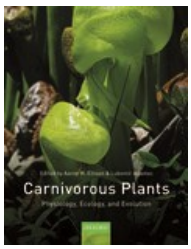

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CHAPTER

14 Motile traps

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Abstract

We review the biomechanics, functional morphology, and physiology of motile traps. The movements of snap traps in *Aldrovanda* and *Dionaea*, motile adhesive traps in *Drosera* and *Pinguicula*, and suction traps in *Utricularia* are driven by active water displacement processes leading to reversible turgor changes of motor cells, irreversible growth, or mechanical pre-stressing of tissues. In some cases, the motion is amplified by the release of elastic energy stored in these tissues. The only known case of a passive motile trapping movement is the 'springboard' trapping mechanism of *Nepenthes gracilis*, in which a rapid vibration of the pitcher lid is actuated by the impact force of raindrops. Open research questions are summarized and future studies are suggested.

Keywords: Aldrovanda, Dionaea, Drosera, elastic instability, electrophysiology, hydraulic movement, Nepenthes gracilis, passive movement, Pinguicula, Utricularia

Subject: Plant Sciences and Forestry, Animal Pathology and Diseases

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14.1 Introduction

Motile traps are found in the genera *Aldrovanda* and *Dionaea* (snap-traps), *Drosera* and *Pinguicula* (adhesive traps with movable trap leaves and emergences), *Nepenthes* (passive-dynamic springboard traps), and *Utricularia* (suction traps). The traditional definition of moving traps as "active" and immobile traps as "passive" (Lloyd 1942) is somewhat blurred because the trap of *Nepenthes gracilis* moves, but this movement is externally driven and so it is still considered to be passive (Bauer et al. 2015b). Plants with active motile traps—snap-traps, motile adhesive traps including the catapulting flypaper traps of *D. glanduligera*, and suction traps—invest metabolic energy to produce movement, or for bringing the trap into a movable state (usually by mechanical pre-stressing of tissues). Plants with passive motile traps (springboard pitfalls) make no such investments, but instead exploit external energy sources. Note that the underlying "costs" of trap production and development (Chapter 18) are not considered here.

In our review of the physiology and biomechanics of carnivorous plant traps and their movements, we explain three general principles of movement actuation that are common to plants, carnivorous or not (reviewed by Forterre 2013, Poppinga et al. 2013b).

The first principle is that external mechanical forces (e.g., wind or rain) lead to elastic deformation of plant organs, causing passive motions. For example, plant stems bend in the wind and return to their original configuration when the wind stops.

The second principle is that water displacement between cells and tissues leads to differential expansion or contraction, thereby causing hydraulic movement. The movement velocity depends on the mechanical properties of the tissue, its permeability to water, and on the distance the water has to travel. Smaller structures principally move faster than larger ones when being actuated purely hydraulically. Two processes may be at work here. First, passive water transport, such as hygroscopic water uptake under wet environmental conditions or evaporative water loss under dry conditions, leads to swelling or shrinking of plant tissues. This does not require metabolic energy. Passive water transport typically actuates movements in dead plant structures such as seed capsules and cones, but is not known to play a role in carnivorous plant traps. Second, physiologically costly active water transport leads to cell turgor changes, causing either irreversible plastic cell deformation (growth) or reversible elastic cell deformation (e.g., in the guard cells of stomata).

The third principle is that the sudden release of elastic energy stored in cell walls and tissues as a result of (usually slow) passive or active hydraulic deformation processes can cause very fast motion.

14.2 Active motile traps

14.2.1 Snap-traps

Snap-traps are found in aquatic *Aldrovanda vesiculosa* and terrestrial *Dionaea muscipula*. Both species have mechanosensory structures for perceiving and processing stimuli, and motile zones that evoke the trapping motion after triggering (Sibaoka 1991). The snapping mechanics differ between these two species. The
p. 181 differences originally were hypothesized to reflect evolutionary adaptions to their different ↳ habitats and surrounding media (Poppinga and Joyeux 2011), but Poppinga et al. (2016a) showed that the kinematics and closure duration of the *Dionaea* trap are similar in air and water. Moreover, *Dionaea* plants can become seasonally inundated and the traps reportedly capture prey underwater (Bailey and McPherson 2012). Hence, the differences in snapping mechanics are unlikely to have evolved in response to the surrounding media, but instead may be adaptations to different prey. *Dionaea* typically catches large strong terrestrial arthropods one at a time (Gibson and Waller 2009), whereas *Aldrovanda* captures small to medium-sized prey such as zooplankton and mosquito larvae and also can capture several animals at once (Cross 2012a; Chapter 21).

The snap-trap of *Dionaea muscipula*.

The *Dionaea* leaf consists of a basal green petiole and an apical, bilobed leaf blade forming a ≈2-cm-long snap-trap (Bailey and McPherson 2012). The bilaterally symmetric, doubly curved trapezoidal lobes are connected by a midrib. Each lobe bears 14–21 marginal teeth (Juniper et al. 1989). In the fully open state, there is a ≈80° angle between the lobes (Poppinga et al. 2016a). Prey are attracted to a band-like region with extrafloral nectaries on the inner trap surface, adjacent to the teeth (Chapter 12). The area between this region and the midrib contains numerous large digestive glands (Chapters 13, 16), and three or four mechanosensitive trigger hairs per lobe (Figure 14.1).

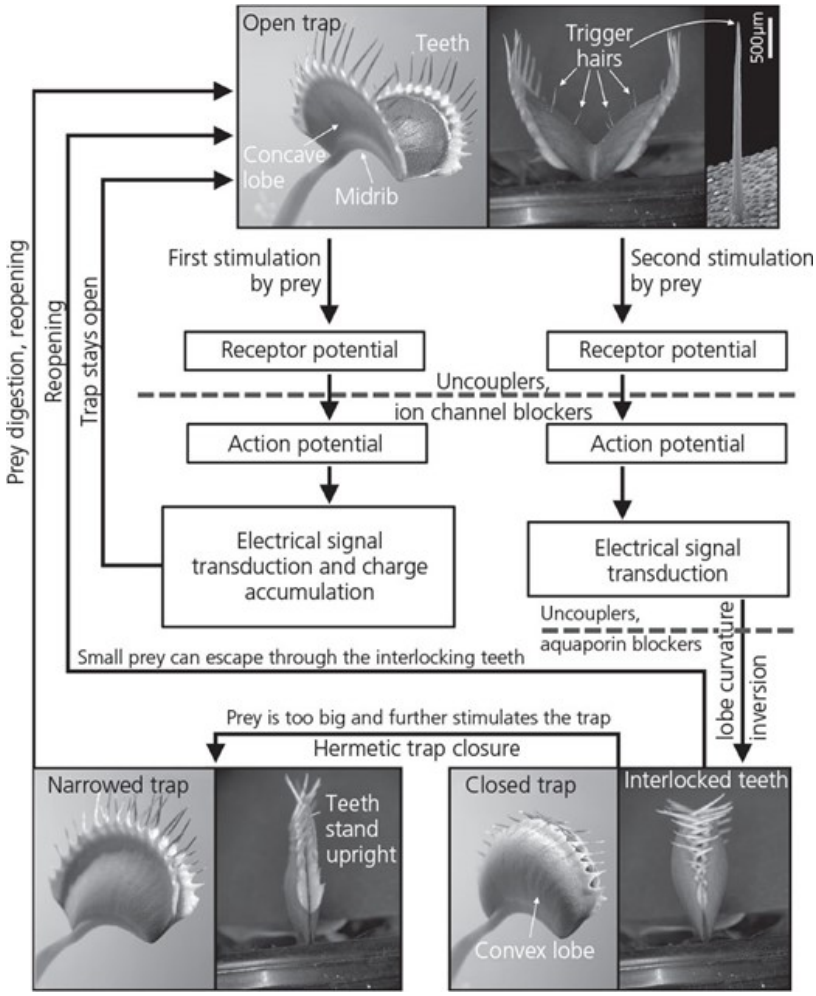

Figure 14.1 The snap-trap of *Dionaea muscipula*. Touching the trigger hairs of an open trap leads to the generation of receptor and action potentials. At least two consecutive mechanical stimuli are necessary for trap closure. Snapping comprises rapid curvature inversions of the two lobes. The electrophysiological processes of the sensory system and the physiological processes of trap lobe movement can be blocked biochemically. The closed trap is characterized by interlocking teeth. If small prey escape, the trap reopens. Prey that cannot escape further stimulate the trap, leading to hermetic closure with the teeth pointing more or less upwards. An enzymatic cocktail is released, prey are digested, and the trap re-opens once again.

Sketch based on an original idea from Volkov et al. (2008b).

At room temperature (≈20 °C), touching a trigger hair at least twice within 20–30 seconds causes the trap to shut rapidly (Williams and Bennett 1982, Hodick and Sievers 1988). At higher temperatures (28–40 °C), a single touch entails closure. Each trigger hair has a circular constriction near its base that contains a single concentric row of mechanosensory cells connected to neighboring cells via multiple plasmodesmata. Their interior appears symmetrically polarized, with complexes of endoplasmic reticulum (ER) cisternae concentrated around vacuoles with polyphenolic contents at the basal and apical pole of each cell (Buchen et al. 1983, Juniper et al. 1989). Whereas the basal region of the hair consists of soft parenchymatous tissue, the distal part is reinforced by thick cell walls and very stiff (Buchen et al. 1983). When touched, the trigger hair bends mainly at the constriction, leading to deformation and stimulation of the sensory cells. As a result, mechanosensitive ion channels open, the cell membrane is depolarized, and a receptor potential is generated (Hodick and Sievers 1988, Sibaoka 1991, Król et al. 2006, Escalante-Perez et al. 2011). During stimulation, the ER-vacuole complexes may act as pressure transducers with the phenolic contents supplying the ions necessary for electrical stimulus generation (Buchen et al. 1983, Juniper et al. 1989).

Voltage-gated ion channels then amplify the receptor potential and generate an action potential that is propagated through the trap tissue with constant amplitude, duration, and speed (Juniper et al. 1989, Volkov et al. 2008b, 2014). This process depends on cross-membrane fluxes of calcium, chloride, and potassium ions (Hodick and Sievers 1986, 1988, Sibaoka 1991, Volkov et al. 2008b, 2008d). Ion and water channel blockers (e.g., NaN_3) and uncouplers (e.g., 2,4-dinitrophenol [DNP]) can reduce or inhibit completely the response to physical and electrical stimuli (Hodick and Sievers 1989, Fagerberg and Allain 1991, Król et al. 2006, Volkov et al. 2008d) (Figure 14.1). Action potentials also are generated when the lobe epidermis or mesophyll cells are directly stimulated. The entire internal trap surface (but not the margins) is sensitive to touch, light, temperature, and electric or wounding stimuli (DiPalma et al. 1966, Hodick and Sievers 1988, Juniper et al. 1989, Trebacz and Sievers 1998).

Trap closure is all-or-nothing: there is no reaction to stimuli below a certain threshold and the speed of closing is independent of the strength (intensity) of stimuli above the threshold (Juniper et al. 1989, Volkov et al. 2007). At room temperature, a single stimulus is insufficient to achieve closure. The restoration of the resting potential after depolarization takes roughly 20–30 s. Because every stimulus causes a depolarization of equal magnitude, a second stimulus within this time frame has an additive effect. This "counting" or "memory" of mechanical perturbations by *Dionaea* may prevent "false" closing if leaves or soil particles land on the trap. The summation of receptor potentials has been demonstrated through repetitive application of small electrical stimuli (Volkov et al. 2007, 2008a, 2008b, 2008c, 2008d).

p. 182 Drought stress can affect mechanoreception, signal transduction, and hence prey capture in *Dionaea* (Escalante-Perez et al. 2011). Traps of water-stressed plants have lowered sensitivity and require three consecutive stimuli to close at room temperature. This makes sense because prey digestion (Chapter 16) is strongly water-dependent. Under dry conditions, the concentration of the phytohormone abscisic acid (ABA) is elevated in the traps. ABA is generally associated with stress responses in plants and plays an important role in water-balance by initiating the drought-induced closure of stomata (Roelfsema et al. 2004).

The closing of the *Dionaea* trap is very fast. It begins just 0.1–0.2 s after triggering (Volkov et al. 2008b, 2008d) and typically is completed within 0.1–0.5 s (Forterre et al. 2005, Volkov et al. 2007, 2008b, 2008d, Escalante-Perez et al. 2014, Poppinga et al. 2016a). After triggering, the lobes first start to move slowly toward each other. It is not clear whether this initial movement is actuated purely hydraulically by water displacement processes between different layers within the lobes, or whether it is additionally supported by the relaxation of pre-stressed mesophyll tissue (Hodick and Sievers 1989, Fagerberg and Allain 1991, Colombani and Forterre 2011). Possible scenarios of hydraulic actuation include irreversible growth processes of cells of the outer lobe surfaces induced by acid-induced cell wall loosening (acid growth; Williams and Bennett 1982), or reversible deformation processes of cells in the different lobe layers due to the opening of water channels (aquaporins; Markin et al. 2008, Volkov et al. 2008b, 2011, Escalante-Perez et al. 2014). The resulting deformation of the two lobes takes place mainly in directions perpendicular to the
p. 183 midrib, ↳ slowly driving the entire trap toward a closed state (Forterre et al. 2005). During closure, the amount of ATP in the lobes drops by ≈30% (Williams and Bennett 1982, Volkov et al. 2012) and their configuration as seen from the outside changes from concave to convex (Darwin 1875) (Figure 14.1).

Hydraulics alone cannot account for the rapid trap closure, and two hypotheses have been advanced to explain it. The first proposes that elastic curvature energy is stored in the lobes due to a difference in hydrostatic pressure between the hydraulic layers, and that its release drives the fast closing movement (Hodick and Sievers 1989, Markin et al. 2008). When water channels between the layers open, the pressure difference can equilibrate and the lobes rapidly relax to the closed configuration.

Alternatively, elastic instabilities may play a crucial role in trap closure. In a widely accepted model by Forterre et al. (2005), the concave lobe curvature acts as a geometrical constraint resisting the initial motion

until the accumulated strain is released suddenly and the lobe rapidly flips into a convex state ("snap-buckling"). The amount of elastic energy released during the curvature inversion, and hence the trapping speed, increases with the dimensionless geometrical parameter $\alpha = \frac{L^4K^2}{h^2}$, where L is the length of the lobe, K is its mean curvature in the open state, and h is its thickness. The parameter α equals the ratio between the energy barrier separating the two states of lobe curvature (the geometrical constraint) and the bending energy supplied by the change of the rest-state curvature (i.e., by the initial motion of the lobes), and depends only on trap morphology and geometry (Forterre et al. 2005, Forterre 2013). The model predicts that larger traps should snap shut faster than smaller ones, but this prediction was not confirmed experimentally (Volkov et al. 2008a, Poppinga et al. 2016a).

The *Dionaea* trap closes with considerable force. Volkov et al. (2013) measured a peak snapping force of 149 mN and a pressure between the narrow trap rims of 41 kPa. The force necessary for escaping from the closed trap reached 4 N, allowing little chance for prey to escape. If one lobe is cut off, the other lobe shows exaggerated bending toward the midrib because its movement is not blocked (Hodick and Sievers 1988, Fagerberg and Allain 1991). Differences in lobe morphology, stimulus processing, or movement actuation also may lead to asynchronous snapping in otherwise intact traps (Poppinga et al. 2016a). Seedling traps have smaller opening angles (≈50°) than adult plants and take much longer (up to several seconds) to close, probably because elastic instabilities play a minor, if any, role. As a result, seedlings may catch only relatively slow-moving prey (Poppinga et al. 2016a).

After snapping quickly, final closure occurs much more slowly because of internal dampening of the hydrated lobes (Forterre et al. 2005). The distance between the lobe edges immediately after snapping remains at 15–20% of the initial distance (Volkov et al. 2008b, 2008d). The teeth on the lobe margins interlock loosely, leaving numerous small gaps (Figure 14.1). This allows small animals to escape, ensuring that the plant does not initiate the metabolically costly digestion process for prey that yield little metabolic benefit. Only larger animals are retained and continue to stimulate the trigger hairs during their struggle to escape. This generates further action potentials (Lichtner and Williams 1977) and causes an increase in the cytosolic concentration of calcium (Escalante-Perez et al. 2011). Together with the perception of N-containing substances (e.g., urea) from the prey, this initiates a further narrowing of the trap. Eventually the trap lobes flatten, causing the teeth to stand more-or-less upright on the lobe margins, and the trap closes hermetically (Figure 14.1). The lobes exert mechanical force up to 450 mN on the inside of the trap, corresponding to a maximum pressure of 9 kPa acting on the prey (Volkov et al. 2013). The formation of a sealed digestion chamber is then followed by the release of digestive enzymes (Escalante-Perez et al. 2011; Chapter 16).

In most cases, the trap re-opens after prey is digested. A single trap can snap and re-open up to 12 times (Bailey and McPherson 2012). The re-opening process occurs over 1–2 days (Fagerberg and Howe 1996, Volkov et al. 2014, Poppinga et al. 2016a) and is controlled either by irreversible growth processes (Ashida 1934) or by hydrostatic pressure changes in the inner and outer tissue layers of the lobes (Markin et al. 2008). A noticeable bulge appears on each of the sealed lobes before the trap margins start to separate and the trap gradually re-opens (Fagerberg and Howe 1996). Reverse snap-buckling does not occur (Poppinga et al. 2016a).

The snap-trap of *Aldrovanda vesiculosa*.

The aquatic *Aldrovanda vesiculosa* develops rootless floating shoots with whorls of six to nine leaves at each node. Each leaf consists of a flattened, air-filled petiolus that splits into three to eight bristles, and a leaf blade that is transformed into a 2.5–6-mm long, 4–7-mm wide snap-trap (Cross 2012a) (Figure 14.2). The two convex (as seen from the outside) trap lobes are attached to a midrib—an extension of the petiolus—and the whole trap is twisted approximately 90° counter-clockwise and tilted 30–40° backwards. As a result, one lobe is turned toward the bristles (the "bristle-side lobe"), whereas the other is turned away (the "free-side lobe") (Ashida 1934) (Figure 14.2a). The bristles are hypothesized either to serve as a mechanical barrier preventing objects other than prey from entering and triggering the trap, or to guide substrate-dwelling prey toward the trap (Cross 2012a). The twisted trap orientation toward the open water may help to maximize exposure to potential prey.

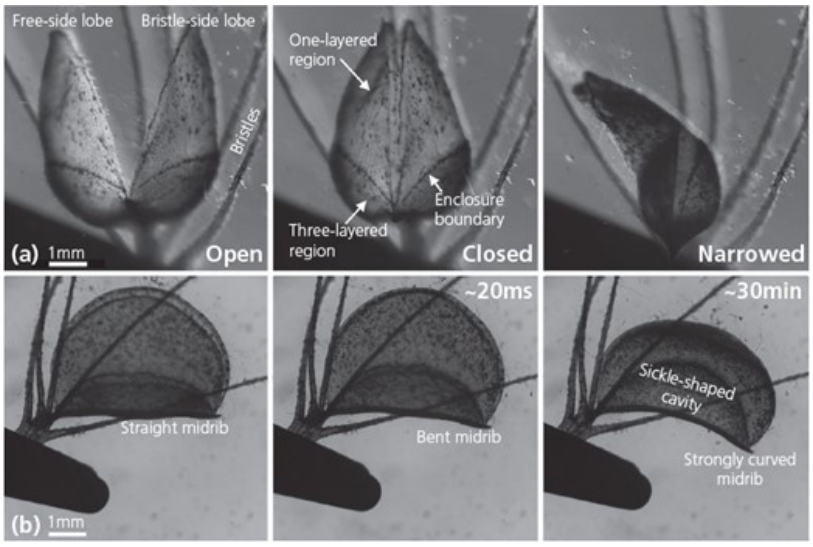

Figure 14.2 The snap-trap of *Aldrovanda vesiculosa*. Frontal views of a trap (**a**) and lateral views of the same trap (**b**) at the same points in time. The left images show the open trap before triggering; the middle images show the closed trap immediately after triggering with an electric charge; and the right images show the narrowed trap. Each lobe consists of a three-layered region and a one-layered region, which are fused by an enclosure boundary. The midrib connects the free-side lobe with the bristle-side lobe. During closure, the midrib notably bends, and its curvature is strongest when the trap is narrowed. At this stage, the free-side lobe has inverted its curvature, and the sickle-shaped cavity contains the caught prey.

Each lobe is divided into a central and a peripheral region by a band-like enclosure boundary (Ashida 1934) (Figure 14.2a). The central, "three-layered" region consists of two epidermal cell layers on either side of a parenchymatous layer. Its interior surface has a multitude of trigger hairs and glands, which are especially densely arranged along the midrib. The peripheral, "one-layered" region is very thin, and consists only of two epidermal layers. Its inner surface is covered in four-armed (quadrifid) glands similar to those inside the *Utricularia* suction traps (Chapter 13). The lobe margin is bent inwards and densely lined with small, tooth-like projections.

Twenty to 40 trigger hairs are concentrated along the midrib and along the enclosure boundary of each trap (Lloyd 1942, Cross 2012a). The hairs are ≈1.5 mm long and 0.05 mm thick. A double articulation in their basal and median regions probably prevents fracture during trap closure (Darwin 1875). It is speculated that the hairs mimic filamentous algae and attract grazing prey (Cross 2012a). A single stimulation of a trigger hair is sufficient to effect trap closure (Lloyd 1942, Williams 1976). The characteristics of resting, receptor, and action potentials, and the patterns of signal transduction, all are similar to *Dionaea*. Upon triggering, Ca^{2+} ions are thought to enter the excitable cells of the three-layered region and cause a receptor potential

(Juniper et al. 1989, Sibaoka 1991). Electrical and chemical stimuli also lead to trap closure (Ashida 1934). Trap sensitivity depends on trap age and water temperature, and spontaneous trap closure occurs when the water temperature is <10 °C or >40 °C (Czaja 1924).

Several consecutive phases of trap movement after triggering have been described (Ashida 1934, Lloyd 1942). Prey are captured during the first, rapid movement phase (trap shutting) (Figure 14.2). At 25 °C, traps
p. 185 can shut within 10 milliseconds, but ↳ this speed declines with decreasing temperatures. The inner epidermal cells of the three-layered region, which are located ≈0.15–0.25 mm from the midrib, constitute the "motor zone" responsible for the movement of the lobes. While the trap is open, the thick-walled motor cells are turgid and resist mechanical pressure exerted by the middle parenchymatous and outer epidermal layer. After triggering, turgor decreases (Ashida 1934, Sibaoka 1991) and the trap closes, probably aided by an acid growth response of cells on the outside of the lobe (Williams 1992). Both lobes move synchronously and smoothly without sudden accelerations or decelerations (Poppinga and Joyeux 2011). After closure, the small teeth on the trap margins interlock (Juniper et al. 1989).

It is still debated whether the shutting motion is supported by a release of stored elastic energy. The epidermis of the outer lobe is undulated when the trap is open but it is smooth in the closed state, indicating some degree of pre-stressing (Ashida 1934, Williams 1992). Moreover, the midrib is more or less straight when the trap is open and curved when the trap is shut (Figure 14.2b), indicating that it may be pre-stressed in the open state (Poppinga and Joyeux 2011). In contrast to *Dionaea*, the lobes of the *Aldrovanda* trap do not invert their curvatures during closure (Figure 14.2a), ruling out snap-buckling instability (Skotheim and Mahadevan 2005, Poppinga and Joyeux 2011). However, deformation of the motor cells alone cannot explain the high closure speed, which is thought to be achieved by mechanical coupling of the motor zone with the rest of the leaf, particularly the midrib. The trap geometry is probably adapted to amplify the bending of the midrib so that a small midrib movement results in a large displacement of the lobes (Poppinga and Joyeux 2011, Joyeux 2013).

The initial rapid trap closure leads to the formation of a cavity in which small prey can still move around freely, but continued stimulation of the trigger hairs initiates further narrowing (Ashida 1934; Figure 14.2). For approximately 30 minutes, both lobes continue moving toward each other until both enclosure boundaries almost touch. The free-side lobe then inverts its curvature in the one-layered region, forming a small, sickle-shaped cavity in the central trap zone that brings prey into contact with the digestive glands (Figure 14.2; Chapters 13, 16). The pressure continues to increase, and large animals may be crushed (Cross 2012a). The narrowing motion is caused by rising turgor resulting from water uptake, followed by elongation of the outer epidermal cells (Ashida 1934). The quadrifid glands also may pump water out of the trap (cf. *Utricularia*; Chapters 13, 16, 19), thereby sealing the trap tightly for digestion (Juniper et al. 1989). Without prey, closed traps stay in the narrowed phase for approximately 6–12 h until they reopen (Lloyd 1942).

Prey digestion lasts approximately 3–10 d (Czaja 1924, Cross 2012a; Chapter 16). Re-opening starts with curvature inversion of the free-side lobe before both lobes gradually open as the inner epidermal cells elongate (Ashida 1934). Opening is much slower than shutting or narrowing because of the mechanical resistance of the middle parenchymatous and outer epidermal cell layers, and because of the necessary water flow into the trap lumen during the inversion of the free-side lobe curvature. As with *Dionaea*, opening of the *Aldrovanda* trap involves irreversible trap growth.

14.2.2 Motile adhesive traps

Actively moving flypaper traps (Chapters 13, 15) are found in several species of *Drosera* and *Pinguicula*. Leaf laminae (*Pinguicula* and *Drosera*), emergences (*Drosera* tentacles), or both may move. Only a subset of *Pinguicula* and *Drosera* species uses movement for trapping, and movement patterns and speed vary greatly. Some *Drosera* species employ moving traps only during part of their ontogeny, which may be an adaptation to different prey targeted during different developmental stages (Poppinga et al. 2013a).

Motile *Drosera* traps.

An insect struggling on a sticky *Drosera* leaf triggers movements of individual tentacles or the entire leaf. This not only hinders escape by bringing further glue-laden tentacles into contact with the prey (Chapters 13, 15), but also aids digestion by forming an "outer stomach" (Figure 14.3a; see Chapter 16). The animal eventually dies from suffocation due to clogging of its tracheae by mucilage (Juniper et al. 1989; Chapter 13).
p. 186 The speed of the tentacle movement depends on the ↳ species, the tentacle type, the intensity of stimulation, the plant's vigor, and on environmental conditions (Darwin 1875, Williams and Pickard 1972, Poppinga et al. 2013a). Bending can take as little as 75 ms in the catapulting tentacles of *D. glanduligera*, or up to several minutes as e.g., in *D. capensis* (Poppinga et al. 2012) (Figure 14.3a–d). Movements of the entire leaf tend to be even slower, typically lasting between several minutes and a few hours (Figure 14.3a).

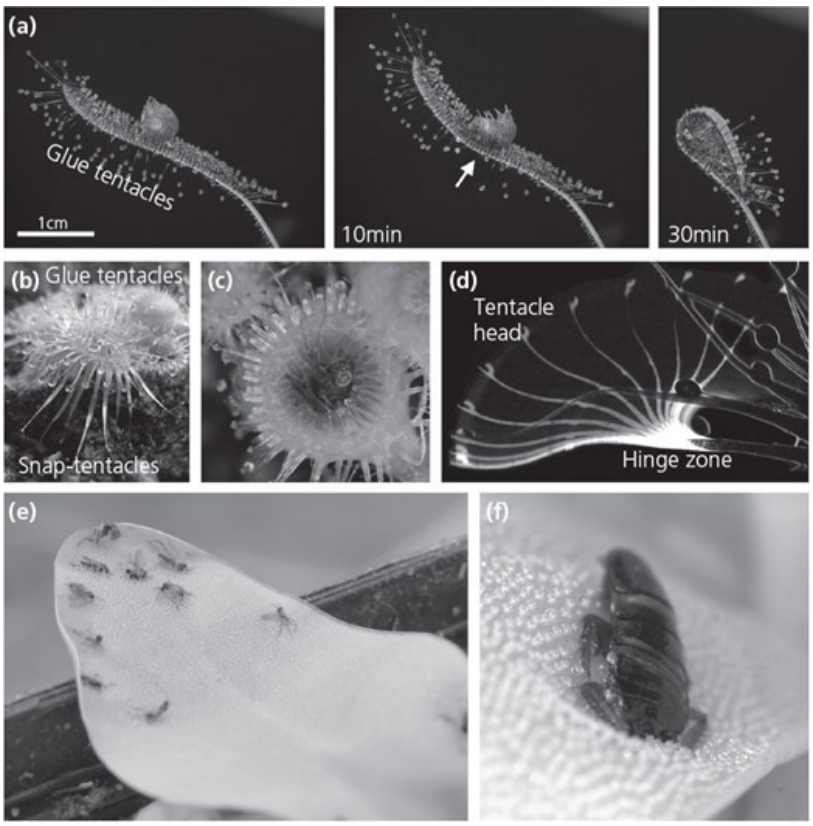

Figure 14.3 The motile traps of *Drosera* and *Pinguicula*. (**a**) A time-lapse recording of a manually fed *D. capensis* trap leaf. Ten minutes after prey is deposited on the leaf, the glue tentacles have bent upwards to hinder prey escape (arrow), and the leaf has begun to bend. Thirty minutes later, the leaf has completely wrapped around the animal, and digestion begins in the outer stomach. Afterwards, the leaf uncurls. (**b**) *D. glanduligera* possesses marginal, mucilage-free snap-tentacles in addition to the glue tentacles that are developed more centrally on the trap leaf. (**c**) Prey (here, a manually placed fruit fly) are catapulted onto the leaf of *D. glanduligera* and then slowly drawn within the concavity by sticky tentacles. (**d**) A high-speed recording of the motion of a *D. glanduligera* snap-tentacle (grayscale inverted for clarity). The period between the first two steps of the motion, which begins on the bottom left of the image, is 20 milliseconds, and the period between the other motion steps is 5 milliseconds. Bending takes place at the hinge zone, whereas the apical tentacle part with the head does not undergo bending deformation. (**e**) The leaf margin of *P. grandiflora* curls inwards as a response to the presence of stuck prey (see also Figure 6.3h). (**f**) A depression forms on the leaf lamina of *P. hirtiflora* at the place where the prey is stuck, leading to a sinking of the prey into a digestive bath.

Figures (**b**), (**c**), and (**d**) are modified from Poppinga et al. (2012).

Drosera tentacles are multicellular glandular emergences. They are typically several mm long, cylindrical in cross-section, and secrete sticky mucilage at the tip (Darwin 1875, Juniper et al. 1989, Seine and Barthlott 1993; Chapter 13). Bending begins a few seconds–minutes after stimulation and occurs in a distinct zone at the base of the tentacle. The site of mechanoreception is situated in stalk cells just below the constricted tentacle head, where the greatest deformation occurs during mechanical stimulation (Darwin 1875). The stalk cells are homologous to the receptor cells of *Dionaea* (Williams and Pickard 1972, Williams and
p. 187 Spanswick 1972, Williams 1976). Mechanical triggering ↳ generates a graded receptor potential with amplitude approximately proportional to the intensity of the stimulus. Once a threshold value is reached, a series of short action potentials travels rapidly from the receptor site to the bending zone. They are transmitted along the excitable outermost two cell layers of the cylindrical tentacle stalk (Williams and Spanswick 1972). The tentacle moves, probably due to differential growth processes, as long as a threshold number of action potentials reach the bending zone (Williams 1976). The tentacles on the leaf margins are typically longer, more sensitive to mechanical stimulation, and show a stronger bending response than the

central tentacles. Stimulation of marginal tentacles alone does not entail any other trap movements (Darwin 1875). Stimulation of central tentacles leads to membrane potential oscillations and jasmonate accumulation at the area of stimulation, entailing a delayed motion of (further) non-stimulated marginal tentacles (Nakamura et al. 2013, Krausko et al. 2017). Wounding of the trap leaf petiolus also leads to tentacle movement (Krausko et al. 2017).

Several tentacle types with distinct morphologies have been described (Seine and Barthlott 1993, Poppinga et al. 2013a). Especially noteworthy are the snap-tentacles found on the leaf margins of various species (Hartmeyer and Hartmeyer 2010). Snap-tentacles move much faster than normal glue tentacles. They are not cylindrical, but bilaterally symmetric, and have a raised gland that does not produce glue. Similar to glue tentacles, snap-tentacles are triggered by mechanical stimulation of the tentacle head, and move by deformation of a distinct bending zone. In *D. glanduligera*, movement occurs ≈400 ms after stimulation and lasts 75 ms. Prey are literally catapulted onto the sticky leaf surface, where mechanosensitive and motile glue tentacles are situated (Poppinga et al. 2012; Figures 14.3b, c). Theoretically, the rapid motion of snap-tentacles could be achieved by pure hydraulic actuation due to their small size. However, elastic instabilities caused by pre-stressing of tentacle tissue also may contribute. *Drosera glanduligera* snap-tentacles function only once, a phenomenon that could be explained by irreversible cell-buckling effects resulting from the high bending speed (Poppinga et al. 2012). In contrast, the snap-tentacles of some species with slower movements (several seconds–minutes) function repeatedly and reset within a day. Some small species of *Drosera* sect. *Bryastrum*, however, possess very fast snap-tentacles that bend within a fraction of a second but function repeatedly (Hartmeyer and Hartmeyer 2015).

Entire leaves move slowly when live prey or prey extracts are placed on the laminae (Darwin 1875, Nakamura et al. 2013; Figure 14.3a), often leading to the development of an "outer stomach" (Darwin 1875; Chapter 16). Leaf movements differ among species and can entail the formation of depressions and deflections of the leaf margins (e.g., *D. rotundifolia*; Darwin 1875), curving and folding of leaves (e.g., *D. capensis*; Bopp and Weber 1981, Bopp and Weiler 1985), or spiral curling (e.g., *D. regia*). The observed kinematics further depend on the location of the prey. For example, Bopp and Weber (1981) found that *D. capensis* leaves bend at the site of prey attachment, and the degree of bending was determined by the distance between prey and leaf tip. Leaf bending originally was thought to be based on auxin-mediated growth processes (Bopp and Weber 1981, Bopp and Weiler 1985, Juniper et al. 1989), but Nakamura et al. (2013) and Mithöfer et al. (2014) reported prey capture-induced accumulation of jasmonates in the leaf tissue and showed that these phytohormones alone can trigger leaf bending. Jasmonates are universally involved in asymmetric growth, herbivore defense, and wounding responses.

Motile *Pinguicula* traps.

The slow leaf movements of *Pinguicula* spp. still are poorly understood. No scientific advances have been made on the physiology, functional morphology, or biomechanics of these traps since Juniper et al. (1989). Only some *Pinguicula* species (e.g., *P. vulgaris*) show movement responses within hours or days after prey capture (Darwin 1875), but others never move (e.g., *P. gypsicola*). The diet of some *Pinguicula* may consist mainly of pollen and other plant debris (Karlsson et al. 1994).

Pinguicula leaves are covered with sessile digestive glands and stalked, glue-producing trapping glands (Chapter 13). They trap mostly small dipterans, especially fungus gnats. In some species, mechanical stimulation in combination with nitrogenous matter leaching from prey induces an upward bending of the
p. 188 leaf margins (Figures 6.3h, 14.3e). ↳ When prey is placed near the center of the leaf, the leaf margins may curl toward the center. These movements are based on differential growth processes (Lloyd 1942) and may boost digestion by bringing additional digestive glands into contact with the prey (Juniper et al. 1989). This may be further aided by the formation of a depression of the leaf lamina around the prey (Figure 14.3f). The

development of this cavity results from turgor loss of the basal cells of the glands and of neighboring epidermal cells (Heslop-Harrison and Knox 1971). As a consequence, prey is immersed in a digestive pool. Once digestion is completed, the leaf unfolds again, and the cavities disappear within approximately 24 hours (Darwin 1875, Lloyd 1942).

14.2.3 Suction traps

Suction traps are the fastest carnivorous plant traps and unique to *Utricularia* spp. (Figures 14.4, 14.5; Chapters 8, 13, 19). Prey animals are sucked into the trap ("bladder") within half a millisecond, which is ≈20 times faster than the *Aldrovanda* snap-trap, 150 times faster than the snap-tentacles of *Drosera glanduligera*, and >200 times faster than the *Dionaea* snap-trap. Most work so far has focused on the relatively large traps of aquatic species (*U.* sect. *Utricularia*, comprising ≈16% of the genus), as they are comparably easy to observe. How the traps of non-aquatic species—approximately 80 % of the genus—function remains largely unknown. Our description of functional morphology, physiology, and biomechanics of *Utricularia* suction traps therefore focuses on aquatic species (*U. vulgaris* trap type; Lloyd 1942).

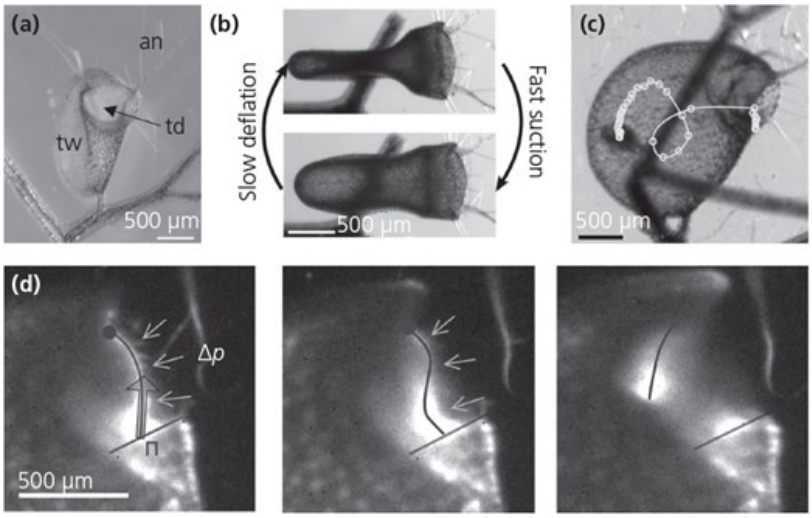

Figure 14.4 General morphology and kinematics of the *Utricularia vulgaris* type of suction trap. (**a**) The trap (bladder) is a hollow vesicle with flexible, lateral trap walls and an entrance region that is closed watertight by the trapdoor. Antennae are crucial for attracting prey and for leading them toward the trapdoor. (**b**) The bladderwort trap works in two phases. First, the trap slowly deflates as water is pumped out of the lumen, and elastic energy is stored in the deformed walls. Second, triggering entails trapdoor opening and relaxation of the trap walls, accompanied by a very fast suction of water and prey. (**c**) High-speed recording of the capture of a small crustacean. The path of the prey during suction is indicated, showing that the animal loops inside the trap. (**d**) Trapdoor kinematics, as visualized by high-speed cinematography under laser sheet fluorescence microscopy. The trapdoor possesses an outward curvature when the trap is ready to fire (left). The force exerted on the door due to the water pressure difference (Δp) between the trap interior and exterior is counterbalanced by friction forces (π) on the threshold. Also, the door resists inwards buckling due to its double curvature. Once the pressure difference is high enough (middle), small mechanical perturbations on the trigger hairs, which protrude from the trapdoor (see Figure 14.5), are sufficient to entail trapdoor buckling. The door is now unlocked and swings open rapidly as water flows in rapidly (right). A critical negative pressure inside the trap leads to spontaneous firing. Abbreviations: an = antennae, td = trapdoor, tw = trap wall.

All images modified from Vincent et al. (2011a).

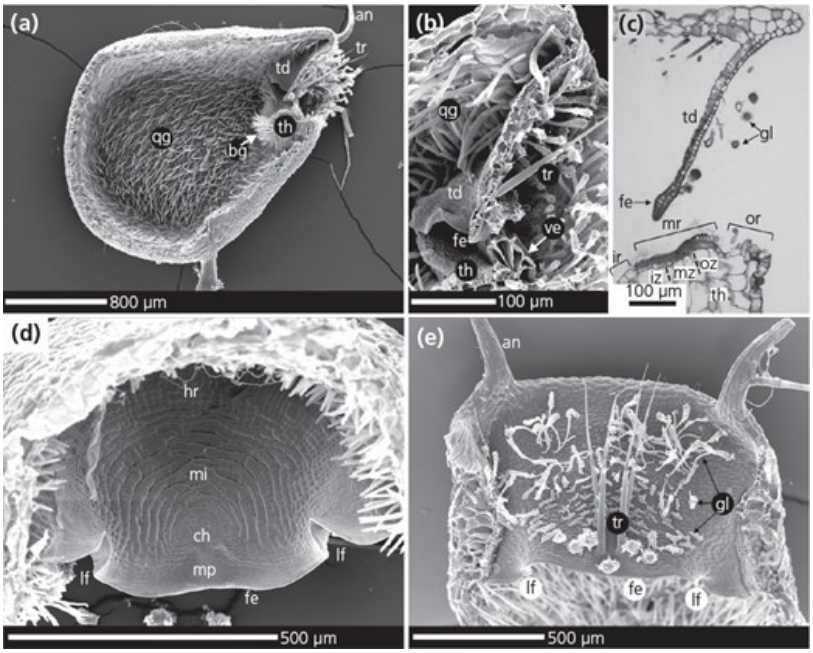

Figure 14.5 Functional morphology of the *Utricularia vulgaris* type of suction trap. (**a**) Scanning electron micrograph of a longitudinal section of an *U. vulgaris* trap. The quadrifid and bifid glands, and the threshold, trapdoor, and trigger hairs are visible. The door rests at an approximate 90° angle to the threshold, and the entrance forms a short tube. (**b**) Scanning electron micrograph of the trap entrance. Note the cut trapdoor with its free edge, the trigger hairs, and the velum on the threshold. (**c**) Light microscopic image of a 10-µm-thick longitudinal section of the trap entrance. The trapdoor consists of two cell layers. The three regions of the threshold, as well as the three zones of the pavement epithelium are visible. (**d**) The inner trapdoor surface is strikingly compartmentalized. The concentric constrictions are hypothesized to act as pre-folds for channeling the process of door buckling and unbuckling (see also Figure 14.4d). Two lateral folds on the free edge help in positioning the door on the pavement epithelium when it is closed, and, by unfolding, in the process of door opening. (**e**) The outer door surface is, in contrast, not compartmentalized. Note the multitude of glands and the long trigger hairs. Abbreviations: an = antennae; bg = bifid glands; ch = central hinge of the door; fe = free door edge; gl = glands of unknown function; hr = hinge region of the door; ir = inner region of the threshold; iz = inner zone of the pavement epithelium; lf = lateral door folds; mi = middle region of the door; mp = middle piece of the door; mr = middle region of the threshold (= pavement epithelium); mz = middle zone of the pavement epithelium; or = outer region of the threshold; oz = outer zone of the pavement epithelium; qg = quadrifid glands; td = trapdoor; th = threshold; tr = trigger hair(s); tw = trap wall; ve = velum.

(a) modified from Poppinga et al. (2016b); **(d)** and **(e)** modified from Vincent et al. (2011a).

The architecture of bladders of the *U. vulgaris* trap type is uniform, with trap diameters ranging from 0.5–6 mm. Some species (e.g., *U. vulgaris*) have bladders that are dimorphic in size and shape (Chapter 13). The bladders are hollow, water-filled, lentil-shaped vesicles with flexible lateral walls (Figure 14.4a, 14.4b, 19.4). The reinforced ↳ entrance forms a short tube and is kept watertight by a trapdoor (Lloyd 1942). The functional morphology of the trapdoor is highly sophisticated (Poppinga et al. 2016b). It consists of two cell layers (Figures 14.5b, 14.5c) and is only 20–40 µm thick. The cells of the outer layer are uniform. In contrast, the inner layer is compartmentalized into several distinct regions, including a central hinge and, immediately below, the so-called middle piece (Lloyd 1942, Vincent et al. 2011b; Figure 14.5d). Several trigger hairs protrude from the outer surface of the trapdoor in this central region (Figures 14.5b, 14.5e). Further antennae and bristles are located at the entrance region (Figures 14.4a, 14.4b, 14.5a, 14.5b). These appendages are crucial for leading prey toward the entrance (Chapter 12).

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The hinge region connects the trapdoor to the arched upper end of the entrance. The lower trapdoor edge rests on the collar-like threshold, forming an angle of approximately 90° (Figures 14.5a–14.5c). The

threshold can be subdivided into three regions. The outer region bears stalked glands of unknown function and the inner region extends into the trap lumen (Lloyd 1942, Poppinga et al. 2016b; Figure 14.5c). Sandwiched in between is the middle region which is the part where the free edge of the trapdoor rests. It is
p. 190 characterized by a pavement epithelium formed by short ↳ glandular cells, and is subdivided into an outer, middle, and inner zone. The cells of the outer zone are bloated like balloons and are characterized by exfoliated cuticles. They form the so-called velum (Figure 14.5b) which is, in combination with secreted mucilage, responsible for keeping the trap watertight. The outer and middle zones together form a large bump; and the adjacent inner zone forms a separate smaller bump. Both elevations run along the whole pavement epithelium, and the furrow between them holds the free edge of the trapdoor securely in place while the trap is closed. Lateral folds of the free door edge may help to position the door accurately in the furrow (Lloyd 1942, Vincent et al. 2011b; Figures 14.5b–14.5e), and probably add displacement space into the lumen when the trap fires.

Two types of glands are found inside the trap. Almost the entire inner surface is covered with four-armed glands (quadrifids) that probably secrete the digestive enzymes (Chapters 13, 16). Two-armed glands (bifids) near the trap entrance presumably pump water out of the trap continuously (Sasago and Sibaoka 1985a, 1985b, Juniper et al. 1989, Adamec 2011d). This assumption is based on the observation that water bubbles form around the entrance region when the trap is submersed in paraffin oil (Sasago and Sibaoka 1985a). The energy-demanding pumping process generates a negative hydrostatic pressure of approximately −12 to −16 kPa inside the trap (Sydenham and Findlay 1973, Sasago and Sibaoka 1985a, Singh et al. 2011). Once this pressure difference is reached, the outward flow may be equalized by inward flows due to trap wall permeability and trapdoor leakage (Adamec 2011d, Vincent et al. 2011a). Vincent et al. (2011b) estimated a Young's Modulus of 5–20 MPa for the trap body, similar to fully turgescent parenchymatous tissue. Trap deflation takes at least 15 minutes. During deflation, the lateral trap walls deform and curve inward (Figure 14.4b). This leads to storage of elastic energy as the trap becomes increasingly pre-stressed. Meanwhile, the trapdoor is held in place by the furrow on the threshold, and stabilized by its convex curvature (Figure 14.4d).

The ultrafast firing of the trap is triggered when prey (typically small crustaceans) touch one of the trigger hairs (Figures 14.4c). It is not yet fully understood whether the underlying process is purely mechanical, with the trigger hairs acting as levers, or whether electrical signaling (as in *Dionaea, Aldrovanda*, and *Drosera*) is involved. Masi et al. (2016) measured electrical responses in *Utricularia* trap cells but did not demonstrate signal transduction. Attempts to trigger *Utricularia* traps electrically have not been successful (e.g., Sydenham and Findlay 1973), and low temperature, ion channel blockers, and cytochrome oxidase inhibitors affect trap deflation, but not triggering (Adamec 2012a). These findings strongly support a purely mechanical trigger mechanism.

A mechanical buckling scenario sufficiently explains how the mechanical sensitivity of the trapdoor increases with decreasing internal pressure until very small perturbations (i.e., prey touching the trigger hairs) suffice to trigger door opening. As water is continuously pumped out of the trap, negative pressure builds up inside, putting the domed trapdoor under increasing tension. Eventually, the deflection of a single trigger hair on the surface is sufficient to induce buckling and a rapid inversion of the door curvature (Vincent et al. 2011b; Figure 14.4d). The deformation is initiated by bulging of the central hinge and middle piece and further amplified by numerous concentric constrictions on the inner door surface (Figure 14.5d) so that it progressively spreads across the rest of the door. The resulting inversion of the door curvature unlocks the free edge, and the door swings open within 0.5 ms (Poppinga et al. 2016b; Figure 14.4d). As the pressure equalizes, the trap walls relax and the bladder suddenly expands, sucking in water and prey with velocities of up to 4 m/s and accelerations of up to 2800 *g*. Phases of very high acceleration during onsets of suction are immediately followed by phases of similarly high deceleration (max.: -1900 *g*) inside the bladders, leading to immobilization of the prey which then dies (Poppinga *et al.* 2017). The rapid influx of

water makes escape virtually impossible, and vigorous turbulence may cause prey to swirl inside the trap (Figure 14.4c). Further investigations are needed to determine whether these turbulences aid in prey retention.

In contrast to the *Dionaea* trap, both the initial inversion of the *Utricularia* trapdoor and the reversion to the
p. 191 convex configuration involve buckling. This ↳ allows the trapdoor to re-close extremely quickly, within approximately 2.5 ms. The hinge region of the trapdoor may promote unbuckling by acting as a spring (Lloyd 1942). The trapdoor remains insensitive to mechanical triggering until the negative pressure inside the trap has reached a threshold value. Immediately after suction, the lateral trap walls remain slightly concave, indicating that they still store some elastic energy and that the pressure difference between interior and exterior has not yet fully equilibrated (Lloyd 1942, Poppinga et al. 2016b). In contrast, piercing the trap (e.g., with a fine needle) leads to fully relaxed trap walls. This indicates that the trapdoor re-closes as soon as the resetting force exceeds suction force. This fast closing may prevent the escape of prey, and minimize the outflow of nutrient-rich water. Prey die due to anoxia (Adamec 2007b) and are enzymatically digested (Chapters 13, 16, 19). Remarkably, the trap can continue to capture prey while digesting.

Traps also may fire spontaneously when a critical negative pressure inside the trap is reached (Adamec 2011d, 2011f, Vincent et al. 2011b). The mechanical relaxation might help to avoid fatigue of the trap tissue (Poppinga et al. 2016b). Spontaneous firings can occur at regular intervals, randomly, or in bursts (Vincent et al. 2011a). The mode of spontaneous firing is characteristic for each individual trap and is species-independent. Small differences in door positioning on the pavement epithelium may contribute to this variation (Poppinga et al. 2016b). The critical pressure for spontaneous firings (−3.9 to −44.9 kPa) varies among species (Adamec and Poppinga 2016). Small algae, protozoa, bacteria, or detritus may be sucked into the bladder during spontaneous firing events and add to the nourishment of *Utricularia* (Koller-Peroutka et al. 2015).

The trap diversity among bladderwort species from various habitats is extraordinary. Many non-aquatic species have elongated tubular trap entrances with lower door-to-threshold angles of only ≈20–60°, and large amounts of mucilage are speculated to aid in door fastening (Lloyd 1942). The respective trapdoor movements also vary. For example, in some species (e.g., *U. uniflora*) no door curvature change takes place prior to opening, and the free door edge detaches from the threshold in a comparably slow manner (Westermeier et al. 2017). Trigger-hair morphology also is highly variable, and some species do not have trigger hairs at all. Westermeier et al. (2017) could not stimulate *U. multifida* traps and they speculated that these traps may function as lobster traps similar to those of *Genlisea* (Reifenrath et al. 2006; Chapter 15). Spontaneous firings also were not observed in *U. multifida*, further corroborating the assumption that it employs passive (i.e., non-motile) traps.

14.3 The passive motile trap of *Nepenthes gracilis*

Nepenthes pitchers are typically passive pitfalls that trap prey using slippery surfaces and retentive fluids (Chapters 12, 15). The roof-like pitcher lid is widely thought to prevent fluid dilution and prey loss during heavy rains. *N. gracilis* is the only species known to directly use the pitcher lid for capturing prey with an externally powered passive movement. The impact force of rain drops leads to a deformation of part of the pitcher, causing a rapid downward movement and subsequent oscillation of the pitcher lid which is crucial for prey capture (Figure 14.6). The passively induced lid movement depends on environmental physical factors (rain) and hence cannot be actively controlled by the plant.

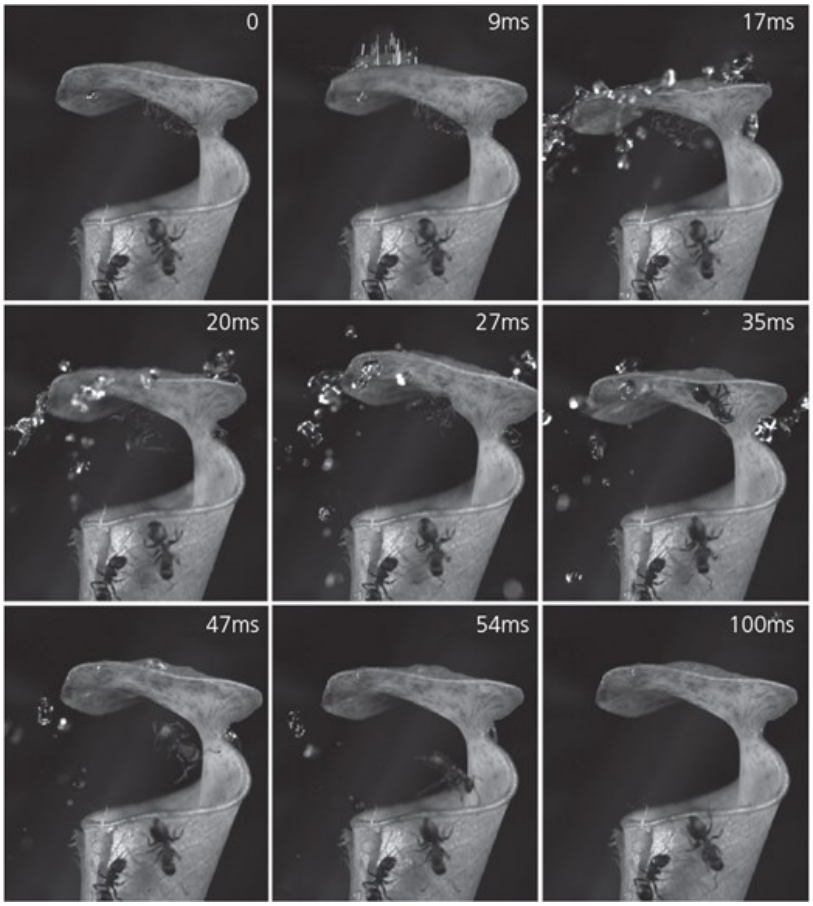

Figure 14.6 The passive motile trap of *Nepenthes gracilis* illustrated with single frames from a high-speed recording of a trapping sequence from a laboratory feeding experiment. In the first image, the ant that will later be trapped is situated at the underside of the pitcher lid and searches for nectar. Other ants can be seen on the outer pitcher surface. At $t = 9$ ms, the splash of the impacting water drop can be seen on the upper lid surface. Afterwards, the lid moves rapidly downward and subsequently oscillates. The ant loses its grip and falls down into the pitcher, which is filled with digestive and retentive fluid.

The unique trapping mechanism of *N. gracilis* relies on a combination of surface and material adaptations. Similar to the inner pitcher wall of many *Nepenthes*, its lower lid is covered with epicuticular wax crystals (Chapters 12, 15); however, the crystal morphology is strikingly different (Figure 15.2g). In contrast to the delicate platelets found on the inner pitcher wall, the lid wax forms dense clusters of flat-topped pillars. These provide sufficient grip for insects to walk upside down under the lid and harvest nectar from highly prolific nectaries, but not enough to withstand severe perturbation. Coating the lower lid surface with an anti-slip polymer caused a significant reduction of captured prey in the field (Bauer et al. 2012b).

The mechanical properties of the *N. gracilis* lid similarly are well-adapted to its trapping function (Bauer et al. 2015b). The lid is very stiff and will break before it bends significantly. However, the rear of the pitcher
p. 192 just below the lid attachment is ↳ flexible. Upon impact of a rain drop, this region deforms and acts as a hinge about which the stiff lid pivots. During the initial downstroke, the lid tip can reach a top speed of 1.5 m s^{-1} and a maximum acceleration of approximately 30 *g*. Velocity and acceleration increase linearly from the base of the lid to its tip, confirming that the lid does not bend but instead functions as a torsional spring that responds to drop impacts with highly stereotyped damped oscillations (Bauer et al. 2015b). The combination of specialized material and surface properties provides *N. gracilis* with a highly effective additional trapping mechanism that may be partly responsible for the great ecological success of this widespread and abundant species. The importance of the lid for prey capture is further corroborated by the fact that *N. gracilis* allocates

a much higher proportion of its attractive nectar to the lower lid surface than other investigated species (Bauer et al. 2012b).

14.4 Future research

Motile traps of carnivorous plants are ideal candidates for in-depth investigations of plant movements. Although their general kinematics and underlying physiological processes have been investigated in detail, the precise mechanisms are not yet fully resolved. Particularly on cellular and molecular level, many processes remain poorly understood (Forterre 2013). Open questions include: how do biological signals such as action potentials affect the post-stimulatory mechanical responses (e.g., turgor changes); how is active water transport maintained (e.g., out of *Utricularia* traps) and how do water channels work; which channels regulate ion transport across membranes, and how do the mechanical and electrical properties of cells and cellular constituents affect this? Commercially available loss-of-function mutants in *Dionaea* offer an
p. 193 exciting opportunity to study ↳ these mechanisms (Bailey and McPherson 2012, Poppinga et al. 2013b).

In addition to controlled laboratory experiments, it is important that trap movements and trapping mechanisms are investigated in the field. These can reveal if trap movements are fine-tuned to exploit prey behavior; how plants avoid being triggered by rain, wind, or debris; how trap sensitivity is modulated by environmental factors; and whether some animals are adapted to avoid traps or escape from them. The ecological implications of motile traps have barely been studied and are likely to provide exciting and surprising discoveries in the future.

Motile traps also can inspire technical devices such as structures that autonomously respond to the environment (Chapter 20). The interest in plant movement for the development of biomimetic applications is constantly increasing. For example, the trapping movements of carnivorous plants have become important sources of inspiration for "elastic architecture" such as biomimetic façade-shading systems (Schleicher et al. 2015). Furthermore, plants in general and carnivorous plants in particular provide ample inspiration for resilient hinge-free movements that function reliably over long time spans while requiring minimal maintenance.

Poppinga, S., Bauer, U., Speck, T., and Volkov, A. G., *Motile traps*. In: *Carnivorous Plants: Physiology, ecology, and evolution*. Edited by Aaron M. Ellison and Lubomír Adamec: Oxford University Press (2018). © Oxford University Press. DOI: 10.1093/oso/9780198779841.003.0014