One remarkable example is *Dionaea muscipula*,the Venus' flytrap, which has modified leaves into snap traps that close rapidly when triggered by unsuspecting prey (Darwin, 1875). The plant has adapted to nutrient-poor soils by supplementing its diet with insects and small arthropods (Gaascht et al., 2013). These specialised features and behaviour are the fundamental elements shaping plants' ecological strategies (e.g. selective investment in trap sizes), enabling them to optimise their interactions with the environment and maximise their chances of survival and reproduction (Westoby et al., 2002).

Although carnivorous plants have been the subject of interest and study for almost 150 years after Darwin’s book “*Insectivorous Plants*”, the origin of the *Utricularia* plant trap has remained mysterious. Even resolving the basic mechanism of trap function required the contributions of several notable figures in botany, including Charles Darwin and John William Lloyd.

## Adhesive Traps

Adhesive traps are characterised by specialised structures on the plant’s surface, typically leaves, that secrete adhesive substances (Mithöfer, 2021). These secretions may serve a dual purpose: they attract unsuspecting prey through their alluring scent, and upon contact, the adhesive substances ensnare the prey, preventing escape (Tagawa & Watanabe, 2021). This trapping mechanism is particularly effective for capturing flying or crawling insects, providing these carnivorous plants with an additional source of nutrients vital for their survival (Tagawa et al., 2018). Most *Drosera* species (commonly known as sundews), such as *Drosera schizandra* from the *Droseraceae* family deploy ground-level adhesive leaves, whereas some species like *Drosera regia*, commonly known as the King Sundew, have filiform (long and skinny) leaves. *Byblis*, another carnivorous plant genus and Some *Pinguicula* species, like *Pinguicula filifolia*, a member of the Butterwort family, employ a similar strategy, with adhesive leaf surfaces that lure and capture prey, despite its genus mostly consisting of ground-level traps. *Roridula*, like *Roridula gorgonias* features glandular hairs on its filiform leaves that secrete a sticky mucilage, but unlike the adhesive substances found in fully carnivorous plants like *Drosera*, the mucilage produced by *Roridula* does not have digestive enzymes (Voigt et al., 2009). Instead, the plant relies on a mutualistic relationship with insect predators, specifically bugs (*Pameridea reut*) that feed on the trapped insects, absorbing their nutrients (Voigt et al., 2009). The *Roridula* plant benefits indirectly from the nutrients the bugs release during their feeding process; thus, some researchers consider them as protocarnivorous plants (Voigt & Gorb, 2010). These plants suggest a shared trapping niche despite their taxonomic differences.

## Snap Traps

Native to the warm-temperate wetlands of North and South Carolina, the Venus’ Flytrap (*Dionaea muscipula*) has specialised snap trap leaves with sensitive trigger hairs, which rapidly close when an insect contacts these trigger hairs to ensnare the prey (Gaascht et al., 2013; Böhm et al., 2016). In contrast, *Drosera burmannii*, also known as Burmann's Sundew, presents a different approach to carnivory. Its trapping mechanism involves sticky glandular hairs on its leaves like other *Drosera* species; however, it goes beyond conventional stickiness. Upon capturing prey, the tentacles undergo a rapid “snap” motion resembling the rapid closure of a snap trap, with the remarkable ability to reversibly bend toward the captured prey (Poppinga et al., 2013). Both *Dionaea muscipula* and *Drosera. burmannii* are known to survive in wetlands (Juniper et al. 1989). The Waterwheel Plant (*Aldrovanda vesiculosa*) is native to nutrient-poor freshwater habitats on several continents, and its aquatic snap trap is a specialised mechanism to capture aquatic invertebrates (Westermeier et al., 2018). The plant's submerged leaves are equipped with delicate trigger hairs, and when these hairs are disturbed by unsuspecting prey, the lobes of the leaf swiftly close together, entrapping the aquatic organisms within a fraction of a second (Adamec, 2018).

## Pitcher Traps

Monotypic family, *Neoenthaceae*, commonly known as Pitcher plants possess leaves that form deep cavities, making escape difficult for prey that fall in (Lee et al., 2016). The alluring design of the pitcher trap is enhanced by a combination of factors, in which they emit enticing scents and produce nectar, serving as irresistible invitations for insects (Hotti et al., 2017). The interior of the pitcher is lined with a slippery, waxy substance that makes it difficult for insects to maintain their footing; therefore, the insects struggle to escape, and they inevitably slip and fall into the liquid-filled cavity below (Moldowan et al., 2019). The pool of water at the pitcher's base may contain digestive enzymes or rely on symbiotic relationships with bacteria to break down the captured prey (Moldowan et al., 2019). Pitfall traps, exemplified by *Sarracenia*, *Nepenthes*, and *Heliamphora* are highly effective at ensnaring insects by the downward-pointing hairs and slick walls of the pitcher prevent most escape attempts, ensuring that the trapped insects remain within the confines of the trap. Among *Nepenthes*, many species feature two forms of pitchers on the same plant, with aerial or ground specialisations, often termed upper or lower traps (Moran, 1996). The upper pitchers of *Nepenthes rafflesiana* are suspended like chalices, and the lower pitchers are at the ground-level, which suggests the dimorphic approach to diversify its prey capture tactics, catering to insects from above and below (Di Giusto et al., 2010).

## Transitional Traps

Members of the *Nepenthaceae* family are traditionally considered pitcher plants, which trap prey via a pitfall mechanism; however, there are some exceptions. *Nepenthes inermis* exhibits characteristics of both sticky and pitcher traps within a single structure (Rice, 2007). The aerial pitcher trap of *Nepenthes inermis* boasts the classic shape associated with pitfall traps, yet its inner walls are adorned with a sticky substance (Rice, 2007), suggesting the possibility of trapping strategies intermediate between two pitfall and sticky trap carnivorous mechanisms. In the category of ground traps, *Pinguicula lutea* and many other *Pinguicula* species suggest an intermediate strategy between sticky and pitcher plant traps. Many Pinguicula exhibit slow leaf motion after prey capture, usually analogized to the sticky tentacle traps seen in *Drosera*. However, in *Pinguicula*, the whole leaf often curls (Scorza & Dornelas, 2011), with some species producing leaves that are highly curled even without prey capture, suggesting a possible first step towards the evolution of a pitfall trap.

## Eel Traps

*Sarracenia psittacina* and *Sarracenia purprea*, characterised by its hooded, decumbent pitchers, employs a eel trap mechanism for capturing prey instead of the conventional fluid-filled pitcher trap. This distinctive approach involves elongated inward-pointing hairs that impede prey exit, as Lloyd (1942) and Juniper et al. (1989) observed and documented. Remarkably, they have been observed capturing aquatic prey (protozoa and water bugs) even when submerged, affirming its unequivocal amphibious nature, thriving in areas prone to flooding (Schnell, 2002). Moreover, *Darlingtonia californica* mechanisms operate similarly through an eel trap mechanism; while the adult *Darlingonia* are typically erect, the juvenile pitchers often exhibit a decumbent orientation (Lloyd, 1942; Schnell, 2002), although trapping in the juvenile stage has not been confirmed. The enigmatic semi-aquatic plant *Genlisea*, which has received relatively limited scientific attention, possesses intriguing traps that primarily develop below the surface of wet environments (Płachno et al., 2020). The traps of *Genlisea* consist of tiny tubes adorned with specialised hairs that allow entry for unsuspecting prey but prevent their escape, featuring two outward-twisting arms that emanate from the mouth of the structure (Carmesin et al., 2021). The arms of the *Genlisea* trap incorporate a channel that is also lined with hairs, forming a directional guiding surface (Carmesin et al., 2021). This elaborate arrangement is believed to be a guiding mechanism, directing small organisms (e.g. protozoans) towards the mouth and digestive region of the trap (Carmesin et al., 2021).

## Aquatic Pitcher Traps

The suction traps of *Utricularia*, commonly known as bladderworts, are renowned for their rapid trapping mechanisms (Westermeier et al., 2017). They have evolved specialised tiny bladder-like structures, functioning as intricate underwater traps (Albert et al., 2010). *Utricularia* species are predominantly aquatic or semi-aquatic, inhabiting various freshwater environments across the globe (Westermeier et al., 2017). The unique aspect of *Utricularia* traps lies in their ability to generate a suction force for prey capture. These traps comprise a bladder or vesicle connected to the external environment through a trigger mechanism, and a slender stalk called the utricle (Singh et al., 2020). The utricle contains numerous small, hair-like structures called trigger hairs, susceptible to mechanical stimulation (Singh et al., 2020). The trigger hairs require only a slight touch or displacement to initiate the trapping process (Westermeier et al., 2017). The precise details of the process vary among species, but the general mechanism involves the rapid expulsion of water from the bladder, creating a sudden decrease in internal pressure (Laakkonen et al., 2006). This pressure differential generates a powerful suction force, causing the prey to be forcefully drawn into the bladder within a fraction of a second (Laakkonen et al., 2006). The efficiency of *Utricularia* traps is further enhanced by the presence of inward-facing bristles or valves at the entrance of the bladder, which allow water and smaller particles to pass through but prevent the escape of captured prey (Singh et al., 2020). Once inside the bladder, the prey becomes trapped and is subsequently digested by the plant's enzymatic secretions (Singh et al., 2020).

Darwin, renowned for his groundbreaking work on evolutionary theory, showed a keen interest in the carnivorous adaptations of plants, including *Utricularia*. In his book *Insectivorous Plants,* published in 1875, Darwin extensively studied bladderworts and provided valuable insights into their trapping mechanisms, although he did not realise or describe the incredible suction mechanism of the trap, despite observing and describing protozoans “suddenly” appearing in the trap. Darwin did recognise the remarkable complexity of their traps and discussed their adaptive significance in nutrient-poor environments. While Darwin cleared up the functional aspects of *Utricularia* traps, John William Lloyd, an American botanist, made significant contributions to our understanding of the plant's evolutionary history. In the early 20th century, Lloyd (1942) conducted extensive fieldwork, meticulously studying the distribution and diversity of bladderworts in North America. His observations and studies of *Utricularia* populations across different habitats provided critical insights into the plant's adaptive radiation and speciation. Recent research combining molecular phylogenetics, comparative morphology, and ecological studies has provided further insights into the origin of *Utricularia*. Phylogenetic analyses based on DNA sequencing have revealed the relationships between different *Utricularia* species and made clear their evolutionary history, confirming that bladderworts likely originated from a common ancestor and subsequently The previously-suspected relationship of *Utricularia* to the other genera in the *Lentibulariaceae* (sister to Genlisea; the sister group of *Utricularia*+*Genlisia* is *Pinguicula*) was also confirmed.

Givnish et al. (1984) proposed a cost/benefit model for the evolution of plant carnivory, which suggests that the costs of carnivory, including the production of secreted mucilage and the acquisition of specialised carnivorous structures, are balanced against the benefits of nutrient acquisition from prey.

According to conventional taxonomy, *Dionaea*, *Aldrovanda*, *Drosera*, as well as *Drosophyllum* and *Triphyophyllum*, are considered closely related (Kubitzki, 2003). This classification is based on shared floral, pollen, and glandular characteristics (Kubitzki, 2003).

In terms of suction traps of *Utricularia*, converting a primitive eel trap into a sophisticated suction trap is conceivable. However, all of the arguments above essentially add up to a hypothesis or evolutionary scenario, which might be criticised as a “just-so story”. Many of the proposed intermediates are hypothetical: for example, this scenario suggests that, between the divergence of *Pinguicula* from *Genlisea*+*Utricularia*, and the *Genlisea*+*Utricularia* split, there must have been a diversification of *Lentibulariaceae* pitcher plants which are now all extinct.

Molecular phylogenies confirmed previous insights, as Ellison and Gotelli (2001) outlined, suggesting that complex traps, including *Utricularia* bladder and pitcher traps, have evolved from simpler adhesive leaf traps, either aerial or ground-based. This suggests a progressive transformation from an adhesive trap to a pitcher trap; if pitchers typically evolved from adhesive traps, then *Pinguicula* traps could be seen as proto-pitcher analogues. In the case of *Pinguicula*, which is considered a transitional trap, the adaptation involves adhesive leaves that serve as adhesive traps. These leaves produce a sticky mucilage that captures and retains prey. The leaf movement in the *Pinguicula*, traditionally considered on the path to more complex motions, involves curling via a growth response (Lloyd, 1942). This curling is hypothesised to enhance leaf contact with prey, minimise nutrient loss, and protect prey from external elements. These functions are perfected to a greater degree in pitcher traps. The persistence of leaf curling in *Pinguicula*, even before prey capture, suggests a sacrifice of photosynthesis for an increased benefit in prey capture and retention, consistent with Givnish’s cost-benefit model. As well as *Pinguicula* reinterpreted as transitional traps, *Nepenthes inermis* also exemplifies the transitional traps by integrating both pitcher and adhesive trap mechanisms within its unique structure (Rice, 2007).

Revisiting the origin of the *Utricularia* trap, the evolution of the Utricularia trap likely involved the gradual transition, including the addition of trigger hairs and vertical doors, especially in more aquatic habitats. The gap between a simple *Pinguicula*-type flypaper trap and the hypothesised eel trap-pitcher (*Genlisea*) could be bridged by analogising the evolutionary history of other pitcher genera that transitioned from adhesive trap ancestors. On this hypothesis, the transition from a *Pinguicula*-like ancestor to *Utricularia* involved the adaptive radiation of pitcher traps similar to those seen in modern genera, challenging the misperception of pitcher plants as predominantly large and *Utricularia* traps as microscopic.

WebPlotDigitizer is a valuable tool for extracting data from graphical representations, such as phylogenetic trees, facilitating their quantitative analysis. Firstly, the *Utricularia* phylogenetic tree image was uploaded to the WebPlotDigitizer platform. Once the image is loaded, the tool allows calibrating the axes, ensuring accurate scaling for subsequent data extraction. The image may be calibrated by referencing features like scale bars or estimated time. With calibrated axes, it is manually digitised data points by adding points corresponding to tips, nodes and corners positions in the tree.

As Darwin (1875) observed the movement of sticky leaf traps, motion acquisition could occur gradually, which suggests that transition from aerial to ground adhesive or reverse can be considered (Rate 3). Moreover, *Dionea* and *Aldrovanda* may have evolved from ground adhesive traps like *Drosera* (Lloyd, 1942; Juniper et al., 1989), which are expressed in the model, transitioning from ground adhesive to amphibious snap trap (Rate 4), and from amphibious snap to aquatic snap trap (Rate 5). *Nepenthes*: tropical pitcher traps may have both upper and lower pitchers (Adlassnig et al., 2011), and the transition from aerial to ground pitcher traps or reverse are imaginable (Rate 6), as well as the transition of amphibious pitchers like *Sarracenia psittacina* from ground pitchers (Rate 7). Some species of Genlisea, with features like stomata on their underground tubers and mucilage-producing trichomes, exhibit adaptations for water interaction and nutrient absorption, which are vital in both amphibious and aquatic environments (Płachno et al., 2020). The evolution of starch-rich tubers in both Genlisea and Utricularia indicates a shared lineage (Płachno et al., 2020), suggesting that similar adaptive mechanisms could lead to the transition into aquatic suction traps (Rate 8). *Pinguicula*, a genus closely related to *Utricularia* (Silva et al., 2016), exhibits pitcher-like tendencies, making it easier to envision transitional forms between flypaper traps and pitcher traps (Rate 9 & 11: adhesive to transitional traps, and Rate 10 & 12: transitional to pitcher traps).

Felsenstein's Pruning Algorithm was employed to calculate likelihoods – the probability of the observed trap type data under each proposed phylogenetic model. Felsenstein's Pruning Algorithm utilises the phylogenetic tree structure to calculate the probabilities of ancestral character states under proposed transition rates (Kosakovsky Pond et al., 2011). Starting from the tips of the assembled phylogenetic tree, with each species labelled according to their observed trap types (e.g., bladder traps, pitcher traps, flypaper traps), the algorithm proceeds recursively toward the tree's root. The algorithm calculates the probability of each trap type being ancestral to the observed tip data above it, for each internal node of the tree. If all descendant species share the same trap type, the ancestral node is assigned that trap type. If the descendant species have different trap types, the ancestral node is assigned likelihoods for each state. The algorithm continues to traverse the tree until the root is reached, assigning trap type likelihoods to each ancestral node. Once the algorithm has traversed the entire tree, the likelihoods are multiplied across all states, producing a total likelihood under the proposed model.

Maximum likelihood analysis under different models aims to assess the likelihood of the observed trap type distribution given each model and determine which model best fits the data. Maximum likelihood analysis is a statistical method commonly used in phylogenetics to estimate the parameters of a given model that maximises the probability of observing the observed data (Price et al., 2010). The analysis utilises a likelihood function that calculates the probability of observing the trap-type scores given the model's parameters for each model. The likelihood function considers the transition rates between trap types, the assignment of ancestral trap types, and the observed trap type scores for each species.

In the context of the maximum likelihood analysis for model comparison, the Akaike Information Criterion (AIC) is a widely used statistical measure to assess the relative goodness-of-fit of competing models. By running the maximum likelihood analysis on the score matrices derived from the null hypothesis model and the pitcher hypothesis model, we can quantitatively evaluate the support for each model and determine which model best fits.

that have not been directly observed. By combining the likelihood calculations described above with an “up-pass” passing probabilities from the root of the tree to the tips, the algorithm can assign probabilities to each possible ancestral trap type and for each node.

Under a givenchosen model, the probability of different ancestral trap types wascan be estimated for ancestral species using ancestral character estimation. that have not been directly observed. By combining the likelihood calculations described above with an “up-pass” passing probabilities from the root of the tree to the tips, the algorithm can assign probabilities to each possible ancestral trap type and for each node. To estimate the number and timing of transitions, ancestral character estimation wascan be supplemented with stochastic mapping (function simmap (?) in phytools).

Under the best model selected based on AIC and equal-rates null model, ancestral character estimation was performed to infer the most likely trap types of ancestral species in the phylogenetic tree using ‘phytools’ (Revell, 2024) and ‘BioGeoBEARS’ (Matzke, 2013). Ancestral character estimation allows reconstructing the trap-type evolution throughout the evolutionary history of the carnivorous plant lineage (Wilson et al., 2022).

Phylogenetic stochastic mapping extends the traditional ancestral character estimation by acknowledging that character evolution is inherently stochastic. The approach allows for the exploration of alternative scenarios in which different trap types may have arisen at ancestral nodes, providing a more nuanced understanding of the potential states of these common ancestors. This probabilistic framework gives us insights into the likelihood of transitions between different trap types and the associated uncertainty in these evolutionary events. This integrative approach, combining the best model selected through AIC with phylogenetic stochastic mapping, enhances the robustness of our ancestral state reconstructions. It acknowledges the inherent complexity and uncertainty in the evolution of trap types within the carnivorous plant lineage. It provides a more comprehensive and realistic depiction of the ancestral states and their associated confidence intervals across the phylogeny.