What's new in the world of carnivorous plants?

by Firman Alamsyah

CARNIVOROUS PLANT NEWSLETTER

Journal of the International Carnivorous Plant Society

Volume 47, No. 1 March 2018

What's new in the world of carnivorous plants – Summary of two symposia held in July 2017

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Dozens of scientific papers about carnivorous plant research are published each year on diverse topics ranging from new species descriptions, through phylogenetic approaches in taxonomy and systematics, to ecology and evolution of botanical carnivory, biomechanics and physiology of traps, among many others. By the time a paper is published, however, it is already "old news" because the salient results often are presented months or even years earlier at scientific conferences. Such meetings are the perfect venues to discuss ongoing research and "hot" topics and present them to colleagues from around the world.

The first and last authors of this report were in the lucky situation to organize symposia about carnivorous plant biology during two major conferences: Simon Poppinga chaired a one-day session—"Carnivorous plants - Physiology, ecology, and evolution"—on July 6, 2017, as part of the Annual Main Meeting of the Society for Experimental Biology (SEB) in Gothenburg, Sweden. This first symposium included two keynote and two invited talks given by renowned carnivorous plants experts and six additional lectures. Aaron Ellison chaired a half-day session co-organized with Bartosz Płachno—"Evolution, ecology, and physiology of carnivorous plants"—on July 25, 2017, as part of the XIX International Botanical Congress (IBC) in Shenzhen, China. This second symposium included 11 invited talks.

These two symposia harkened back to the 1980 SEB symposium on carnivorous plants organized by Barrie Juniper (Fig. 1; see also the review by Williams (1981)) that led to the well-known book The Carnivorous Plants (written by Juniper, Richard Robins, and Danny Joel, published in 1989), and presaged the new publication (December 2017) of Carnivorous Plants: Physiology, Ecology, and Evolution (edited by Aaron Ellison and Lubomír Adamec). This summary aims to inform the CPN readership about the research presented at these two symposia.

Present at both symposia, Dr. Andreas Fleischmann discussed the multiple evolutionary lines of carnivorous plants. Current research shows that carnivory has evolved at least ten times in flowering plants, resulting in 19 carnivorous plant genera containing at least 800 species (Fig. 2). Five basic trap

Thursday, 18 December

SOCIETY *for* EXPERIMENTAL BIOLOGY

OXFORD CONFERENCE — DECEMBER 1980

CARNIVOROUS PLANTS I

(Botany Lecture Theatre)

Organised by: B. E. JUNIPER

Chairman: B. E. JUNIPER

9.00 J. HESLOP-HARRISON (Aberystwyth): The physiology of secretion and absorption by leaf glands of *Pinguicula*.

Enzyme secretion is driven by the passage of water through the gland accompanying the movement of Cl^- ions from a basal reservoir cell, apoplastic flow being blocked by an intervening endodermal cell. During resorption, control is lost, and the digest pool enters the leaf through endodermal and reservoir cells.

9.40 R. J. ROBINS and B. E. JUNIPER (East Anglia and Oxford): The secretory cycle of *Dionaea muscipula*.

Stimulation of the digestive organs evokes the release of hydrolytic activity from stores within the smooth endoplasmic reticulum, a subcompartment of the vacuole and the cell wall. Release primarily appears to occur by fusion of the smooth endoplasmic reticulum to the plasmalemma. Additional *de novo* synthesis provides further protein for secretion and replenishes the stores.

10.20 P. REA (Oxford): Fluid secretion and absorptive activity in the glands of *Dionaea muscipula*.

Stimulation of the digestive glands of *Dionaea* elicits a secretion of chloride ions together with protons. Evidence is presented concerning the mechanism of chloride transport and the relevance of proton extrusion to amino acid uptake.

10.40 COFFEE.

11.00 Y. HESLOP-HARRISON (Aberystwyth): The comparative morphology of the enzyme secretory glands of *Genlisea*, *Pinguicula* and *Utricularia* (Lentibulariaceae) and *Byblis* (Byblidaceae).

The digestive glands of carnivorous plants have a basic architecture of three cell types: (a) secretory, (b) endodermal and (c) reservoir or communicatory. There are, however, some departures in detail in gland morphology, both fine structural and cytochemical, and probably also in function. These features will be compared in four genera.

11.40 U. LÜTTGE (Darmstadt): Transport by the glands of carnivorous plants in relation to other glands and comparable systems.

12.20 S. E. WILLIAMS (Lebanon Valley College, U.S.A.): The comparative physiology of the prey capture mechanism of the Droseraceae.

The capture movements of *Dionaea* and *Drosera* are controlled by mechanically initiated action potentials and a chemically initiated hormonal mechanism. The rapid movements of *Drosera* result from changes in wall plasticity while those of *Dionaea* appear to involve a combination of a turgor change mechanism with a plasticity change mechanism.

1.00 LUNCH.

28

CARNIVOROUS PLANTS II

Chairman: R. J. ROBINS

2.15 THE BOTANIC GARDEN, HIGH STREET.

J. K. BURRAS (Oxford): The culture and propagation of carnivorous plants.

4.00 TEA (in the Botany School, South Parks Road).

4.30 D. JOEL and B. E. JUNIPER (Jerusalem and Oxford): The structure of the glands of *Drosophyllum lusitanicum* and *Dionaea muscipula* in relation to absorption.

The dye neutral red cannot be absorbed by the glands of *Drosophyllum* when young nor by those of *Dionaea* before stimulation. Both sets of glands have very thin cuticles; that of *Drosophyllum* becomes permeable at maturity and that of *Dionaea* after stimulation. The ultrastructural changes will be described and a hypothesis for this absorption control proposed.

5.30—6.10 THE TENDER TRAP. A film of carnivorous plants by Oxford Scientific Films.

32

Figure 1: Schedule of the 1980 symposium on carnivorous plants presented at the Oxford Conference of the Society of Experimental Biology, December 1980. Thanks go to Prof. Stephen Williams for providing the scans.

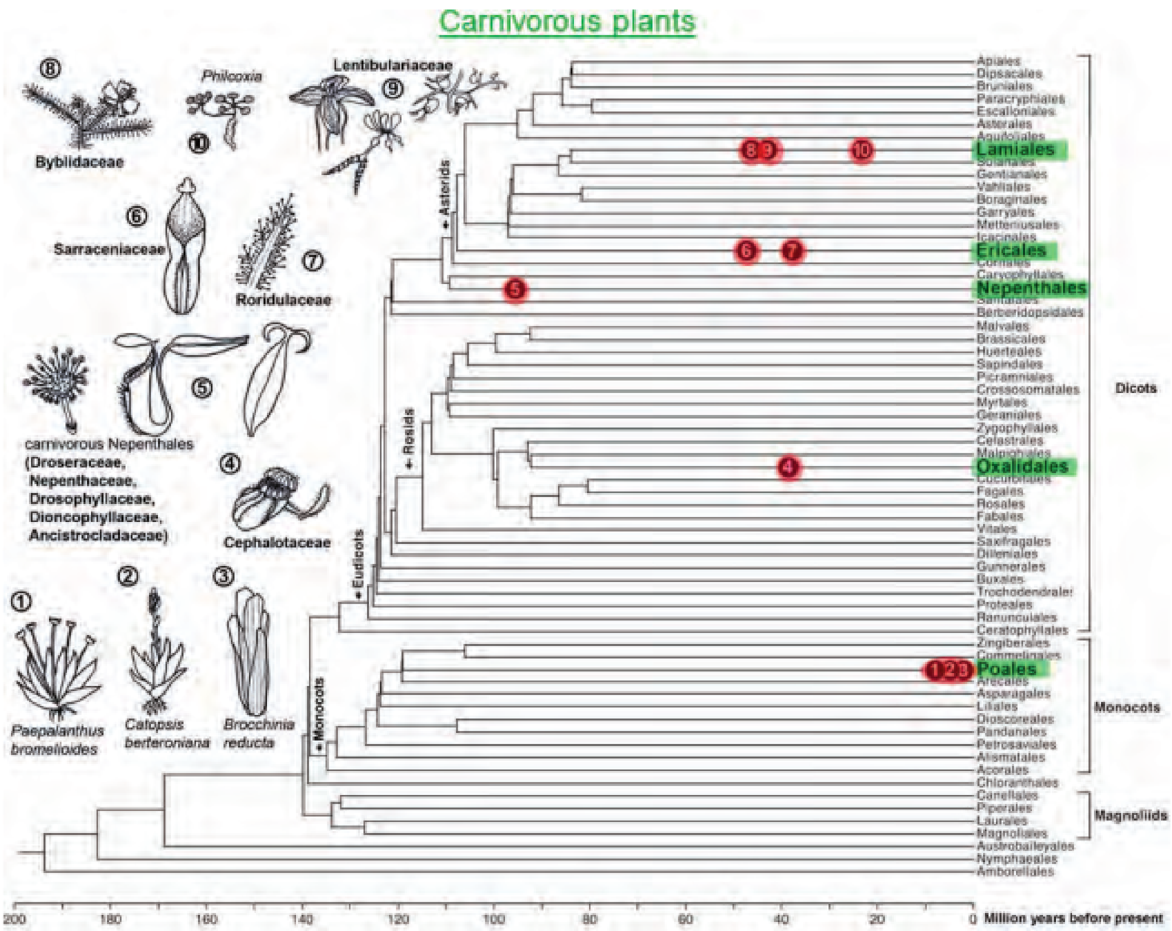

Figure 2: Family tree of the flowering plants, with botanical orders containing carnivorous plants highlighted in green. Evolutionary origins of carnivorous lineages indicated by red dots. The further to the left the dot on a branch, the older the carnivorous lineage. Figure modified from Fleischmann *et al.* 2017, and reprinted with permission of Oxford University Press.

types are found among carnivorous plants (pitfall traps, adhesive traps, snap traps, eel traps, and suction traps; Fig. 3). Some trap types (especially motile traps such as suction traps or snap traps) have evolved as modifications of passive flypaper-type traps within the same lineage ("homology"), but others have evolved in parallel in distantly related groups ("homoplasy" or convergent evolution). Prof. Aaron Ellison also gave talks in both symposia, where he presented a comprehensive synopsis on how carnivorous plants can be used as experimental systems to address contemporary scientific problems. His review included discussions of how carnivorous plants have illuminated studies of evolutionary convergence, inspired biomimetic materials, been used to study complex ecological questions about food-web assembly, and led to the development of school curricula and citizen science programs.

Studies of the morphology and the genomes of carnivorous plants continue to yield new and often surprising results. At the IBC symposium, Mathias Scharmann showed that population genomics of naturally co-occurring *Nepenthes* species in Southeast Asia are clearly distinct but not yet reproductively isolated (Fig. 4). The maintenance of genetic and phenotypic identities in the presence of gene flow indicates adaptive processes, presumably through selection against certain hybrids. Mr. Firman Alamsyah used both molecular data (internal transcribed spacer sequences of nuclear DNA) and morphological data on peristome structure to illuminate evolutionary trends in

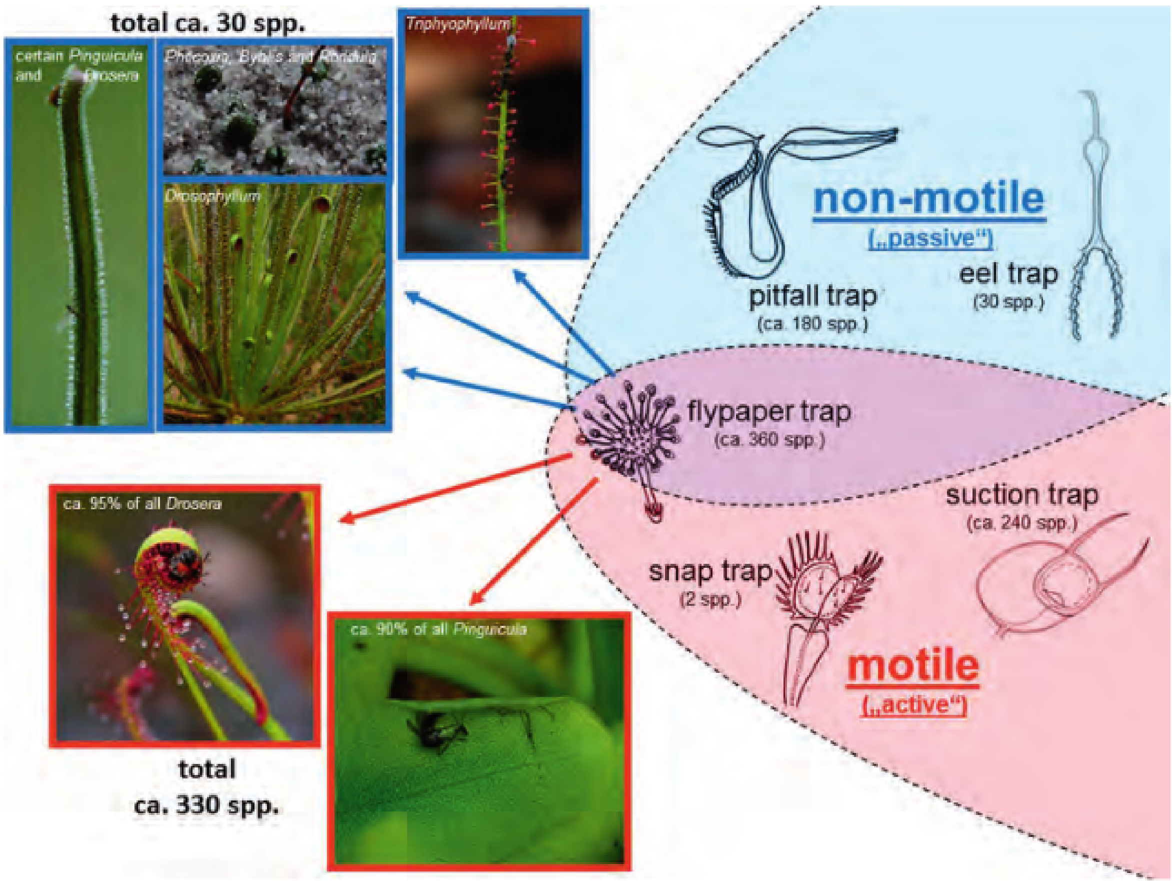

Figure 3: Distribution of the 5 basic trap types among the ≈800 species of currently known carnivorous plants. The trap types can be classified as motile or non-motile, depending upon capability of motion for prey capture or retention. Among the plants with sticky traps, there are those motile and non-motile passive leaves. Photographs and drawings by Andreas Fleischmann.

Nepenthes. He reported that narrow (< 10-mm) peristomes appear to be the ancestral ("plesiomorphic") condition in the genus, and that larger (10–20-mm or > 20-mm) peristomes likely evolved at least 7 and 8 times, respectively, whereas the narrow peristome evolved again at least 4 times from lineages with wider peristomes (Fig. 5). In a second talk, Alamsyah reported new results on molecular evolution of the nepenthesin II digestive enzyme in 29 species of *Nepenthes*. These results soon will be submitted for peer review and eventual publication.

Dr. Bartosz Płachno and colleagues (Małgorzata Stpiczyńska, Richard W. Jobson, Hans Lambers) presented new research on glands and other features of the flowers of carnivorous plants. Although most carnivorous plant enthusiasts focus on the traps, the flowers not only are beautiful (Fig. 6) but also need specific adaptations so pollinators don't end up as prey (Cross *et al*. 2017). Like the unique glandular hairs of carnivorous traps, the entomophilous species of *Pinguicula*, *Genlisea*, and *Utricularia* also have specialized glandular hairs on their flowers. These produce fragrances or nectar to attract pollinators.

Prey capture and its importance for carnivorous plant growth continues to inspire both basic and applied research. In the SEB symposium, Prof. Ulrike Müller explained the fluid mechanics during prey capture by the suction traps of bladderworts (*Utricularia vulgaris* and *U. gibba*) and presented fascinating and new insights into these enigmatic and extremely complex mechanical trap devices. Dr. Sebastian Kruppert and Martin Horstmann reported research on carnivorous plants from the

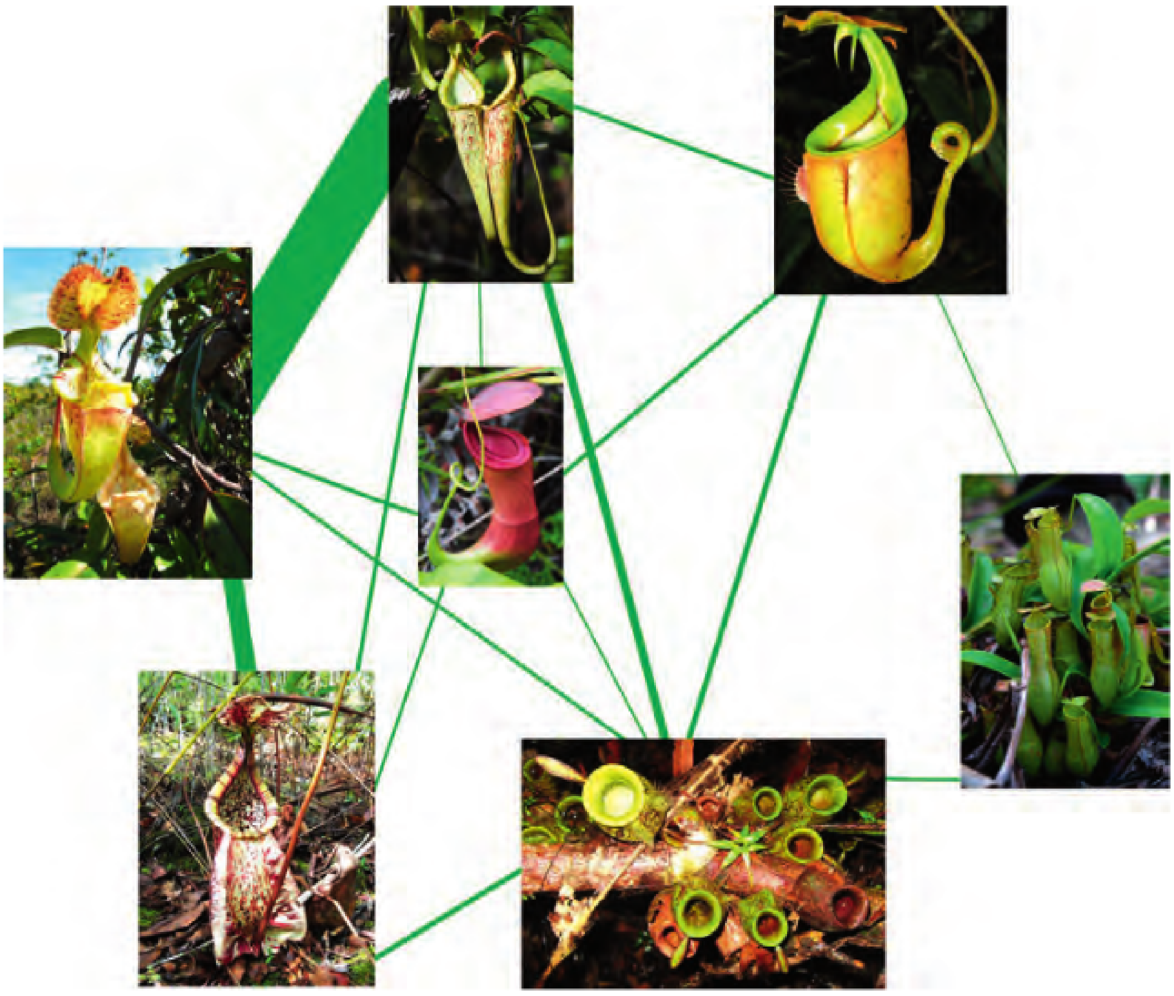

Figure 4: Network of gene flow between seven *Nepenthes* spp. that grow together in the same or adjacent habitats in the lowlands of Borneo (clockwise from above): *Nepenthes hemsleyana*, upper pitchers; *N. bicalcarata*, upper pitcher; *N. gracilis*, lower pitchers; *N. ampullaria*, rosette with lower pitchers; *N. rafflesiana* giant form, lower pitcher; *N. rafflesiana* typical form, upper pitchers; center: *N. mirabilis*, upper pitcher. Population genomics have revealed that hybridization and back-crossing has been occurring between some of these species for thousands of generations. Gene flow and its estimated strength is shown by the thickness of the green bars. All photographs by Mathias Scharmann.

perspective of the prey. They showed how freshwater crustaceans react to botanical predators with inducible morphological changes that impede capture. Three weeks later at the IBC symposium, Ms. Saskia Klink (with her colleagues Philipp Giesemann and Gerhard Gebauer) presented new estimates of the amount of nitrogen obtained from prey by *Pinguicula* and *Utricularia* growing in Austria and Germany. By measuring the concentration of stable isotopes of nitrogen, Klink *et al*. showed that prey contribute about as much nitrogen to *Pinguicula* and *Utricularia* as they do for other sticky leaf (*Drosera* spp.) and aquatic (*Utricularia* subgenus *Polypompholyx*) carnivorous plants. They conclude that a closer look at the trophic levels of prey organisms can improve our understanding of the performance of carnivorous plants in their specific habitats.

In the IBC symposium, the themes of evolutionary convergence and prey capture came together in Ms. Laura Skates's talk. She presented part of her ongoing PhD research (done in collaboration with Maria Paniw, Fernando Ojeda, Kingsley Dixon, Gerhard Gebauer, Jason Stevens, and Adam

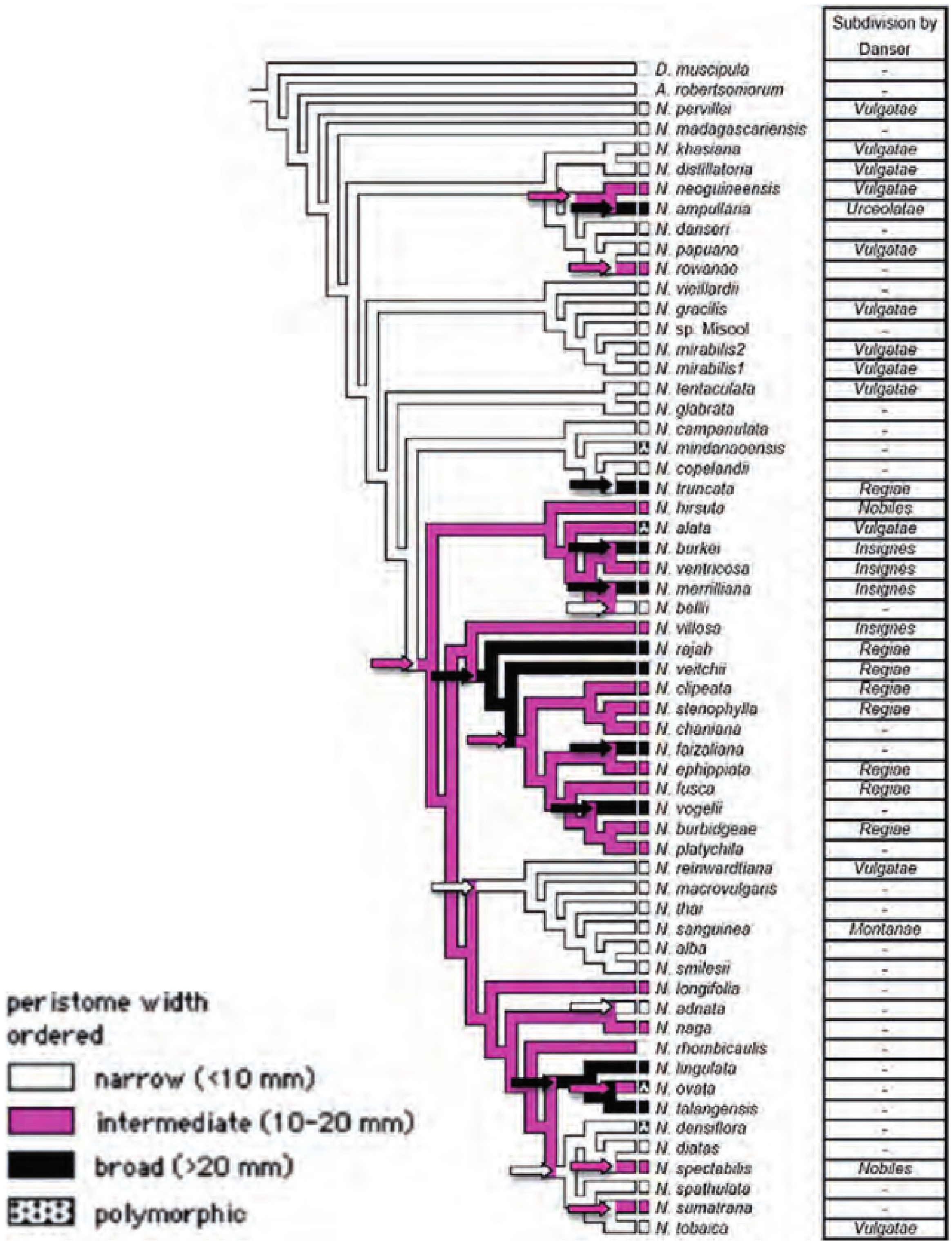

Figure 5: Character state reconstruction of *Nepenthes* for peristomes. Arrows indicate repeated evolution of narrow, intermediate, and broad peristomes (figure modified from Alamsyah & Ito 2013).

Cross) on the convergent evolution of the rainbow plant, *Byblis gigantea*, and the dewy pine, *Drosophyllum lusitanicum*, with respect to the relationship between their investment in carnivorous structures and the reliance on carnivory of these two species (Fig. 7). She discussed the ecological relevance of prey capture for each species and the implications for their management and conserva-

Figure 6: Flowers of *Utricularia bremii* photographed by Bartosz Płachno in sand-pit Cep I in Suchdol nad Lužnicí, S. Bohemia (Czech Republic).

tion. Tom Givnish presented an updated version of his influential cost/benefit model for the evolution of carnivory in plants.

In the SEB symposium, Dr. Ulrike Bauer reviewed the biomechanics of pitfall traps, explained how arthropods lose their foothold on them, and how such slippery pitcher-plant surfaces are inspiring novel technologies. Anna Westermeier gave new and fascinating insights into the trapping mechanics of the Venus' flytrap's little aquatic sister, the waterwheel plant (*Aldrovanda vesiculosa*), based on comprehensive biomechanical experiments and theoretical modelling. Dr. Simon Poppinga presented an overview of recent research about the snapping behavior of the Venus' flytrap. Westermeier's and Poppinga's projects both are within the Collaborative Research Centre 141 and are part of a broader effort at the University of Freiburg in which the movements of carnivorous plants are being studied for development of biomimetic applications (Poppinga *et al*. 2016).

Two presentations, one at SEB and the other at IBC, examined commensal organisms, also known as inquilines, that inhabit the traps of different carnivorous plants. At the SEB, Dr. Dagmara Sirová discussed the highly complex plant-microbe interactions in the carnivorous bladderworts (*Utricularia*). Many researchers have observed living and reproducing algae and eukaryotes inside the bladders, and Sirová and her colleagues are developing the *Utricularia* system as a model for studying host-microbe interactions and their ecological dynamics (Sirová *et al*. 2017). At the IBC, Ms. Amanda Northrop presented work that she and her colleagues (Rachel Brooks, Jéssica Duarte Sousa, Aaron Ellison, Bryan Ballif, and Nicholas Gotelli) are doing to develop the purple pitcher plant, *Sarracenia purpurea* and its bacterial inquilines as a model system for understanding and predicting the dynamics of aquatic ecosystems and tipping points between aerobic and anaerobic

Figure 7: Leaves of *Byblis gigantea* (left) and *Drosophyllum lusitanicum* (right). Photographs by Laura Skates.

states. Northrop *et al*. use metagenomics and metaproteomics to identify differences in the composition and function of bacteria in pitchers with or without excess prey (Fig. 8). They showed that the *S. purpurea* micro-ecosystem can be experimentally manipulated to undergo a state change, that such states can be distinguished using environmental proteomics methods, and that these findings from the *S. purpurea* model micro-ecosystem may be applicable to larger aquatic ecosystems.

Finally, one speaker at each symposium discussed possible new additions to the carnivorous flora. At the SEB, Dr. Anneke Prins presented her ongoing investigations into the proto-carnivorous properties of common teasel (*Dipsacus fullonum* [Caprifoliaceae: Dipsacales]). At the IBC, Mr. Qianshi Lin discussed his dissertation work (co-authored with T. Gregory Ross, Fushi Ke, and Sean Graham) on the possibilities of carnivory in Canadian species of *Triantha* (Tofieldiaceae: Alismatales) that grow in bogs side-by-side with *Drosera* and *Pinguicula*. In both cases, further experimental work is ongoing to determine whether these plants possess all the characteristics of the "carnivorous syndrome" (Ellison & Adamec 2017).

With many people in the audience actively working on carnivorous plants, each talk was accompanied by thorough discussion. The inspiring and exciting atmosphere also was supported by the great venues. The many original research presentations about carnivorous plant-prey interactions, sophisticated fluid mechanics, evaluation of the "carnivorous status" of a certain species, and trapping mechanics will, once published, surely have a great impact in a variety of research fields. Many of the speakers who presented at the symposia can be seen in the group photos (Fig. 9). Because the SEB symposium was on the same day as the birthday of our highly esteemed colleague and friend,

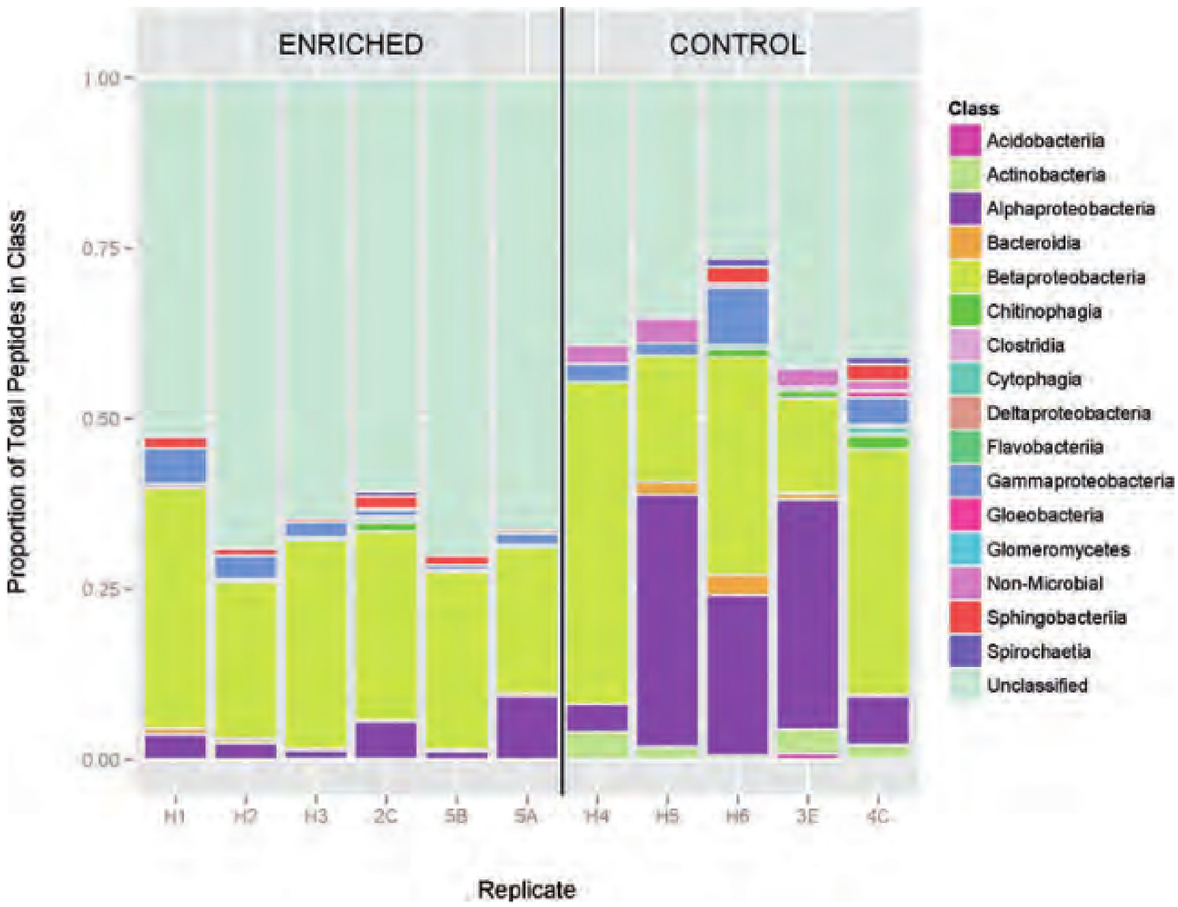

Figure 8: Distinctly different microbial communities contribute to protein expression in unfed and fed *Sarracenia purpurea* pitchers. The bars illustrate the proportion of total peptides from the top 220 proteins associated with specific microbial classes. Figure from Northrop *et al.* (2017) and reproduced with permission of the Ecological Society of America.

Figure 9: Left: SEB group photo with birthday greetings to Dr. Lubomir Adamec, and participants (left to right): Sebastian Kruppert, Ulrike Müller, Martin Horstmann, Anneke Prins, Dagmara Sirová, Aaron Ellison, Anna Westermeier, Simon Poppinga, Andreas Fleischmann. Presenter Ulrike Bauer is not in the photograph. Right: ICB group photo, with participants (left to right): Mathias Scharmann, Firman Alamsyah, Aaron Ellison, Saskia Klink, Bartosz Płachno, Amanda Northrop, Qianshi Lin, Laura Skates, Adam Cross. Presenter Tom Givnish is not in the photograph.

Dr. Lubomir Adamec (Trebon, Czech Republic), we added a special greeting to him, which we sent to him from the conference (Fig. 9).

Acknowledgments: SP & AW's projects are supported within the Collaborate Research Centre 141. UB is funded by a Royal Society University Research Fellowship. FA's participation at the XIX IBC was supported by a Scholar award from the IBC Committee and funds from Prof. Dedy Darnaedi (Researchers Care Group). UKM is supported by grant 13-52130 from the US National Science Foundation (NSF). AN was funded by NSF grants 11-44055 and 11-44056 and an Institutional Development Award (IDeA) from the National Institute of General Medical Sciences of the National Institutes of Health under grant number P20GM103449. The Botanical Society of America provided partial support for AN to attend the XIX IBC. LS is supported by a Research Training Program scholarship, and her research presented at the XIX IBC was supported by the International Carnivorous Plant Society and the School of Biological Sciences at the University of Western Australia. AME was supported by grant 11-44056 from the US NSF.

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