falcons, shorebirds, and hummingbirds, the primaries are extremely asymmetric. In poor fliers, such as galliform birds, the asymmetry is less pronounced. Ostriches (*Struthio*) and rheas (*Rhea* and *Pterocnemia*) are flightless and are thought to have evolved from flying birds (*6*). They apparently have retained the wing and flight feathers for display and perhaps for thermoregulation and balance in running. In these birds the vanes of the primaries have reverted to symmetry. In other island birds that have presumably become secondarily flightless more recently (*7*), such as the Kagu (*Rhinochetos jubatus*) and the Brown Mesites (*Mesoenas unicolor*), the rectrices are perfectly symmetric; the primaries show only a slight asymmetry. The flightless Galapagos Cormorant (*Phalacrocorax harrisi*) has nearly symmetric vanes on the primary feathers but has retained asymmetric vanes in the retrices, presumably for a hydrodynamic function, as it swims through the water. Flying species of modern cormorants have asymmetric primary and tail feathers. The flightless grebes *Centropelma micropterum* and *Podilymbus gigas* of Lake Titicaca and Lake Atitlán, respectively, have asymmetric primary vanes but use their wings to some degree. The rails (Rallidae) show the greatest proclivity among modern birds to become flightless, and in this family one sees all degrees of flightlessness and a corresponding diminution in the degree of asymmetry of the vanes of the primaries (*3*) (Fig. 2). Such absolutely flightless rails as *Atlantisia rogersi* and *Gallirallus australis* have perfectly symmetric vanes on the primaries.

The shape and general proportions of the wing and wing feathers in *Archaeopteryx* are essentially like those of modern birds. The fact that the basic pattern and proportions of the modern avian wing were present in *Archaeopteryx* and have remained essentially unchanged for approximately 150 million years (since late Jurassic time), and that the individual flight feathers showed the asymmetry characteristic of airfoils seems to show that *Archaeopteryx* had an aerodynamically designed wing and was capable of at least gliding. Any argument that *Archaeopteryx* was flightless must explain selection for asymmetry in the wing feathers in some context other than flight.

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Capture Enhancement in a Carnivorous Aquatic Plant: Function of Antennae and Bristles in *Utricularia vulgaris*

Abstract. *Traps of the carnivorous hydrophyte* Utricularia vulgaris *Linnaeus (Lentibulariaceae) have structures termed antennae and bristles around their trapdoors that increase their rate of entrapment of the substrate-dwelling prey* Chydorus sphaericus *(Chydoridae, Crustacea). The kind and number of these structures are important in determining capture rate. Experimental data and corresponding behavioral observations support Darwin's hypothesis that antennae and bristles function as a "funnel" leading potential prey toward the trapdoor and their capture by offering the prey a favorable substrate that exploits their natural locomotor and feeding behavior.*

Utricularia, commonly known as bladderwort, encompasses over 250 species, more than any other genus of carnivorous plant, and is distributed throughout the tropical and temperate climates of the world (*1–4*). A member of the family Lentibulariaceae, *Utricularia* is unique among carnivorous plants because of (i) the structural complexity of its traps, thought to be the most intricate in the plant kingdom (*2*), and (ii) the rapid movement of the opening and closing of its trapdoors, by far the fastest-acting botanical trapping mechanism known (15 to 25 msec) (*2, 5*). *Utricularia vulgaris* Linnaeus, the most widely distributed species of bladderwort, is a free-floating hydrophyte common in shallow, still, circumboreal waters, although its range extends into the tropics (*1, 3, 6*). Morphologically, this plant is composed of a central stem from which radiate at various intervals finely dissected leaves (*7*) (Fig. 1A). To each leaf are attached 20 or more traps (Fig. 1B).

A trap or "bladder" is a hollow, egg-shaped structure 0.3 to 5.0 mm long and having a trapdoor at its tapered end (*4*) (Fig. 1C). Darwin, in his classic treatise *Insectivorous Plants*, termed the multicellular, branched extensions arising from the top corners of the trapdoor arch "antennae," and the unbranched, filamentous projections occurring in sets on either side of the door frame "bristles" (*8*). He used these terms, still in use today (*4, 7, 9*), because a trap and its associated structures reminded him of an aquatic microcrustacean. The functional significance of these structures, he proposed, is to guide potential prey to their doom by creating a "funnel" that directs animals toward the trapdoor. This speculation that antennae and bristles provide an adaptive advantage in prey capture has been generally accepted for more than a century (*2, 4, 9*), but to the best of our knowledge has never been experimentally tested.

We now report results from a series of experiments that support Darwin's "funnel" hypothesis. Selective removal of antennae, bristle-sets, or both significantly reduces the rate of capture by *U. vulgaris* traps on microcrustacean prey (Chydoridae, Cladocera). Prey traveling over antennae and bristles are more likely to be captured than those meandering on the surface of the bladder. Because antennae and bristles structurally resemble filamentous algae, a frequent substrate for Chydoridae, they furnish a pathway similar to an algal strand down which these animals graze off epiphytes while being led toward the trapdoor; consequently, these structures substantially increase the probability of prey entrapment.

The action of the trapping mechanism of *U. vulgaris* has been well studied (*2, 5*). A negative hydrostatic pressure maintained within the trap is released when an animal touches one of the trigger hairs at the base of the trapdoor, causing a rapid opening of the door, expansion of the bladder, and inflow of water and prey (Fig. 1D). The door then shuts, and specialized cells within the

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walls of the trap cause water to be transported from the lumen to the exterior through the door region (*10*) reestablishing the hydrostatic pressure differential, contracting the elastic bladder walls, and resetting the trap in a minimum of 15 minutes (*11*). One trap can be triggered and can reset in excess of 25 times and still retain its functional capability (*12*).

We conducted a series of four experiments to test the effect of antennae and bristle-sets on the rate of capture by *U. vulgaris* on *Chydorus sphaericus* O. F. Müller (Chydoridae, Cladocera), a ubiquitous microcrustacean frequently captured by *U. vulgaris* (*12, 13*). The experiments were identical except that the two in condition 1 began at 0600 hours and those in condition 2 began at 1800 hours. Each experiment was composed of seven treatments that consisted of the removal of one antenna (1A), two antennae (2A), or none (0A) and one bristle-set (1B), two sets (2B), or none (0B) in the following seven combinations: 0A0B (control), 0A1B, 1A0B, 1A1B, 1A2B, 2A1B, and 2A2B (Table 1). In half of the treatments, the structures were removed from the right side (S1), in the other half from the left (S2). Because these structures were cut off with microsurgical scissors, the natural shape and function of the traps were left undamaged (*14*). Treatments consisted of four 25-ml glass petri dishes, each filled with 15 ml of filtered pond water containing one *U. vulgaris* leaf with ten large bladders (*15*) and 25 *C. sphaericus*. Each treatment and condition was replicated with a "brother" or "twin" leaf from the same stem location. Experiments were terminated after 24 hours, and the captures per trap were recorded.

A four-way analysis of variance (treatment by side by brother by condition) revealed that only treatment had a significant effect [F (6 df) = 34.25, $P < .001$]; this allowed values within each experimental treatment to be pooled. Capture rate (Table 1) is thus a mean based on the 16 independent treatment values of the four separate experiments.

Removing any structure resulted in a decline in the rate of entrapment in all six ablation treatments compared with the control (Table 1). For example, the absence of one antenna and one bristle-set (T4) reduced the number of captures by 36 percent; elimination of all projections (T7) corresponded to a 79 percent decrease. A comparison of all seven treatments revealed a linear relationship between the number of prey captured and the number of structures removed ($r = .99$). To evaluate the contribution of individual antennae and bristle-sets to the overall rate of capture, comparisons were made between treatments with and without the respective structure (*16*). The removal of one bristle-set brought about an 11 percent reduction; two, 29 percent; one antenna, 29 percent; and two, 64 percent.

Table 1. Effect of antenna (A) and bristle-set (B) removal on the capture rate of *U. vulgaris* on *C. sphaericus*. Rates are expressed as the mean (± standard error) number of captures per *U. vulgaris* leaf with ten large traps in 24 hours. Abbreviations: T, treatment; S, side (S1 ablation from right side, S2 from left); condition 1 (C1) began at 0600 hours, condition 2 (C2) at 1800 hours.

Structures removed (No.)		Treatment	*C. sphaericus* captured (No.)†		Capture rate ($\bar{X}$ ± S.E.)
A	B		C1	C2	
		T1*			
0	0	S1	15†	15	14 ± 0.8
		S2	12	13	
		T2			
0	1	S1	11	13	13 ± 0.7
		S2	15	12	
		T3			
1	0	S1	12	9	11 ± 0.8
		S2	10	12	
		T4			
1	1	S1	9	10	9 ± 0.7
		S2	9	7	
		T5			
1	2	S1	7	7	7 ± 0.6
		S2	8	6	
		T6			
2	1	S1	3	5	4 ± 0.6
		S2	6	3	
		T7*			
2	2	S1	4	2	3 ± 0.4
		S2	3	4	

*No side designations were possible; half the leaves were randomly assigned to each side. †Each number represents a mean of four values—two "brothers" from two experiments.

These results indicate that antennae are twice as important as bristle-sets in enhancing the capture rate. This may be further supported by the observation that small bladders ordinarily produce only antennae. Antennae differ from bristle-sets in the following characteristics: (i) size, approximately 22 percent longer (*17*); (ii) position, above the trapdoor; and (iii) shape, branched. Any or all of these properties could contribute to antennal superiority in determining capture rate.

The removal experiments demonstrated the enhancement of capture rate attributable to antennae and bristle-sets; they did not, however, elucidate the possible plant-animal interaction that accounted for the enhancement. To investigate how antennae and bristles might affect the locomotor behavior of the chydorids, we designed a three-trial experiment. Using the same petri dish "universe" as in the removal experiments, we observed the number of animals that swam to and landed on either an antenna, bristle, or trap, exclusive of antennae and bristles, and the subsequent number of captures preceded by movement on each substrate type until ten captures were recorded for each of the three trials.

The traps themselves were most often landed on, as would be expected from their larger surface area, and antennae the least (Table 2). However, the percent of landings that resulted in capture were significantly higher for chydorids landing on antennae than on either bristles or traps, thus corroborating the antennal superiority distinguished in the removal experiments; bristles accounted for a higher percent than traps. No *C. sphaericus* were seen to swim directly into the trapdoor and be captured. These results support Darwin's "funnel" hypothesis, since prey that are moving on antennae or bristles have a higher probability of capture than those traveling over the surface of a bladder, even though considerably more are landing on the trap. The inference is that the prey are somehow guided to or are arriving at the trapping mechanism with greater regularity.

Table 2. Number of *C. sphaericus* swimming to and landing on antennae (A), bristles (B), and traps (T) (exclusive of antennae and bristles) compared with number captured.

Substrate inhabited before capture	Trials			Total number landing	Total number captured	Total landing (%)	Landing resulting in capture (%)	Level of significance*
	1	2	3					
Antenna								
Landing	26	11	30	67		26		
Captured	5	3	6		14		21	.05(A, B)
Bristle								
Landing	14	49	20	83		30		
Captured	2	6	3		11		13	.05 (B, T)
Trap								
Landing	40	53	31	124		41		
Captured	3	1	1		5		4	.05 (T, A)

*Fisher exact probability test.

The key to understanding how antennae and bristles direct potential prey toward the trapdoor is a knowledge of the feeding behavior of *C. sphaericus*. Chydoridae are substrate-dwelling organisms often found in association with filamentous algae (*18*). In particular, *C. sphaericus* uses two feeding modes when in contact with this substrate: (i) grazing on epiphytes while traversing an algal strand and (ii) filter-feeding while grasping a strand and remaining stationary. These modes of feeding are also used on antennae and bristles of *U. vulgaris* (*19*), whose structure closely resembles that of filamentous algae. Traveling and feeding along these filamentous extensions apparently increases the probability that a chydorid will arrive at the base of a projection located on the door arch, move out onto the trapdoor, and trigger the trapping mechanism. The likelihood that an animal will contact the bladder door may be augmented by sugary secretions of the door itself that are thought to act as a prey lure (*20*).

Chydorids are only a portion of the prey consumed by *U. vulgaris*. Crawling forms, such as chironomid or other insect larvae (*2, 12*), and free-swimming victims that include daphnids or water fleas (*13*) are also reported to be ingested. Antennae and bristles are used as a feeding pathway by chironomids in the same manner as chydorids (*12*). Whether their adaptive value is similar in the entrapment of free-swimming prey remains to be tested; from an inspection of the contents of over 1000 bladders collected from various localities in temperate North America, however, daphnids were found to be an extremely rare dietary component (*12*). This would seem to indicate that antennae and bristles are better adapted to complementing the capture of substrate-dwellers or crawling prey.

Antenna and bristle forms vary from one species of *Utricularia* to another (*2, 3*). Their functional significance, as well as morphological variability, may be dependent on habitat type—aquatic, mud, or wet sandy soil and wet moss (*2*). In water-dwelling species like *U. vulgaris* these structures are thought to be an elaboration of the trapping mechanism (*2, 4, 9*), thus reinforcing Darwin's hypothesis. It has also been proposed, however, that their absence does not affect the number of prey captured (*2*). Although our study does not establish the sole functional significance of antennae and bristles, it does present experimental evidence that supports the validity of Darwin's "funnel" hypothesis and indicates an adaptive value of these trap extensions in enhancing capture success by providing a favorable substrate that exploits the natural feeding modes of littoral, substrate-dwelling prey.

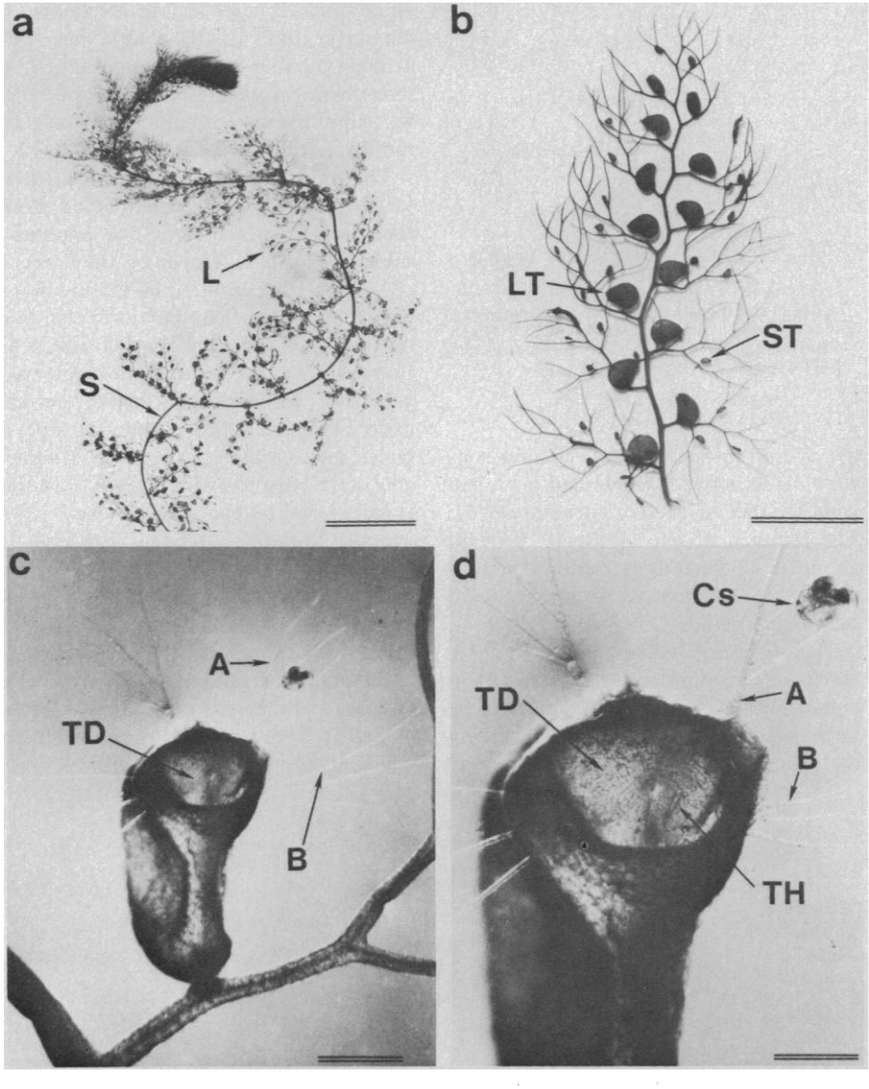

Fig. 1. (a) Morphology of *U. vulgaris* showing the central stem (*S*) from which radiate the trap-bearing leaves (*L*) (bar = 3 cm). (b) Leaf containing large traps (*LT*) and small traps (*ST*) (bar = 1 cm). (c) Anterior view of a trap or bladder and its associated structures, antennae (*A*) and bristles (*B*), surrounding the trapdoor (*TD*) (bar = 1 mm). (d) Close-up of the trapdoor region of a bladder depicting the proximity of the base of the antennae and bristles to the trapdoor and trigger hairs (*TH*). A *C. sphaericus* (*Cs*), common prey animal of the plant, is perched on a bristle (bar = 0.5 mm).

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14. Surgical removal of antennae and bristle-sets from traps in the set or concave position did not trigger the bladders or alter their shape. Further observations preceding the formal experiments indicated *C. sphaericus* approached the trapdoors of these traps and touched the trigger hairs just as they did bladders without removals; the traps were as effective in capturing one prey, resetting, and then capturing a second prey. These observations coupled with the mechanical nature of the trapping mechanism led us to believe that the removals had little, if any, effect on the functional ability of the traps or the behavior of the prey.
15. *Utricularia vulgaris* was collected one day

preceding each experiment from Lidyhites Pond, New Haven, Conn. In the laboratory, leaves with healthy, functional traps were cut from the plant stem and cleaned of entangling filamentous algae. Secondary or small bladders were removed from the leaf periphery, leaving ten large traps near the midvein of each leaf. Distinctions of trap type, small or large, were made according to the scheme of R. L. Wallace [*Freshwater Biol.* 7, 301 (1977)].

16. Mean number of captures per antenna or bristle-set is based on treatment comparisons. For example, the contribution of 1B was calculated from the summation of the subtractions of the mean of treatment 2 (T2) from T1, T4 from T3, T5 from T4, and T7 from T6, and the resultant divided by 4 (Table 1). The variance between the compared treatments was significant for the contribution of 1B ($P < .05$), 2B ($P < .01$), 1A ($P < .005$), and 2A ($P < .005$) (Bonferroni multiple comparison t statistic). Bonferroni inequality was applied to the levels of significance of Student's t test according to R. J. Harris [*A Primer of Multivariate Statistics* (Academic Press, New York, 1975), pp. 98-101].
17. Antenna length, including branches and bristle-sets, was measured on 258 randomly chosen traps: antenna, 2.92 mm ± 0.14 mm; bristle-set, 2.29 mm ± 0.11 mm (mean ± standard error).
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Radiation from Tritiated Thymidine Perturbs the Cell Cycle Progression of Stimulated Lymphocytes

Abstract. *Tritiated thymidine was found to affect the cell cycle progression of phytohemagglutinin-stimulated human lymphocytes. By means of flow cytometry a statistically significant increase in the G_2 and M phases of the cell cycle was observed in cultures with low concentrations of tritiated thymidine added 18 hours before the cultures were harvested.*

Tritiated thymidine is widely used for labeling newly synthesized DNA in proliferating cells. The incorporated radioisotope can be rapidly measured by liquid scintillation counting and autoradiography. However, in the late 1950's evidence was obtained that incorporated [^{3}H]thymidine suppressed cell proliferation (*1*). Colony count inhibition (*2*), quantitation of chromosome aberrations (*3*), inactivation of transforming DNA (*4*), production of mutations (*5*), and the induction of DNA strand breaks (*6, 7*) have all been used to demonstrate the deleterious effects of [^{3}H]thymidine, and have shown that these effects are a function of specific activity, concentration, and exposure time.

Flow cytometry (FCM) has become a popular method for quantitating DNA content on a per cell basis (*8*). Cells or nuclei stained with a fluorescent dye such as propidium iodide (PI) are suspended in a fluid stream that passes through an argon-ion laser beam (488 nm). As the cells pass through the laser, at rates of 100 to 3000 cells per second, a photomultiplier tube detects the amount of fluorescence emitted per particle, and this information is collected on a multichannel analyzer or computer. When a relatively specific dye for double-stranded nucleic acid, such as PI, is used, the resultant histogram displays the number of cells on the ordinate against the fluorescence intensity (proportional to DNA content) on the abscissa. These histograms are therefore a "snapshot" representation of the proportion of cells distributed about the phases of the cell cycle and can be used to estimate the percentages of cells in G_0+G_1, S, and G_2+M (*9*). Also, groups of histograms (for example, quadruplicate cultures of two test groups) can be averaged and compared statistically (*10*). This statistical comparison shows areas of significant differences between the averaged histograms.

We have used FCM to study cell cycle changes caused by the addition of [^{3}H]thymidine to phytohemagglutinin-stimulated lymphocyte microcultures. These 0.2-ml cultures were made up of human peripheral blood lymphocytes separated by Ficoll-Paque (Pharmacia). Each well contained 1×10^5 cells suspended in Medium 199 buffered with 0.23 percent bicarbonate and supplemented with 2m*M* L-glutamine, 20 percent heat-inactivated fetal calf serum, and a 1× antibiotic-antimycotic mixture (Gibco). Lymphocytes were stimulated with optimum PHA concentrations (PHA-P, Difco) for 90 hours and [^{3}H]thymidine was added 18 hours or 20 minutes before the culture was harvested. Cultures were treated with 0.03 ml of medium with or without [^{3}H]thymidine of specific activity 1.9 Ci/mmole (Schwarz/Mann), or 50 Ci/mmole (New England Nuclear) or $2.6 \times 10^{-7}M$ unlabeled thymidine (Sigma) (see Figs. 1 to 3). Flow cytometric analyses were performed on PI-stained nuclei (*11*). Each FCM analysis shown (Figs. 1 to 3) is a statistical comparison between two groups of quadruplicate smoothed, translocated, and averaged histograms (*10*). Figure 1 shows the differences observed when 0.1 μCi of [^{3}H]thymidine (1.9 Ci/mmole) was added per culture, or when medium alone was added for the last 18 hours. The 18-hour labeling period was used because labeling times of 12 to 24 hours are commonly used with PHA-stimulated lymphocyte cultures. The cultures exposed to [^{3}H]thymidine showed a marked buildup of cells in G_2+M with a reduced proportion of cells in S. These differences in S and G_2+M were significant to $P < .01$. To determine whether the effect elicited by [^{3}H]thymidine was due to the concentrations of thymidine employed, we tested unlabeled thymidine at the same concentration ($2.6 \times 10^{-7}M$).

Figure 2 compares the effects of adding unlabeled thymidine with the effects of adding medium containing no thymidine. Only two points were significantly

Table 1. The incorporation of [^{3}H]thymidine by cultures exposed to either 0.1 μCi of [^{3}H]thymidine (1.9 Ci/mmole) for 18 hours or 1.0 μCi (50 Ci/mmole) for 20 minutes. At 90 hours the microcultures were harvested onto glass fiber filters by means of a Titertek Cell-Harvester (Flow Labs). Dried filters were counted (3255 Packard Scintillation Spectrometer) in 5 ml of scintillation fluid containing 8.0 g of butyl-PBD [2-(4′-tertiarybutylphenyl)-5-(4″-biphenyl)-1,3,4-oxadiazole] and 0.5 g of PBBO [2-(4′-biphenyl)-6-phenylbenzoxazole] (Beckman) per liter of Scintanalyzed Toluene (Fischer). The stimulation index (SI) was calculated by the formula: SI = [cpm (with PHA) − cpm (no PHA)]/cpm (no PHA), where cpm is counts per minute.

Amount of [^{3}H]thymidine added (μCi per culture)	PHA added	Radioactivity (count/min)*	Stimulation index
	Cells exposed for 18 hours		
0.1	−	132 ± 27	
0.1	+	42,190 ± 1,500	319
	Cells exposed for 20 minutes		
1.0	−	158 ± 54	
1.0	+	42,825 ± 2,377	270

*Mean ± standard deviation.

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