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学位論文題目 Evolution of complex traits in carnivorous plants

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論文内容の要旨
Summary of thesis contents

Gradual, stepwise evolution occurs by the accumulation of small changes, but how complex traits evolve remains unclear, since evolutionary intermediates may be less adaptive than the starting state, or the final state. In the evolution of carnivorous plants, the use of insects as a nutrient source requires multiple novel traits, such as the production of specialized leaf morphology and the secretion of digestive fluids; together, these traits are known as ‘carnivorous syndrome’. Acquisition of partial components of carnivorous traits may not be adaptive without concurrent establishment of other traits. Therefore, evolutionary pathways may have circumvented less-adaptive intermediates. In this study, I examined development of pitcher leaves and evolution of digestive enzymes of carnivorous plants to understand how complex traits evolve.

In carnivorous plants, morphological evolution often involves changes that facilitate a trapping strategy and construction of functional pitfall traps requires drastic morphological changes. Here, I first review the developmental mechanisms of leaf shape diversification in flowering plants, and then describe developmental analyses of pitcher leaves in *Sarracenia purpurea*. I show that the pitcher leaves of *Sarracenia purpurea* develop through cell division patterns that are distinct from those in bifacial and peltate leaves, subsequent to regular expression of adaxial and abaxial marker genes. Differences in the orientation of cell divisions in the adaxial domain cause bifacial growth in the distal region and adaxial ridge protrusion in the middle region. These different growth patterns in the leaf establish the pitcher morphology. A computer simulation suggests that the orientation of the cell division plane is critical for the acquisition of the pitcher morphology. Our results imply that

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tissue-specific changes in the orientation of cell division underlie the development of a morphologically complex leaf.

To facilitate molecular understanding of carnivorous syndrome, my colleagues and I established *Cephalotus follicularis* as a new model system. This plant can produce both carnivorous pitcher and non-carnivorous flat leaves. Using this phenotypic plasticity, we can compare the two types of leaves in a single species to infer evolutionary processes. By analyzing leaf fates in response to various environmental factors, I succeeded in controlling the leaf dimorphism under experimental conditions. In addition, the *C. follicularis* nuclear genome has been sequenced and gene knockdown techniques have been developed, making this species tractable for molecular and genetic analyses. Using these resources, I identified transcription factors that show expression changes correlated with leaf fates. This model system will enable further analyses of the molecular mechanisms of carnivorous syndrome.

Carnivorous plants repeatedly evolved from non-carnivorous ancestors, indicating multiple, independent origins of carnivorous traits, including secretion of digestive enzymes. To understand the genetic basis of repeated emergence of carnivorous traits, I analyzed digestive enzyme genes from four carnivorous plants covering three independent origins of carnivorous syndrome. First, partial amino acid sequences of secreted proteins were determined, and then the corresponding genes were identified by transcriptome sequencing of trap leaves. The identified genes were not specific to carnivorous plants, but rather were homologs of pathogenesis-related hydrolytic enzymes in non-carnivorous plants. These orthologous genes likely were co-opted as digestive enzymes in parallel. Furthermore, several digestive enzymes share convergent amino acid substitutions, particularly in exposed residues at the protein-environment interface; these convergent substitutions may affect molecular adaptation to digestive fluid-specific micro-environments.

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The evolution of leaf morphology and digestive enzymes has likely co-opted preexisting mechanisms and modified these mechanisms to serve novel functions. Such evolutionary modifications may require fewer genetic changes than constructing these traits from ground zero, and thus have the potential to drive evolution of complex traits.