



A contribution to the study of floral morphological and ontogenetic evolution

Florian Jabbour

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Document présenté pour obtenir
L'HABILITATION A DIRIGER LES RECHERCHES
par

Florian Jabbour

CONTRIBUTION A L'ETUDE DE L'EVOLUTION
DE LA MORPHOLOGIE ET DE L'ONTOGENIE FLORALES

10 novembre 2017

RAPPORTEURS

Julien Bachelier. Professeur. Freie Universität, Berlin

Vincent Debat. Maître de Conférences, HDR. MNHN, Paris

Paula J. Rudall. Directrice de Recherches. Royal Botanic Gardens, Kew

EXAMINATEURS

Pierre-Henri Gouyon. Professeur. MNHN, Paris

Erik Smets. Professeur. Leiden & Leuven Universities, and Naturalis Biodiversity Center



HABILITATION THESIS

Florian Jabbour

A CONTRIBUTION TO THE STUDY OF FLORAL MORPHOLOGICAL AND ONTOGENETIC EVOLUTION

10 November 2017

EXAMINERS

Julien Bachelier. Professor. Freie Universität, Berlin

Vincent Debat. Associate Professor, HDR. MNHN, Paris

Paula J. Rudall. Senior Researcher. Royal Botanic Gardens, Kew

OTHER COMMITTEE MEMBERS

Pierre-Henri Gouyon. Professor. MNHN, Paris

Erik Smets. Professor. Leiden & Leuven Universities, and Naturalis Biodiversity Center

A mon grand-père Elie

*Parfois on regarde les choses
Telles qu'elles sont
En se demandant pourquoi*

*Parfois, on les regarde
Telles qu'elles pourraient être
En se disant pourquoi pas*

Gaëtan Roussel, « Il y a »



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I thank Catherine Damerval, Thierry Deroin, and Emily Meineke for proofreading this thesis.

I thank the members of the *MADP* team for their support and for making the daily work (experiments, supervisions of students, meetings, writing manuscripts and proposals) such a pleasure.

I must as well say few words about five researchers, who influenced my way of conducting research and being a researcher. Most of them were former supervisors; many of them are current collaborators. Tatiana Giraud, Sophie Nadot, Catherine Damerval, Susanne Renner, and Thierry Deroin – thank you!

I thank all my former and current students for regularly making me reappraise the way I supervise them. Special thanks are due to Felipe Espinosa, Lucas Batory, and Lucile Jourdain-Fiévet for showing such an enthusiasm for science and botany in particular.

I thank Evelyne Ollivier, Sophie Nadot, and Manuela Lopez-Villavicencio for giving me the opportunity to co-supervise PhD students.

I thank the colleagues from the MNHN, be they botanists, ornithologists, paleontologists, or entomologists, technicians or researchers, for all the fruitful and pleasant interactions.

I heartily thank my very close collaborators Wei Wang, James Byng, and Stefan Dressler for putting their trust in me.

Many thanks to my friends Andreas and Marie, for their loyalty and support.

I thank Stephan for all the sacrifices he made and for his unconditional support. The Earth will always be “bleue comme une orange”.

FOREWORD

As a child and teenager, I used to collect almost everything: gemstones and minerals, fossils, shells, feathers, dried plants, wine labels. Each of these collections was classified according to simplistic (and very personal!) systems. I remember I regularly reorganized my collections to optimize space and to be able to find back a particular object the fastest possible. It was a game, and with hindsight, an unconscious attempt to bring “order out of chaos”.

I sometimes think that me working in a Museum of Natural History is no coincidence, when looking at the influence two men had on me. On the one hand, my father taught me how interesting it can be to establish and take care of a collection. On the other hand, my maternal grandfather gave me the opportunity to accompany him during his walks in parks and forests. He could identify all kind of birds and plants, and was a true lover of natural history (see Fig. 1). He had to quit school relatively early, but as a self-taught person, and thanks to his endless curiosity and enthusiasm, he was one of the most cultivated people I have ever known. I dedicate this humble thesis to him.

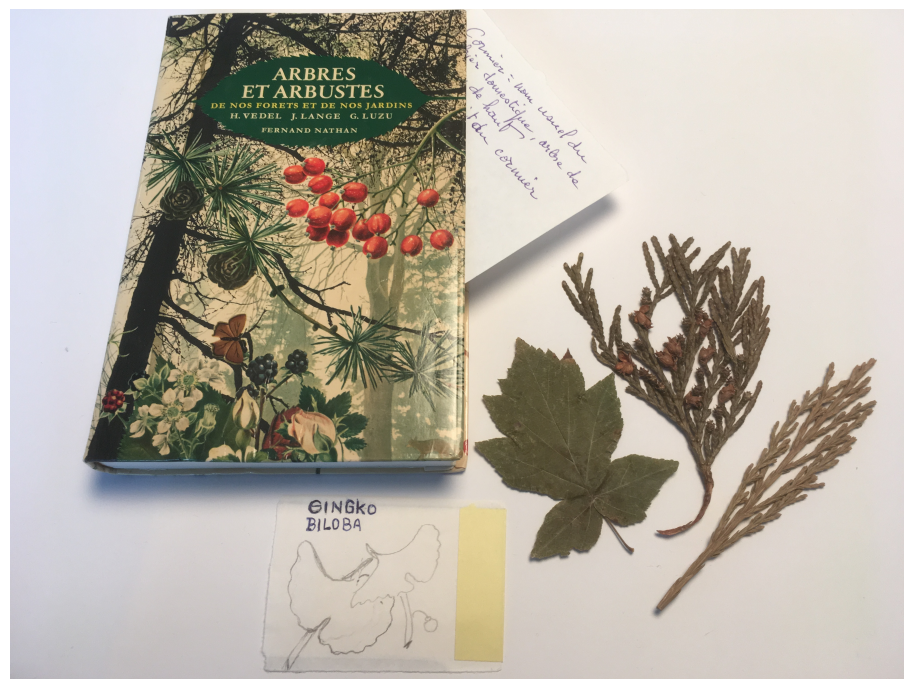


Figure 1: Personal memories. A book about trees and shrubs that belonged to my grandfather, in which a drawing of a *Ginkgo* leaf, handwritten notes, and dried plant parts were slipped.

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Dr. Florian JABBOUR
Born, Lebanon, April 28, 1983
French and Lebanese citizenships

CURRICULUM VITAE

Assistant Professor at the National Museum of Natural History, Paris, France
PhD in Evolutionary Biology
Engineer in Agronomical Sciences

EDUCATION

- 2006 – 09 **PhD student**, lab ESE (Ecology Systematics Evolution), Univ. Paris Sud, France (Dir.: Sophie Nadot) and lab Génétique Quantitative et Evolution, Gif-sur-Yvette, France (Dir.: Catherine Damerval)
Thesis title: Recurrent evolution of zygomorphy in eudicots.
Investigation of floral architecture, development and genetic bases
- 2006 **MSc student**, lab ESE (Dir.: Tatiana Giraud)
- 2005 **Research intern**, LBBE lab (Biometry and Evolutionary Biology), Lyon, France (Dir.: Blandine Doligez)

Research intern, CRBPO (Research Centre for the Biology of Bird Populations), National Museum of Natural History, Paris, France (Dir.: Frédéric Jiguet)

2003 – 06 AgroParisTech (Paris Institute of Technology for Life, Food and Environmental Sciences - Engineering school)
MSc of Ecology, Biodiversity and Evolution at AgroParisTech

2001 – 03 Lycée Sainte Geneviève, Versailles, France. Preparatory classes for the national examination for admission to the French “Grandes Ecoles” system (graduate level engineering schools), majoring in Mathematics, Physics, Chemistry, Biology, and Geology

2001 Baccalauréat (French secondary school leaving diploma, examination taken in Beirut, Lebanon), majoring in Biology and Geology, awarded with high honours

EMPLOYMENT

2013 – **Assistant Professor**, MNHN, Paris, France
Curator at Paris Herbarium (P)

2010 – 12 **Postdoctoral fellow**, DFG fellowship (German Science Foundation). Lab of S. Renner at the Institute of Systematic Botany, Ludwig Maximilians University (LMU), Munich, Germany
Project: Flower evolution in the Delphinieae (Ranunculaceae): morphology, development, molecular phylogeny, and biogeography

2010 **Teaching fellow**, LMU, Munich, Germany

2006 – 09 **Teaching Assistant**, Univ. Paris Sud, France

COLLECTIVE RESPONSIBILITIES AND MEMBERSHIPS

- 2017 Member of the CNL (Centre National du Livre, under the supervision of the French Ministry for Culture and Communication) for scientific and technical literature
- 2016 – Co-team leader, together with T. Deroin, team *Morphology, Anatomy and Development of Plants* (5 permanent members, 7 people in November 2017)
- 2016 – Member of the ISYEB Research Council
- 2013 – 16 Organizer of the bimonthly scientific meetings for botany at the MNHN
- 2013 – 16 Co-organizer of the ISYEB monthly Journal Clubs, with J. Fuchs
- Member of the Société Française de Botanique
 - Member of the Euro Evo Devo association
 - Member of the *Delphinium* Society

CURATION

- 2013 – Curator at P Herbarium
- Curator of Ceratophyllales, Ranunculales, Sabiales, Proteales, Trochodendrales, Buxales, Gunnerales, Dilleniales, Saxifragales, Vitales, Zygophyllales, and Asterales (ca. 750,000 specimens)

EDITORIAL BOARDS

- 2017 – Botany Letters

REVIEWER FOR

Acta Societatis Botanicorum Poloniae	Genetica
Adansonia	Int. J. Plant Sci.
Ann. Bot.	New Phytologist
Annales Botanici Fennici	Perspect. Plant Ecol. Evol. Syst.
Biol. J. Linn. Soc.	Phytologia Balcanica
Bot. J. Linn. Soc.	Plant Syst. Evol.
Botany Letters	PLoS One
Caryologia	Proc. R. Soc. B
Flora	Taxon
Frontiers Plant Sci.	

National and international funding agencies

Polish National Science Centre
ATM MNHN (Action Thématique du Muséum)
SEP2D (Sud Expert Plantes Développement Durable)

TEACHING

L1–3: 3 years of undergraduate studies, M1–2: 2 years of MSc

- 2013 – **Assistant Professor** at the MNHN, Paris
- Angiosperm taxonomy, morphology, anatomy (MNHN M1 students)
 - Angiosperm phylogenetic classification (MNHN/UPMC M2 students)
 - Plant adaptations to environment (AgroParisTech & Univ. Paris Sud M1 students)
 - Plant teratology (continuing education and teacher education, MNHN)
- 2010 **Teaching fellow**, LMU, Munich, Germany (undergrads)
- Systematic botany

- 2006 – 09 **Teaching Assistant**, Univ. Paris Sud (undergrads and M1 students)
- Systematic botany, plant morphology
 - Evolution of sexual systems in Angiosperms
 - Reconstructing phylogenies
 - Ecology, biodiversity and conservation

SUPERVISION OF STUDENTS

Supervision of 1 postdoc, 2 PhD, 3 M2, 3 L3, and 2 engineering students. My relative involvement in the supervision is indicated by the percentage (100% if not specified).

- 2017 **Yiyun Chen** M2 student (funding: ATM, co-supervision with Sylvain Gerber, 50%)

Evolution of floral forms in Delphinieae (Ranunculaceae).

Morphometric geometrics on herbarium specimens

- 1 publication: Chen et al. in prep. for *Botany Letters*

- Lucile Jourdain-Fiévet** L3 student (co-supervision with Felipe Espinosa, 50%)

Floral development in *Delphinium elatum* (Ranunculaceae)

- 2016 – 19 **Felipe Espinosa** PhD student (funding: Colombian grant from Colciencias, co-supervision with Sophie Nadot [HDR], 90%)

Evolution of floral morphological diversity in Ranunculaceae and in Delphinieae in particular

- 3 publications: Xiang et al. 2017 *Taxon*, Espinosa et al. 2017 *International Journal of Plant Sciences*; Espinosa & Derooin in prep. for *Botany Letters*

- 2016 **Wafa Ben Othman** 2nd year AgroParisTech student (funding: ISYEB)

Evolution of the distribution area of *Nigella damascena* (Ranunculaceae) since the early 19th century

- 1 publication: Damerval et al. in prep. for *Botany Letters*

Lucas Batory L3 student

Nomenclatural revision of the genus *Consolida* (Ranunculaceae)

- 1 publication: Du Pasquier et al. in prep for *Phytokeys*

2 TIPE students (school students; project on the different uses of *Papaver* species)

- 2015 **Felipe Espinosa** M2 student (funding: ISYEB)
Morphology and anatomy of teratological flowers of Ranunculaceae
• 1 publication: Jabbour et al. 2015 *Flora*
- 2013 – 16 **Marion Chartier** Postdoc (funding: Austrian FWF, supervised by Jürg Schönenberger, Univ. Vienna; 10%)
Diversity and evolution of the Angiosperm floral morphospace
• 4 publications: Chartier et al. 2014 *New Phytologist*; Chartier et al. 2016 *Taxon*; Chartier et al. 2017 *Proceedings of the Royal Society B*, Chartier et al. in prep for *Evolution*
- 2013 – 16 **Chhavarath Dary** PhD student (funding: French Ministry for Research, supervised by E. Ollivier, HDR, Univ. Aix-Marseille; 20%)
Systematic, phytochemical, and pharmacological studies of the genus *Stephania* in Cambodia
• 6 publications: Hul et al. 2014, *Phytotaxa*; Dary et al. 2015, *Edinburgh Journal of Botany*; Dary et al. 2017, *Natural Product Research*; Hul et al. 2017 *Phytotaxa*; Dary et al. submitted to *Natural Product Communications*; Dary et al. submitted to *Comptes Rendus Chimie*
- 2010 – 11 **Alfonso Rojas** MSc student (co-supervision with S. Renner, 90%)
Molecular phylogeny and biogeography of the African *Delphinium* (Ranunculaceae)
• 1 publication: Chartier et al. 2016, *Taxon*

- 2008 **Erwan Cherel** 2nd year engineering student in agronomical sciences
Evo-devo of floral symmetry in Ranunculaceae
- Julie Leroux** L3 student (co-supervised with Catherine Damerval, 10%)
Evo-devo of floral symmetry in Papaveraceae - Ranunculaceae

COMMITTEES

- 2017 **Gwenaëlle Saulnier** M1, MNHN. Thesis title: Morphometric analysis in three species of Hymenophyllaceae. Main examiner
Julian Lazard M1, MNHN. Thesis title: Development of a computerised lexicon for leaf characters for indexing herbarium specimens. Main examiner
- 2016 **Chhavarath Dary** PhD, Univ. Aix-Marseille, France. Thesis title: Systematic, phytochemical, and pharmacological studies of the genus *Stephania* in Cambodia. Examiner
Antoine Larré. M1, MNHN. Thesis title: Temporal evolution of the phenology of selected mountain plant species. Main examiner
- 2014 **Julien Massoni** PhD, Univ. Paris Sud, France. Thesis title: Phylogeny, molecular dating, and floral evolution of Magnoliidae (Angiospermae). Main examiner
Lucie Bauret M2, MNHN. Thesis title: Biogeographical connections between South America and the Malagasy region, evidenced by a morphological and phylogenetic study of the fern genera *Abrodictyum* and *Trichomanes* (Hymenophyllaceae). Main examiner
- 2013 **Bader Kezzim** M2, MNHN. Thesis title: Molecular phylogeny of the Myodocarpaceae. Main examiner
Boris Domenech Diplôme d'Etudes Supérieures (MSc level), Univ. Paris Sud, France. Thesis title: Evolution of floral morphology in the

Ranunculaceae. Examiner

Elisabeth Reyes Diplôme d'Etudes Supérieures (MSc level), Univ. Pierre et Marie Curie, Paris, France. Thesis title: Evolution of floral symmetry in the Proteaceae. Main examiner

I took part in two “comités de thèse” (group of researchers following the work of a PhD student and giving advices to the student and to the supervisor):

- Anaëlle Soulebeau (MNHN, Dir.: P. Lowry and T. Haevermans)
- Lucie Bauret (MNHN, Dir.: M.A. Selosse, G. Rouhan, and M. Gaudeul)

LANGUAGES

French & Arabic native speaker, **English** near native speaker, **German** good command, **Spanish** basic communication skills

GRANTS

- | | |
|------|---|
| 2017 | • Annual support received from the ATM (Action Thématique du Muséum) blanche of the French National Museum of Natural History. 2,600 € |
| 2016 | <ul style="list-style-type: none">• Visiting scholarship from the MNHN, Paris, France, for Dr. Andriy Novikoff to spend one month at Paris Herbarium. The grant was obtained for a project designed by A. Novikoff and me.• National Geographic Society, Committee for Research and Exploration. Exploring interspecific genetic exchanges between populations of <i>Delphinium</i> (Ranunculaceae, flowering plants) on sky-islands in the Great African Rift. Field trip in 2018 (Coordinator of the project; with S. Dressler). 15,000 USD• Annual support received from the ATM (Action Thématique du Muséum) blanche for a M2 student in 2017. 3,500 € |

- 2015 • Visiting scholarship from the French Embassy and French Institute in Serbia for Dr. Jelena Aleksić to spend one month at Paris Herbarium. The grant was obtained for a project designed by J. Aleksić and me.
• Annual support received from the ATM (Action Thématique du Muséum) “Possible shapes, realized shapes” of the French National Museum of Natural History. 2,600 €

- 2014 • Annual support received from the ATM “Living collections” of the French National Museum of Natural History. 7,000 €

- 2013 • Annual support received from the ATM “Barcode” and “Biodiversity” of the French National Museum of Natural History. 1,300 € and 5,000 €, respectively

- 2012 • Postdoctoral fellowship (3 years) from the Austrian Science Fund (FWF: Fonds zur Förderung der wissenschaftlichen Forschung). Project leader: J. Schönenberger; project P25077-B16 (I wrote the grant application). 246,500 €

- 2010 • Postdoctoral fellowship (2 years) from the German Science Foundation (DFG: Deutsche Forschungsgemeinschaft). Project leader: S. Renner; project RE603/12-1 (I wrote the grant application). 97,500 €

- 2007 • Support received from the SYNTHESYS European Program. 4,000 €

- 2006 • PhD fellowship from the French Ministry of Research. 71,000 €

I applied for an ANR *Jeune Chercheur* grant in 2015/2016, without success (even though the project passed the first selection step). On behalf of the team MADP, I applied for the *Emergences Ville de Paris* grant in 2016, without success. The team sent a new application in spring 2017 (result in November 2017). In September 2017, together with collaborators from three other labs, I will apply for an ANR grant (see § VI.e.).

PUBLICATIONS (supervision)

- 2017 34 Sauquet H, von Balthazar M, Magallón S, Doyle JA, Endress PK, Bailes
(9) E, Barroso de Morais E, Bull-Hereñu K, Carrive L, Chartier M, Chomicki G, Coiro M, El Ottra JHL, Epicoco C, Foster C, **Jabbour F**, Haevermans T, Hernández R, Little SA, Löfstrand S, Luna JA, Massoni J, Nadot S, Prieu C, Reyes E, dos Santos P, Schoonderwoerd K, Soulebeau A, Städler Y, Tschan G, Wing-Sze Leung A, Schönenberger J (2017) The reconstructed ancestral flower and its subsequent diversification. *Nature Communications* 8: 16047.
- 33 Espinosa F, Deroin T, Xiang KL, Wang W, Pinedo Castro M, Byng JW, Aytaç Z, Nadot S, **Jabbour F** (2017) The Turkish endemic *Pseudodelphinium turcicum* (Ranunculaceae) : an unusual population of *Delphinium* with peloric flowers that has persisted in the wild for 20 years. *International Journal of Plant Sciences* 178(7): 546–555.
- 32 Xiang KL, Aytaç Z, Liu Y, Espinosa F, **Jabbour F**, Byng JW, Zhang CF, Erst AS, Wang W (2017) Recircumscription of *Delphinium* subg. *Delphinium* (Ranunculaceae) and implications for its biogeography. *Taxon* 66(3): 554–566.
- 31 Kang Y, **Jabbour F**, Cao S, Wang Y, Huang J, Guo J (2017) Leaf epidermal features of Chinese *Stephania* Lour. (Menispermaceae) and their systematic significance. *Kew Bulletin* 72: 26.
- 30 Chartier M, Löfstrand S, von Balthazar M, Gerber S, **Jabbour F**, Sauquet H, Crane PR, Schönenberger J (2017) How (much) do flowers vary? – Unbalanced disparity among flower functional modules and a mosaic pattern of morphospace occupation. *Proceedings of the Royal Society B: Biological Sciences* 284: 20170066.
- 29 Hul S, Dary C, Jacques F, Ollivier E, Bun SS, Cheng SK, Kim S, Peou Y, **Jabbour F** (2017) The world checklist of *Stephania* (Menispermaceae), with notes on types. *Phytotaxa* 298(2): 101–118.
- 28 Le Bras G, Pignal M, Jeanson M, Muller S, Aupic C, Carré B, Flament G, Gaudeul M, Gonçalves C, **Jabbour F**, Lerat E, Lowry P, Offroy B, Pérez E, Poncy O, Rodrigues Invernón V, Rouhan G, Haevermans T

- (2017) The vascular plant collection (P) at the Herbarium of the Muséum National d'Histoire Naturelle (MNHN-Paris). *Nature Scientific Data* 4: 170016.
- 27 Xiang KL, Zhao L, Erst AS, Yu SX, **Jabbour F**, Chen ZD, Wang W (2017) A molecular phylogeny of the eastern Asian endemic genus *Dichocarpum* (Ranunculaceae): Implications for the biogeography of the area encompassing Mainland China, Taiwan, and Japan. *Molecular Phylogenetics and Evolution* 107: 594–604.
- 26 Dary C, Bun SS, Herbette G, Mabrouki F, Bun H, Kim S, **Jabbour F**, Hul S, Baghdikian B, Ollivier E (2017) Chemical profiling of tuber of *Stephania cambodica* Gagnep. (Menispermaceae) and analytical control by UHPLC-DAD. *Natural Product Research* 31(7): 802–809.
- 2016 25 Chartier M, Dressler S, Schönenberger J, Rojas Mora A, Sarthou C, (3) Wang W, **Jabbour F** (2016) The evolution of afro-montane *Delphinium* (Ranunculaceae): morphospecies, phylogenetics, and biogeography. *Taxon* 65(6): 1313–1327.
- 24 Xiang KL, Wu SD, Yu SX, Liu Y, **Jabbour F**, Erst AS, Zhao L, Wang W, Chen ZD (2016) The first comprehensive phylogeny of *Coptis* (Ranunculaceae) and its implications for character evolution and classification. *PLoS ONE* 11(4): e0153127.
- 23 Cossard G, Sannier J, Sauquet H, Damerval C, Ronse De Craene L, **Jabbour F**, Nadot S (2016) Subfamilial and tribal relationships of Ranunculaceae: evidence from eight molecular markers. *Plant Systematics and Evolution* 302(4): 419–431.
- 2015 22 Xie D, He J, Huang J, Xie H, Wang Y, Kang Y, **Jabbour F**, Guo J (7) (2015) Molecular phylogeny of Chinese *Stephania* Lour. (Menispermaceae) and reassessment of the subgeneric and sectional classifications. *Australian Systematic Botany* 28: 246–255.
- 21 **Jabbour F**, Nadot S, Espinosa F, Damerval C (2015) Ranunculacean flower terata: records, a classification, and some clues about floral developmental genetics and evolution. *Flora* 217: 64–74.
- 20 **Jabbour F**, Dressler S (2015) Neotypification of *Delphinium dasycaulon* (Ranunculaceae). *Phytotaxa* 231(2): 197–200.

- 19 Dary C, Hul S, Kim S, **Jabbour F** (2015) Lectotypification of *Stephania pierreii* (Menispermaceae). *Edinburgh Journal of Botany* 72(3): 423–428.
- 18 Soulebeau A, Aubriot X, Gaudeul M, Rouhan G, Hennequin S, Haevermans T, Dubuisson JY, **Jabbour F** (2015) The hypothesis of adaptive radiation in evolutionary biology: Hard facts about a hazy concept. *Organisms Diversity and Evolution* 15(4): 747–761.
- 17 **Jabbour F**, Udron M, Le Guilloux M, Gonçalves B, Manicacci D, Nadot S, Damerval C (2015) Flower development schedule and *AGAMOUS*-like gene expression patterns in two morphs of *Nigella damascena* L. (Ranunculaceae) differing in floral architecture. *Botanical Journal of the Linnean Society* 178: 608–619.
- 16 Deroin T, Damerval C, Le Guilloux M, **Jabbour F** (2015) Floral vascular patterns of the double-flowered and wild-type morphs of *Nigella damascena* L. (Ranunculaceae). *Modern Phytomorphology* 7: 13–20.
- 2014 15 Chartier M, **Jabbour F**, Gerber S, Mitteroecker P, Sauquet H, von (4) Balthazar M, Staedler Y, Crane PR, Schönenberger J (2014) The floral morphospace – a modern comparative approach to study Angiosperm evolution. *New Phytologist* 204: 841–853.
- 14 Hul S, Dary C, Jacques F, Ollivier E, Bun SS, **Jabbour F** (2014) Lecto- and epitypification of *Stephania rotunda* (Menispermaceae). *Phytotaxa* 172(2): 133–136.
- 13 **Jabbour F**, Cossard G, Le Guilloux M, Sannier J, Nadot S, Damerval C (2014) Specific duplication and dorsoventrally asymmetric expression patterns of *CYCLOIDEA*-like genes in zygomorphic species of Ranunculaceae. *PLoS ONE* 9(4): e95727.
- 12 Novikoff AV, **Jabbour F** (2014) Floral anatomy of Delphinieae (Ranunculaceae): Comparing flower organization and vascular patterns. *Modern Phytomorphology* 5: 35–44.
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- Chen Y, Gerber S, Novikoff A, **Jabbour F**. Analysis of floral shape diversity in the tribe Delphinieae (Ranunculaceae) using geometric morphometrics on herbarium specimens. In prep. for a Special Issue in *Botany Letters*, about the different uses of herbarium specimens in modern science
- **Jabbour F**. A study of the anatomy and physiology of nectaries. A translation from Bonnier G (1878) *Bulletin de la Société Botanique de France* 25(8): 262–271, and review of subsequent works. In prep. for *Botany Letters*
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- Du Pasquier PE, Batory L, **Jabbour F**. Nomenclatural (re)integration of *Consolida* and *Aconitella* in *Delphinium* and new combinations in *Delphinium* (Ranunculaceae). In prep. for *Phytokeys*

BOOKS AND BOOK CHAPTERS

- 2 Damerval C, **Jabbour F**, Nadot S, Citerne H. Evolution of symmetry in plants (2018) In: Nuño de la Rosa L, Müller GB (eds.), *Evolutionary Developmental Biology – A reference guide*, Springer International Publishing Switzerland, 1250 pp.
- 1 Aupic C, Allorge L, Aymonin G, Carré B, Deroin T, Dupont J, Gaudeul M, Haevermans T, Hul S, **Jabbour F**, Lamy D, Le Gall L, Poncy O, Rakotondrainibe F, de Reviers B, Rouhan G, Sarthou C, Vadon C (2013) *L'Herbier du Muséum – L'aventure d'une collection*. Artlys – Muséum national d'Histoire naturelle.

CONFERENCES (speaker's name italicized. **: invited)

- 2018 ** **Institute seminar** at Goethe Universität, January, Frankfurt, Germany. Talk

- 2017 *Jabbour F.* Systematics of Delphinieae (Ranunculaceae) and insight into the evolution of "Rittersporne" and "Eisenhüte" flower morphology
 ** **PhD Days** at Univ. Paris Sud, November, Orsay, France. Talk.
 I turned down the proposal as the talk is planned the same day as my Habilitation defence
 • 21st **AETFAT** conference, May, Nairobi, Kenya. Talk
Jabbour F, Chartier M, Dressler S, Schönenberger J, Rojas A, Sarthou C, Wang W. The evolution of afro-montane *Delphinium* (Ranunculaceae): morphospecies, phylogenetics and biogeography.
 ** **International Botanical Conference**, July, Shenzhen, China. Talk (invitation passed to my PhD student, F. Espinosa)
Espinosa F, Deroit T, Wang W, Xiang KL, Pinedo Castro M, Byng JW, Aytac Z, Nadot S, **Jabbour F.** The Turkish endemic *Pseudodelphinium turcicum* (Ranunculaceae): an unusual population of *Delphinium* with peloric flowers that has persisted in the wild for 20 years. Poster
- 2016 • 8^e **journée IDEEV**, Paris, France. Talk.
Nadot S, Sauquet H, Damerval C, **Jabbour F**, Domenech B. Perianth evolution in Ranunculales.
 • 6th **Euro Evo Devo** meeting, Uppsala, Sweden. Posters
Jabbour F, Gonçalves B, Le Guilloux M, Manicacci D, Nadot S, Damerval C. Flower development schedule and BC gene expression patterns in two morphs of *Nigella damascena* (Ranunculaceae) differing in floral architecture.
Espinosa F, Deroit T, Damerval C, Nadot S, **Jabbour F.** Ranunculacean flower terata: morpho-anatomical characterization and clues about floral developmental genetics and evolution.
 ** **RISE**, the first Ranunculacean International Seminar, Lviv, Ukraine. Talk
Jabbour F, Espinosa F, Deroit T, Manicacci D, Nadot S, Damerval C. Development, anatomy, and genetic control of some teratological phenotypes of Ranunculaceae flowers.
 • **Evolution 2016**, Austin, USA. Talk
Sauquet H, [14 authors], **Jabbour F**, [15 authors], Schönenberger J.

- The reconstructed ancestral flower and its subsequent diversification.
- 2015
- **Botany 2015**, Edmonton, Canada.
 - Chartier M*, [3 authors], **Jabbour F**, [2 authors], Schönenberger J. How (much) do flowers vary? The floral morphospace of Ericales. Talk
 - Sauquet H*, [14 authors], **Jabbour F**, [14 authors], Schönenberger J. Fifteen clues to the early diversification of flowers: first results from the eFLOWER initiative. Poster
 - **6th Balkan Botanical Congress**, Rijeka, Croatia. Talk
 - Espinosa F, Damerval C, Derooin T, Manicacci D, Nadot S, **Jabbour F**. Development, anatomy, and genetic control of some teratological phenotypes of Ranunculaceae flowers.
 - **Botanical research in Tropical Asia**, Vientiane, Lao PDR. Poster
 - Dary C*, Hul S, **Jabbour F**, Kim S, Bun SS, Ollivier E. Systematic and phytochemical studies of the genus *Stephania* in Cambodia.
- 2014
- **UNESCO International Conference**: “Botanists of the 21st century: Roles, challenges and opportunities”, Paris, France. Talk
 - Sauquet H*, [11 authors], **Jabbour F**, [15 authors], Magallón S. eFLOWER: Synthesizing data on flowers in the 21st century.
 - **5th Euro Evo Devo meeting**, Vienna, Austria. Talk
 - Jabbour F**, Cossard G, Le Guilloux M, Sannier J, Nadot S, Damerval C. *CYCLOIDEA*-like genes and floral symmetry in Ranunculaceae.
 - **Evolutionary Plant Radiations meeting**, Zurich, Switzerland. Talk
 - Sauquet H*, [11 authors], **Jabbour F**, [15 authors], Magallón S. eFLOWER: A framework for understanding the evolution and diversification of flowers. Poster
 - Atchison G*, Nürk NM, Koch M, **Jabbour F**, Boucher FC, Hughes CE. Comparative montane plant radiations: from the Andes to the Hengduan Mountains.
- 2013
- **Annual meeting of the French Systematics Society**, Paris, France. Talk
 - ** 17th **Evolutionary Biology Meeting**, Marseilles, France. Talk
 - ** **Séminaire de l'UMR Génétique Quantitative et Evolution**, la Ferme du Moulon.

- Jabbour F* and Renner S. Systematics, biogeography, and perianth evolution in the Delphinieae (Ranunculaceae).
- 2012 **** Seminars of the Dept. of Structural and Functional Botany**, Vienna, Austria. Talk *Jabbour F* and Renner S. Evolutionary trends in Delphinieae (Ranunculaceae). A focus on life histories and perianth structure.
- 2011 • **Botany 2011**, St. Louis, USA. Talk
Jabbour F, Rojas A, Renner S. A phylogeny of the Delphinieae (Ranunculaceae) reveals that *Aconitum* is embedded in *Delphinium*: implications for flower evolution.
• **7th Int. Congress of Systematic and Evolutionary Biology**, Berlin, Germany. Talk
Jabbour F and Renner S. The spatiotemporal unfolding of the *Delphinium/Consolida* clade (Ranunculaceae) in the eastern Mediterranean area.
- 2009 • **25th Plant Biology** symposium, University of California, Riverside, USA. Poster and talk
Jabbour F, Nadot S, Damerval C. Developmental features and evolution of zygomorphy in the tribe Delphinieae (Ranunculaceae).
- 2008 • **2nd Euro Evo Devo** meeting, Ghent, Belgium. Poster
Jabbour F, Ronse de Craene L, Nadot S, Damerval C. The developmental bases of floral symmetry in Ranunculaceae. Constraints on the evolution of zygomorphy in basal eudicots.
- 2007 • **11th Evolutionary Biology Meeting**, Marseille, France. Talk
Jabbour F, Damerval C, Nadot S. Comparative evolution of floral symmetry in monocots, basal and core eudicots. A morphological and phylogenetic approach.
• **6th Biennial Meeting of the Systematics Association**, Edinburgh, Scotland. Poster
Jabbour F, Nadot S, Damerval C. Diversity and evolution of *CYCLOIDEA*-like genes in Ranunculaceae - Papaveraceae.
- 2006 • **Annual meeting of the French Systematics Society**, Paris, France. Poster

Jabbour F, Le Gac M, Giraud T. Inferring phylogenies of *Microbotryum violaceum* and of its host plants for delimiting parasite species and study cospeciation.

TABLE 1: Publications

Total number = 34, number with IF ≥ 1 = 28, G Scholar: H = 11, citations > 420

Journal	IF	#	Position in the sequence of authors			Following a supervision
			First	Contributing author	Last	
Int. J. Plant Dev. Biol.	-	1	1			
Modern Phytomorphology	-	2			2	
Edinburgh Journal of Botany	-	1			1	1
Kew Bulletin	0.6	1		1		
Australian Systematic Botany	0.8	1		1		
Phytokeys	1.1	1	1			
Comptes Rendus Biologies	1.1	1	1			
Flora	1.1	1	1			1
Phytotaxa	1.2	3	1		2	2
Plant Systematics and Evolution	1.2	1		1		
Advances in Botanical Research	1.3	1		1		
International Journal of Plant Sciences	1.7	2	1		1	1
Natural Product Research	1.8	1		1		1
Organisms Diversity and Evolution	2.3	1			1	
Botanical Journal of the Linnean Society	2.5	1	1			
Taxon	2.5	3	1	1	1	2
Plos One	2.8	2	1	1		
BMC Evolutionary Biology	3.2	1		1		
Annals of Botany	4.0	2	2			
Molecular Phylogenetics and Evolution	4.4	2	1	1		
Nature Scientific Data	4.8	1		1		
Proceedings of the Royal Society B	4.9	1		1		1
Plant Journal	5.9	1		1		
New Phytologist	7.3	1		1		1
Nature Communications	12.1	1		1		

Webpage (will be transferred to a new website in autumn 2017):

<http://isyeb.mnhn.fr/annuaire-et-pages-personnelles/pages-personnelles/Florian-JABBOUR,325>

Team webpage (will be transferred to a new website in autumn 2017):

<http://isyeb.mnhn.fr/departements/departement-systematique-et-172/morpho-anatomy-and-development-of/>

I. MY SCIENTIFIC TRAJECTORY (OR HOW I BECAME A LIFELONG STUDENT OF PLANT AND FLOWER FORM EVOLUTION)

Morphology, or the study of organismal forms, is at the crossroads of genomes, developmental and historical (phylogenetic) constraints, and environment. By definition, it is an integrative discipline building bridges between, for instance, evo-devo and ecology, systematics and physiology.

I consider myself as a student of plant and flower form evolution, and I organized this thesis around this scientific topic. In this manuscript, I made the choice to use the term morphology rather than phenotype for two reasons: 1) these terms are not synonymous. A phenotype is the set of observable features of an organism, such as its morphology, but also, for instance, its metabolism and behaviour; 2) I think it is important to highlight the very long history of morphology as a discipline.

In this thesis, I will first say few words about the history of plant and flower morphology, and highlight its integrative nature. Second, I will give some ideas about the supervision of students, before developing a selection of past, current, and prospective research projects. Third, I will explain my involvement in the other tasks of the MNHN.

In the following paragraph, I will shortly explain how I became a researcher dedicated to the study of plant and flower morphology.

Starting in 2005 with a MSc on the molecular phylogenetics of phytoparasitic fungi, I embarked on a PhD project focusing on the evo-devo of floral symmetry under the supervision of Sophie Nadot and Catherine Damerval, before doing a postdoc in plant systematics. I can now say that my passion for flower morphology and development was triggered by a visit to the Royal Botanic Garden Edinburgh in 2017, where I conducted my first study of floral development together with Louis Ronse De Craene. I could not invest more time in morphology-development during my PhD, as the evo-devo experiments were time-consuming. During my postdoc in the lab of Susanne Renner, I conducted a developmental study, after re-building on my own a critical-point drying system from separate parts, and I insisted on writing a paper based on flower morphological evolution (Jabbour and Renner 2012a). The second postdoc project I designed with Jürg Schönenberger was exclusively based on flower morphology. In my opinion, it got funded by the FWF (Austrian Science Fund) mainly

because the biological question was relevant (see Chartier et al. 2014, 2017), but also because the project uniquely integrated botany and the mathematics of a morphospace approach. Before even starting this second postdoc (which was brilliantly taken in charge of by Marion Chartier), I got hired at the MNHN for an Assistant Professorship focusing on plant radiations on islands (I had studied the radiation of Delphinieae Warm. on the Himalayas and the mountains of SW China, [Jabbour and Renner 2012b]). While studying radiations on islands (Soulebeau et al. 2015), I pursued my studies on flower morphology, getting trained in plant anatomy, and supervising a PhD student on a flower-morphology-based topic. In January 2016, some colleagues and I got together in a team entitled *Morphology, Anatomy and Development of Plants*, in order to gather our expertise and know-how.

II. MORPHOLOGY: THE RENAISSANCE OF AN OLD DISCIPLINE

Since Goethe (1790), morphology as a discipline has been not only descriptive but explanatory too. Johann Wolfgang von Goethe proposed that the different parts of a flower result from the “metamorphosis” (meaning transformation) of a basic organ, the “ideal leaf”. Goethe’s hypothesis was validated by the students of the ABC model, in which combinatorial interactions between different classes of floral homeotic genes (A, B, and C, among others) determine the identity of the floral organs (Theissen and Saedler 2001).

Morphology and its central concept, homology, are pre-Darwinian in origin, and as a result obsolete and arguable in the eyes of many (Richter and Wirkner 2014).

The pre-Darwinian idealistic homology concept was not anchored in organismal evolutionary history. According to this concept, two characters were thought to be homologous because they were built based on the same plan or archetype. This concept, already used by Goethe, is older than the term homology, which was defined in a modern way by Owen (Mayr 1982). Two structures are now called homologous if they represent corresponding parts of organisms, which are built according to the same body plan. The existence of corresponding structures in different species is explained by derivation from a common ancestor that had the same structure as the two species compared (Wagner 1989).

Descriptions, comparisons and explanations of forms refer primarily to single organisms, morphemes (parts of an organism; units of description without reference to evolution; see Richter and Wirkner 2014) or semaphoronts (characters expressed at any stage of ontogeny, Sharma et al. 2017).

Modern morphology is the heir of a long tradition. Many famous morphologists deeply influenced the evolution of concepts and techniques in their field. Old theories are still currently discussed and contribute to the maturity of the discipline. For instance, Haeckel’s theory of recapitulation proposes that parts of the evolutionary history of a lineage are conserved in the ontogeny of its constituting extant species (Haeckel 1866). Although this concept received some criticism later on (e.g. Gould 1977), its essence is still the basic principle of evo-devo (Niklas and Kutschera 2017), namely that it is generally possible to reconstruct organismal evolution and potentially

phylogenetic relationships by comparing developmental processes (see semaphoronts) of different organisms (Wanninger 2015).

However, being an old discipline may have its drawbacks. We may think everything was described, we might hear that morphology cannot teach us anything anymore in our days of omics-driven science, students often run away from plant morphology because the word is spread that it is a classical and obsolete discipline, that one has to read many old publications before initiating any study, and most of all, because “no one gets any position doing (only) morphology”.

In the context of a steady decline in interest in morphology both at research institutions and funding agencies (Schönenberger et al. 2016), where morphology is mostly perceived as a provider of characters for systematic circumscription (Kaplan 2001), there has been a trend in recent years to justify the necessity of research in this field and to provide evidence that the discipline has renewed itself (while on the one hand, this behaviour of calling into question is healthy, on the other hand it is a sign that morphologists feel insecure in the current scientific world). Some publication titles or paragraph titles are explicit in this respect: “Why is it important to maintain a research program in morphology?” (Giribet 2015), “Morphology is dead – long live morphology!” (Wanninger 2015), and linguistic innovations were proposed to modernize the field of morphology (and probably to compete with the disciplines that are usually the most funded), such as “high-throughput morphology”, “next-generation histology”, “phenomics” (Giribet 2015), “MorphoEvoDevo” (for evolutionary developmental morphology; parallel with EcoEvoDevo [Gilbert and Epel 2015]; Wanninger 2015).

After a long period of absence from mainstream evolutionary biology, morphology experienced a renaissance within the field of evo-devo (Richter and Wirkner 2014, Specht and Bartlett 2009). Model-based reconstruction of ancestral states (e.g. Sauquet et al. 2017), taking into account the phylogenetic framework and recent paleobotanical discoveries, and morphospace analyses (Chartier et al. 2014, 2017) have also breathed new life into the field of morphology. A striking feature of morphological evolution is that due to developmental, functional, and phylogenetic constraints, not all theoretically possible architectures have been explored during evolution. Morphospaces are theoretical spaces describing and relating organismal phenotypes. Although widely applied in zoology, morphospace analyses have so far been largely

disregarded in botany (but see Mander 2016), with notable exceptions in the field of pollination biology (Ollerton et al. 2009, Schönenberger et al. 2016).

We now are in need of a new generation of morphologists and anatomists (ca. 2,000 plant species described each year [Christenhusz and Byng 2016]). These scientists have to be able to understand genetics, genomics, molecular phylogenetics, and evo-devo, in addition to mastering the old literature (often in English, but also in German and French). More than understanding the results, they should be able to communicate with the researchers in those disciplines, and design research projects hand in hand with them. Hardly any morphology-based project will get funded nowadays (at a national or international level) and morphology has to be combined with other approaches to become appealing.

The following boxes present the biographies of a selection of botanists who were influential in the fields of plant (and flower) morphology and anatomy. Three of them had strong links with the MNHN. A last box deals with the evolution of imaging techniques, most of which revolutionized the study of plant morphology.

BOX 1: Biography and works of Jean-Baptiste Payer (1818-1860, †42)

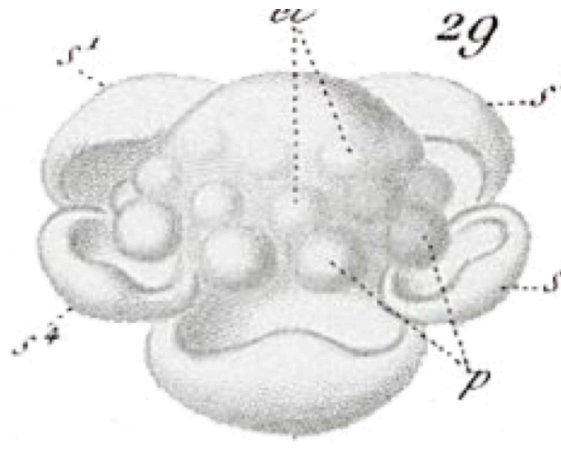


Illustration: Payer JB (1857) *Traité d'organogénie comparée de la fleur*. Planche 56, Nigelles.

Portrait: <http://www.asfeldjuzancourt.fr/le-saviez-vous.html>

Jean-Baptiste Payer comes from a family of millers from the North-East of France. He starts his academic career in 1840 as professor of geology and mineralogy in Rennes. In 1841, he becomes Assist. Prof. in Botany at the Ecole Normale Supérieure in Paris.

In 1848, he is involved in the French Revolution, and takes afterwards political responsibilities until the 1851 coup. He then dedicated himself fully to Botany.

In 1852, he becomes professor of plant organography at the Faculty of Sciences of Paris, taking over from Auguste de Saint-Hilaire.

Although Payer's contributions to botany are numerous, his most famous work is indisputably the *Traité d'organogénie comparée de la fleur*. This book, compiling personal observations on floral development for most Angiosperm orders, was published in 1857 (Payer was then 39!), after 13 years of dissecting floral buds, observing the preparations under a binocular, comparing and synthesizing his observations and presenting hypotheses of homology among structures from different taxa.

The plates illustrating the successive developmental stages of the meristems or of selected organs are of high quality, and are still useful nowadays.

Most of the biological material he studied was provided by the MNHN. For this reason, he followed the classification of Angiosperms that the MNHN was using back then.

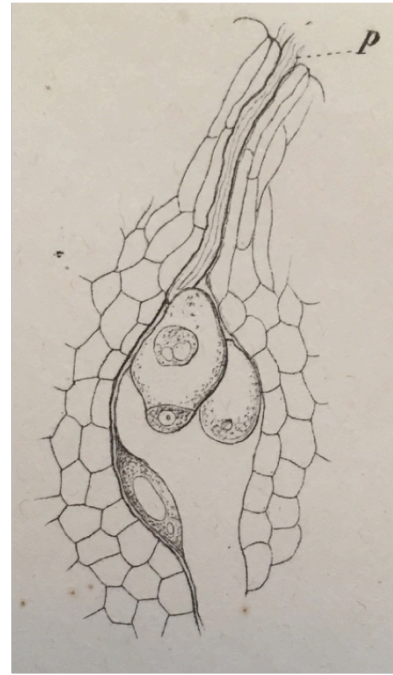
Payer acknowledges in le *Traité* the influence of Charles-François Brisseau de Mirbel, who was, according to him, the father of plant organogenesis. de Mirbel started his career at the MNHN before settling at the Sorbonne. He is also known for his deep impact on the fields of cytology and physiology that were emerging at that time.

The *Traité d'organogénie* has been cited more than 500 times (G-Scholar, August 2017), in articles focusing on floral development, morphology, floral evolution, plant systematics, or evo-devo. Payer's *Traité* is an unmissable work for all students of flower morphology and development.

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BOX 2: Biography and works of Wilhelm Hofmeister (1824-1877, †53)



Portrait: https://fr.wikipedia.org/wiki/Wilhelm_Hofmeister

Illustration: Hofmeister W (1859) Neue Beiträge zur Kenntniss der Embryobildung der Phanerogamen. XXIV *Lamium purpureum*.

Friederich Wilhelm Benedikt Hofmeister is known as the discoverer of the alternation of generations (sporophyte-gametophyte) and for his fundamental studies of plant embryology.

Hofmeister was an autodidact in botany; he had no university education, much less a Ph.D. degree, but ultimately was appointed Professor of Botany at Heidelberg at age 39.

Hofmeister investigated the causal bases for the morphological diversity of seed plants. To answer this question, he introduced in his research concepts and tools from physics and chemistry, all of which he also taught himself.

As one of the earliest plant biophysicists, Hofmeister was so far ahead of his time that he was not understood by his contemporaries or many who followed him.

Hofmeister's principal contribution to the field of plant morphology was his book *Allgemeine Morphologie der Gewächse* (General morphology of growth;

Hofmeister, 1868). In this complex, hardly accessible book, he presented an analytical view of the developmental basis underlying the diversity of plant form, but also biophysical interpretations of a range of phenomena including phyllotaxis and the effects of gravity and light on plant morphology.

Hofmeister's contribution to biology is still far from widely acknowledged. However, Kaplan and Cooke (1996) conclude that "his reputation became eclipsed because he was so far ahead of his contemporaries that no one could understand or appreciate his work". The study of Hofmeister's work is also limited because it is published in German, though translations for some articles have been made.

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BOX 3: Biography and works of Philippe Van Tieghem (1839-1914, †75)



Portrait from Bonnier (1915).

General and close view of the histological slides of the Van Tieghem collection at the MNHN.

Philippe Edouard Van Tieghem started to work on microscopic fungi in the laboratory and under the supervision of Louis Pasteur. He gave his name to a device – the Van Tieghem cell – that allows following the mycelium development under a microscope.

Van Tieghem joins the MNHN in 1878. His contribution to the study of plant anatomy in France was essential in many aspects (Van Tieghem 1891). Looking at the inner structures of plants, he aimed at elaborating hypotheses of homology. He was the first one to systematically organize this field of botany. Through his

publications and teaching, he defended an approach of plant anatomy integrated into the more general discipline of evolutionary biology. His work is mainly based on highlighting the geometrical properties of the observed structures, as it was a usual practice in science in the middle of the 19th century (Bachelard 1938).

All the slides prepared by Van Tieghem and his students are kept at the MNHN. This collection consists of ca. 20,000 slides, which corresponds to one third of the slide library of the MNHN. Many samples come from rare or important specimens (type specimens and herbarium specimens collected in the 18th and 19th centuries). Almost all the samples are in good state and are cited in Van Tieghem's publications (available at the libraries of the MNHN). The project of digitizing this collection has still to be funded. Although this collection is of an immense scientific importance, it is so far rarely used.

References

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- Van Tieghem P (1891) Traité de Botanique. 2^{ème} éd. vol. 1. Paris: Savy.

BOX 4: Biography and works of Michel Guédès (1942-1985, †43)

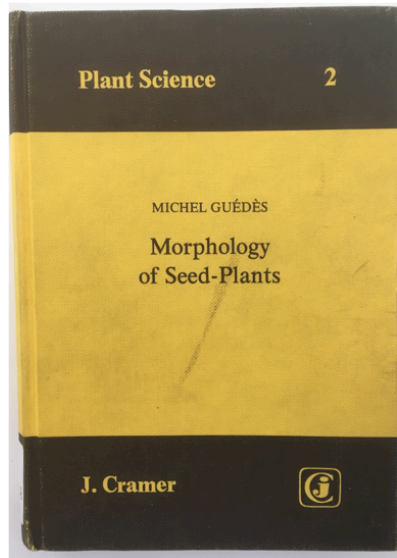


Illustration: picture of a book cover taken at the Library of Botany at the MNHN.

Portrait from Aymonin (1987).

Michel Guédès was a self-trained morphologist. He joined the staff of Paris Herbarium in 1971. He adopted a generalist approach of botany, investigating many taxonomic groups within Angiosperms, and being keen on morphology, plant architecture, systematics, teratology, floristics, nomenclature, history of science (e.g. Guédès 1973). He had an excellent knowledge of the German botanical literature and his work on floral structures reflected the theory of Goethe.

Although he passed away quite young, he published >170 publications, often in foreign journals such as *Taxon*, *Flora*, *Botanische Jahrbücher*, and *Phyton*. His book “Morphology of seed plants” (1979), with about 900 references, stimulated a renewed interest in the subject. He also published popular books for the general public (*Les bienfaits des plantes*; *Les plantes sauvages*; *Baies et fruits de nos bois et jardins*).

According to the biographical information available at the library of the MNHN, Michel Guédès had a complicated and thwarted career history. He did not seem to be a man of compromise, and was convinced of his hierarchy’s disregard. In his

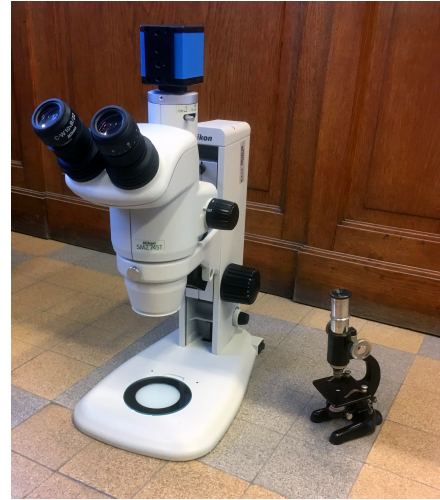
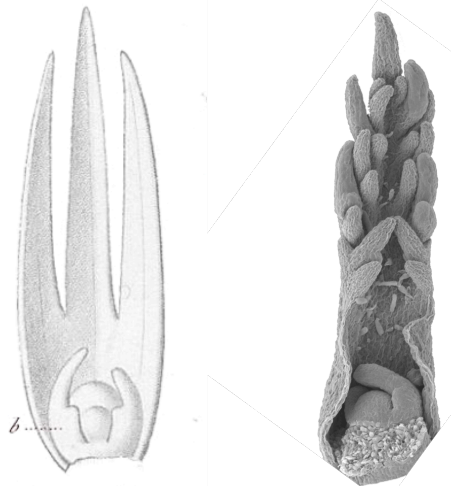
opinion, he did not get any promotion at the MNHN because his directors believed he could not travel far and long, and because of his lack of servitude.

People who knew him add that he mastered the botanical literature (in French and other languages), and that he always found time to discuss students' or colleagues' projects, address their conceptual or technical problems, and give them advice.

Reference

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BOX 5: The evolution of imaging techniques for the study of plant morphology



Left: Ranunculaceae flower meristem showing the bract and the bracteoles. Drawing from Payer (1857, plate about *Nigella*) and SEM image of an *Aquilegia alpina* L. flower bud. Right: Stereomicroscope (bought in 2013) and antique microscope (19 cm high, bought on a flea market in 2017).

Imaging technique (approximate date of first use)

1. Principle
2. Objective
3. Selected example

Light or optical microscopy (17th century)

1. Uses visible light and a set of lenses to magnify the image of a sample.
2. Simple 2D observation at a magnification reaching 1,500x (product of the powers of the ocular and the objective lens).
3. Melo-de-Pinna GF, Hernandez-Lopes J, Ogura AS, Santos LK, Silva DC, Haevermans T (2016) Growth patterns and different arrangements of vascular tissues in succulent leaves. *International Journal of Plant Sciences* 177(8): 643–660.

Transmission Electron Microscopy, TEM (1930's)

1. A beam of electrons is transmitted through a sample (less than 100 nm thick) to form an image. The image is magnified and focused onto an imaging device.

2. 2D observations at a magnification reaching 500,000x.
3. Antoń S, Kamińska M (2015) Comparative floral spur anatomy and nectar secretion in four representatives of Ranunculaceae. *Protoplasma* 252(6): 1587–1601.

Confocal microscopy (1950's)

1. It is an optical microscope reconstructing 3D structures from sets of images obtained at different depths within a thick object. It uses reflected light or fluorescence. The user does not directly observe the object, he or she rather sees a computer-generated image.
2. 2D observations of fixed material or living material, using the GFP (Green Fluorescent Protein). It can reveal gene expression patterns.
3. Harrison CJ, Rezvani M, Langdale JA (2007) Growth from two transient apical initials in the meristem of *Selaginella kraussiana*. *Development* 134(5): 881–889.

Scanning Electron Microscopy, SEM (1970's)

1. Destructive method, it requires many samples to obtain a consecutive series of states. Samples are critical point dried and coated with conductive materials (e.g. gold, platinum, graphite). In the SEM, an electron beam is emitted under vacuum and scans the surface of a sample. The most common SEM mode is detection of secondary electrons emitted by atoms excited by the electron beam. The number of secondary electrons that can be detected depends, among other factors, on specimen topography. By scanning the sample and collecting the secondary electrons that are emitted using a special detector, an image displaying the topography of the surface is created. SEM can achieve resolution better than 1 nm.
2. 3D images at a magnification reaching 100,000x. It allows reconstructing developmental steps of an ontogenetic sequence.
3. Ren Y, Chang HL, Endress PK (2010) Floral development in Anemoneae (Ranunculaceae). *Botanical Journal of the Linnean Society* 162(1): 77–100.

Replica molds (1970's)

1. Indirect method of capturing the form of a structure. An impression mould of a structure is filled with epoxy. Once removed from the mould, an impression is retrieved, which is a positive reproduction of the initial structure.

2. Allows in vivo observations and retrieves high structural details. It allows for instance the direct measurement of phyllotactic parameters.
3. Barabé D, Lacroix C, Jeune B (2007) Following the initiation and development of individual leaf primordia at the level of the shoot apical meristem: the case of distichous phyllotaxis in *Begonia*. *Annals of botany* 99(3): 555–560.

Light sheet microscopy (2000's)

1. It achieves optical sectioning by the selective illumination of a single plane of the sample with a sheet of laser light while simultaneously recording emitted fluorescence orthogonally to the illumination plane. A 3D image of the sample can then be generated with a temporal resolution ranging from seconds to several days, and at scales ranging from subcellular to whole organ.
2. It provides fast imaging, and low phototoxicity, two key criteria for live imaging under physiological conditions.
3. Berthet B, Maizel A (2016) Light sheet microscopy and live imaging of plants. *Journal of microscopy* 263(2): 158–164.

High Resolution X-ray Computed Tomography, HRXCT (2000's)

1. It is based on the property of low X-ray absorption of most plant tissues. It uses contrasting agents to reveal inner structures. The maximal resolution that can be obtained is 30 nm with synchrotron radiation. Compared with HRXCT, **Micro Magnetic Resonance Imaging (microMRI)** requires large and expensive magnets and cannot currently achieve resolution below 50-25 µm, and **Optical Projection Tomography (OPT)** requires that samples be transparent (treatment with caustic soda), a sample size of a few mm and allows a resolution of ca. 15-10 µm. HRXCT requires minimal sample preparation and is not destructive.
2. It delivers detailed 3D phenotypical data and allows virtual dissections in all directions.
3. Staedler YM, Masson D, Schönenberger J (2013) Plant tissues in 3D via X-ray tomography: simple contrasting methods allow high resolution imaging. *PloS one* 8(9): e75295.

***In vivo* live imaging based on Epi-Illumination Light Microscopy, ELM (2014)**

1. Non-destructive, it requires a single growing meristem. The drawback of live ELM is the difficulty in keeping the tissue healthy for several days.
2. It reveals the absolute time of organ initiation and duration of growth.
3. Jerominek M, Bull-Hereñu, K, Arndt M, Claßen-Bockhoff R (2014) Live imaging of developmental processes in a living meristem of *Davidia involucrata* (Nyssaceae). *Frontiers in Plant Science* 5: 613.

III. INVESTIGATING THE DIVERSITY AND EVOLUTION OF PLANT AND FLORAL FORMS: ONE FOR ALL AND ALL FOR ONE!

Although studying plant (and floral) morphology and development requires investing a lot of time to make observations at the binocular or at the SEM, endlessly dissecting floral buds and reading a fairly abundant literature, morphology is everything but a solitary discipline. Interacting with students, interns, and collaborators indeed makes the daily work more rewarding and interesting, and incomparably more fruitful.

I would suggest to the students of floral morphology to design the most integrative studies possible. This may sound like a simplistic statement but it is not easy to achieve. To carry out an excellent morphological study, one would need to have knowledge – and be able to design and conduct research – in various fields, such as anatomy, paleobotany, geometric morphometrics, phylogenetics, and evo-devo (Fig. 2, Debat and David 2002). Indeed, the morphology of an organism is at the interface of genome and environment, and its thorough analysis requires investigating its molecular bases, the developmental processes underlying it, and its functions in a given environment.

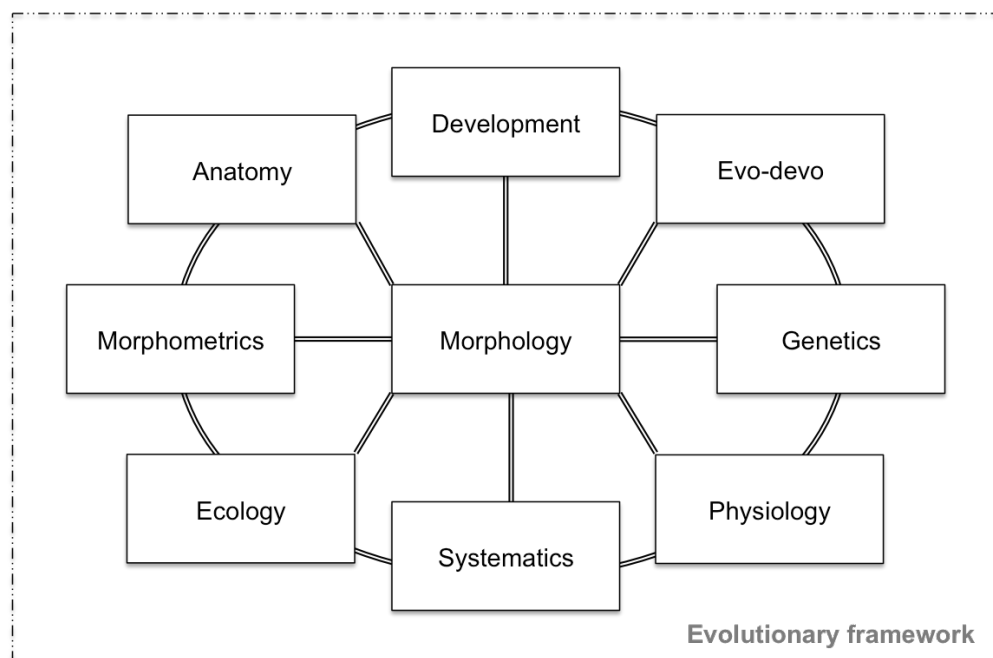


Figure 2: Relations of (plant) morphology with other disciplines. Links among disciplines are shown with double lines. All disciplines in relation with morphology are potentially linked to one another. Adapted from Kaplan (2001).

This list may seem restricted to methods, but each of the fields cited over is linked to a set of concepts and schools of thought, and is hence much more than a method.

Students of plant (and floral) morphology have to deal with ancient and old literature in depth (e.g. Jabbour et al. 2015a), as well as with conceptual adjustments (Ronse De Craene 2010, Ronse De Craene et al. 2014) and technical advances (e.g. High Resolution X-ray Computed Tomography, Stuppy et al. 2003, Staedler et al. 2013; *In vivo* live imaging of meristem development, Jerominek et al. 2014; see Box 5; Davies et al. 2017).

As it is almost impossible to master all these disciplines, especially at an early career stage, collaborations are crucial to achieve a thorough research project focusing on plant (and floral) morphology, in order to gather huge amount of data (Sauquet et al. 2017, Fig. 3), analyze morphological evolution using innovative methods (Chartier et al. 2017), or interpret morphological evolution in the light of other disciplines (Mouly et al. 2016). For instance, in the study led by Hervé Sauquet and Jürg Schönenberger, designed to shed new light on the structure of the ancestral flower of all living Angiosperms, 36 researchers worked together during six years to gather the largest data set of floral traits ever assembled (13,444 referenced data points), sampling 792 species from 63 orders (98%) and 372 families (86%) of Angiosperms. We reconstructed the ancestral Angiosperm flower as bisexual and actinomorphic, with more than two whorls of three separate perianth organs each (undifferentiated tepals), more than two whorls of three separate stamens each, and more than five spirally arranged separate carpels (Fig. 3a).



Figure 3a: The hypothetical ancestral flower of Angiosperms (Sauquet et al. 2017).

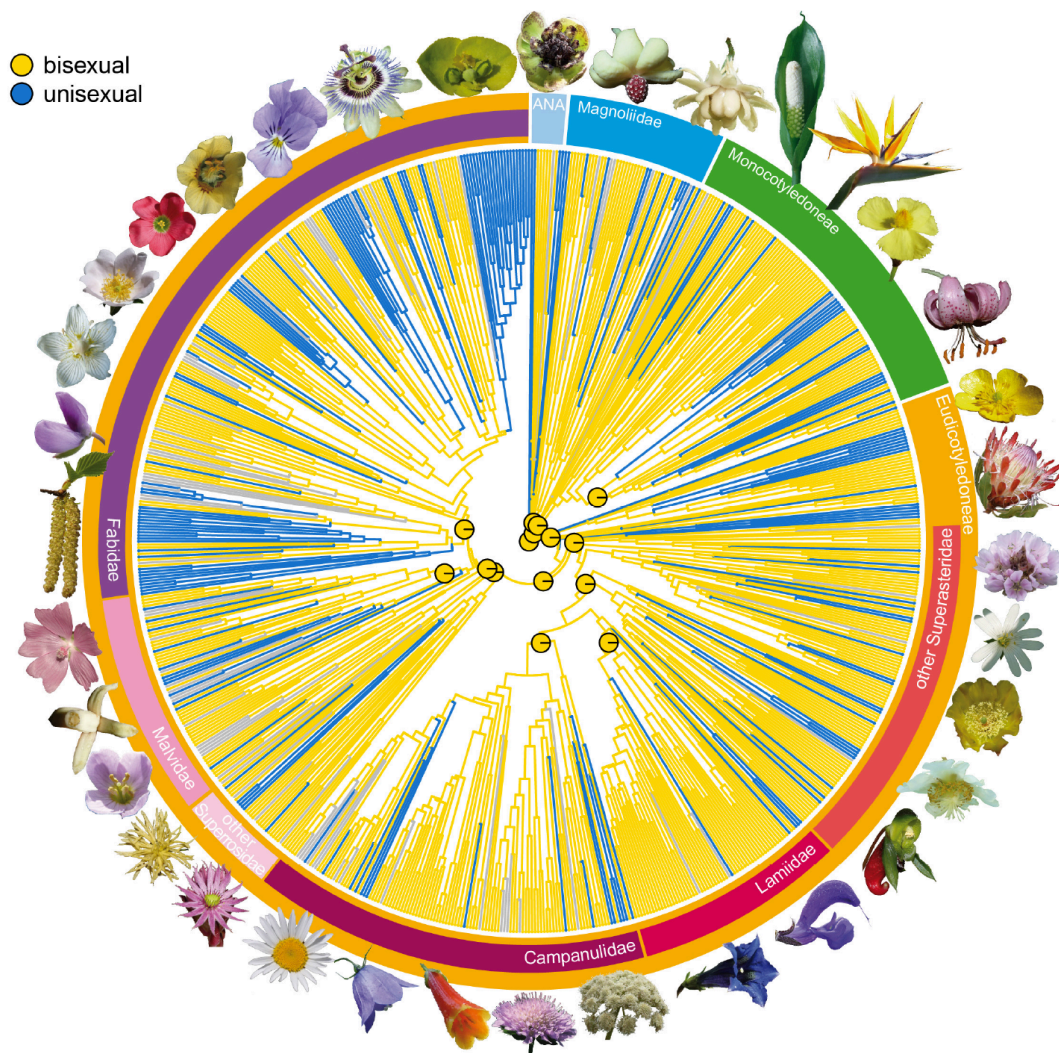


Figure 3b: The hypothetical ancestral flower of Angiosperms. Maximum likelihood ancestral state reconstruction of functional sex of flowers in Angiosperms, showing that bisexual flowers are ancestral and that unisexual flowers evolved many times independently. The pie charts at the centre of the figure indicate the proportional likelihoods for reconstructed ancestral states at 15 key nodes.

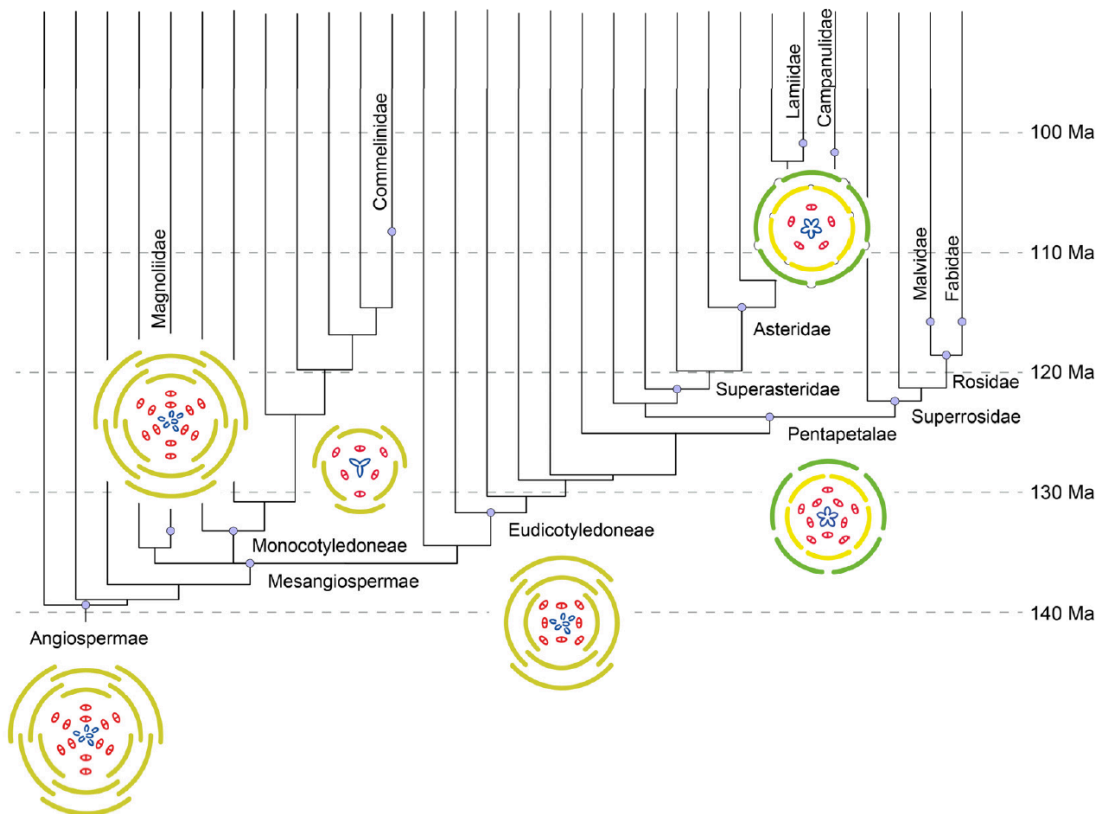


Figure 3c: The hypothetical ancestral flower of Angiosperms. Scenario for the earliest phase of floral diversification as inferred from the analyses of Sauquet et al. (2017). Floral diagram colour code: light green = undifferentiated tepals; green = sepals; yellow = petals; red = stamens; blue = carpels.

Building a network of collaborations does not only guarantee high-quality research, it also facilitates the access to funding.

Last, I will highlight what contributed significantly to my status of evolutionary morphologist at the MNHN. Being a curator at the National Herbarium is a fantastic opportunity for me as a lifelong student of plant and flower form evolution. Indeed, reading, making observations, and meeting researchers from different backgrounds are extremely enriching. Among all the colleagues I welcomed at the Herbarium, several have become collaborators and contributed to the evolution of my thinking in the field of morphology.

IV. SUPERVISION OF STUDENTS AND OF RESEARCH PROJECTS

Since I got hired at the MNHN, I co-supervised a postdoc (Marion Chartier) and a PhD student (Chhavarath Dary), and I supervised a MSc student (Felipe Espinosa), two undergraduate students (Lucas Batory, Lucile Jourdain-Fiévet), and an engineering student (Wafa Ben Othman).

I currently co-supervise the PhD work of Felipe Espinosa and the MSc internship of Yiyun Chen. In July 2017, an Iranian student (Masoumeh Khodaverdi) applied for a PhD contract at the MNHN. Unfortunately, she was not successful, but Catherine Damerval (co-supervisor) and me hope we can find an alternative PhD fellowship. The projects of Chhavarath, Felipe, Yiyun, and Masoumeh are detailed in Box 6. Later, when enough afro-montane *Delphinium* L. specimens will be collected, I would like to design a PhD project focused on the phylogeography and systematics of this group. The student would be co-supervised by Stefan Dressler, Guillaume Besnard, and me.

Training students and future researchers is a duty and a pleasure. Due to the diversity of personalities and to the different perceptions of science, supervising a student is always a challenge, but a very rewarding task as well. My objective is to help students become more autonomous and develop their curiosity, and most of all encourage them to cultivate their own skills and scientific affinities.

Among the projects I organized and led (eight papers as last author + a pair of papers for which I chose to be the first author [Jabbour and Dressler, 2015; Jabbour et al. 2015a]), three are special to me. The first one was a collaborative study I initiated after I arrived at the MNHN. It was a scientometric study about radiations, focused on insular systems, and not restricted to plants (Soulebeau et al. 2015). Anaëlle Soulebeau was then a PhD student, and six other colleagues (including a postdoc, four Assistant Professors, and one Professor) contributed to the study. It was quite challenging to standardize a protocol for extracting data from the literature and to make everybody respect the deadlines.

The second was a neat and thorough nomenclatural revision for an afro-montane species of *Delphinium*, co-authored with Stefan Dressler. This work was linked with an ongoing research project but also with my curatorial activities. Stefan was at that time a colleague/curator from Frankfurt Herbarium, and we only knew each other

from writing emails to each other. Since then, he visited Paris Herbarium, we designed a project that we submitted to the National Geographic Society, and we will do our first field trip together in Kenya next year.

The third was the first paper of Felipe Espinosa as a first author, Felipe being the first PhD student I am in charge of. Besides the fact that Felipe had to write for the first time a full manuscript, he successfully dealt with collaborators from the MNHN on the one hand, and from Turkey, China, and the Netherlands on the other hand.

BOX 6: Former, current, and prospective MSc and PhD students

Portrait 1 (past)

Dr. Chhavarath DARY

Assist. Prof., Univ. Phnom Penh



The PhD project of Chhavarath focused on the systematics of the genus *Stephania* Lour. (Menispermaceae) and on the pharmacological properties of some species of *Stephania* found in Cambodia.

He was supervised by Prof. Evelyne Ollivier and Dr. Sok-Siya Bun at the University of Marseilles, and by Dr. Hul and me at the MNHN.

His PhD work led to four publications so far, and we still collaborate on his PhD topic to publish his last results.

He is since September 2016 an Assistant Professor at the University of Phnom Penh.

Portrait 2 (present)

Felipe ESPINOSA

PhD student, MNHN



Felipe investigates the evolution of floral structures and floral organization in the Ranunculaceae, combining morphology-anatomy, development and molecular phylogeny.

He is supervised by Prof. Sophie Nadot (Univ. Paris Sud) and me.

As a MSc student under my supervision, he co-authored an article in *Flora* (Jabbour et al. 2015a). His first PhD paper got accepted in April 2017 in *Int. J. Plant Sci.* (Espinosa et al. 2017).

After his PhD defence (planned in May 2019), Felipe will go back to Colombia.

Portrait 3 (present)

Yiyun CHEN

MSc student (M2), MNHN



Yiyun is currently a MSc student under the supervision of Dr. Sylvain Gerber (MNHN) and me. She conducts a comparative analysis of floral shapes in the tribe Delphinieae, using geometric morphometrics, and based on herbarium specimens. She will defend her MSc thesis in September 2017.

Yiyun will then go back to China where she will work at a panda conservation centre.

Portrait 4 (future?)

Masoumeh KHODAVERDI

Applicant for a PhD contract at the MNHN



Masoumeh contacted me one year ago to build a PhD project combining floral development and evo-devo.

Together with Dr. Catherine Damerval (CNRS, Le Moulon-Génétique Quantitative et Evolution), we designed a project addressing the possible genetic causes of differential petal development in Ranunculaceae.

Masoumeh was invited to the competition of the Doctoral School of the MNHN in July 2017. She was unfortunately not selected, but she would still have the possibility to work in our team in case we get the ANR grant in early 2018.

Prof. Shahin Zarre (Univ. Tehran) would be a third co-supervisor.

V. EVOLUTION OF FLOWER FORM IN A PHYLOGENETIC CONTEXT: SELECTION OF PAST AND CURRENT RESEARCH PROJECTS

I have investigated the evolution of flower forms in Angiosperms since my time as a PhD student. I tackled this issue through different disciplines such as comparative analyses, evo-devo, systematics, and morphology-anatomy. Figure 4 shows the different Angiosperm taxa I have investigated so far.

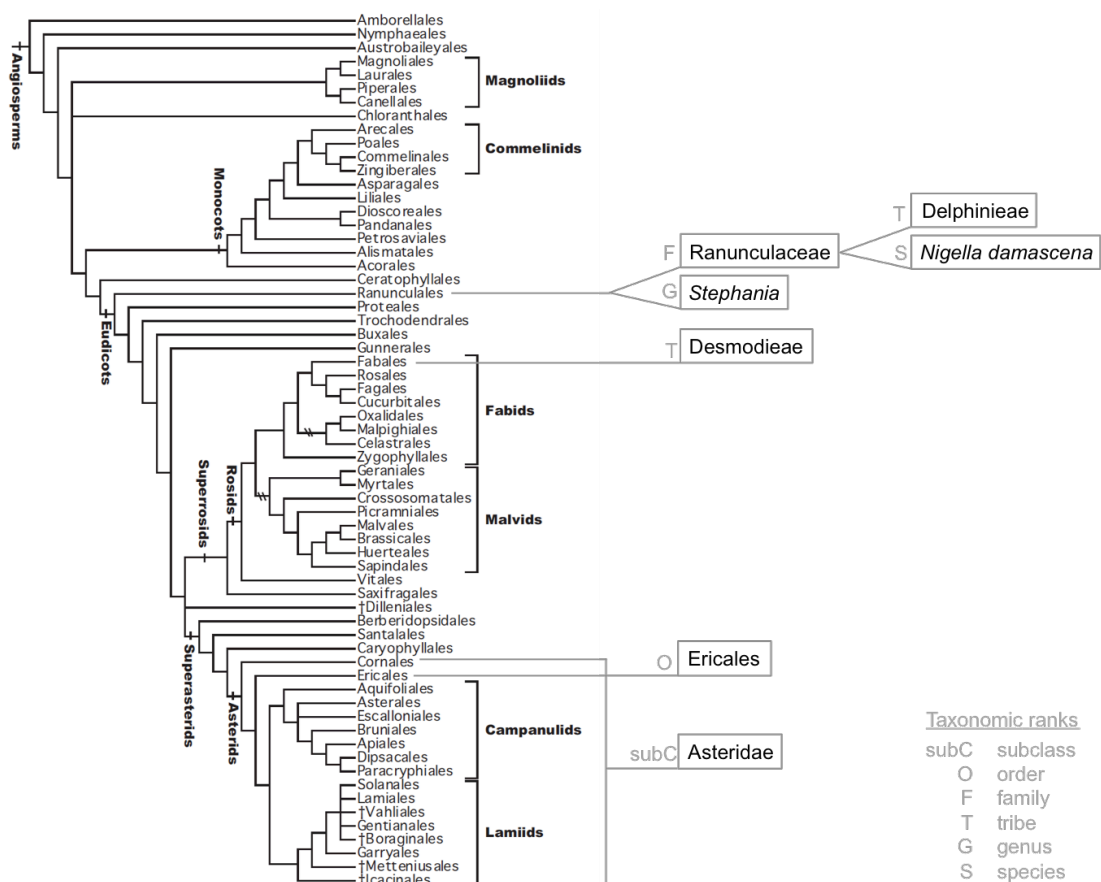


Figure 4: The taxa I have investigated so far. The Angiosperm tree topology is from APG IV (2016).

The research I currently conduct focuses on Angiosperm systematics, a growing part of it being dedicated to taxonomy. I have studied more particularly the evolution of floral forms in selected taxa from Ranunculales, in a phylogenetic context. This order of flowering plants is not the least studied, and many research groups focus on the molecular phylogeny (e.g. Wang et al. 2009), flower development (e.g. Zhao et al.

2012, 2016) and evo-devo (e.g. Rasmussen et al. 2009, Pabón-Mora et al. 2013), or pharmacological properties of the plants (e.g. Hao and Yang 2016). It is the first order to diverge within Eudicots, and it is characterized by a tremendous flower disparity (Damerval and Nadot 2007, Damerval and Becker 2017).

These projects were conducted and completed thanks to students I supervised (Fig. 5) and in collaboration with a group of reliable and enthusiastic collaborators.

Staying in close contact with some fields (e.g. evo-devo) and initiating projects in fields I was not trained in (e.g. pharmacological and chemical properties of plants) are important to me. It allows getting a more comprehensive understanding of the evolutionary processes having shaped current biodiversity. On a more personal ground, it helps me discovering new aspects of science and meeting new collaborators with different ways of apprehending morphological evolution. Whilst supervising students and transmitting the knowledge I have accumulated through the years is very satisfactory, I like to remain in the mental position of the student, pushing myself to discover new areas of botany (see paragraph VI.i.), and always trying to question my own reasoning, especially in fields where my personal scientific routine got settled.

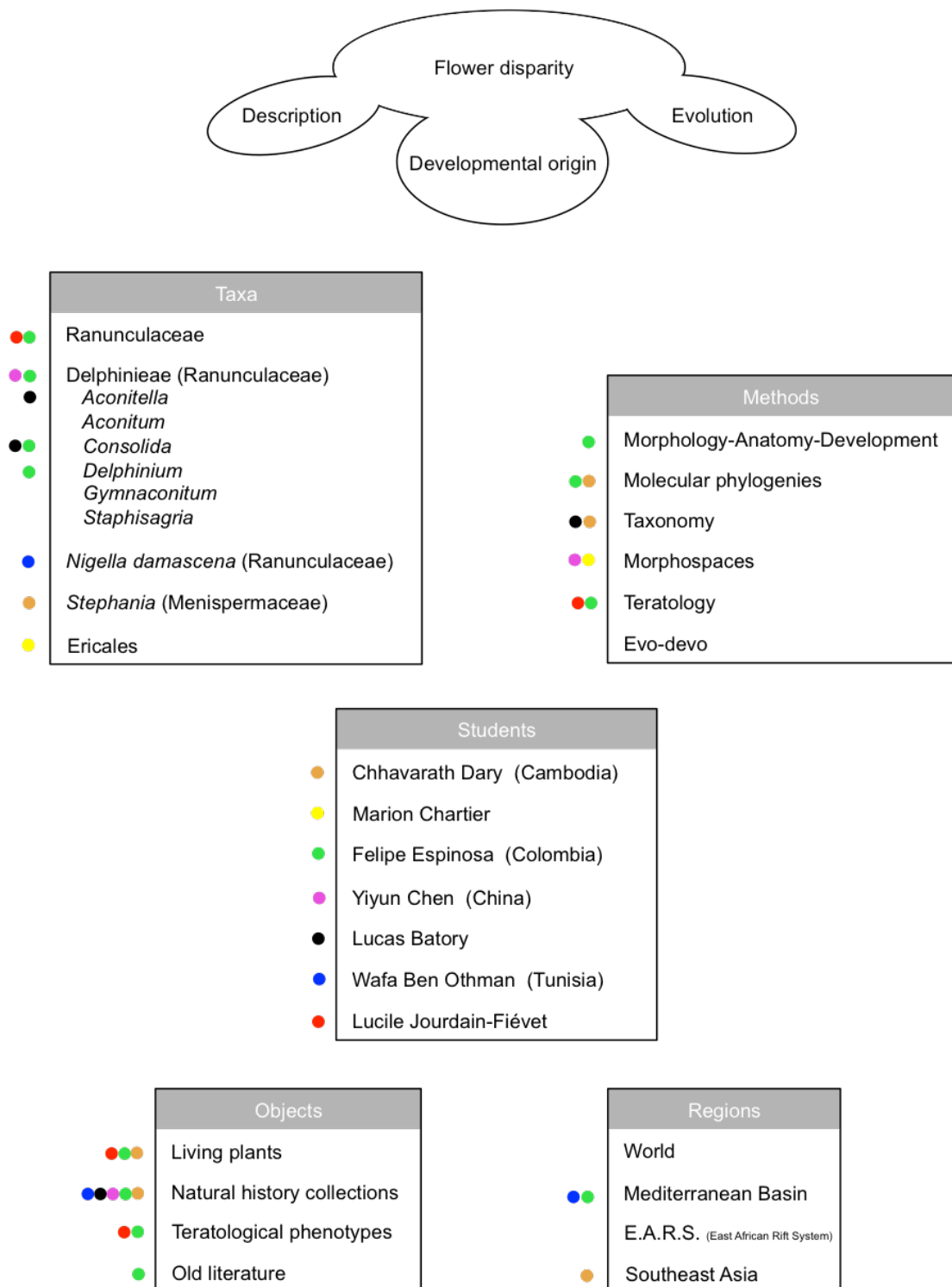


Figure 5: Synthesis of the main research projects I was involved in or led so far. The involvement of my former and current students in each project is shown.

V.a. FLOWER SYMMETRY: DEVELOPMENT, EVO-DEVO, AND EVOLUTION

Flower symmetry is a feature of floral bauplan that plays an important role in the pollination process (e.g. pollinator attraction, optimisation of pollen deposition on the pollinator's body). Its establishment during development, and its molecular bases have been investigated in many taxonomic groups (Endress 1999, Citerne et al. 2010), and it was shown that zygomorphy (bilateral symmetry) evolved ca. 200 times in Angiosperms from ancestral lineages with actinomorphic flowers (Reyes et al. 2016). My work as a PhD student aimed at investigating 1) the morphological correlates of flower symmetry of the subclass Asteridae in a phylogenetic framework and 2) the molecular bases of zygomorphy in the tribe Delphinieae (the only lineage within Ranunculaceae for which zygomorphy is a synapomorphy).

This PhD project combined two approaches: 1) phylogenetic comparative analyses of the evolution of selected floral traits to detect correlates of and constraints on the evolution of zygomorphy in Asteridae, and 2) a candidate-gene evo-devo investigation of floral symmetry in selected species of Ranunculaceae.

We demonstrated that the transition between different states of floral symmetry in Asteridae is conditioned by both androecium organ number and perianth merism, and that zygomorphy is a prerequisite to the emergence of spurs (Jabbour et al. 2008).

In selected actinomorphic and zygomorphic species of Ranunculaceae, we described the developmental events leading to the establishment of floral symmetry, and identified the developmental stages at which zygomorphy is settled in Delphinieae (Jabbour et al. 2009).

In the same family, 28 species (18 genera) sampled throughout the phylogeny of Delphinieae were used for characterizing the *CYC*-like gene sequences and infer their evolution in the tribe and family, and three species with actinomorphic flowers and a couple of species with zygomorphic flowers (*Aconitum carmichaelii* Debeaux and *Consolida regalis* Gray) were used to study the expression of the different paralogues during development.

We found that a gene duplication possibly predated the emergence of the Delphinieae lineage, resulting in up to four gene copies in zygomorphic species (a first duplication may have predated the divergence between Lardizabalaceae and Ranunculaceae).

The paralogs were expressed early in floral buds and the duration of their expression varied between species and paralog class. At most one paralog was expressed during the late stages of floral development in the species with actinomorphic flowers whereas all paralogs from the species with zygomorphic flowers were expressed, composing a species-specific identity code for perianth organs (Jabbour et al. 2014; Fig. 6).

I had the opportunity during my PhD to co-author a review article about the researches conducted on flower symmetry (Citerne et al. 2010). My contribution was mostly about the establishment of the different types of symmetries during flower development (Fig. 7).

Evo-devo of floral symmetry is not a major focus of my research anymore, although I still collaborate on this topic with my former PhD supervisors, Sophie Nadot and Catherine Damerval. During my three years as a PhD student working on floral symmetry, I had the opportunity to supervise an undergraduate student, Julie Leroux, and an engineering school student, Erwann Cherel. Both were trained in molecular biology and worked on *RANACYL* sequencing in Ranunculaceae.

During my PhD time, I considered myself an evolutionary biology student. It is years after that plants became more than a model and a material for my experiments and that I started to consider myself as a botanist.

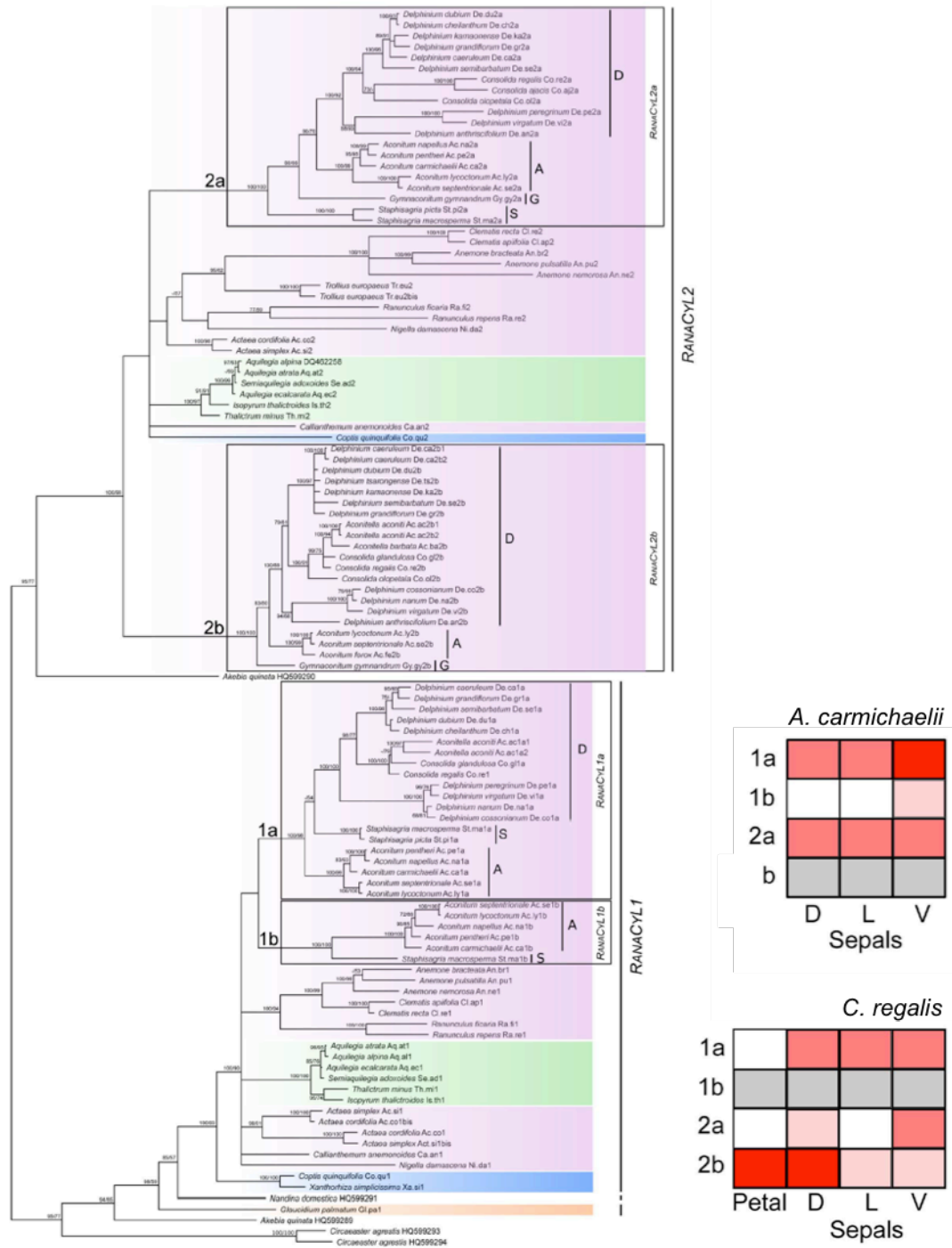


Figure 6: *RANACYL* genes: Phylogenetic relationships and expression pattern. Phylogenetic tree of the *CYC*-like sequences in Ranunculaceae (the lineages of species with zygomorphic flowers are highlighted in pink) and expression level of the *RANACYL* paralogs for *Aconitum carmichaelii* and *Consolida regalis* in the different perianth compartments (Jabbour et al. 2014). D: dorsal, L: lateral, V: ventral.

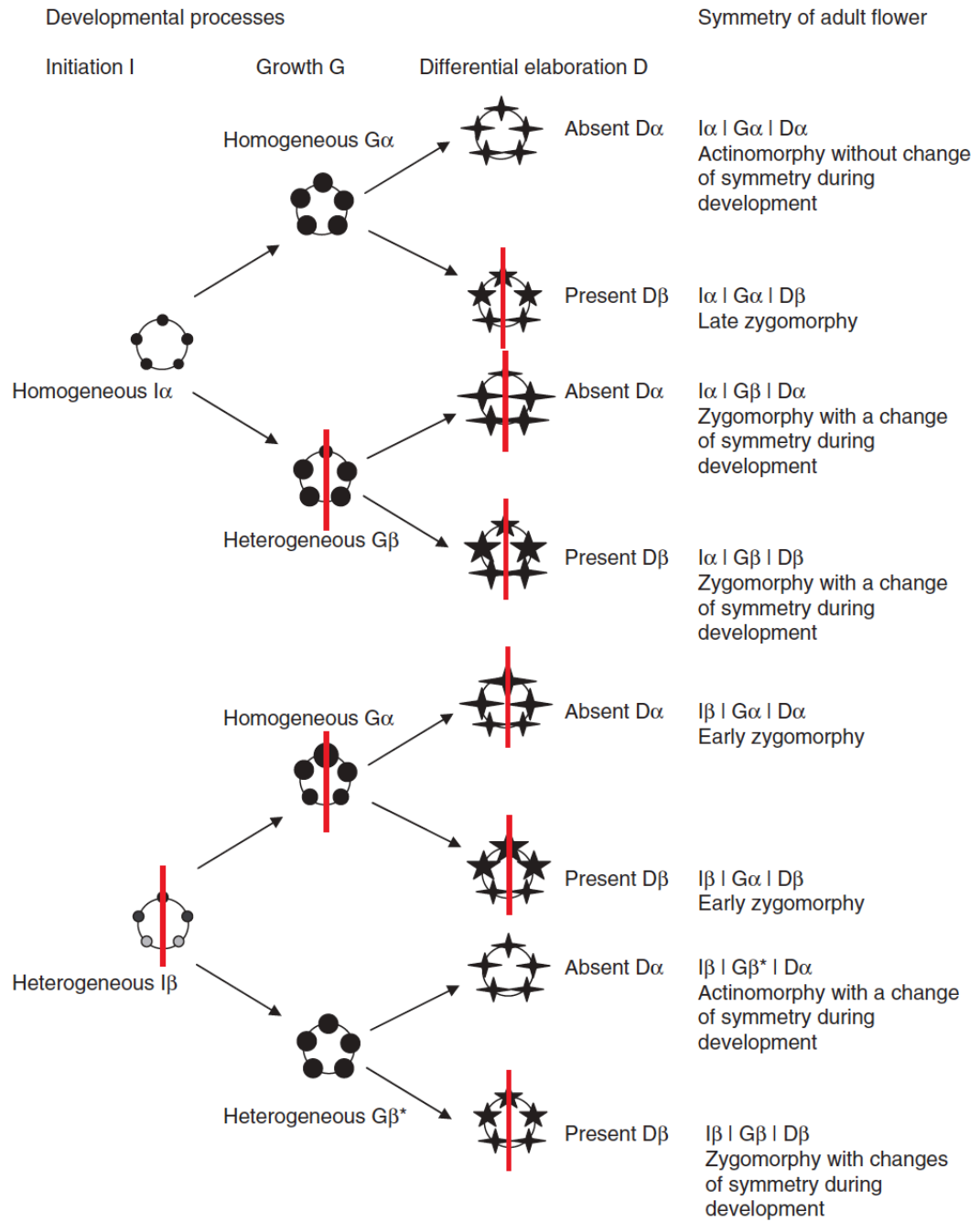


Figure 7: Theoretical developmental trajectories combining different states for three processes (organ initiation, growth, and differential elaboration) resulting in different types of floral symmetry. See Citerne et al. (2010) for details.

V.b. SYSTEMATICS AND FLOWER EVOLUTION IN DELPHINIEAE (RANUNCULACEAE)

I did not expect as a PhD student to be still working on Delphinieae ten years later. I was first attracted by the diversity of their floral forms, looking at them as a simple plant model for my evo-devo experiments. I discovered as time went by that Delphinieae are an excellent model to study floral morphological evolution, lineage evolution and biogeographical history of temperate plants, and the evolution of pollination systems.

The research I conduct on Delphinieae aims at understanding lineage evolution within the tribe in order to clarify its systematics.

Another objective is to understand the developmental and genetic bases of synorganisation in the dorsal part of the Delphinieae flower (Fig. 8). Synorganisation is the intimate structural connection of two or several neighbouring floral organs to form a functional system (hyperorgan). It may occur by congenital or postgenital fusion or by coordination of organs without fusion (definition given by Specht and Bartlett [2009]). The vocabulary relative to the perianth organs of Delphinieae follows Rasmussen et al. (2009).

Regarding the floral morphology in the tribe, I am particularly interested in the modalities of the transitions among the different architectures displayed by such zygomorphic and highly synorganized flowers. I defined categories of floral organizations differing in the structures producing and protecting nectar (Fig. 9). Convergences in flower form and organization were evidenced in this tribe (see below), and most of my research on Delphinieae is designed to understand the phylogenetic and environmental constraints having shaped these convergences.

The research on Delphinieae has been conducted in collaboration with many colleagues and students. Their names and roles are cited and detailed below.

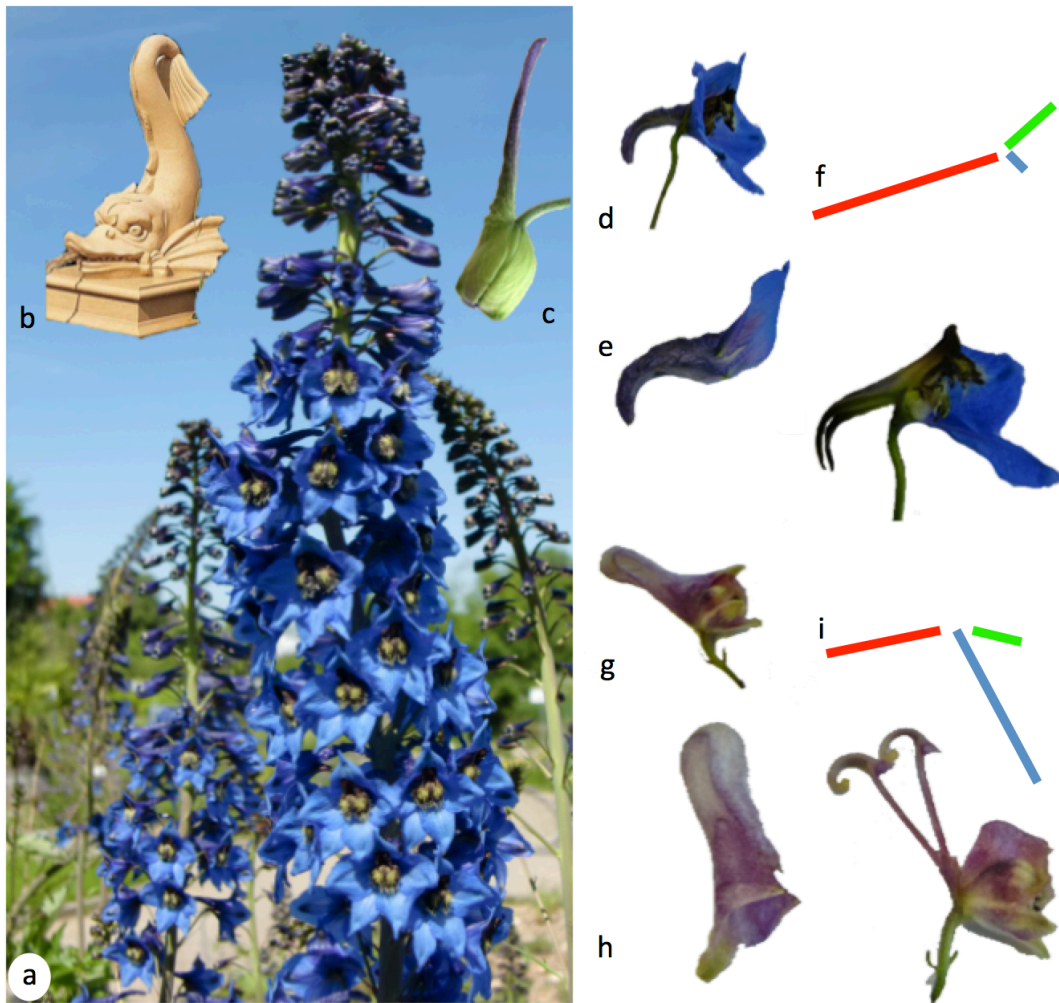


Figure 8: Delphinieae floral groundplan; a. Inflorescences of *Delphinium elatum* L. (Munich botanical garden), b. Antique dolphin fountain, c. *Delphinium* flower bud, resembling the shape of dolphin as depicted in antique art, d. Flower of *Delphinium elatum*, e. Dorsal spurred sepal of the same flower, put aside to show the pair of dorsal spurred petals. One lateral and one ventral sepal were removed, f. Petal organisation in *Delphinium*, showing the proportion of each part of the petal. Red: spur, green: labium, blue: stalk, g. *Aconitum lycoctonum* subsp. *moldavicum* (Hacq.) Jalas, h. Dorsal spurred sepal of the same flower, put aside to show the pair of dorsal spurred petals, i. Petal organisation in *Aconitum* L., showing the proportion of each part of the petal. Red: spur, green: labium, blue: stalk.

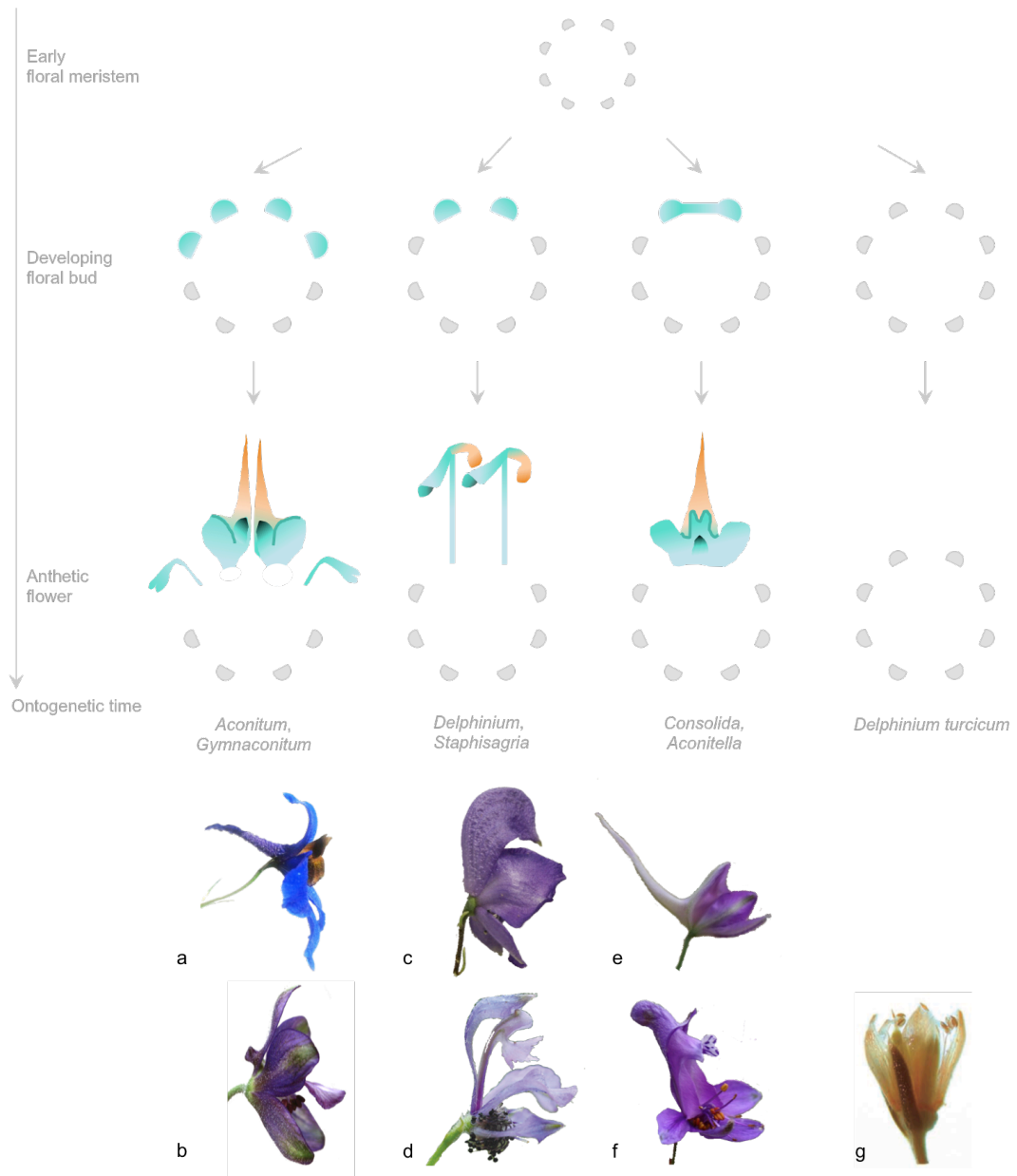


Figure 9: The types of corolla development identified in Delphinieae (Jabbour et al. 2009, Jabbour and Renner 2012a); a. *Delphinium elatum* (credit: F. Espinosa), b. *Staphisagria macrosperma* Spach, c. *Aconitum napellus* L., d. *Gymnaconitum gymnandrum* (Maxim.) Wei Wang & Z.D.Chen (Wang et al. 2013), e. *Consolida regalis* (credit: A. Gröger), f. *Aconitella hohenackeri* Soják (credit: A. Gröger), g. *Delphinium turcicum* (H.Duman, Vural, Aytaç & Adigüzel) Espinosa (credit: F. Espinosa). Photographs are not to scale. Green: developing petals; orange: nectar spur.

As a PhD student, I used Delphinieae as part of my species sampling for the study of the molecular causes of the zygomorphic phenotype in Ranunculaceae. Also, thanks to a Synthesys funding, I visited Louis Ronse De Craene at the Royal Botanic Garden Edinburgh. It was a wonderful time learning the bases of a developmental study using SEM. I discovered that I could spend hours dissecting floral buds under a binocular, and that I liked it! I was at that time exclusively involved in my genetics and evo-devo oriented PhD project, reading only the most recent papers in the field. What a surprise it was when Louis suggested me to read “Payer”. Payer meant nothing to me then, and I have to confess I had not thought that such an old book could contain information relevant to scientists using 21st century techniques to investigate floral development. This small event had lots of effects on my scientific way of thinking. I learned that old does not mean obsolete, that observations made with simple techniques do not mean wrong or out-of-date observations, and that any new research project should build on all the available literature, be it from different schools of thinking, centuries, or languages.

Following this work, I got frustrated not having any clue about the evolution of the species of Delphinieae, and even not being able to describe properly how their flower was organized. I designed a first postdoc project to tackle those issues. Learning plant systematics and pursuing developmental studies in a lab such as the one led by Susanne Renner was a great experience.

I used for the first time herbarium specimens and got familiar with the herbarium work (see Malécot and Dubuisson 2004). I built a molecular phylogeny of the tribe Delphinieae, reconstructed its biogeographical history, and found that the particular floral morphology of the *Consolida* (DC.) Gray/*Aconitella* Spach genera was the result of a postgenital fusion of two petal primordia (Jabbour and Renner 2011a, 2011b, 2012a, 2012b; Fig. 9). Since then, I continuously updated the phylogeny of Delphinieae, and made the necessary taxonomical changes. This work has been done in close collaboration with Wei Wang (Espinosa et al. 2017, Xiang et al. 2017; Fig. 10).

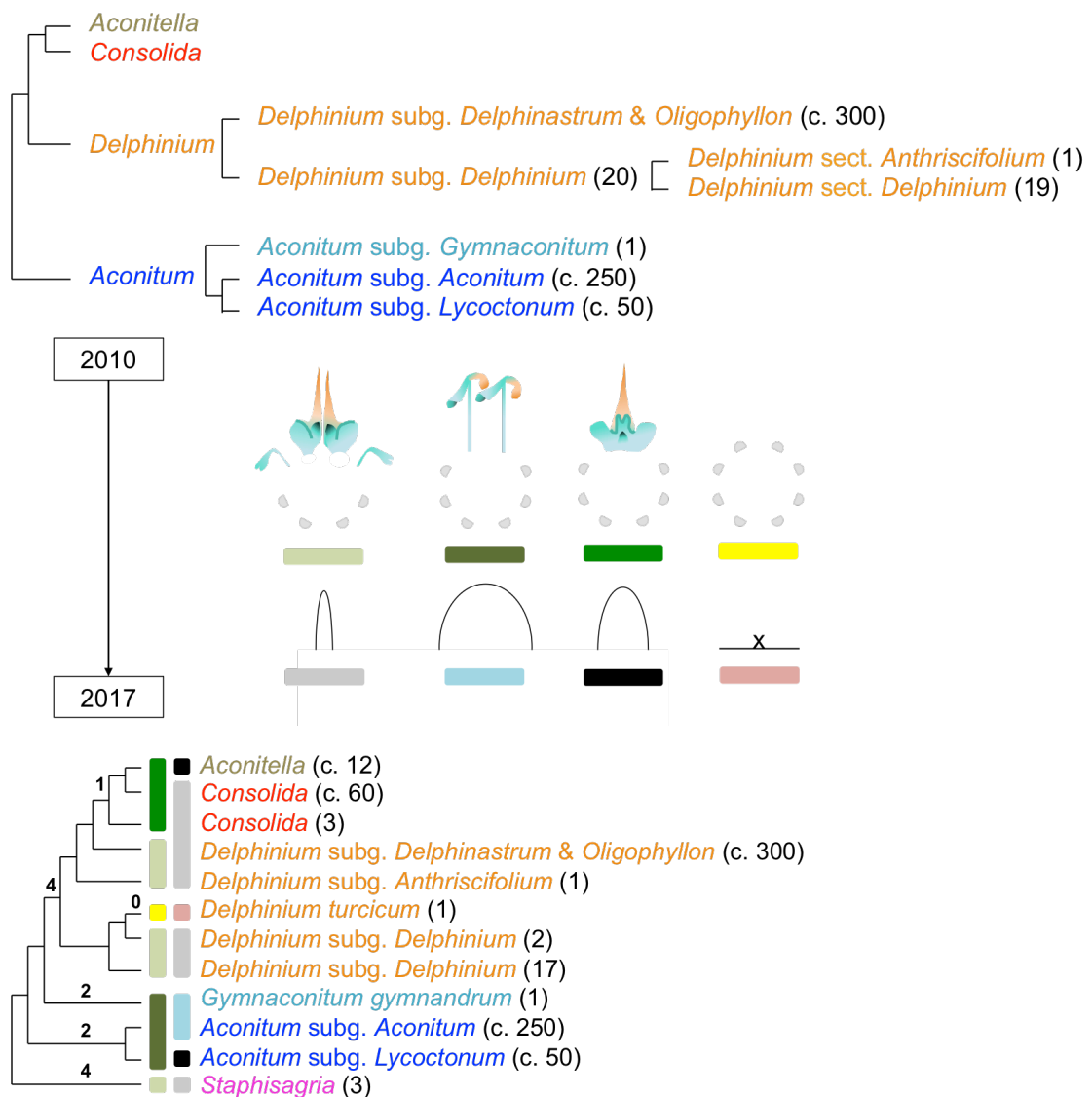


Figure 10: Improvements in the phylogeny of Delphinieae since 2010. This date corresponds to the start of my postdoc during which I built the first molecular phylogeny of the *Consolida*+*Aconitella* group (Jabbour and Renner 2011a), and then the first molecular phylogeny of the tribe Delphinieae (Jabbour and Renner 2011b, 2012a). My colleague Wei Wang built on my results one year later (Wang et al. 2013), focusing on the phylogenetic placement of the monotypic genus *Gymnaconitum* (Stapf) Wei Wang & Z.D.Chen. The subsequent studies about infratribal taxa in Delphinieae were conducted in collaboration with Wei Wang and his team (Espinosa et al. 2017, Xiang et al. 2017). The three species of *Staphisagria* J.Hill were once included in the genus *Delphinium*. *Delphinium turcicum* was formerly published as *Pseudodelphinium turcicum* H.Duman, Vural, Aytaç & Adigüzel (Vural et al. 2012). Numbers in parentheses correspond to the number of species in the taxon. Numbers on the branches correspond to the number of fully developed petals in the flowers of the corresponding lineage (see Fig. 9). Coloured bars refer to the corolla type (first column next to the tips of tree; see Fig. 9) and to the sepal shape (second column; spurred, hooded, cylindrical hood, flat).

My research on Delphinieae has been pursued and widened after I got hired at the MNHN. I still use molecular phylogenetics and biogeographical methods to address issues such as lineage evolution and morphological evolution (thanks to morphometrics applied to herbarium flower samples). Together with students, I look now at the evolution of Delphinieae at the infra-subgeneric level. Felipe Espinosa (second year PhD student) investigated the phylogenetic relationships and flower morphology and anatomy in a newly described species from Turkey, *Delphinium turcicum* (Espinosa et al. 2017).

Marion Chartier (former postdoc at Univ. Vienna) was involved in the study of the afro-montane species of *Delphinium* (Chartier et al. 2016). Whilst I designed the study and conducted the molecular biology experiments and morphometric measurements on herbarium samples, Marion was in charge of the statistical and morphospace analyses based on the morphometric data (Fig. 11). This study was co-authored by Alfonso Rojas, a student I supervised when I was a postdoc. Other collaborators from the MNHN (Corinne Sarthou) or from other institutions (Stefan Dressler [Frankfurt], Jürg Schönenberger [Vienna], Wei Wang [Beijing]) were associated to this study.

I remember an advice Sophie Nadot and Catherine Damerval gave me when I was a PhD student, and this advice had a great impact on the trajectory of my research in the few years following my defence. I hope I translate it here without too many changes: “Don’t spend so much time doing development or morphology. Even if this is interesting, this will not bring big papers. Better focus now on your evo-devo experiments, you need molecular papers in your CV. Nobody will offer you a permanent position nowadays with only morphology and development in your CV”.

I followed this advice, and kept the proportion of morphological studies relatively low during my PhD and postdoc, although it was important for me to build some minimal expertise in this field (Jabbour et al. 2009; Jabbour and Renner 2012a). I now have the opportunity to dive into the fields of morphology, development and anatomy, to train students in such disciplines (Felipe Espinosa, Lucile Jourdain-Fiévet), and to build projects with collaborators who are keener on the investigation of the molecular causes of floral phenotypes.

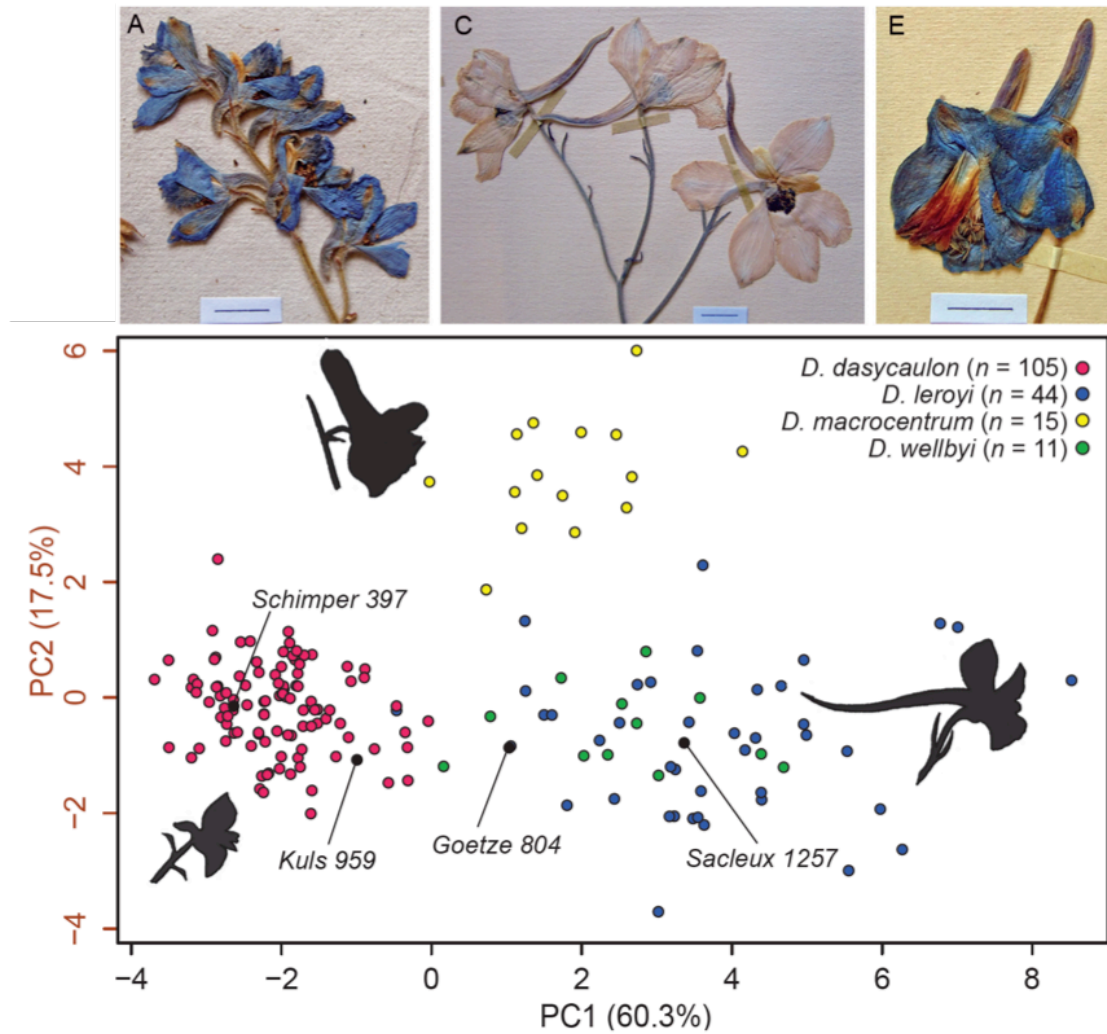


Figure 11: The morphospecies of afro-montane *Delphinium* and their phylogenetic relationships. PCA showing the circumscription of the three morphospecies based on the analysis of 13 metrics taken from flowers from herbarium specimens. See Chartier et al. (2016) for details.

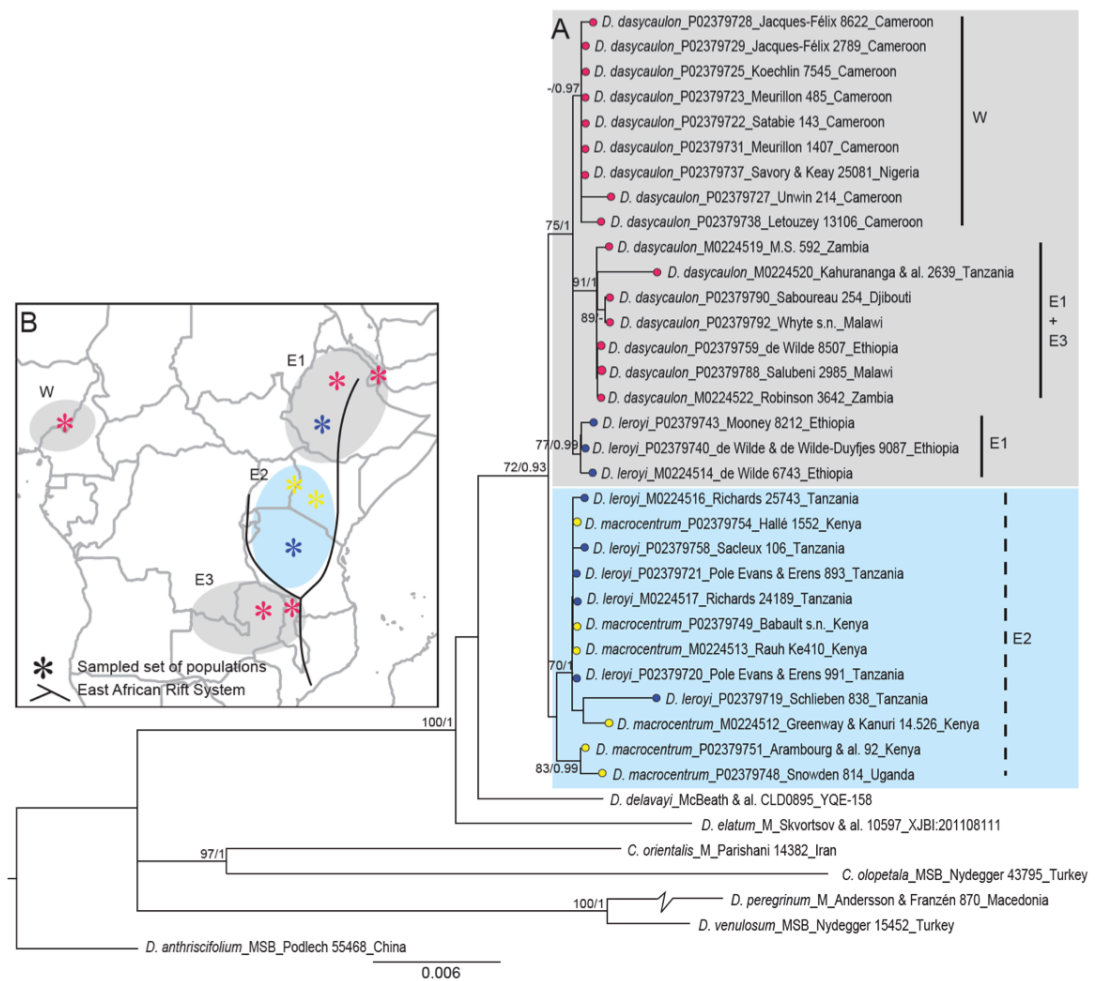


Figure 11: Continued. Plastid phylogeny of the afro-montane morphospecies of *Delphinium*. The two clades (blue and grey) are depicted on the map of Africa. The asterisks on the map represent monophyletic sets of accessions. The hypothesis of a convergent evolution towards a *D. leroyi* flower type in both the blue and grey clades due to ecological constraints was proposed.

Together with Andriy Novikoff (State National History Museum Ukraine), I studied the floral anatomy of representative species from different genera of Delphinieae (Novikoff and Jabbour 2014, Fig. 12). I invited Andriy as a guest researcher in our Institute in March 2016 to initiate with me a study of Delphinieae floral shape, using herbarium specimens and applying geometric morphometric methods. This project is now being carried out by a Masters student, Yiyun Chen, who is co-supervised by Sylvain Gerber (palaeontologist and morphometricians at the MNHN) and me. Further anatomical studies are conducted by Felipe Espinosa (PhD student) and Thierry Deroin, on Ranunculaceae flowers with atypical phenotypes, with the objectives of

characterizing the anatomical identity of organs in those flowers, and providing hypotheses about the flower parts that are the most prone to homeotic changes. The species investigated belong to the genera *Aquilegia* L. and *Delphinium sensu lato* (including *Consolida*).

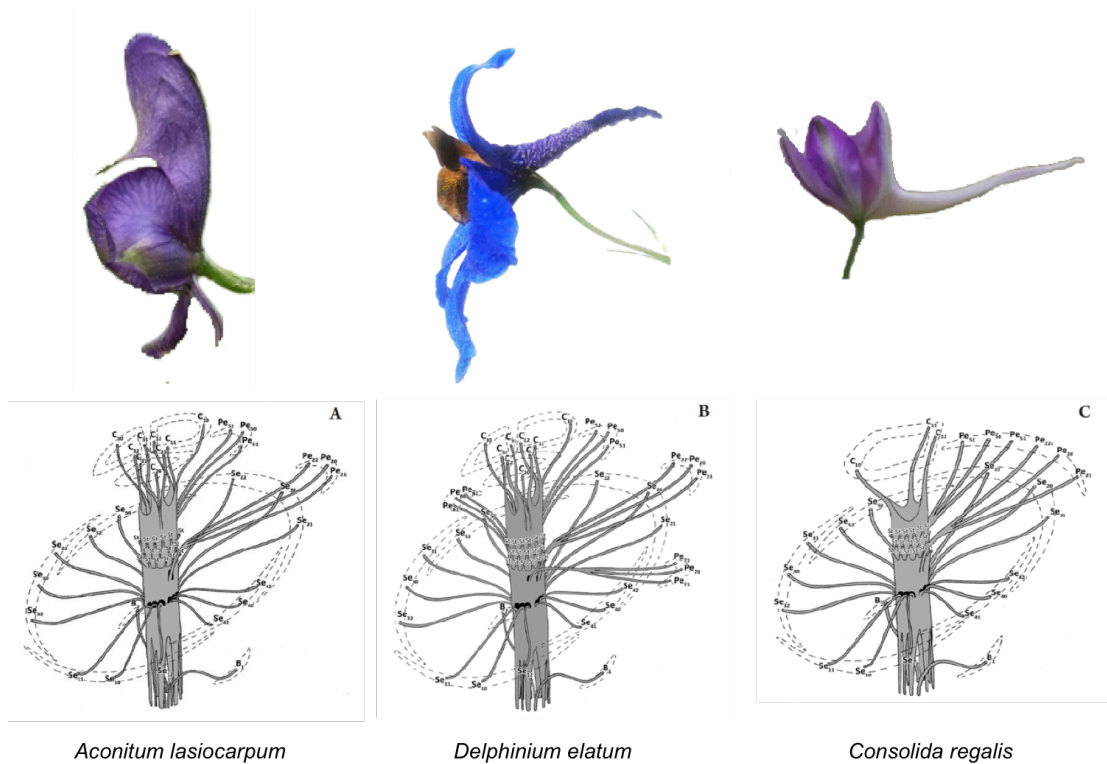


Figure 12: Floral vascular organization in three species representative of the three main floral types (with a developed corolla) found in Delphinieae (Novikoff & Jabbour 2014). Credits: *A. lasiocarpum* Gáyer (http://www.kul.pl/gal_12532.html), *D. elatum* (Felipe Espinosa).

Floral development studies are conducted by Felipe Espinosa and Lucile Jourdain-Fiévet (undergraduate student) on buds from horticultural varieties of *Aquilegia* and *Delphinium* and in *D. elatum* (Fig. 13). Both Felipe and Lucile work under my supervision.



Figure 13: The corolla of a developing flower of *Delphinium elatum*. View from above. Dissected floral bud showing the corolla consisting of four ventral petals with an arrested development, two flat dorso-lateral petals, and two spurred dorsal petals.

These works in the fields of systematics and morphology-anatomy led to the re-circumscription of several groups and to taxonomic revisions. The findings implying that neither *Consolida* and *Aconitella* (Jabbour and Renner 2011a), nor *Pseudodelphinium* H.Duman, Vural, Aytac & Adigüzel (Espinosa et al. 2017) are separate genera, but rather belong in *Delphinium*, call for nomenclatural revisions of the three groups. *Pseudodelphinium* (monotypic) was synonymised with *Delphinium* by Espinosa et al. (2017). The names of the ca. 70 species of *Consolida* and *Aconitella* are being transferred to *Delphinium* by Pierre-Emmanuel du Pasquier (Herbarium and Botanical Garden, Geneva), Lucas Batory (undergraduate student) and me in a manuscript we have in preparation.

Eventually, the description of the genus *Delphinium* will have to be amended, taking into account the presence within the genus of species with actinomorphic spurless flowers lacking a corolla (*Pseudodelphinium*). This taxonomic act will be done in collaboration with Thierry Derooin, Felipe Espinosa, Pierre-Emmanuel du Pasquier, James Byng (Naturalis Leiden) and Wei Wang. James and Wei co-authored Felipe's

article on *Pseudodelphinium*, and Wei and I developed through the years a very active collaboration on the systematics of many Ranunculaceae genera.

V.c. FLOWER DIMORPHISM IN *NIGELLA DAMASCENA* L. (RANUNCULACEAE)

The “*Nigella damascena* story” all started during my PhD, as *N. damascena* was one of the two species of Ranunculaceae with actinomorphic flowers (the other one being *Clematis recta* L.) I chose to serve as references in the evo-devo study of floral symmetry in the family. When growing plants from seeds for my experiments, I was surprised to find two kinds of flowers. Some plants bore flowers with (petaloid) sepals and (nectariferous) petals; some others had flowers with only (petaloid) sepals, hence missing a corolla. At that time, I did not know of the abundant literature on this particular floral dimorphism, although I was familiar with the research conducted on the dimorphism in other biological systems (e.g. Darwin 1877, de Vos et al. 2014). My supervisors and I thought it would be interesting to understand the molecular and developmental bases of the two floral architectures, as well as the plant mating system and pollination ecology characterizing each floral morph.

We gathered people to work on this very exciting topic, and tackled all these issues in the past few years. Some aspects are still under investigation.

Flower morphology (Jabbour et al. 2015), anatomy (Deroin et al. 2015), and development (Zhao et al. 2011, Jabbour *et al.*, 2015b) were described and compared between the two morphs, and the molecular basis of the floral dimorphism was unravelled (Gonçalves et al. 2013, Fig. 14). We demonstrated that the floral dimorphism is controlled by a single locus, which perfectly co-segregates with the *N. damascena* *AP3-3* gene. This gene is not expressed in the apetalous morph and exhibits a dynamic expression during early floral development in the petalous morph. We hypothesized that *NdAP3-3* plays a role not only in petal identity but also in meristem patterning, possibly through regulation of perianth organ number and the perianth/stamen boundary.

Although we suffered from competition from another research group (Hongzhi Kong’s lab: Zhang et al. 2013, Wang et al. 2015), we continue our study in order to make it

the most integrative possible. Results about mating systems, fitness, and pollination ecology were obtained and have now to be published.

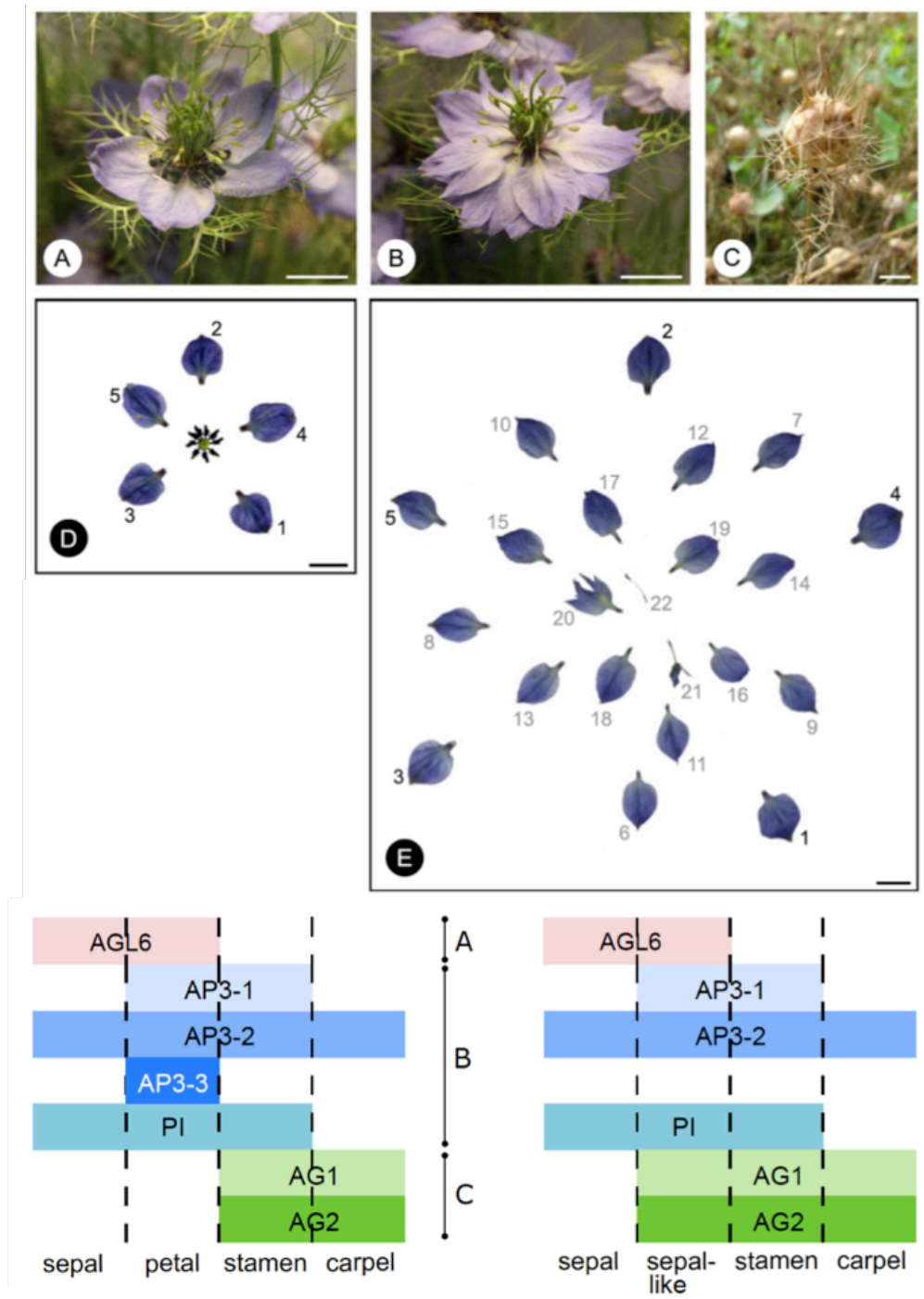


Figure 14: The expression pattern of class A, B, and C genes in the two morphs of *Nigella damascena*. The two floral morphs (flowers and dissected flowers) and a fruit. The expression pattern of the ABC genes is shown for the two morphs (left: wild-type [petalous] morph; right: apetalous morph [with supernumerary perianth organs]). See Jabbour et al. (2015b) for details.

Also, we want to analyze the evolution of the distribution of each morph, to test for the conservation of particular geographic patterns through time. We hence georeferenced more than 3,000 herbarium specimens from 45 herbaria, and could reconstruct distribution maps for each morph, during the last two centuries, and by intervals of 50 years. The gene responsible for the floral dimorphism (*NdAP3-3*) is currently being sequenced from a sample of herbarium specimens collected from different areas in the Mediterranean Basin, to test whether the apetalous phenotype is always determined by the same molecular factor.

V.d. SYSTEMATICS OF *STEPHANIA* (MENISPERMACEAE)

The research project about the taxonomical circumscription within *Stephania* was initiated by my colleague Sovanmoly Hul (Assistant Professor and curator at P). She was the one starting the collaboration with a team of researchers in pharmacology from Marseille, aiming at demonstrating the pharmacological activity of the tubers of some Cambodian species from this genus.

We co-supervised a PhD student, Chhavarath Dary, who studied the systematics of the genus (Hul et al. 2014; Dary et al. 2015; Hul et al. 2017) and the chemical properties of selected species (Dary et al. 2016). Chhavarath reconstructed a molecular phylogeny of the genus (species sampling ratio = 64%) under my supervision. The manuscript has still to be worked on before submission. Building on the world checklist of *Stephania* we published (Hul et al. 2017), Sovanmoly, Chhavarath and I will now work on the Menispermaceae Flora of Cambodia, Laos and Vietnam. *Stephania* is the most species rich of all the genera of Menispermaceae recorded in this region. Chhavarath went back to Phnom Penh where he works as an Assistant Professor.

During the last years, I had the opportunity to work on Chinese *Stephania* with other collaborators. We published a molecular phylogeny (sampling ratio = 74% for China, 48% worldwide; Xie et al. 2015), and a study about the diversity of leaf epidermal features in the subset of Chinese species (Kang et al. 2017).

V.e. FLOWER DISPARITY IN ERICALES

After a PhD in evo-devo (molecular biology techniques, focus on Ranunculaceae), a first postdoc in systematics (molecular biology and herbarium work, focus on Delphinieae), I was eager to address more theoretical issues in the field of flower morphological evolution. This idea was already in my mind during my PhD, and it led to an article about modelling flowers and inflorescences (Jabbour and Citerne 2010). Reading articles from the abundant literature about morphological evolution in various kinds of organisms (e.g. Foote 1991, Niklas 1994, McGhee 1999) helped me mature the project. The idea was to apply mathematical methods to ordinate and analyze the discrete and continuous botanical data.

With this idea in mind, and following the advice Elvira Hörandl (Univ. Göttingen) gave me, I contacted Jürg Schönenberger (Univ. Vienna). Visiting his lab in 2012 was a great opportunity to meet Maria von Balthazar and Yannick Staedler, two of Jürg's collaborators. My idea to look at the profuse botanical data using a mathematical framework was nothing new, and Jürg and Peter Crane (Yale) had already thought about working on Angiosperm morphospace, reanalysing the data set of Stebbins (1951) in the light of the APG classification and applying refined statistical methods.

This project was designed by Jürg Schönenberger and me and got funded by the Austrian Science Fund. It consisted in investigating the evolution of the floral morphospace occupation in the order Ericales. As I got appointed at the MNHN before the start of this project, Jürg and I hired Marion Chartier as a postdoc. Marion started with a review of the studies having looked at plant morphospaces, and reinterpreted under the APG3-light and with modern statistical analyses the pivotal findings of Stebbins (1951; Chartier et al. 2014). Based on a limited number of floral traits, he determined the frequency of each combination of traits that is observable in nature, and he pinpointed the floral organizations that could not be possibly observed, either because he considered them “nearly impossible” (from a developmental or architectural point of view) or “with a low survival”. Marion's postdoc project led her to study the order Ericales, an order of 381 extant species with many economically important species (e.g. tea [Theaceae], kiwi [Actinidiaceae], or rhododendrons [Ericaceae]) and a huge flower disparity. She demonstrated in a very high quality paper (Chartier et al. 2017, Fig. 15) that the Ericales floral morphospace is organized as a continuous cloud in which most clades occupy distinct regions in a mosaic

pattern, that disparity increases with clade size rather than age, and that fossils fall in a narrow portion of the space. She also found that among functional modules, it is the androecium that contributes most to total floral disparity in Ericales. Marion became a very good collaborator, and we together analysed the floral morphological disparity of the afro-montane species of *Delphinium* (Chartier et al. 2016).

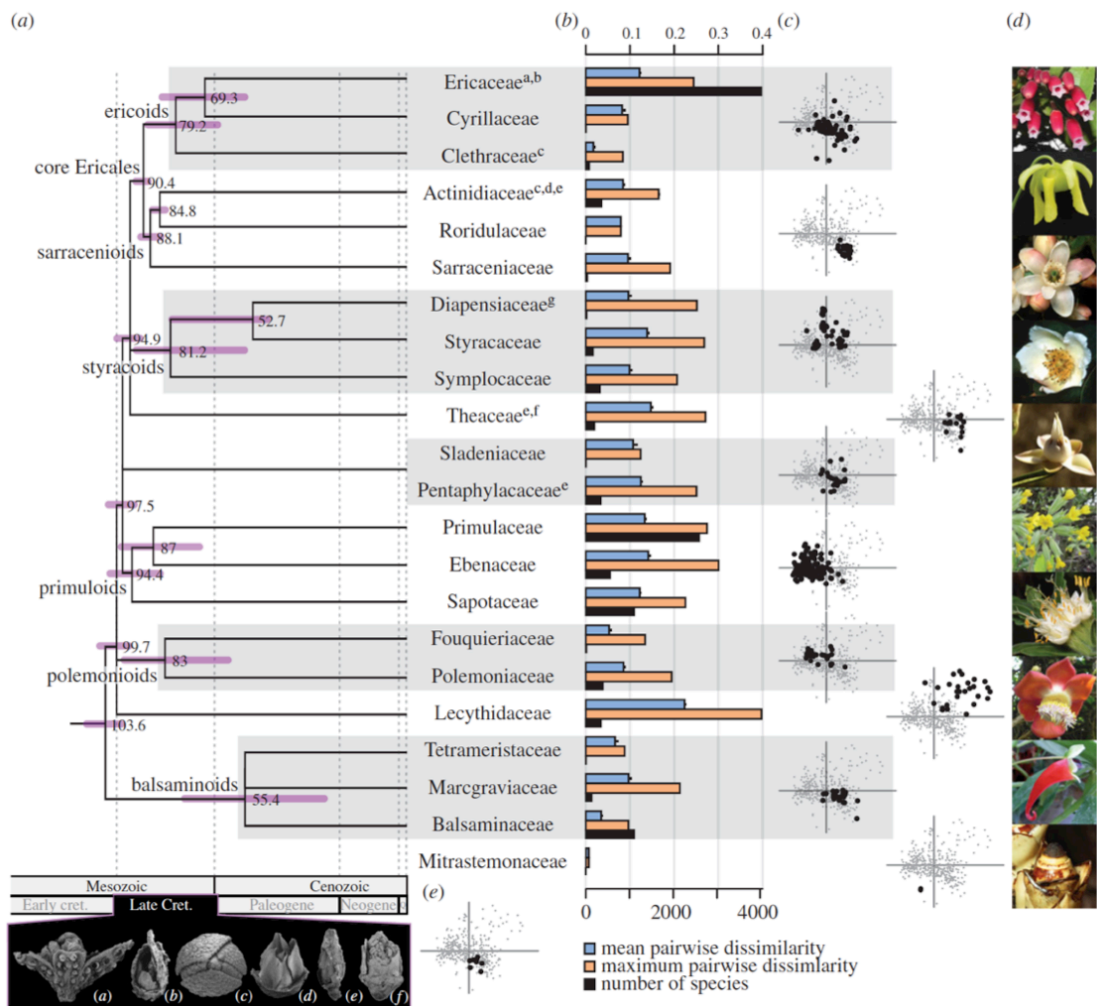


Figure 15: The floral morphospace of Ericales. (a) Phylogenetic relationships among ericalean families. Pictures of six of the fossil genera included in the analyses. Assigned positions of the fossils are highlighted in (a) by superscript letters on the family names. (b) Disparity. (c) 2D-morphospace representation using PCA. Black dots: species of suprafamilial clades or families; grey dots: all remaining ericalean species. (d) Floral diversity in Ericales: from top to bottom: *Satyria* sp. (Ericaceae), *Sarracenia flava* L. (Sarraceniaceae), *Symplocos pendula* Wight (Symplocaceae), *Schima superba* Gardner & Champ. (Theaceae), *Anneslea fragrans* Wall. (Pentaphyllaceae), *Primula officinalis* (L.) Hill (Primulaceae), *Cantua quercifolia* Juss. (Polemoniaceae), *Couroupita guianensis* Aubl. (Lecythidaceae), *Impatiens paucidentata* De Wild. (Balsaminaceae), *Mitrastemon matudae* Yamam. (Mitrastemonaceae). (e) Position of the nine fossil species (black dots) in the morphospace (grey dots).

VI. FUTURE AND PROSPECTIVE RESEARCH

I intend to pursue my research projects in the fields of systematics and taxonomy, using the results of these studies to analyze flower morphological evolution in a regularly updated phylogenetic framework. It will be particularly interesting to switch among different taxonomical scales.

My future and prospective research projects are presented below in the expected chronological order of achievement. Whilst most of them are focused on Delphinieae, some deal with Ranunculaceae and Angiosperms as a whole.

VI.a. AMENDING THE DESCRIPTION OF THE GENUS *DELPHINIUM* (RANUNCULACEAE)

The protologue of *Delphinium* (Linnaeus, 1753) places the genus in the *Polyandria Trigynia* section. Six groups are considered by Linnaeus in *Delphinium*, depending on whether the flower bears a single or three capsules and a single or two nectariferous petals. Other discriminant traits are the branching of the stem and the leaf shape. So the first description of *Delphinium* already included the species belonging to *Consolida* and *Aconitella*.

Now that a species of *Delphinium* with apetalous peloric flowers (Rudall and Bateman 2003) was found (Espinosa et al. 2017), the description of the genus *Delphinium* has to be amended and should include, among other characteristics, the following character states: zygomorphy or actinomorphy, dorsal sepal spurred or not, corolla present or absent (petals not developed), corolla consisting of four or a single fully developed petal, when present.

This will be an important taxonomical act as this genus consists of ca. 300 species distributed worldwide. This manuscript will be prepared together with Felipe Espinosa, Thierry Derooin, Pierre-Emmanuel du Pasquier, and James Byng. Felipe and I will be the first and last authors, respectively.

VI.b. FLOWER DEVELOPMENT IN THE GENUS *STAPHISAGRIA* (RANUNCULACEAE)

The genus *Staphisagria* is the earliest diverging in the tribe Delphinieae. It consists of three Mediterranean species, two of them (*S. requienii* (DC.) Spach and *S. picta* (Willd.) F.Jabbour) being narrow endemics. Material from *S. macrosperma* was collected in spring 2015 and spring 2017 in the Botanical Garden of the MNHN, Paris. Seeds from the two other species will be sown in order to get floral buds in spring 2018. The comparative analysis of the floral development in the three species will then be conducted. Some very interesting population genetic and pollination ecology studies focusing on this group of species were published (Orellana et al. 2009a, 2009b) but the floral morphology of the three species was never investigated in detail and compared. *Staphisagria macrosperma* has the shortest outer spur in the whole tribe Delphinieae.

Describing the floral development in this genus will be crucial to provide a good model to investigate the evo-devo of nested spur formation, the rhythm of spur development in species with contrasted spur lengths, and the physical constraints exerted by the inner spurs on the outer one, and reciprocally.

VI.c. IDENTIFYING THE SISTER GROUP OF THE DELPHINIEAE (RANUNCULACEAE)

To understand flower evolution in Delphinieae and reconstruct the ancestral flower of the tribe, it is required to include the sister group of the tribe in the analyses. The most recent phylogenies of Ranunculales (Wang et al. 2009; matrix of molecular [plastid and nuclear] and morphological traits) and Ranunculaceae (Cossard et al. 2016; eight markers from the three genomes; Wang et al. 2016; one nuclear and five plastid markers) published to date did not solve this issue.

A methodology inspired from Lehtonen et al. (2016) who found, by simulating many alternative phylogenetic tree topologies under different cost regimes, that *Nigella* L. was likely the sister group of the tribe Delphinieae, could be used here with a

taxonomic sampling better adapted to our question. This work will be conducted in collaboration with Wei Wang.

VI.d. A SYNTHESIS ABOUT THE RESEARCH DONE SO FAR ON DELPHINIEAE (RANUNCULACEAE)

Many studies about Delphinieae have been published in the last ten years. A wide array of questions have been answered, in fields as diverse as molecular phylogeny (Jabbour and Renner 2012b), flower morphology and anatomy (Novikoff and Jabbour, 2014), evo-devo (Rasmussen et al. 2009, Jabbour et al. 2014), teratology (Jabbour et al. 2015a), pollination ecology (Duan et al. 2009), karyology (Bosch et al. 2016), and pharmacology (Xiao et al. 2006).

The taxonomic circumscription of many groups within Delphinieae has been particularly impacted by the regular updates of the phylogeny of the tribe. For instance, the genus *Staphisagria* was resurrected (Jabbour and Renner 2011b), *Pseudodelphinium* was sunk into *Delphinium* (Espinosa et al. 2017), *Consolida* and *Aconitella* are nested in *Delphinium* (Jabbour and Renner 2011a) and will be synonymized with *Delphinium*, *Gymnaconitum* was taken out from *Aconitum* (Wang et al. 2013), and *Delphinium* sect. *Delphinium* was erected to the subgenus level (Xiang et al. 2017). The advances in floral evo-devo, and the new data about the morphology and anatomy of Delphinieae flowers, and the very abundant literature about the chemical properties of species from this tribe now have to be synthesized.

Furthermore, new data about flower modularity and integration were obtained by Yiyun Chen (Masters student, co-supervised by Sylvain Gerber and I) at the end of the summer 2017 (Fig. 16). These results obtained with geometric morphometrics on flowers from herbarium specimens will be included in the Special Issue of *Botany Letters* I co-organize with Guillaume Besnard (CNRS Toulouse).

On the long term, Wei Wang and I plan to revise the taxonomy of the genus *Delphinium* (ca. 300 species), building on our publications on the group. The last treatment of the genus was made by Malyutin (1987) based on seed characters. The

recent re-circumscription of some infrageneric taxa will be taken into account, and we expect that many species will need to be synonymized.

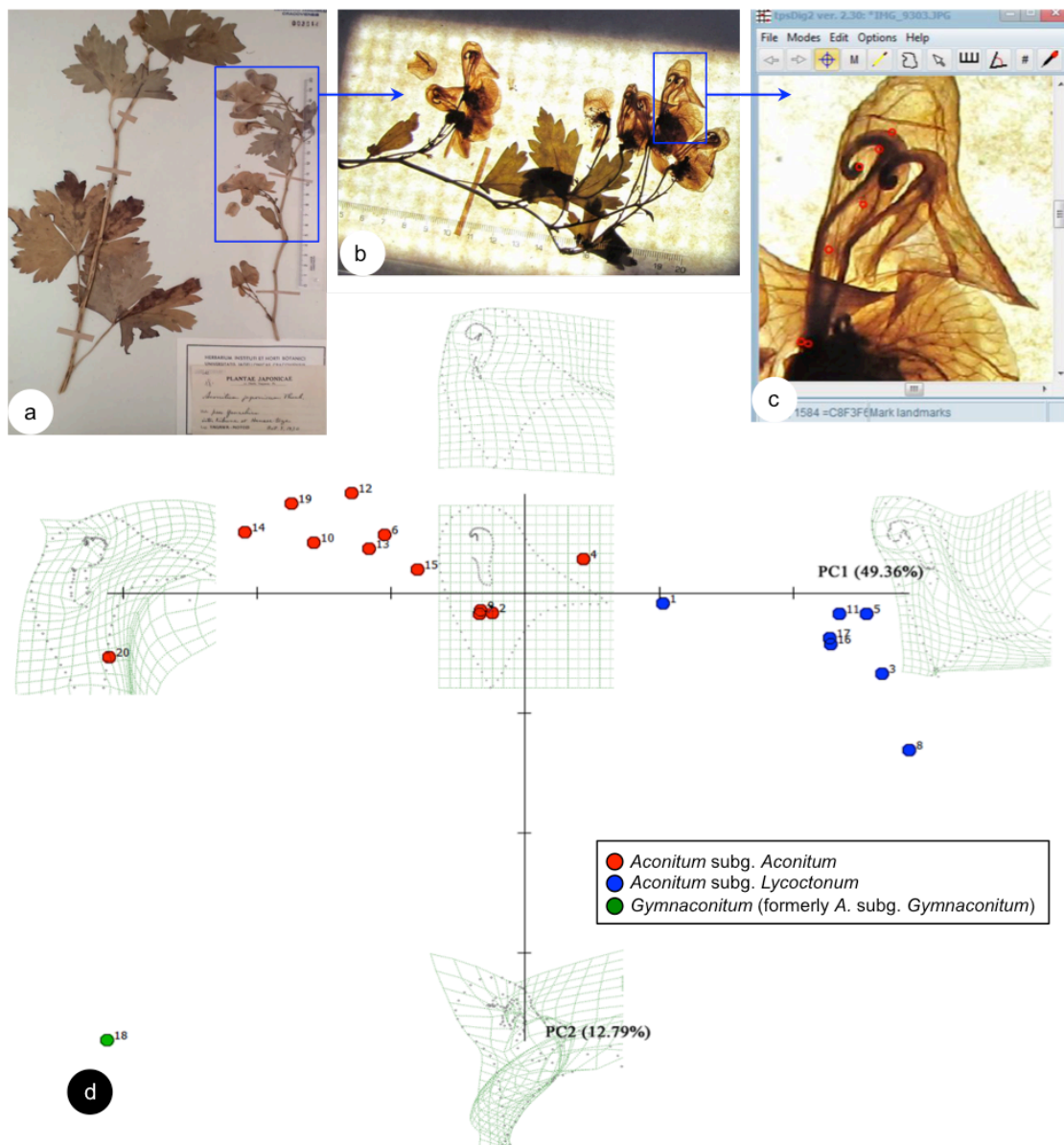


Figure 16: Geometric morphometric study of Delphinieae floral shape based on herbarium specimens: Example of species with *Aconitum*-like flowers; a. Specimen of *A. japonicum* Thunb. from KRA Herbarium (Jagiellonian University, Kraków, Poland), b. Trans-illuminated inflorescence, c. Landmarks put by Yiyun Chen on a dorsal petal, d. 2D geometric morphometric analysis of shape variation. Principal component 1 (PC1) and PC2 account for 49% and 13% of the total variance in the sample, respectively. Virtual flower shapes were produced to visualize the sample mean shape (centre of the graph), as well as modes of floral shape variation along PC1 and PC2. Pictures in a and b, credit: Andriy Novikoff.

VI.e. EVO-DEVO OF PERIANTH DIMORPHISM IN *NIGELLA DAMASCENA* (RANUNCULACEAE)

The teams of Catherine Damerval and of Sophie Nadot, and the MADP team will submit a project to the ANR in September 2017. This project will include an investigation of perianth organ anatomy and development in both floral morphs, as our recent anatomical observations showed that the composition of the perianth of the apetalous morph is more complex than previously thought. Additionally, after having reconstructed the evolution of the distribution area of both floral morphs during the last three centuries thanks to an excellent sampling of the world collection of *N. damascena* herbarium specimens (Jabbour et al. in prep), we will test whether the apetalous morph is always (in time and space) caused by the insertion of a transposon at the *NdAP3-3* locus. Preliminary results suggest that it is not the case.

This project will be extended to other models of Ranunculaceae in order to compare the morphogenesis of perianth organs, and especially petals, at the family level.

VI.f. COMPARATIVE STUDY OF PETAL DEVELOPMENT IN RANUNCULACEAE

This project was designed by Catherine Damerval and me to investigate the developmental and cellular processes involved in petal form diversity. The genesis of petal morphology in some representative genera of Ranunculaceae will be studied by combining morphological and evo-devo approaches.

For this purpose, and to understand the mechanisms responsible for the cellular and morphological development and growth of petals, the PhD student will apply anatomical investigations and histological analyses using microscopic observations, quantitative measurements as well as geometric morphometrics (or CT-scanning if possible). The sampling would include ca. 10 species representing various tribes of the Ranunculaceae differing in corolla aspect and petal morphology. Species from the Delphinieae, from the genera *Aconitum*, *Consolida*, and *Delphinium* will be selected. Interestingly, this tribe comprises more than one-quarter of the species of the family, all being characterized by zygomorphic flowers but differing in perianth structure and composition.

For comparison, species will be selected from other genera showing a broad range of petal morphology (e.g. *Adonis* L., *Aquilegia*, *Helleborus* L.). In order to examine how different petal forms might evolve in correlation with changes in the regulation of cell division and expansion, the student will carry out *in situ hybridization* experiments to discriminate territories of gene expression relating to the cell division and cell differentiation processes by tracking histone H4 in DNA-replicating cells (Fobert et al. 1994).

This comparative study on growth and development of petals should help reconstructing ancestral and derived developmental modules involved in the evolution of floral form in Ranunculaceae. Compared with results in other Angiosperm species, this study will help understanding how the orientation and timing of cell division and predominant growth directions contribute to the origin of flower variation within Angiosperms.

VI.g. EVOLUTION OF EXTRA- AND INTRAFLORAL NECTARIES IN ANGIOSPERMS

Many of the plant taxa I use for my research are species that reward their pollinators with nectar. For instance, *Aconitum* and *Delphinium* flowers have nectar spurs, whereas small pocket-like petals are found in *Nigella*. Many more examples of genera and species characterized by flowers with secretory structures can be found in the literature (e.g. *Diascia* Link & Otto, *Satyrium* Sw., Johnson et al. 2011; Monocots, Smets et al. 2000, see Fernández-Mazuecos and Glover, 2017, Fig. 17).

I would like to gather all existing data relative to extra- and intrafloral secretory structures from the literature, and map the different traits on a phylogeny of Angiosperms. We would get crucial information about the number of transitions towards each type of structure (e.g. nectar pouch, nectar spur, oil spur, nectar canals) and their location in the phylogenetic tree. This result will inspire evo-devo studies investigating the development of such secretory structures and will facilitate the selection of the taxa with similar morphologies (but from different lineages) to be investigated.

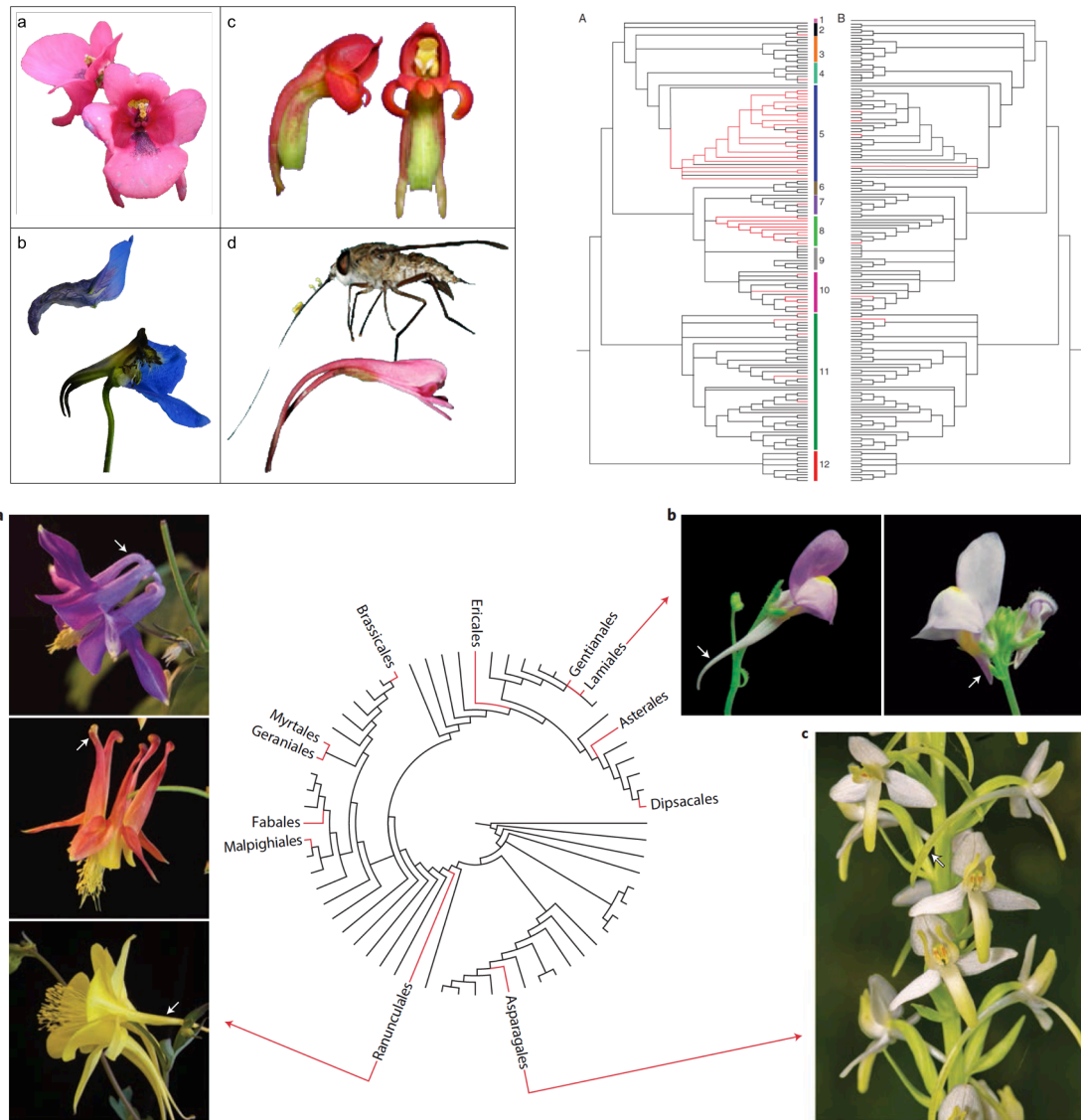


Figure 17: Evolution of spurred flowers in Angiosperms. Pictures of four species producing twin-spurred flowers. a. *Diascia integerrima* E.Mey ex Benth. (Scrophulariaceae) and its pair of oil spurs (<http://www.randomharvest.co.za/South-African-Indigenous-Plants/ShowPlant/PlantId/259?Plant=Diascia+integerrima+Pink>), b. *Delphinium elatum* (Ranunculaceae) and the pair of inner nectar spurs, c. *Satyrrium sceptrum* Schltr. (Orchidaceae) with its pair of nectar spurs, d. *Satyrrium macrophyllum* Lindl. with its pollinator, the long proboscis fly *Prosoeca ganglbaueri*. c and d from Johnson et al. (2011).

Mirror trees of the Asteridae showing the evolution of perianth symmetry and the number of spurs optimized using the maximum parsimony method. (A) Evolution of perianth symmetry. Black: actinomorphy; red: zygomorphy. (B) Evolution of the number of spurs. Black: 0 or equal to perianth merism; red: inferior to perianth merism. Coloured lines and numbers refer to the orders of Asteridae: 1, Garryales; 2, Untitled Group 1; 3, Gentianales; 4, Solanales; 5, Lamiales; 6, Aquifoliales; 7, Apiales; 8, Dipsacales; 9, Untitled Group 2; 10, Asterales; 11, Ericales; 12, Cornales. From Jabbour et al. (2008).

Model systems to study the evolution of nectar spurs. Ordinal-level phylogeny of flowering plants, with

red branches indicating orders in which nectar spurs have evolved (Fernández-Mazuecos and Glover 2017). Three phylogenetically disparate genera in which evolution of nectar spurs is being investigated are shown. a, *Aquilegia*: species with different pollination syndromes display contrasting spur lengths, as exemplified by *A. sibirica* Lam. (c. 10 mm, bee-pollinated, top), *A. formosa* Fisch. ex DC. (ca. 20 mm, hummingbird-pollinated, centre) and *A. chrysantha* A.Gray (ca. 70 mm, hawkmoth-pollinated, bottom). b, *Linaria* Mill.: *L. salzmännii* (ca. 13 mm, left) and *L. clementei* Haenseler ex Boiss. (ca. 3 mm, right) are two closely related species with nearly identical floral morphology but contrasting spur lengths. c, *Platanthera* Rich.: intraspecific variation in spur length in *P. bifolia* (L.) Rich. (ca. 15–40 mm) correlates with the proboscis length of local pollinators.

This work could be suitable for a MSc student or a PhD student, and will be done in collaboration with Thierry Deroin (MNHN), Sophie Nadot (Univ. Paris Sud), Catherine Damerval (CNRS Le Moulon), and potentially with Beverley Glover (Univ. Cambridge) and Eberhard Fischer (specialist of *Impatiens* L.; Univ. Koblenz, Germany).

Although we have at hand a preliminary database, this project has not started yet.

I was asked by the journal Botany Letters (formerly Acta Botanica Gallica, and initially known as Bulletin de la Société Botanique de France) to pick in their archives one of their highly cited papers, to translate it into English, and to add a concise synthesis of the research conducted so far on the same topic.

In order to fuel this project on secretory structures in Angiosperms, I selected an article entitled: “Etude sur l’anatomie et la physiologie des nectaires”, by Gaston Bonnier (1878, Bulletin de la Société Botanique de France).

VI.h. PHYLOGEOGRAPHY OF *DELPHINIUM* IN THE EAST AFRICAN RIFT SYSTEM

The investigation of flower morphological diversity, phylogeny and biogeography of the afro-montane *Delphinium* provides excellent bases for further studies focusing on the population genetics and on the phylogeography within the group, possibly at finer geographical scales. In addition, the hypotheses of hybridization among morphospecies, and of the evolutionary convergence towards the *D. leroyi*-like flower morphology in the two clades of afro-montane *Delphinium*, have still to be tested.

New collections are needed, and the first trip in East Africa will take place in Kenya and Malawi, thanks to a funding form the National Geographic Society, in collaboration with Stefan Dressler (Senckenberg Museum, Frankfurt; Fig. 18), Itambo Malombe (Director of the EA Herbarium, Nairobi), and Esther Kioko (Head of Zoology Department, National Museums of Kenya; for the observations of floral visitors).

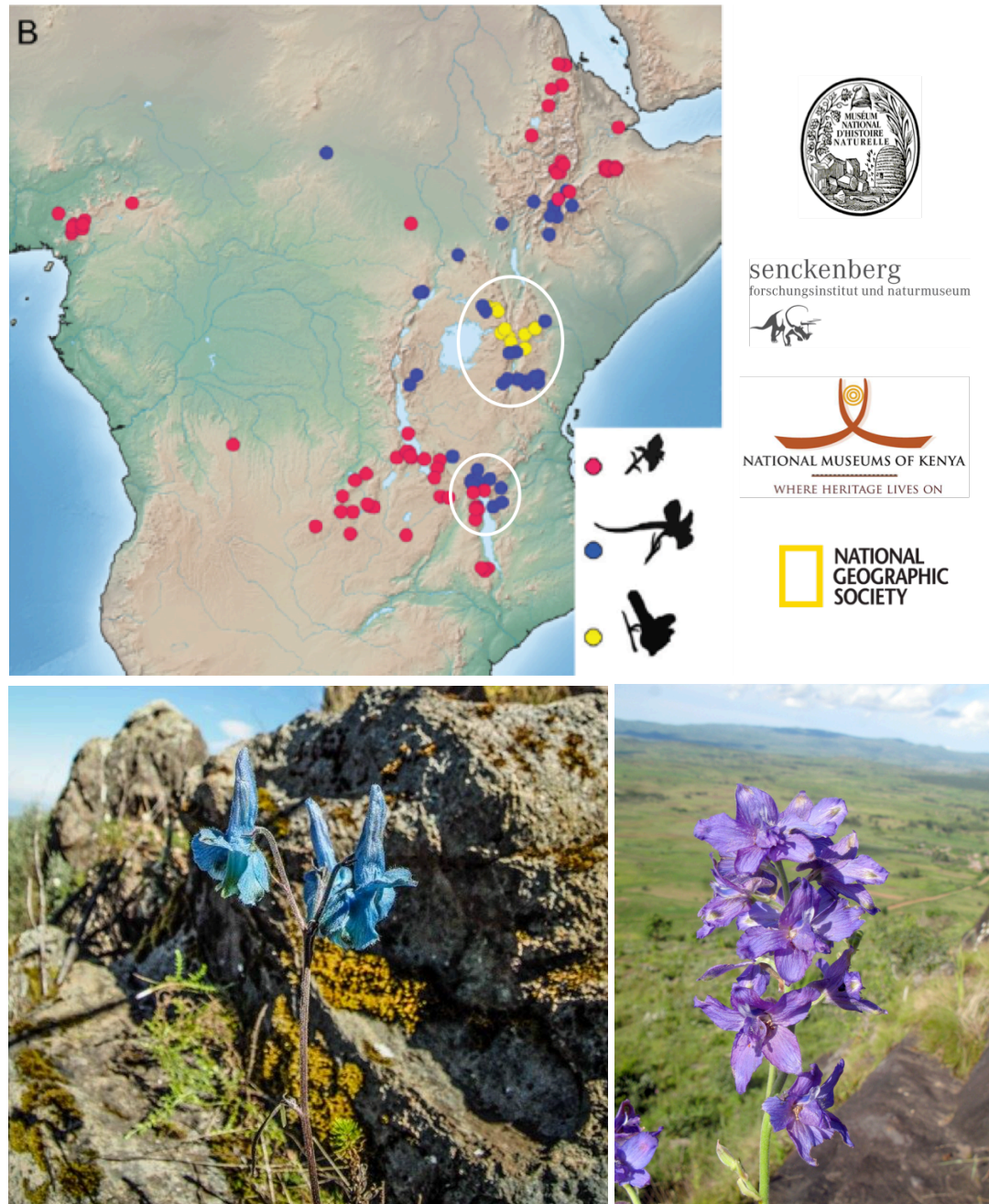


Figure 18: Collecting afro-montane *Delphinium* in Kenya and Malawi in 2018. Distribution area of the three morphospecies of afro-montane *Delphinium*. The high altitude areas (in Kenya and Malawi)

Stefan Dressler and I will visit in August 2018 are circled in white. The project gathers partners from the MNHN, the Senckenberg Museum (Frankfurt), and from the National Museums of Kenya. The field trip is funded by the NGS. Picture of *D. macrocentrum* Oliv. in its natural habitat on Mt. Elgon (Kenya; credit: David Gwynne-Evans). Picture of *D. dasycaulon* Fresen. in its natural habitat, Tala Hill Kasense, Rukwa (Tanzania; credit: Robert v. Blittersdorff; <http://www.africanplants.senckenberg.de>).

The continuation of this project calls for more field trips, in priority in Ethiopia and Tanzania, but also in Cameroon (contact: Thomas Couvreur, IRD, Montpellier, <https://sites.google.com/site/plantbiodiversityadaptation/members/permanents/thomas-couvreur>).

The newly collected data will be analysed together with my collaborators in this project, as well as with Guillaume Besnard (CNRS Toulouse, <http://www.edb.upstlse.fr/Besnard-Guillaume.html>) who is an expert in conducting genomic studies on herbarium specimens.

These prospective studies will only be possible with the contribution of my European, Asian, and African collaborators. Each of these studies will give us the opportunity to train students in various disciplines, from plant anatomy to phylogeny, and from taxonomy to the history of science.

VI.i. LONG-TERM PROJECTS

On the long term, I would like to train myself in embryology and palaeobotany in order to be able to answer in a more integrative way questions in the fields of plant systematics, phylogeny, and morphological evolution. I am already in contact with a paleobotanist (Dario de Franceschi) and an archeobotanist (Aurélié Salavert) at the MNHN, and it would be relatively easy for me to learn from them and look at the very rich fossil plant collection. I feel that getting familiar with embryology would be a more difficult task. It would probably be necessary to spend some time in a specialized laboratory where I could learn the techniques and get intensive training.

I would also like to invest some time in thinking about science and its evolution (probably with my colleagues Thierry Deroin and Corinne Sarthou, see Lamy et al. 2016), particularly about the evolution of concepts in plant morphology and

development, adapting the methodology of Fisler and Lecointre (2013) who studied the evolution of the use of trees in systematics (Fig. 19).

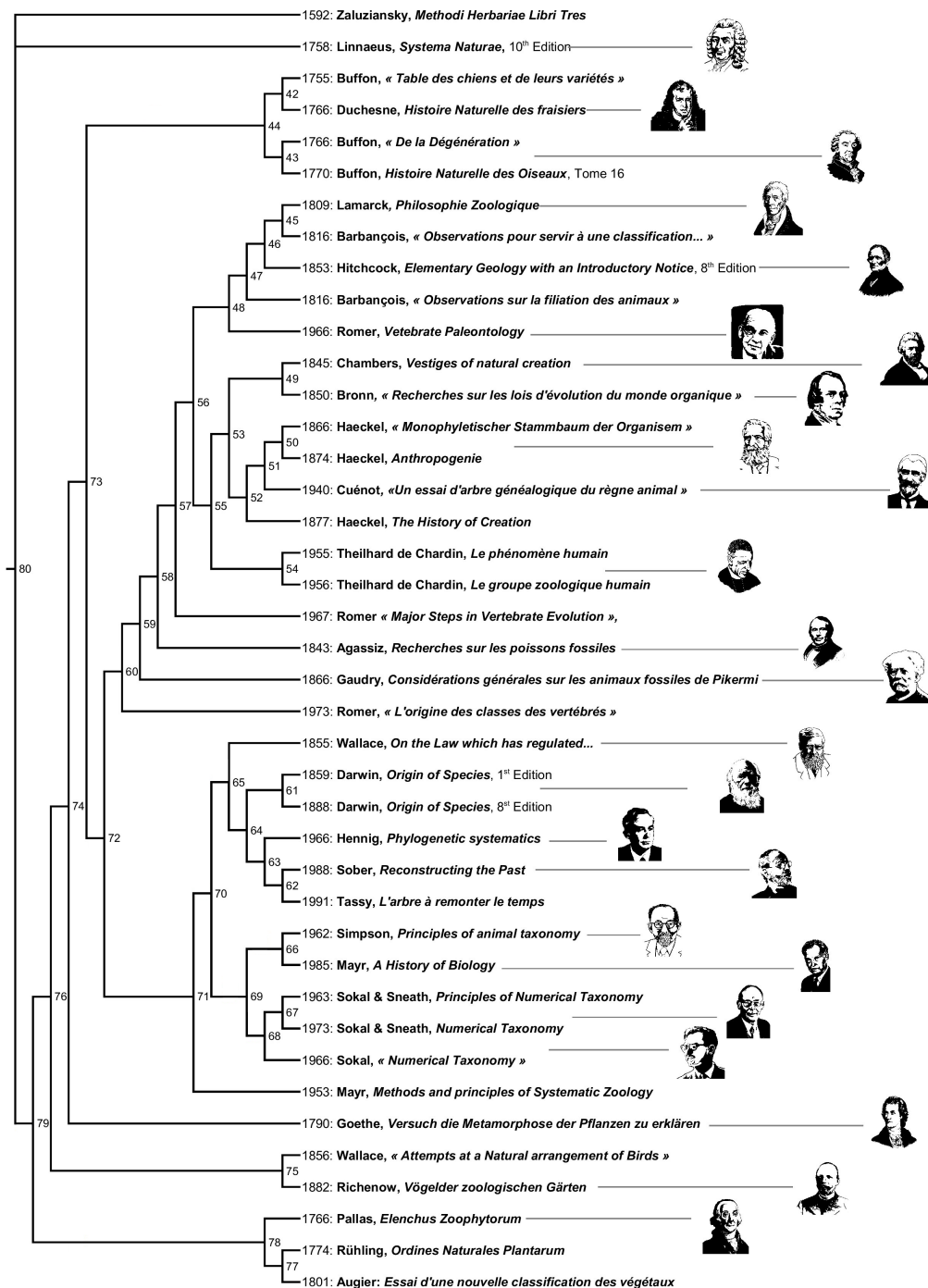


Figure 19: A phylogenetic tree showing the relationships among different concepts of trees (in a systematic meaning). Conceptual parts of ideas, writings and drawings about trees were discretized and coded as 91 characters into a matrix. Examples of characters are “time taken into consideration” (Yes or No), “the tree has a classificatory aim” (Yes or No), and “Use of monophyly” (Yes or No). Adapted from Fisler & Lecointre (2013).

VII. THE MANY FUTURES OF PLANT MORPHOLOGY AT THE MNHN (AND BEYOND)

Many of the botanists at the MNHN study plant morphology to complement a study focusing on a phylogeny of a group of taxa or to bring evidences for a taxonomic treatment. So the knowledge about plant morphology exists, is shared among colleagues, and is transmitted to the interns and students. However, detailed studies designed to answer a question about the evolution of morphological or anatomical structures, or studies aiming at discussing a concept in the fields of plant morphology and plant anatomy are less common, as they require genuine expertise. The team *Morphology-Anatomy and Development of Plants* is the only team in the Botany section, and even in the *Institute of Systematics, Evolution and Biodiversity* that makes clear that its members are the local experts in these fields. We made this choice to highlight our assets, and show our originality, although we conduct research in the fields of plant systematics, plant development in space, and history of sciences.

Choosing to build a team based on research projects about plant morphology, anatomy and development have some obvious effects. Even if this is not applicable to all our research projects, publishing in high impact factor journals can be difficult. Getting funding for plant morphology-oriented projects could be even more difficult in the current scientific context in France, or even in Europe (Jürg Schönenberger and I were extremely happy to get a FWF funding from the Austrian government to work on the evolution of the floral morphospace).

Students of plant morphology have to face many prejudices and have to repeatedly answer the same critics and explain why this discipline is important in the botanical research of the 21st century. How many times did I hear the following sentences:

- Plant morphology is so old-fashioned!
- When you study plant morphology, obtaining results is such a long process!
- You cannot obtain ground-breaking results (anymore) in this field.
- You use simple (simplistic) and old-fashioned methods.
- The objects you study are less noble or less complex then, let's say, a genome, or a phylogenetic tree with hundreds of accessions.

This discipline may seem unrewarding at first sight, owing to the time one should invest in the dissections, experiments, and observations, and to the difficulty to publish

the results in high impact journals. However, studying the morphology, anatomy, and development of plants can be fascinating. The community of botanists studying flower morphology is not large, and it is possible for a flower morphologist in his/her middle career to know and to have contacts with all the other members of the community (Fig. 20).



Chelsea Specht	Berkeley	Maxim Nuraliev	Moscow
Shirley Tucker	Santa Barbara	Alexei Oskolski	Moscow
Denis Barabé	Montreal	Andrey Sinjushin	Moscow
Joachim Vieth	Montreal	Dmitry Sokoloff	Moscow
Rolf Sattler	Montreal	Mohammad Reza Dadpour	Tabriz
Christopher R. Hardy	Millersville	Shahin Zarre	Tehran
Natalia Pabón-Mora	Medellín	Yi Ren	Shanxi
Simone de Pádua Teixeira	São Paulo	Liang Zhao	Shanxi
Kester Bull-Hereñu	Santiago		

Figure 20: Contemporary (floral) morphologists-anatomists throughout the world. See p. 80 for a focus on Europe. I offer my apologies to those I have forgotten.



Louis Ronse de Craene	Edinburgh	Somayeh Naghiloo	Mainz
Paula Rudall	Kew	Peter Leins	Heidelberg
Gerhard Prenner	Kew	Claudia Erbar	Heidelberg
Thierry Deroin	Paris	Rolf Rutishauser	Zurich
Florian Jabbour	Paris	Peter Endress	Zurich
Sophie Nadot	Orsay	Jürg Schönenberger	Vienna
Catherine Damerval	Gif-sur-Yvette	Maria von Balthazar	Vienna
Erik Smets	Leiden	Yannick Städler	Vienna
Julien Bachelier	Berlin	Andriy Novikoff	Lviv
Anette Becker	Gießen	Anastasiya Odintsova	Lviv
Regine Claßen-Bockhoff	Mainz	Livia Wanntorp	Stockholm

Figure 20: Continued.

Different scenarios for the future of plant (and flower) morphology could be thought about, depending on the geographical level considered (an Institute, a country, worldwide) and on the actions and decisions taken by different entities (individuals, head of University, funding agencies, governments setting the next public research priorities).

In the most optimistic (but unlikely) scenario, priority will be put on exploring, describing, and analysing the evolution of biodiversity, more funding opportunities will become available, the number of taxonomists will increase, and a new generation

of plant morphologists will be trained and will find positions in line with their expertise. The opposite scenario would involve a decrease in the number of experts in plant morphology, and consequently of teachers and mentors. The new generations of botanists would overlook the discipline of plant morphology (this trend is already noticeable as some courses in botany disappear in many Universities). Locally, this trend may lead to the loss of expertise in plant morphology-anatomy. This situation may last several decades before this discipline would be re-discovered, knowing that building new group of experts is not straightforward, especially in plant morphology-anatomy. Indeed, (but I am perhaps wrong), the role of mentors and colleagues is crucial in this discipline, for the transmission of the experimental know-how and of the theoretical knowledge (evolution of concepts, schools of thought, knowledge of recent and old publications, possibly in different languages).

In my opinion, the most realistic scenario would be a compromise between the two previous ones, and highly depends on the personal involvement of individuals rather than on an improvement of the funding policies or the scientific priorities of Universities, although these two aspects are important. Researchers in the field of plant morphology should 1) work on multiplying the connections of their network, 2) teach and train more students and make them travel within their network to get familiar with different methods and “families” of researchers, 3) build collaborations to be more successful when applying for funding. Teaching is essential as this is the only way to show the students that their prejudice against plant morphology and anatomy are unfounded. Students and interns should be wisely trained, i.e. trained in a way that they know as well the bases of evolutionary biology, evo-devo, systematics, physiology, and paleobotany. Such disciplines are a chance for plant morphology, as they highlight its importance and arouse new approaches and concepts. Researchers should invest in the young ones at early stages in their career.

As plant morphologists-anatomists, it is our duty to go towards the other researchers from other disciplines. If they do not include any investigation of plant morphology-anatomy-development, it is often because they do not know how crucial the results would be to better understand their model system and target the most useful structure and/or developmental stage for their own study.

Plant morphology-anatomy is neither a minor discipline nor a discipline from the past. On the contrary, the roots of plant morphology-anatomy are very deep. Many advances, especially in the imaging techniques, have been made in the last 50 years, and morphology-anatomy deserves a place among the -omics. Why could not we argue that we are conducting studies in the field of morphomics and anatomics, if this is a way to get more funding and visibility from other fields of science?

Few disciplines allow a single researcher to conduct all the steps of the research (from material sampling to writing a manuscript through the experimental part) his-/herself. Plant morphology is one of them. In this context, one should focus even more on collaborating with colleagues, locally and internationally, training students tirelessly, and integrating his/her research in the broad context of evolutionary biology.

VIII. INVOLVEMENT IN THE DIFFERENT TASKS OF THE MNHN

At the MNHN, the Assistant Professors and Professors are assigned five missions: conducting research, curating collections, teaching, making expert assessments, and popularizing science. I kept this part deliberately short as the Habilitation thesis focuses on research.

VIII.a. RESEARCH TEAM RESPONSIBILITY

My research projects are developed in § V and VI. I add here information about my recent experience as a team leader. Since January 2016, I share with Thierry Deroin the responsibility of the MADP (Morphology, Anatomy, and Development of Plants) team. The team consists of five permanent members: three Assistant Professors, one engineer, and one technician. We investigate the morphology, anatomy and development of plants (mostly flowers, but also roots) in a phylogenetic framework, in model (*Arabidopsis thaliana* (L.) Heynh., *Aquilegia* sp.) or non-model (e.g. *Hyacinthoides* sp., *Delphinium* sp.) species. Our objectives are to reconstruct the evolution of our structures of interest (e.g. the shoot meristem, the floral meristem, the carpel) and to study the impact of the environment (contrasted habitats, microgravity and spatial radiations) on their development.

We submitted earlier in 2016 a project to a call for proposals of the city of Paris, in order to get an additional funding for our study on the impact of radiations on the development of the plants in spatial conditions.

Next spring, the MADP team will ask the MNHN for the opening of an Assist. Prof. position, to fill important needs in teaching plant morphology and anatomy at the MNHN. One option would be to design the research part of the job description focusing on the evolution of the morphological-anatomical structures of plants and on their development, in relation with environmental constraints, and based on living material and on the herbarium, spirit and slide collections. The taxonomic and geographical focus of the position will be specified if necessary. The Assist. Prof. would work as a curator as well.

VIII.b. CURATION AT P HERBARIUM

I am a curator for 12 orders (ca. 750,000 specimens) of flowering plants (e.g. Asterales, Ranunculales) at Paris Herbarium (P, Le Bras et al. 2017). The job consists in updating the classification of specimens according to the recent taxonomic revisions, welcoming visitors and preparing loans for other institutions. I published several nomenclatural acts in relation with the part of the collection I curate (in Menispermaceae: Hul et al. 2014, Dary et al. 2015, Hul et al. 2017; in Ranunculaceae: Jabbour and Dressler 2015, Espinosa et al. 2017, Xiang et al. 2017).

My own collections are deposited at P, and I plan to go on a field trip with Stefan Dressler (Senckenberg Museum, Frankfurt) in July 2018 in Kenya and Malawi to collect specimens of *Delphinium*. This trip has been funded by the National Geographic Society.

In 2015 and 2016, I invited two colleagues at P to work on our collections. Jelena Aleksić (Serbia) and Andriy Novikoff (Ukraine) worked on Serbian spruces and on Delphinieae, respectively.

Many bridges exist between the curation and the research parts of my job at the Museum. Indeed, some of the visitors I welcomed became collaborators. Stefan Dressler works with me on the systematics of the afro-montane *Delphinium*, Pierre-Emmanuel du Pasquier (Geneva Herbarium) contributes to the nomenclatural revision of *Consolida* and *Aconitella* (Ranunculaceae), James Byng (Naturalis, Leiden) collaborated with my PhD student on the study of *Pseudodelphinium turcicum* (Espinosa et al. 2017), and Limin Lu (Institute of Botany, Beijing) included me in a project about Asian Vitaceae.

VIII.c. TEACHING

I teach systematics and evolutionary botany to Masters students and Agronomy engineering students. I supervise Masters or undergraduate interns each year.

VIII.d. EXPERT ASSESSMENTS

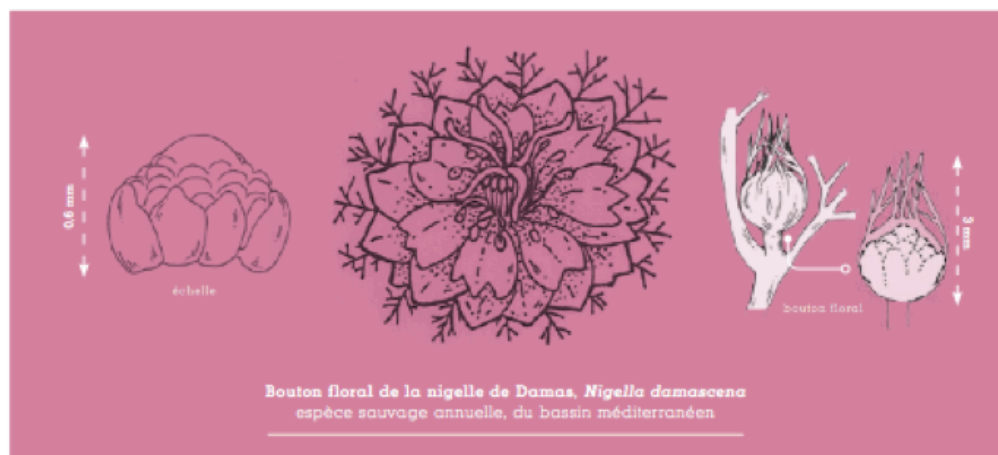
I reviewed manuscripts submitted to 18 scientific journals, and proposals submitted to different authorities at the Museum and to the Polish National Science Centre. I am currently an associate editor for the journal *Botany Letters* (formerly *Acta Botanica Gallica*), and a member of the commission for scientific and technical literature at the French Centre National du Livre. This public organization financially helps the work of editors, authors and translators. In each commission, a dozen of members are designated for three years.

VIII.e. SCIENCE POPULARIZATION

Together with my colleagues at the MNHN, I contributed to the permanent exhibition in the Botany building. The team of curators also worked on a book entitled “L’Herbier du Muséum” (Aupic et al. 2013), and since I got hired at the Museum, I participated each year in the “Fête de la Science” national event, during which labs open their doors to the public and present their work. In 2018, an open-air exhibition in the Jardin des Plantes will highlight projects currently conducted at the Museum. Our project about the floral dimorphism of *Nigella damascena* got selected (see Fig. 21).



Figure 21: Science popularization at the MNHN. The poster and panel (SEM picture) that will be displayed in the Jardin des Plantes at the MNHN, explaining the floral dimorphisms in *Nigella damascena* and the purpose of studying the development of the floral buds. The bottom picture was taken during a previous exhibition in 2016 called “Planète Grenouille” (Credit: Cyril Ruoso, <http://www.cyrilruoso.com/?Planete-grenouille>).



Qu'est-ce que le dimorphisme floral ?

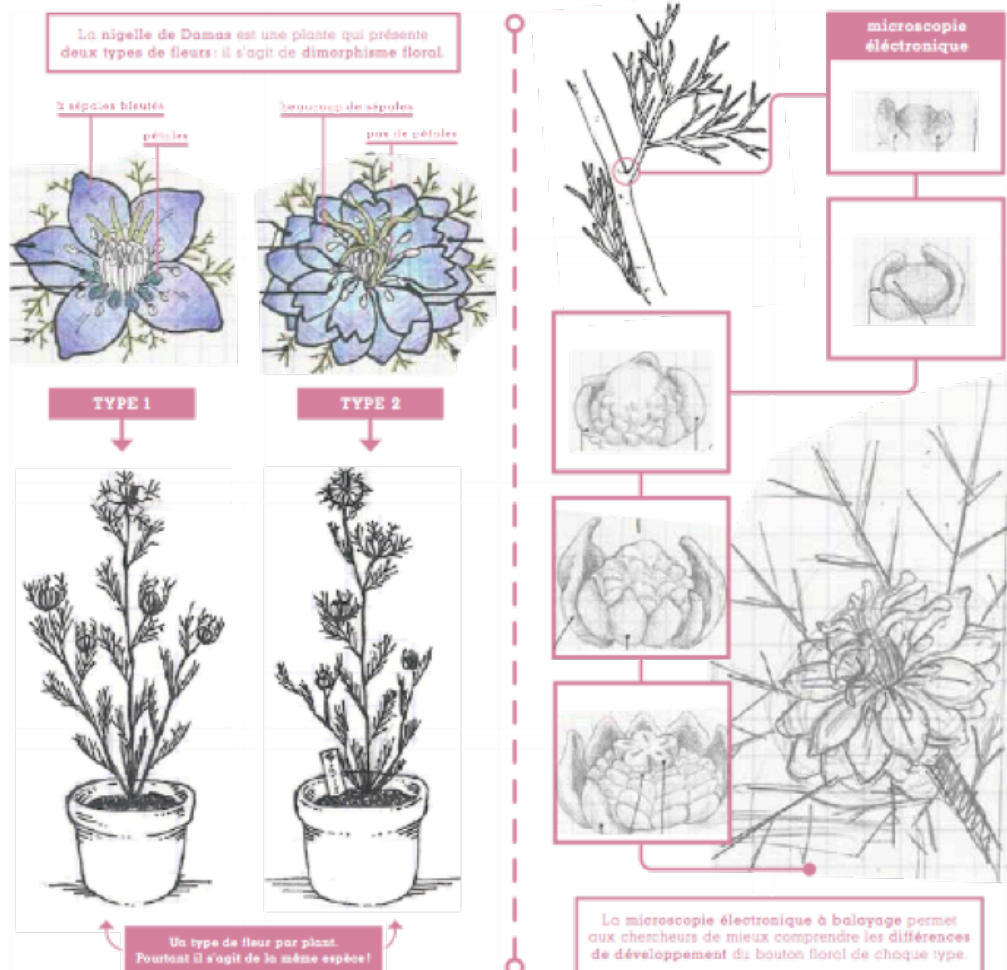


Figure 21: Continued.

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