# Evolution and Development of Carnivorous Plants

# 食虫植物の発生と進化

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## Introduction

Carnivorous plants possess complex traits composed of multiple unique evolutionary novelties. How such complex traits emerged is a frequent question in evolutionary and developmental biology. Studying how carnivory and related traits, like the digestion and absorption systems and the specific trap morphologies evolved can help to shed light on this question.

## Results

In this study, first I focused on Droseraceae carnivorous plants, namely on *Drosera spatulata*, *Dionaea muscipula* and *Aldrovanda vesiculosa*, and by assembling genomes from each representative genus in the family, I reconstructed the evolutionary events of their genomes. It was shown that whole genome duplications, massive gene space reductions, and sudden transposable element increases parallelly shaped these plants. The origin of carnivory appears to be related to these genomic phenomena, suggesting the role of genomic plasticity in the evolution of complex traits. This, however did not give much information about the relationships between the complex carnivorous traits: attraction, digestion, nutrient absorption and transport, and the development of the special trap leaves in the family.

Secondly, to understand the relationships between development of trap shapes and other carnivorous traits in the Droseraceae, I analyzed the temporal developmental transcriptome of two representative species, *Drosera spatulata* with adhesive traps and *Dionaea muscipula* with snap traps. *Drosera* tentacles were speculated to originate from lobed or compound leaves, however there were no experimental supports. We showed that genes involved in lobed or compound leaf development in some angiosperms are expressed during the leaf development of *Drosera spatulata* and *Dionaea muscipula*. This supports the previous hypothesis and gives a direction for future research in the development and evolution of Droseraceae traps. Furthermore, I found that genes related to carnivorous functions, such as digestion and nutrient transport are predominantly expressed just before the maturation, which brought a drastic change in the transcriptional profile compared to those in previous stages. This transition was unexpectedly similar to that of a senescing leaf in Arabidopsis. Looking into the detailed processes of senescence and comparing those of the carnivory, it turned out that these two processes share a substantial number of transcription factors and other proteins. Hydrolytic processes, nutrient absorption, and transportation are the core processes for both leaf senescence and carnivory. Thus, I hypothesize that carnivory is originated as an exaptation of leaf senescence, which is concordant with the simultaneous evolution of digestion and absorption in carnivorous traits.

Thirdly, I focused on the development of pitcher shaped leaf in *Cephalotus follicularis*. *C. follicularis* is a pitcher-bearing carnivorous plant in the order Oxalidales and it is unique in the sense that it forms both carnivorous pitcher leaves and photosynthetic flat leaves, which makes it ideal to compare their development within one genetic background. The leaf fate changes under seasonal temperature and photoperiodic conditions. In this thesis, I found that nutrient availability in the substrate can override this program. As pitchers can serve as a nutrient capture organ as roots, this demonstrates the importance of carnivory in the plant's nutrient homeostasis in connection to development. Furthermore, I present the transcriptome of shoot apices in various environmental conditions and also a single cell level transcriptomic map of pitcher development in comparison to that of flat leaf. I found that cell types characterized by the single cell transcriptomic maps differentiate at the young leaf primordia between pitcher and flat leaves, suggesting that the leaf fate is determined before their morphological differentiations. I could also detect specific cell types potentially related to carnivory, such as waxy epidermal cells and digestive gland cell. Genetic analyses with transformed *C. follicularis* should facilitate to examine my hypotheses, thus I also report my trials to establish the technique.

## Discussion

Overall, carnivorous plants can serve as a useful material for evolutionary and developmental studies as they present novel and interconnected physiological traits with the complex leaf morphology. Genomic rearrangements provided potential toward the evolution of carnivory by recruiting duplicated genes and altering their regulatory networks. Such events result in co-option of multiple physiological processes simultaneously, that is the senescence in the Droseraceae. This leverages larger systems in order to establish novel complex traits. It is worth to emphasize that the carnivorous morphology and physiology are combined traits in carnivory and their simultaneous evolution may be related to interlacing of their regulatory networks, which would serve as a fascinating research field in the future.