Book review

From Darwin to today: what modern biology tells us about the life of the green flesh-eater

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Carnivorous Plants: Physiology, Ecology, and Evolution
Edited by Aaron Ellison and Lubomir Adamec
(Oxford University Press, New York, NY; 2018)
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In the animal world, species that consume animals, plants or both have not attracted people in the same way as plants that live on an animal diet — the so-called carnivorous plants. Ever since their discovery in the 18th century, scientists have asked how these plants can make use of meat. Based on observations and field experiments, laboratory scientists went out to find answers to the basic questions: how plants can catch prey, decompose them, and consume the animal-derived nutrients.

Darwin pioneered this field and, in 1875, was the first to publish a book on carnivorous plants [1]. Scientists continued to explore these unique creatures and new investigations provided the basis for follow-up books by Lloyd [2] and Juniper *et al.* [3]. Now, in the fascinating times of modern biology, a new book on carnivorous plants has become available. It is edited by Aaron Ellison and Lubomir Adamec, the leading experts in the field over recent years and among the most cited scientists in *Carnivorous Plants* (2018). The book intends to keep a balance between systematics, ecology, and eco-physiology, i.e. the three major fields in carnivorous plant science, in which the editors are experts.

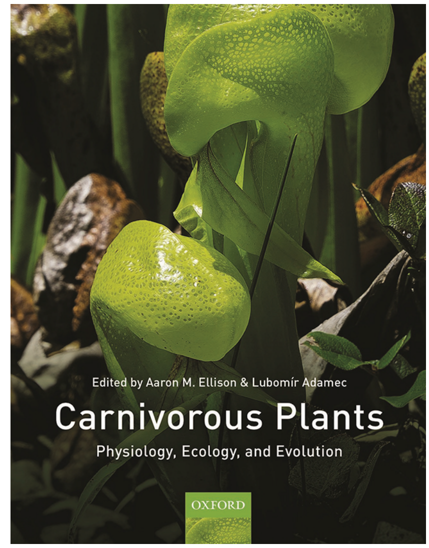
The book is organized in an unusual way, as it is assembled from the contributions of 66 expert co-authors who present the current state of science in their individual field of carnivorous plant research. *Carnivorous Plants* (2018) thus reads like a compendium of reviews, with a good deal of repetition between chapters.

The majority of the compendium focuses on classical topics of plant biology, and one finds a wealth of detailed information about the special features of individual carnivorous plant species. The chapters are well illustrated with high-quality photographs and detailed tables. The comprehensive description of the features of different carnivorous plant types is especially well illustrated with plates and tables. Each of the 28 chapters closes with a note on future research in the field of the expert co-authors, which makes *Carnivorous Plants* (2018) a most valuable, state-of-the-art archive for researchers focusing on systematics, ecology, and conservation biology.

However, given its structure, which presents the subject in a rather fragmented manner, it is hard for the non-expert reader to appreciate the bigger picture as presented in Darwin´s pioneering work [1] or in specific reviews on an individual carnivore such as the Venus flytrap [4]. Although well addressed in the compendium, the fragmentation of information throughout the chapters means that the more general readership cannot easily extract specific features of different carnivorous plants and trap types. Therefore, the general reader does not easily find answers to key questions, such as: why do non-carnivorous plants often tend to outgrow the green flesh-eaters in their nutrient-pure habitats? What difference does the root system make or, in other words, how differently do carnivorous plants with and without roots perform? Which cost–benefit model applies to the different types of carnivorous plants?

One finds a complete list of references dating from 1989 to 2017 (for more recent publications that did not make it before printing, see below). The reader also finds references dating back to the period that the former books already covered. The reader is, however, left uncertain as to whether or not the early findings and hypotheses were confirmed and which of them did not survive rigorous revalidation by modern studies.

Today, an ever-increasing number of plant genomes is being identified, which — together with proteomics and metabolomics — helps scientists to navigate the complex road maps of biological systems. In this way, major



molecular insights have been gained in plant biology, including for example into the C4 and CAM syndrome, which, like carnivory, reflects an adaptation of plant performance to changing environments on our planet.

One reason why I agreed to review this book was that I hoped to learn more about the roots of carnivory, its molecular evolution, and the development of the body plan of organs formed to capture and process animal prey. The last chapter of the part dedicated to systematics and evolution addresses carnivorous plant genomes. This section is very well covered by the experts on plant genome evolution and development. The co-authors have long-standing experience in this field, with plants in general, and recently with carnivorous plants in particular. The chapter's co-authors have recently sequenced and annotated the relatively small genomes of the suction trap–forming *Utricularia gibba* and the pitcher plant *Cephalotus follicularis*. Together with *Genlisea aurea*, which operate lobster pot traps, three carnivorous plant genomes from two families are now sequenced. Given that there are about 800 carnivorous plants subdivided over 12 families, one does not have to mention that the current database is insufficient for the comprehensive identification of genomic features specific to carnivorous plants and for understanding the adaptive evolution of carnivory.

Although one must await genomic data and transcriptome sets from a

An ant, the next meal of the carnivorous Darwin plant *Dionaea muscapula*, visiting the snap trap.
When the animal prey touches the sensory hairs protruding from the trap's surface, the capture organ will snap closed, digest the meal and consume the nutrients derived. (Photo: Sönke Scherzer.)

larger number of carnivorous species and families, the non-expert reader learns two key things from the available data. Firstly, the genome of the rootless, aquatic carnivore *Utricularia* apparently lacks genes for nutrient transporters, which are functionally expressed in the roots of non-carnivorous plants. It is very likely that the submersed trap of the carnivore acts as a substitute for the root by taking up prey-derived nutrients. Given that the reader does not learn anything about the trap-expressed transporters, this subject still seems open for further investigation in the species presented in the genome chapter (for trap transporters in the Venus flytrap, see references below). Secondly, *Cephalotus* can switch between non-carnivorous leaves and carnivorous pitchers. This switch seems to be associated with the expression of transcription factors that control leaf patterning. Reading this section, one might speculate on whether nutrient starvation could serve as a signal that causes the transition to the carnivorous syndrome.

Prior to the next version of the book, it will be important to test the current hypotheses and models predicting key molecular players in determining the carnivorous habit. This will certainly have to involve the testing of trap and non-trap transporter gene/protein function in the carnivorous plant under investigation as well as after heterologous expression of these genes in non-carnivorous plants and animal systems (addressed in [5–7]). In model plants, the analysis of mutants has paved the way for the understanding of complex behavior. In contrast to model plants, few mutants of carnivorous plants are currently available and carnivorous plants are not yet subject to large-scale transformation or genetics. Given that spontaneous mutations can be found and that the first carnivorous species have successfully been transformed [8], directed and undirected mutagenesis approaches offer a scientific playground for the future. Hopefully, genetic screens for the gain and loss of carnivorous features will enable the identification of as yet unknown carnivorous gene functions.

Given the current progress in the field, I personally believe that carnivorous plant genomes and the molecular control of trap development and functions will very likely advance into a major section of the secret life of carnivorous plants in a forthcoming book on this exciting topic.

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Q & A

Vivian Irish

Vivian Irish received her PhD in biology from Harvard University, where she worked on the developmental genetics of dorsal–ventral patterning in Drosophila*. She continued to explore patterning processes during* Drosophila *embryogenesis as a Jane Coffin Childs Fellow with Michael Akam at the University of Cambridge. Long interested in plant biology, she began hanging out at the Plant Breeding Institute, then at Cambridge, to catch up on the latest in plant biology research. Eventually, she pursued a second postdoc, this time as a National Science Foundation Fellow with Ian Sussex in plant developmental genetics at Yale University. She was appointed to the faculty at Yale in 1991 and is currently the Eaton Professor of Molecular, Cellular and Developmental Biology at the university.*

What turned you on to biology in the first place? When I was four years old, my parents took me to the Boston Science Museum and I remember being entranced by a human embryology display; that must have planted the seeds of my fascination with developmental biology. Later on, in sixth grade, I was voted 'best conclusioner' in reference to my science experiment write-ups. Clearly, I was destined to be a researcher!

And what drew you to your specific field of research? I love being able to apply genetic approaches to dissect development. When I was an undergraduate and during my graduate student days, *Drosophila* was by far and away the best system to explore questions of development using genetic approaches. I pondered moving into plant biology as a graduate student but was frustrated by the lack of good plant genetic systems; maize was an obvious possibility, but I didn't have the head for carrying out genetic analyses in the time frame needed for maize crosses. *Arabidopsis* had a renaissance as a plant model genetic system in the 1980s, and many *Drosophila* researchers moved to work on this 'botanical *Drosophila*' at that time, including me. I've worked on different aspects of patterning in *Arabidopsis*, as well as