-F + rp/16 tree*** [of Jobson et al. 2003, *Syst. Bot.* **28**: 157-171] **shows a different branching of major clades compared to the results obtained by *matK/trnK***" Müller and Borsch, p. 41. Thus, at present at least, the molecular basis for a further (larger) revision appears to be somewhat contradictory and rather thin.

Taylor, P. (1989, reprinted 1994): The Genus *Utricularia* - A Taxonomic Monograph. Royal Botanic Gardens, Kew. *Kew Bulletin Additional Series XIV*. London. Her Majesty's Stationary Office. (On *U. neottioides* p. 498 and 500: "...Traps usually few or often apparently absent, paired or solitary on the rhizoids, at the stolon nodes and at the base of the primary leaf branches, obliquely ovoid, c. 1 mm long, shortly stalked, the stalk often curved, so as to invert the trap, the mouth terminal, with a variable number (usually 3) of short simple, or rarely sparsely branched, dorsal setae, the internal 4-armed glands with arms 5-8 times as long as wide (fig. A, 10).")