How the sensory system of carnivorous plants has evolved

Charles Darwin was deeply interested in carnivorous plants and was particularly fascinated by Venus flytrap (Dionaea muscipula) and sundew plants (Drosera spp.) of the Droseraceae family. He was intrigued by fast and slow trap movements in these plants and predicted the existence of a signal that transfers information from sensor to actuator within the trap organ. Based on his request, Sir John Burdon-Sanderson discovered electrical signals in Venus flytrap. Recent success in the transformation of non-model carnivorous plants with a Ca²⁺ sensor has outlined a possible route for the evolution of sensory systems in the carnivorous family Droseraceae.

When an insect lands on the sticky surface of the marginal tentacles of the sundew plant, an amazing reaction in the plant world is initiated. The tentacle heads start to generate a trace of action potentials, which propagate down through the stalks and terminate near the bases. As a result, all the tentacles in direct contact with the insect prey start to bend inward, fixing the prey and placing it on the inner trap surface. Subsequently, other tentacles that were not in previous contact with the prey also start to bend inward. How is this communication achieved? In their seminal works, Barbara Pickard and Stephen Williams concluded that each tentacle behaves electrically independently and that delayed movement of tentacles not directly stimulated by the prey is caused by a phytohormone (reviewed in Williams and Pickard, 1980; Williams, 2002). Krausko et al. (2017) recently observed membrane potential oscillations on the abaxial trap surface after prey contact with the inner tentacles, which resembled Ca²⁺ oscillations and thus communication among tentacles. The recent successful transformation of the sundew plant Drosera spatulata with the Ca²⁺ sensor GCaMP3 shed more light on this process (Procko et al., 2022). Stimulated tentacles send a Ca²⁺ wave from the tentacle head down to the base and outward from the base to the surrounding tissue. The concentric propagation of the Ca²⁺ wave may enter neighboring tentacles that do not have direct contact with the insect prey, likely activating them. This localized Ca²⁺ signaling induces accumulation of a phytohormone from the jasmonate (JA) group, which accumulates only in the bending segment of the trap and induces localized secretion of digestive enzymes (Nakamura et al., 2013; Krausko et al., 2017). Procko et al. (2022) showed that activation of neighboring tentacles is likely to be mediated by a Ca²⁺ wave. However, phytohormonal activation by JAs cannot be completely ruled out, as suggested by Williams and Pickard (1980), and both processes may contribute to tentacle activation.

The findings of Procko et al. (2022) are not surprising in the context of another recent study, which may help us to understand how this sensory system may have evolved. When the leaf trichome of non-carnivorous Arabidopsis thaliana transformed with the same Ca²⁺ sensor (GCaMP3) was mechanically stimulated, a Ca²⁺ wave was triggered, beginning at the trichome base before propagating away from the trichome as a concentric wave (Matsumura et al., 2022). In the cells that received a Ca²⁺ signal, the immune response was initiated in a phytohormone (e.g., JA)-dependent and independent manner. Proteins similar to the digestive enzymes of carnivorous plants (e.g., chitinases, etc.) were found among the upregulated genes. These findings suggest that the prerequisite for the sensory system of Droseraceae was already present in non-carnivorous plants and that evolution only fine-tuned the process for botanical carnivory. Because the Ca²⁺ wave in the Arabidopsis trichome does not enter neighboring trichomes (Matsumura et al., 2022), an increase in tentacle density or a decrease in the resistance to Ca²⁺ wave propagation may lead to coordination and complex trap behavior. Presumably, this hypothesis can be tested using mutants of transgenic GCaMP3 Arabidopsis with increased trichome density. Changes in the cellular architecture of a trap that can convert a biochemical signal (e.g., JA) into tentacle and trap bending responses, together with the secretion of sticky substances, significantly improved insect-capture efficiency. The signaling and biochemistry necessary for prey digestion had already been established during the evolution of the plant defense system; only small modifications of enzyme properties were needed. Then it was time for a significant improvement in trap behavior: the evolution of the snap trap.

It has been generally accepted that snap traps of Dionaea and Al-drovanda evolved from sticky traps (Gibson and Waller, 2009). Recent success in the transformation of Venus flytrap (D. muscipula) with a similar Ca²⁺ sensor (GCaMP6f) enables us to look at Ca²⁺ signaling. When the trigger hair on the trap surface of a Venus flytrap is touched, an electrical signal propagates from the trigger hair into the bilobed trap. At the same time, the Ca²⁺ wave propagates from the trigger hair into the trap lobe and can enter the digestive glands and remaining neighboring trigger hairs (Suda et al., 2020; Scherzer et al., 2022), resembling the behavior in sundew plants. Venus flytrap exhibits significantly greater velocity of Ca²⁺ propagation (20–100 mm s⁻¹) and complexity compared with sundew and Arabidopsis plants (1–3 μm s⁻¹) (Figure 1). This fast velocity, which quickly activates the snap trap, compensates for the loss of sticky mucilage needed for prey retention in slower sundew traps. Anatomical studies revealed that the different trap structures in sundew and Venus flytrap are homologous. The marginal tentacles of sundew-like plants may have been modified...
through evolution into the marginal teeth for retaining prey seen on the Venus flytrap; other tentacles were possibly modified to act as “trigger” sensory hairs, and others likely became sessile digestive glands (Gibson and Waller, 2009). The subsequent downstream sequence of events after the Ca$^{2+}$ wave is similar to that in sundew plants: accumulation of JAs and expression and secretion of digestive enzymes (Pavlovič and Mithöfer, 2019). In both cases, mechanostimulation of non-carnivorous and carnivorous plants represents the first alert: the massive and long-lasting accumulation of JAs and the activation of defense and digestion start after the perception of chemical stimuli from wounding or herbivory (i.e., damage-associated molecular patterns) or insect prey (Pavlovič and Mithöfer, 2019).

Recent studies have also described a possible contribution of different ion channels to the mechanosensing ability of carnivorous plants. Non-carnivorous plants sense mechanical stimuli using mechanosensitive ion channels, including members of the mechanosensitive channel of small conductance-like (MSL) family. Homologous to these channels in Venus flytrap and sundew plants of the family Droseraceae is FLYCATCHER1, which is strongly expressed in sensory cells in the indentation zone of Venus flytrap trigger hairs and in heads of sundew tentacles, where most flexure occurs (Procko et al., 2021). In these structures, FLYCATCHER1 and/or other identified channels may transform a mechanical stimulus into an electrical one. On the other hand, electrical and systemic Ca$^{2+}$ signaling in non-carnivorous plants (i.e., from leaf to leaf) is dependent on GLUTAMATE RECEPTOR LIKE CHANNELS (GLR3.3 and GLR3.6 Mousavi et al., 2013; Toyota et al., 2018). The podium cells of Venus flytrap trigger hairs specifically express DmGLR3.6, which may enable propagation of the Ca$^{2+}$ signal from the trigger hair to the trap lobe (Scherzer et al., 2022). Thus, the mechanism of prey recognition in carnivorous Droseraceae has evolved by co-opting ancestral mechanosensitive channels and other ion channels to sense and propagate touch signals. These results are only indirect to date and need to be verified using loss-of-function mutants in carnivorous plants.

Successful transformation of the model plant Arabidopsis and non-model carnivorous plants with similar Ca$^{2+}$ sensors has shed light on the evolution of the sensory system in carnivorous plants of the family Droseraceae. However, carnivorous plants have evolved independently at least 10 times, and not all use JA signaling for the activation of their traps (Adamec et al., 2021). How these carnivorous genera sense mechanical stimulation, if at all, and whether it can activate carnivorous responses remain to be investigated. For this purpose, we will need more successful transformations of these recalcitrant but beautiful and interesting plants that intrigued Charles Darwin, one of the greatest biologists of all time.

**AUTHOR CONTRIBUTIONS**
A.P. wrote the manuscript.

**ACKNOWLEDGMENTS**
No conflict of interest is declared.

Andrey Pavlovič*

Department of Biophysics, Faculty of Science, Palacký University, Olomouc, Czech Republic

*Correspondence: Andrey Pavlovič (andrej.pavlovic@upol.cz)

https://doi.org/10.1016/j.xplc.2022.100462

**REFERENCES**
Adamec, L., Matusíková, I., and Pavlovič, A. (2021). Recent ecophysiological, biochemical and evolutionary insights into plant carnivory. Ann. Bot. 128:241–259. https://doi.org/10.1093/aob/mcab071.

Gibson, T.C., and Waller, D.M. (2009). Evolving Darwin’s ‘most wonderful’ plant: ecological steps to a snap-trap. New Phytol. 183:575–587. https://doi.org/10.1111/j.1469-8137.2009.02935.x.

Krausko, M., Perutka, Z., Sebela, M., Šamajová, O., Šamaj, J., Novák, O., and Pavlovič, A. (2017). The role of electrical and jasmonate signalling in the recognition of captured prey in the carnivorous sundew plant Drosera capensis. New Phytol. 213:1818–1835. https://doi.org/10.1111/nph.14352.

Matsumura, M., Nomoto, M., Itaya, T., Aratani, Y., Iwamoto, M., Matsuura, T., Hayashi, Y., Mori, T., Skelly, M.J., Yamamoto, Y.Y., et al. (2022). Mechanosensory trichome cells evoke a mechanical stimuli–induced immune response in Arabidopsis thaliana. Nat. Commun. 13:1216. https://doi.org/10.1038/s41467-022-28813-8.

Mousavi, S.A.R., Chauvin, A., Pascaud, F., Kellenberger, S., and Farmer, E.E. (2013). GLUTAMATE RECEPTOR-LIKE genes mediate leaf-to-leaf wound signalling. Nature 500:422–426. https://doi.org/10.1038/nature12478.

Nakamura, Y., Reichelt, M., Mayer, V.E., and Mithöfer, A. (2013). Jasmonates trigger prey-induced formation of ‘outer stomach’ in carnivorous sundew plants. Proc. Biol. Sci. 280:20130228. https://doi.org/10.1098/rspb.2013.0228.

Pavlovič, A., and Mithöfer, A. (2019). Jasmonate signalling in carnivorous plants: copycat of plant defence mechanisms. J. Exp. Bot. 70:3379–3389.

Procko, C., Murthy, S., Keenan, W.T., Mousavi, S.A.R., Dabi, T., Coombs, A., Procko, E., Baird, L., Petapoutian, A., and Chory, J. (2021). Stretch-activated ion channels identified in the touch-sensitive
structures of carnivorous Droseraceae plants. Elife 10:e64250. https://doi.org/10.7554/eLife.64250.

Procko, C., Radin, I., Hou, C., Richardson, R.A., Haswell, E.S., and Chory, J. (2022). Dynamic calcium signals mediate the feeding response of the carnivorous sundew plant. Proc. Natl. Acad. Sci. USA. 119, e2206433119. https://doi.org/10.1073/pnas.2206433119.

Scherzer, S., Huang, S., Iosip, A., Kreuzer, I., Yokawa, K., Al-Rasheid, K.A.S., Heckmann, M., and Hedrich, R. (2022). Ether anesthetics prevents touch-induced trigger hair calcium-electrical signals excite the Venus flytrap. Sci. Rep. 12:2851. https://doi.org/10.1038/s41598-022-06915-z.

Suda, H., Mano, H., Toyota, M., Fukushima, K., Mimura, T., Tsutsui, I., Hedrich, R., Tamada, Y., and Hasebe, M. (2020). Calcium dynamics during trap closure visualized in transgenic Venus flytrap. Nat. Plants 6:1219–1224. https://doi.org/10.1038/s41477-020-00773-1.

Toyota, M., Spencer, D., Sawai-Toyota, S., Jiaqi, W., Zhang, T., Koo, A.J., Howe, G.A., and Gilroy, S. (2018). Glutamate triggers long-distance, calcium-based plant defense signaling. Science 361:1112–1115. https://doi.org/10.1126/science.aat7744.

Williams, S.E. (2002). Comparative physiology of the Droseraceae sensu stricto – how do tentacles bend and traps close. Proceedings the 4th International Carnivorous Plant Conference, pp. 77–81. https://cpn.carnivorousplants.org/articles/ICPS2002confp77_81.pdf.

Williams, S.E., and Pickard, B.G. (1980). The role of action potentials in the control of capture movements of Drosera and Dionaea. In Plant Growth Substances, F. Skoog, ed. (Berlin: Springer), pp. 470–480. https://doi.org/10.1007/978-3-642-67720-5_48.