

Progress in Botany 83

Ulrich Lüttge · Francisco M. Cánovas ·
María-Carmen Risueño ·
Christoph Leuschner ·
Hans Pretzsch *Editors*

Progress in Botany

 Springer

Progress in Botany

Volume 83

Series Editors

Ulrich Lüttge
Department of Biology
Technical University of Darmstadt
Darmstadt, Germany

Francisco M. Cánovas
Department of Molecular Biology and Biochemistry
University of Málaga
Málaga, Spain

Hans Pretzsch
Chair for Forest Growth and Yield Science
School of Life Sciences Weihenstephan
Technical University of Munich
Freising, Germany

María-Carmen Risueño
Pollen Biotechnology of Crop Plants Group
Centro de Investigaciones Biológicas “Margarita Salas” (CIB) CSIC Madrid
Madrid, Spain

Christoph Leuschner
Plant Ecology
University of Goettingen
Göttingen, Germany

Progress in Botany is devoted to all the colourful aspects of plant biology. The annual volumes consist of invited reviews spanning the fields of molecular genetics, cell biology, physiology, comparative morphology, systematics, ecology, biotechnology and vegetation science, and combine the depth of the frontiers of research with considerable breadth of view. Thus, they establish unique links in a world of increasing specialization. Progress in Botany is engaged in fostering the progression from broad information to advanced knowledge and finally deepened understanding. All chapters are thoroughly peer-reviewed.

Ulrich Lüttge • Francisco M. Cánovas •
María-Carmen Risueño • Christoph Leuschner •
Hans Pretzsch
Editors

Progress in Botany Vol. 83

 Springer

Editors

Ulrich Lüttge
Department of Biology
Technical University of Darmstadt
Darmstadt, Germany

Francisco M. Cánovas
Department of Molecular Biology and
Biochemistry
University of Málaga
Málaga, Spain

María-Carmen Risueño
Pollen Biotechnology of Crop Plants
Group
Centro de Investigaciones Biológicas
“Margarita Salas” (CIB) CSIC Madrid
Madrid, Spain

Christoph Leuschner
Plant Ecology
University of Göttingen
Göttingen, Germany

Hans Pretzsch
Chair for Forest Growth and Yield
Science, School of Life Sciences
Weihenstephan
Technical University of Munich
Freising, Germany

ISSN 0340-4773

ISSN 2197-8492 (electronic)

Progress in Botany

ISBN 978-3-031-12781-6

ISBN 978-3-031-12782-3 (eBook)

<https://doi.org/10.1007/978-3-031-12782-3>

© The Editor(s) (if applicable) and The Author(s), under exclusive license to Springer Nature Switzerland AG 2023

This work is subject to copyright. All rights are solely and exclusively licensed by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.

The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

The publisher, the authors, and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, expressed or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature Switzerland AG
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

Contents

Plant Evolution and Systematics 1982–2022: Changing Questions and Methods as Seen by a Participant	1
Susanne S. Renner	
Plants in Space: Novel Physiological Challenges and Adaptation Mechanisms	29
F. Javier Medina, Aránzazu Manzano, Khaled Y. Kamal, Malgorzata Ciska, and Raúl Herranz	
Terrestrialization: The Conquest of Dry Land by Plants	65
Ulrich Lüttge	
Legacies of Human Land Use Impacts in Central European Forests . . .	91
M. Wulf	
Global Forest Biodiversity: Current State, Trends, and Threats	125
C. Leuschner and J. Homeier	
An Overview on Dendrochronology and Quantitative Wood Anatomy Studies of Conifers in Southern Siberia (Russia)	161
Alberto Arzac, Marina V. Fonti, and Eugene A. Vaganov	
Holobionts in the Plant Kingdom	183
Ulrich Lüttge	
Evolution of Holobiont-Like Systems: From Individual to Composed Ecological and Global Units	203
Rainer Matyssek, Ulrich Lüttge, and Wolfgang zu Castell	
Plant Proteolysis in Development: Insights and Functions	249
Ioannis H. Hatzianestis, Andriani Mentzelopoulou, and Panagiotis N. Moschou	

Experimental Evidence for Fruit Memory and Its Applications to Post-harvest Physiology and Technology: An Overview 291
Gabriela N. Reissig, Yutcelia C. Galviz Fajardo, André G. Parise, Rafael V. Ribeiro, and Gustavo M. Souza

Movement of Aquatic Oxygenic Photosynthetic Organisms 315
John A. Raven and Michel Lavoie

An Overview of Water and Nutrient Uptake by Epiphytic Bromeliads: New Insights into the Absorptive Capability of Leaf Trichomes and Roots 345
Cassia Ayumi Takahashi, Antônio Azeredo Coutinho Neto, and Helenice Mercier

Phi Thickenings: Their History, Current Status and Role(s) in Mechanically Strengthening the Plant Root 363
David A. Collings, Maketalena Aleamotu‘a, and David W. McCurdy

Contributors

Maketalena Aleamotu'a Centre for Plant Science, School of Environmental and Life Sciences, The University of Newcastle, Callaghan, NSW, Australia

Alberto Arzac Siberian Federal University, Krasnoyarsk, Russia

Malgorzata Ciska Centro de Investigaciones Biológicas Margarita Salas – CSIC, Madrid, Spain

David A. Collings Centre for Plant Science, School of Environmental and Life Sciences, The University of Newcastle, Callaghan, NSW, Australia
School of Molecular Sciences, The University of Western Australia, Crawley, WA, Australia

Antônio Azeredo Coutinho Neto Department of Botany, Institute of Biosciences, University of São Paulo, São Paulo, SP, Brazil

Marina V. Fonti Siberian Federal University, Krasnoyarsk, Russia

Yutcelia C. Galviz Fajardo Laboratory of Plant Cognition and Electrophysiology (LACEV), Department of Botany, Institute of Biology, Federal University of Pelotas (UFPeL), Capão do Leão, RS, Brazil

Ioannis H. Hatzianestis Department of Biology, University of Crete, Heraklion, Greece
Institute of Molecular Biology and Biotechnology, Foundation for Research and Technology-Hellas, Heraklion, Greece

Raúl Herranz Centro de Investigaciones Biológicas Margarita Salas – CSIC, Madrid, Spain

J. Homeier Plant Ecology, University of Göttingen, Göttingen, Germany

Khaled Y. Kamal Centro de Investigaciones Biológicas Margarita Salas – CSIC, Madrid, Spain
Department of Health and Kinesiology, Texas A&M University, College Station, TX, USA

Michel Lavoie Quebec, Canada

C. Leuschner Plant Ecology, University of Göttingen, Göttingen, Germany

Ulrich Lüttge Department of Biology, Technical University of Darmstadt, Darmstadt, Germany

Aránzazu Manzano Centro de Investigaciones Biológicas Margarita Salas – CSIC, Madrid, Spain

Rainer Matyssek Life Science Center Weihenstephan, Technische Universität München, Freising, Germany

David W. McCurdy Centre for Plant Science, School of Environmental and Life Sciences, The University of Newcastle, Callaghan, NSW, Australia

F. Javier Medina Centro de Investigaciones Biológicas Margarita Salas – CSIC, Madrid, Spain

Andriani Mentzelopoulou Department of Biology, University of Crete, Heraklion, Greece

Institute of Molecular Biology and Biotechnology, Foundation for Research and Technology-Hellas, Heraklion, Greece

Helenice Mercier Department of Botany, Institute of Biosciences, University of São Paulo, São Paulo, SP, Brazil

Panagiotis N. Moschou Department of Biology, University of Crete, Heraklion, Greece

Institute of Molecular Biology and Biotechnology, Foundation for Research and Technology-Hellas, Heraklion, Greece

Department of Plant Biology, Uppsala BioCenter, Swedish University of Agricultural Sciences and Linnean Center for Plant Biology, Uppsala, Sweden

André G. Parise Laboratory of Plant Cognition and Electrophysiology (LACEV), Department of Botany, Institute of Biology, Federal University of Pelotas (UFPeL), Capão do Leão, RS, Brazil

John A. Raven Division of Plant Science, University of Dundee at The James Hutton Institute, Dundee, UK

School of Biological Sciences, University of Western Australia, Crawley, WA, Australia

Climate Changer Cluster, University of Technology Sydney, Ultimo, NSW, Australia

Gabriela N. Reissig Laboratory of Plant Cognition and Electrophysiology (LACEV), Department of Botany, Institute of Biology, Federal University of Pelotas (UFPeI), Capão do Leão, RS, Brazil

Susanne S. Renner Department of Biology, Washington University, Saint Louis, MO, USA

Rafael V. Ribeiro Laboratory of Crop Physiology (LCroP), Department of Plant Biology, Institute of Biology, University of Campinas (IB/UNICAMP), Campinas, SP, Brazil

Gustavo M. Souza Laboratory of Plant Cognition and Electrophysiology (LACEV), Department of Botany, Institute of Biology, Federal University of Pelotas (UFPeI), Capão do Leão, RS, Brazil

Cassia Ayumi Takahashi Department of Botany, Institute of Biosciences, University of São Paulo, São Paulo, SP, Brazil

Eugene A. Vaganov Siberian Federal University, Krasnoyarsk, Russia
V.N. Sukachev Institute of Forest SB RAS, Federal Research Center 'Krasnoyarsk Science Center SB RAS', Krasnoyarsk, Russia

M. Wulf Leibniz Centre for Agricultural Landscape Research (ZALF), Müncheberg, Germany
Institute of Biochemistry and Biology, University of Potsdam, Potsdam, Germany

Wolfgang zu Castell Department of Geoinformation, Helmholtz Centre Potsdam, GFZ German Research Centre for Geosciences, Potsdam, Germany

Curriculum Vitae



Susanne S. Renner

Education

- 1984 Dr. rer. nat. in Biology, University of Hamburg, Germany
1992 Habilitation in Botanical Systematics, University of Hamburg

Appointments

- 1981–1983 Research Associate, Botanical Institute, University of Hamburg, working in Manaus, Brazil
1984–1985 Researcher at Inst. Nat. de Pesquisas da Amazônia (INPA), Manaus, with DFG grant
1985–1987 Postdoctoral Fellow, Smithsonian Institution, Washington, DC, USA
1987–1992 Associate Professor, Botanical Institute, University of Aarhus, Denmark
1993–1996 Professor, Botanical Institute, University of Mainz, Germany
1996–2003 Professor, University of Missouri-St. Louis, MO, USA

2003–October 2020 Professor (chair), Biology, Ludwig-Maximilians University, Munich, Director of the Munich Botanical Garden and of the herbaria in Munich (M and MSB)

2020 Honorary Professor, Washington University, Department of Biology, Saint Louis

Honors

Elected foreign member of the *Royal Danish Academy of Sciences* (2005)

Elected member of the *Bavarian Academy of Sciences* (2009)

Elected member of the *German Academy of Sciences, Leopoldina* (2009)

Elected member of the *American Academy of Arts and Sciences* (2018)

Plant Evolution and Systematics 1982–2022: Changing Questions and Methods as Seen by a Participant



Susanne S. Renner

Contents

1	Introduction: Why I Studied Biology and Ended Up in Systematics	2
2	Monographs, Floras, and Herbarium-Based Species Discovery: The Years in Washington, Aarhus, and Mainz	5
3	The Move to Molecular Data: Likelihood, Molecular Clocks, and Biogeography	7
4	The Discovery of Natural Horizontal Gene Transfer in Seed Plants; Mitochondria, Plastomes, Transposons, and Finally Nuclear Data for Studying Plant Domestication ...	9
5	Functional Morphology, Plant/Animal Interactions, and Discovery of Ant-Cultivated Rubiaceae	11
6	Bee Phylogeny and Behaviour, and a Botanical Garden as a Terrarium	14
7	Plant Sexual Systems and Molecular Cytogenetics	16
8	Phenology and Botanical Gardens as Common Gardens	18
9	History of Botanical Collecting and New Ways to Achieve Stable Scientific Names ...	20
10	Epilogue: The Increasing Role of Collaboration in Systematics and the Changing Position of Systematics Within Biology	21
	References	23

Abstract This review describes, in chronological order, the research topics in which I have been involved over the past 40 years, a time during which the study of plant evolution, systematics, and biodiversity has moved from relying solely on morphology to relying mostly on DNA sequences and now partially assembled genomes. When I began to do systematics, traveling to tropical countries for fieldwork was a big draw and probably influenced my initial choice of plant groups to work on. In 1989, I made a conscious decision to shift my focus from monographs, floras, and herbarium-based species discovery to the evolution of plant sexual systems and the functioning of unisexual flowers, selecting first Siparunaceae and then Cucurbitaceae as suitable groups. I also became an early adopter of

Communicated by Ulrich Lüttge

S. S. Renner (✉)

Department of Biology, Washington University, Saint Louis, MO, USA

e-mail: srenner@wustl.edu

molecular clock approaches in the study of biogeography and plant/animal mutualisms, and was involved in the discovery of natural horizontal gene transfers in seed plants, which in turn led to an interest in mitochondrial and plastid genomes in parasitic plants. Three topics, bee behaviour on flowers, the evolution of ant/plant interactions, and plant phenology, have accompanied me from my dissertation to the present, while others, such as molecular cytogenetics, grew from the interests and expertise of students. The breadth of topics reflects a great change in systematics since the 1980s, namely the increasing role of collaborations. Monographs, floras, and cladistics (when morphology based) used to be done in isolation. With DNA data came lab work, bioinformatics, and both the need and the possibility to collaborate, which brought systematists out of their niche, gave comparative biology a huge push, and resulted in a better integration of biodiversity studies within biology.

Keywords Bees, Biogeography, Botanical gardens, Molecular clocks, Molecular cytogenetics, Natural horizontal gene transfer, Phylogenetics, Plant/animal mutualisms, Sexual systems, Species discovery, Stable naming

1 Introduction: Why I Studied Biology and Ended Up in Systematics

My parents were interested in history and writing, rather than science, but after buying a newly built house surrounded by raw soil in Schleswig-Holstein, my Swabian father developed an interest in gardening. He did this from a book, 'Der praktische Gartenfreund' (I still have it), and as a result the garden had all the ingredients fashionable then, such as odd ornamental conifers, a magnolia, *Delphinium*, and 'Gloria Dei' roses in front. My father would explain the etymology of the plants' scientific names, and to this day, I cannot look at a *Hydrangea* without hearing my father's voice, explaining the name's meaning. In high school, in Norderstedt, German and biology were my favourite subjects, especially behavioural biology. I read the popular books of Karl von Frisch, Konrad Lorenz, Nikolaas Tinbergen, and Irenäus Eibl-Eibesfeldt, and a mini-research project, when I was 15 or 16, on 'Sex symbols in advertisement' in hindsight set me on my path (Sect. 7).

In the summer of 1972, my parents let me spend 6 weeks in Gananoque, Ontario, where I helped an uncle who was a forester, beekeeper, and budgie breeder. The next summer, when I had finished high school, they let me visit another uncle, who worked in Santiago de Chile. After a couple months of volunteering, I began studying marine biology at the University of Chile. This came to an end when the university closed because of the murder of Allende in September 1973, and I will never forget how in early October, my uncle's house was searched by two young men probably my age (19), toting machine guns. After that, I decided to continue my studies at the university of Hamburg. The most wonderful classes for me were those

Fig. 1 Klaus Kubitzki instructing Susanne Renner during her M.Sc. research in 1979 (private photo)



of the zoologists, including Wolfgang Villwock (1930–2014) on fishes, Hans Strümpel (1935–2019) on social insects, and Otto Kraus (1930–2017) on spiders. Kraus, of course, introduced us to Willi Hennig and cladistics.

Unfortunately, the only professor in animal behaviour, which I had planned to specialize in, let us do experiments on imprinting that should never have been permitted. One involved three students, including myself, sleeping next to an incubator with chicken eggs so that we might imprint the newly hatched chickens on a ball. The chickens, sadly, never walked at all because they all had splayed feet and crippled legs. Nobody had told us that just-hatched chickens must never be kept in containers with smooth surfaces. This experience drove me to botany.

Botany in Hamburg was well-represented by, among others, Konrad von Weihe (1923–2013), who taught economic botany (in which I then wanted to specialize), Hans-Dieter Ihlenfeldt (1932–), Heidrun Hartmann (1942–2016), and Klaus Kubitzki (1933–), who taught systematics and evolution. The seminar classes offered by professor Kubitzki, especially one on flower/pollinator coevolution, and an excursion he led to Obergurgl in the Austrian alps stood out. Kubitzki knew every plant and every moss in Obergurgl, but realizing that I knew nothing, he happily demonstrated *Poa annua* to me, explaining that students from Hamburg actually best learn this species on Mount Etna.

Klaus Kubitzki and I shared a love for South America, especially Chile and Brazil. I had spent the summer of 1978 in São Paulo and Rio de Janeiro, with a great-aunt, and so by then I could get by in both Spanish and Portuguese. After my oral examinations in entomology and botany, I therefore embarked on an M.Sc. thesis (1978/79; Fig. 1) focused on *Aiouea*, a South American genus of Lauraceae, under Kubitzki's guidance, later published in the *Flora Neotropica* series of the New York Botanical Garden (Renner 1982). Disappointingly, the project involved Kubitzki

traveling in South America and me going through the hundreds of specimens he had on loan in the herbarium in Hamburg. To identify Lauraceae, one has to boil their minute flowers in hot water and then dissect and draw them under a stereoscope fitted with a drawing tube. I was not keen on this. The best part for me instead consisted in extracting information from the labels. Using label data, I found that two morphologically similar and co-occurring species differed in their flowering time. I also placed every collection on the standard *Flora Neotropica* maps, which required studying old maps and finding out about the collectors' itineraries. While none of this was earth-shattering, my approach taught me how to use label data to study phenological niches, starting an interest that would lead to some of my most innovative research.

For my doctoral research, begun in 1980, professor Kubitzki let me chose between ant/plant interactions or bee/flower interactions. I decided on the latter topic, realizing that Melastomataceae would afford me an opportunity to also study the former (ant plants came back into focus later; Sect. 5). I moved to Manaus for 25 months, doing fieldwork on the reproductive biology of Melastomataceae, which involved traveling all over the Amazon basin and also to Minas Gerais. Part of my work was done within the Minimal Critical Size project north of Manaus, run by Thomas Lovejoy (1941–2021), a leading thinker in the study of 'biological diversity', a term that he coined and which his friend E. O. Wilson (1929–2021) then shortened for a 'National Forum on BioDiversity' at the Smithsonian Institution in Washington in September 1986 that I was fortunate to attend as a postdoc. The Minimal Critical Size project brought numerous visiting researchers from the USA, working on army ants, snakes, frogs, birds, and other animals variously able, or unable, to traverse the burnt strips of land between the blocks of left-over forest (the 'minimal' reserves). It also mapped and tagged thousands of trees, which meant I could do ecological observations, including monitor flowering and fruiting times, another topic to which I returned 20 years later, when changing phenology under climate change became a concern (Sect. 8).

The external examiner for my dissertation, written in German and on a typewriter, and oral defence, back in Hamburg in late 1983, was Stefan Vogel (1925–2015). To prepare, I read all his publications, and, I think, Stefan Vogel is among the biologists who had the deepest influence on me. We stayed in close contact until late 2012. The other person to whom I owe the greatest debt is Klaus Kubitzki, who 4 years after my Ph.D., when I had my first academic position at the University of Aarhus in Denmark, supported my habilitation at the University of Hamburg, which I did as a 'traveling professor' from Aarhus.

2 Monographs, Floras, and Herbarium-Based Species Discovery: The Years in Washington, Aarhus, and Mainz

After defending my dissertation, I obtained my first grant from the German research foundation (DFG) to work on the systematics of the tree genus *Bellucia* (Melastomataceae), which took me back to Manaus. From there, I was invited to participate in an American-led expedition to the Serra da Neblina (1984), a tabletop mountain at the border between Brazil and Venezuela. This was a helicopter-dependent adventure, and because of the fickleness of helicopters, we ended up spending 20 straight days between 1,850 and 2,100 m elevation, which gave me time for pollination observations that remain among the few such studies from any tabletop mountain (Renner 1989). I continued my taxonomic work with a postdoctoral fellowship from the Smithsonian Institution in Washington (June 1985–December 1987) where I worked with John J. Wurdack (1921–1998; Fig. 2), a proponent of the importance of collecting and studying species' geographic distribution. Through John, a gregarious person who often invited visitors to lunch at the Smithsonian's 'Castle', I met some of the heroes of the era, including Joseph Ewan (1909–1999), Armen Takhtajan (1910–2009), and Arthur Cronquist (1919–1992).

Fig. 2 My postdoctoral advisor, John Wurdack, on Serra da Neblina, Venezuela, in 1959 with one of the *Heliampora* plants whose pollination biology I later studied on the same mountain



In 1988, Art Cronquist even took me along on a short plant collecting trip in California during which we camped out under the stars.

Scientifically, I was kind of stuck, monographing ever more genera (*Bellucia*, *Loreya*, *Macairea*, *Rhynchanthera*, *Pterogastra*, *Schwackaea*, *Pterolepis* and more) and contributing treatments to floras and checklists (for Ecuador, Venezuela, Colombia, Thailand, China). Herbarium-focused research continued during my years as assistant, then associate, professor in the botany department of the University of Aarhus (March 1987–December 1992), which had long-established ties with institutions in Greenland, Ecuador, and Thailand, and colleagues there took me along on many field trips, including to Thailand with Kai Larsen (1926–2012), Greenland with Simon Laegaard, and Ecuador with Henrik Balslev.

Thinking about a new direction for my research, I decided to work on plants with sexually specialized sporophytes (dioecious plants) – a sexual system superficially resembling that of animals but making little sense in sedentary organisms, such as land plants. Since I was familiar with Laurales, I chose Monimiaceae, which often have unisexual flowers and which in some classifications included Atherospermataceae, Monimiaceae, Siparunaceae, and even *Amborella* and *Trimenia* (the latter soon excluded and recognized as among the oldest lineages of flowering plants; Renner 1999; Mathews and Donoghue 1999). In Ecuador, one could study the reproductive biology of Monimiaceae and Siparunaceae, and with my first M.Sc. student, Jan Peter Feil (M.Sc. thesis 1989–1990), we did exactly that.

Having published lengthy taxonomic works on various plant groups and with over 100 new species associated with my name, I came to realize that for me, herbarium-based work was too static, even when paired with collecting trips to tropical countries. There are 1.2 million published names for land plants, 46% of which are considered synonyms, and in the flowering plants, there may be 3–4 synonyms for every accepted name. This redundancy, which is a huge problem for evolutionary studies, can only be solved by people trained in finding type specimens, which often involves historic-detective work, and who know how to assess traits, geography, and ideally also DNA data. All my doctoral students, I hope, acquired a basic understanding of this, but only four of 22 (at universities in Aarhus, Mainz, Saint Louis, and Munich) decided to include extensive taxonomic work in their theses: Gudrun Kadereit, née Clausing, who worked on several genera of Asian Melastomataceae and who since the beginning of 2021 holds the Chair of Systematic Botany at the University of Munich (thus being my successor); Karsten Meyer, who worked on the genus *Melastoma*; Norbert Holstein, who worked on the genus *Coccinia* (Cucurbitaceae) and is now a curator at the Natural History Museum in London; and Fernanda Carvalho, who revised the papaya family (Caricaceae) and is now a professor at the university of Minas Gerais in Belo Horizonte. All also generated molecular phylogenies and carried out fieldwork. My own most fulfilling taxonomic work, on the above-mentioned Monimiaceae and Siparunaceae, was done in collaboration with the unforgettable embryologist, mycologist, and born taxonomist Gerlinde Hausner (1939–2008) who worked with me during my 3 years at the university of Mainz (e.g. Renner and Hausner 1997, 2005 another volume in the *Flora Neotropica* series).

3 The Move to Molecular Data: Likelihood, Molecular Clocks, and Biogeography

From mid-1996 onwards, when I moved to the University of Missouri-Saint Louis (UMSL), I focused on obtaining DNA sequences to understand relationships in the ‘Monimiaceae’ (e.g., Renner et al. 1997, 2000), and my lab therefore produced the first sequences of *Trimenia* and *Amborella*, which fell far outside Laurales (Renner 1999; Mathews and Donoghue 1999). I therefore gave aliquots of the DNAs to Yin-Long Qiu at the University of Michigan and Michael Zanis, then a Ph.D. student in the lab of Pamela and Douglas Soltis, who were working on a large phylogeny of the flowering plants (Qiu et al. 1999, 2005), a sharing that led to visits with top people in the developing field of angiosperm phylogenetics.

With DNA sequences in hand, I became interested in molecular-clock dating and set about learning and testing how to apply this tool, inspired by the work of Sanderson who first used multiple fossil calibrations (Sanderson 1997 and onwards). I believe my paper on the history of the Southern Hemisphere family Atherospermataceae, which has fossils in New Zealand and Patagonia, was the first application of molecular-clock-dating in plant biogeography (Renner et al. 2000; Fig. 3). The basic idea with all molecular clocks is to find a genome region that accumulates substitutions suitably fast (with ‘suitably fast’ depending on the questions one is asking) so that they can be ‘seen’ and counted in a DNA alignment,

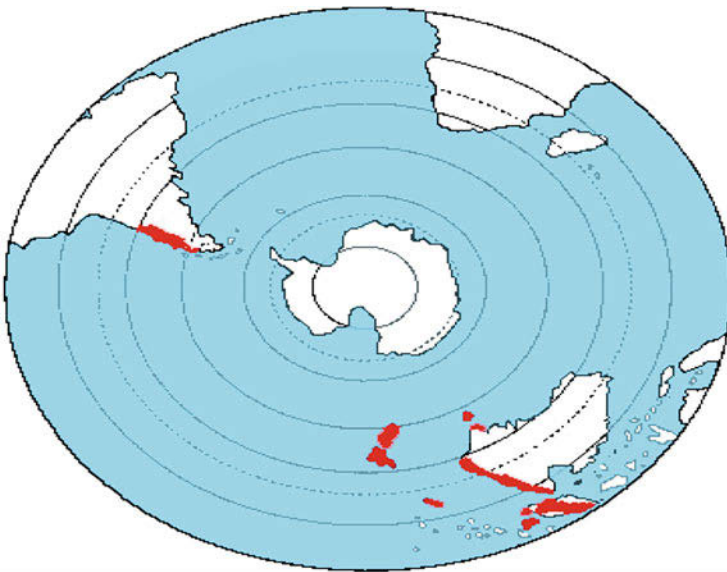


Fig. 3 The distribution of Atherospermataceae, which have two species in Chile and 12 in Australasia, with fossils in Patagonia and New Zealand that we used to calibrate an *rbcL*-based molecular clock (Renner et al. 2000)

and translated into proportional branch lengths (i.e., genetic distances) in a phylogeny. Branch lengths are then calibrated with some external event, such as a volcanic eruption, a characteristic fossil, or the date when a patient's blood was sampled. The obtained rate (number of substitutions per time) can be used to translate the age of any node in the phylogeny into absolute time (in millions of year or years, as the case may be). Modern epidemiology and biology are unthinkable without molecular clocks. Of course, any inferred time has an error range, which can also be calculated. Molecular clocks are the basis for quantifying evolutionary change in absolute time, be it in the SARS-CoV-2 virus human evolution, plant/animal interactions, biogeography, or the first appearance of particular traits of interest, such as carbon-concentrating mechanisms in hornworts (Villarreal and Renner 2012).

Having understood the power of the new approach, my students and I applied clock dating to numerous biogeographic and evolutionary questions, both in case studies (Renner and Zhang 2004 – with a wonderful postdoc, Libing Zhang, now a senior curator at the Missouri Botanical Garden; Won and Renner 2006; Sebastian et al. 2010; Renner et al. 2020) and more general work. The latter included an early review of the so-called relaxed molecular clock approaches (Renner 2005), how to infer the root of a phylogeny, i.e., its evolutionary starting point, with a clock model (Renner et al. 2008), the introduction of fossil-based ‘ghost’ lineages that prove a former geographic presence no longer seen in any of the sequenced living taxa (Mao et al. 2012; Nauheimer et al. 2012), and the application of the ‘Fossilized Birth/Death’ model in which all fossils of a clade (not just the oldest ones) are used for calibration (Grimm et al. 2015; Renner et al. 2016).

In 2002, when molecular-clock approaches were beginning to reveal the frequency of successful long-distance dispersal, casting doubt on earlier plate-tectonic-type explanations for geographic disjunctions, Tom Givnish and I organized a symposium at the University of Madison in 2002 on ‘*Tropical intercontinental disjunctions: Gondwana break-up, immigration from the boreotropics, and trans-oceanic dispersal*’ (Givnish and Renner 2004). My own contribution dealt with plant dispersal across the tropical Atlantic by wind and sea currents (Renner 2004), and I argued that despite the influence of chance, meta-analyses should be able to detect predominant patterns in suitable time spans because of the predictable direction of sea and wind currents. Another meta-analysis focused on the 4 km-high Tibetan Plateau, which geologists tend to agree was already that high by 40 Ma ago. Yet, at least 100 studies of plants and animals have claimed that the rise of the Tibetan Plateau occurred a mere few million years ago, matching their various clock-dated young groups of organisms (Renner 2016a; the 100 papers are listed in my paper's appendix). This is entirely due to copy-and-paste science and is in no way a sign that molecular-clock-dating does not work.

4 The Discovery of Natural Horizontal Gene Transfer in Seed Plants; Mitochondria, Plastomes, Transposons, and Finally Nuclear Data for Studying Plant Domestication

Hyosig Won, my second doctoral student in Saint Louis, arrived in my lab in September 1998, directly from South Korea, and it soon became clear that he had a much more solid understanding of molecular biology than I did. He taught me about intron regions, mobile elements, and splicing, and working with him was great. One day, he came and said he had discovered sequences in the mitochondrial DNA of *Gnetum*, the gymnosperm genus on which he was doing his dissertation, that could only come from some plant in the sunflower family. Of course, Hyosig checked everything multiple times before we submitted our paper to *Nature* on 2 February 2003. As expected, the reviewers (on March 5) said that horizontal gene transfer (HGT) among higher plants could not exist. A couple days after this rejection, Jeffrey Palmer from Indiana University called me out of the blue to tell me that he believed in our results and that I should resubmit our paper to the *Proceeding of the National Society*, which we did on 12 June and where it was accepted on 18 July. By coincidence, a paper from Jeff Palmer's lab with the first case of HGT in flowering plants came out in *Nature* on 10 July 2003 (Bergthorsson et al. 2003). All these cases involved standard mitochondrial genes, encoding ribosomal and respiratory proteins, and since 2003, it has become clear that HGT between distantly related land plants has occurred relatively often. The precise mechanisms are still an open question, but most instances involve parasitic plants that are attached to their host via plasmodesmata through which phloem sap, macromolecules, and entire mitochondria can pass.

For several years, HGTs of mitochondrial genes among higher plants was an exciting area, and when I moved to the university of Munich in June 2003, people in my lab kept an eye open for additional cases. One of my first doctoral students in Munich, Natalie Cusimano, who came from Berlin in February 2005, studied the acquisition and loss of horizontally-transferred mitochondrial introns in Araceae (Cusimano et al. 2008) and later, after we began using Next-Generation sequencing (NGS) in 2011, Natalie and I investigated HGT events between the endoparasite *Cynomorium coccineum* and its various hosts (Cusimano and Renner 2019; Fig. 4). Another student to focus on parasitic plants was Sidonie Bellot, who joined in 2010, coming from an M.Sc. project in France where she had already used NGS and knew how to analyse the data. Sidonie focused on the plastid genomes of the worldwide endoparasite family Apodanthaceae, which led to the discovery that these parasites have lost all but five or six of the 110–130 genes in a typical angiosperm plastome (Bellot and Renner 2016). This may still be the smallest plastid genome known in the embryophytes.

Better sequencing machines eventually allowed systematists to routinely obtain nuclear sequences, but much of what one obtains from next-generation sequencing (NGS) consists of transposons and other types of repetitive DNA. But how to use

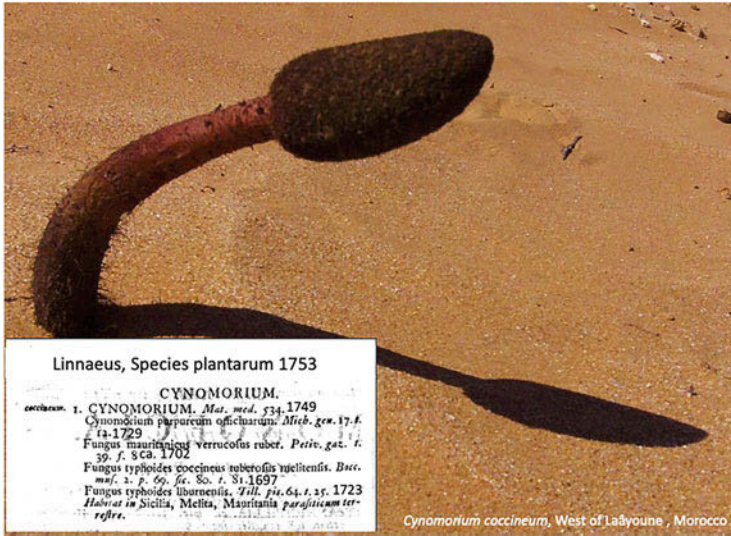


Fig. 4 The inflorescence of a *Cynomorium coccineum* plant, a root holoparasite that Linnaeus and his contemporaries thought was a fungus, as is evident from the synonymous names given in Linnaeus's 1753 *Species Plantarum*. The species occurs in sandy soils from Spain to China and parasitizes a limited number of hosts, which enabled us to study its sequential acquisition of mitochondrial genes from different hosts over geographic space and geologic time (Cusimano and Renner 2019). The species is in its own family, which we placed in the Saxifragales (Bellot et al. 2016)

these difficult-to-align data in comparative biology? One option was to focus on transposons and the question of how they are inherited. Some transposons are highly labile, even during the lifetime of an organism, others are not. With a French postdoc, Mathieu Piednoel, with deep experience in retrotransposons, I submitted a grant request on this topic to the DFG, and when we were funded, Mathieu joined my lab for 3 years (2011–2014). Because of my interest in parasitic plants, we focused on Orobanchaceae, sending material of selected autotrophic, hemi-, and holo-parasitic diploid and tetraploid species to a company for NGS as well as generating a 'traditional' phylogeny in our own lab from short sequences and with dense species sampling. We discovered that major plant LTR-retrotransposon families undergo taxon-specific proliferation are especially chromoviruses of which we found species-specific families (Piednoel et al. 2012, 2013).

The Cucurbitaceae, a family of about 1,000 species with an exceptional number of economically-important crops, wide geographic occurrence, tight coevolutionary interactions with various groups of bees (Sect. 6), and unisexual flowers in monoecious or dioecious species (Sect. 7), became a focus from June 2001 onward. However, obtaining good material took years because many cucurbits are tropical climbers or desert-adapted plants that are difficult to collect because they only

emerge from their underground tubers or leaf-less thick stems with sufficient rain. Once it became easier to obtain nuclear sequences from herbarium material, my students, postdocs, and I started making many unexpected discoveries about the wild relatives (and their geographic distribution) of cucumber, watermelon, honey melon, and others (Renner et al. 2007a, b; Sebastian et al. 2010; Chomicki and Renner 2015, Chomicki et al. 2020d: a review of Cucurbitaceae domestication). Genomic data are crucial for resolving the evolution of cultivated species because the events are so young, usually having occurred over the past 10,000 years. Inferring the domestication of the watermelon therefore took a multi-year, multi-postdoc, multi-national project, as well as the classic taxonomist's detective skills to check old maps, labels, type locations, and small, but important herbaria. It turned out that Sudanese wild melon are the most likely wild progenitors of the domesticated watermelon (Renner et al. 2021b).

I am very grateful to students and collaborators who enabled me to step into the phylogenomic era, foremost among them Guillaume Chomicki (Sect. 5), Oscar Pérez-Escobar, formerly a doctoral student in Munich and now a curator at the Royal Botanic Gardens in Kew, and Wei-Ning Bai and Da-Yong Zhang at Beijing Normal University. With the last two, I am working on the evolution of Juglandaceae, including the walnut, which it turns out originated as a hybrid species, as inferred with population-genetic methods (Zhang et al. 2019).

The functioning of my lab in Munich depended on Dr. Martina Silber, who ran it from January 2010 until my retirement. With her help, we were able to do barcoding, genomics, transcriptomics, and molecular cytogenetics (Sect. 7). She supervised bachelor and M.Sc. students in the lab, was on top of safety protocols, lab inspections, and the orderliness of purchases and budgets, and was genuinely interested in the different questions we were working on, exploring new methods on her own, with much more technical know-how than any of us others. Without Martina, the lab's success would not have been possible.

5 Functional Morphology, Plant/Animal Interactions, and Discovery of Ant-Cultivated Rubiaceae

The evolution of flowering plants cannot be understood without considering their interactions with pollinators because there lies the key to the origin and function of flowers. Early pollinators, back in the late Jurassic and early Cretaceous when flowering plants evolved, must have been certain flies, beetles, and moths that searched out gymnosperm cones as mating sites and for egg-laying. These insects' visits to male and female cones of now extinct gymnosperms must have contributed to efficient (because directed) pollen transfer, setting up the context for the mutual adaptations and coevolutionary divergences that led to the diversity we see today. These topics have always played a large role in my teaching (in Aarhus, Saint Louis,

and Munich), and over the years, M.Sc. students in my lab and students whom I co-advised have carried out studies on pollination by flies and beetles in *Nuphar* in Scandinavia, Germany, and North America, by midges in Ecuador and China, and by pollen-feeding moths in China. This work – along with studies from others – showed that early-evolving angiosperm groups that still survive are mostly pollinated by ovipositing flies. Compared to food reward-based pollination, oviposition-based systems are less wasteful of plant gametes because female insects with herbivorous larvae reliably visit the particular oviposition sites (i.e. flowers) to which their larvae are adapted (Luo et al. 2018).

Collaborations in the field of plant/pollinator interactions came from working with Chinese students and postdocs who over the years became close colleagues, especially Dianxiang Zhang and Shi-Xiao Luo of the botanical garden in Guangzhou and Shuang-Quan Huang from Central China Normal University in Wuhan. The projects involved mutual visits and field trips, seminars at my Chinese host institutions, and lots of wonderful Chinese food. My very first visit to China, in April 2004, yielded the discovery of a new self-pollination mechanism by pollen grains that are sliding down the flower's own style and onto its stigma (Wang et al. 2004). Another project that stands out in my mind involved experiments on the function of morphologically differentiated stamens in buzz-pollinated flowers (Luo et al. 2008). The results supported Darwin's division-of-labour hypothesis, which predicts that the pollen grains from the set of anthers less conspicuous to bees should have a higher chance of reaching a conspecific stigma than the grains from the other more conspicuous set.

Functional analyses often require microscopy and stereoscopy, something of which I felt I had done quite enough during my M.Sc. on the genus *Aiouea*, which has tiny nectar glands like most Lauraceae (Sect. 1). However, a collaboration with the morphologist Florian Jabbour, who spent 2 years in my lab (2010–2012) as a postdoc with funding from the DFG rekindled my interest in the functioning of nectaries, this time inside the complex perianth of the Delphinieae (Ranunculaceae), a group that Florian is an expert on (Jabbour and Renner 2012a, b). Florian is now working at the Museum National d'Histoire Naturelle in Paris, with a continued focus on the Ranunculaceae. Because of their huge role in plant/pollinator interactions, nectar spurs and nectar production remained a focus in my work. With an M. Sc. student, I applied molecular-clock dating to the African moths and the long-spurred *Angraecum* star orchids that fascinated Darwin, and we discovered that – against my expectation – the longest-spurred orchids and the longest-tongued *Xanthopan* moths on Madagascar are of the same age, namely ~7 my, supporting that their extreme traits are the result of coevolution, despite the orchid probably being more dependent on the moths than the other way around (Netz and Renner 2017; more field work is needed).

Nectar selectively offered in suitable spurs also is the sine qua non in hummingbird pollination, a topic on which I worked with another postdoc, Stefan Abrahamczyk (2012–2014), now at the Natural History Museum in Stuttgart. We investigated the timeframe over which hummingbirds, which provide great pollination services and thereby 'drive' flower evolution, have interacted with different



Fig. 5 The sword-billed hummingbird, *Ensifera ensifera*, with an up to 11 cm long bill, visiting *Passiflora mixta*. With molecular clocks applied to a hummingbird phylogeny and several plant phylogenies we inferred that this hummingbird diverged from its sister species ~11.6 million years ago and that at least 45 plant species in seven genera and five families now depend on this bird for pollination, many of them having evolved in a step-wise process. Photo Rolf Nussbaumer, Ecuador

plant genera and even entire families, leading to classic cases of convergent evolution, the parallel acquisition of similar traits in unrelated species. The results show that this can take just a few million years, followed in some groups (such as the Passifloraceae that we focused on) by ‘evolutionary escapes’ from ancestral bird pollination to pollination by bats, moths, or bees (Abrahamczyk et al. 2014; Abrahamczyk and Renner 2015; Fig. 5).

In April 2013, Guillaume Chomicki visited to discuss possible topics for a doctoral project. Within 30 min, we discovered a shared interest in ant/plant interactions, which had interested me since my own doctoral research (which included observations of the ant-occupied genus *Tococa*) and ever since (Renner and Ricklefs 1998). We both thought that the evolution of ant/plant symbioses, the permanent physical living of ants inside plant-formed nesting structures, had not been studied with the full arsenal of comparative biology, including field experiments, lab-based developmental studies, molecular-phylogenetics (including transcriptomics, Pu et al. 2021), and molecular-clock dating. As the focal ant/plant clade, we selected a group of Rubiaceae with about 100 species in SE Asia, with fieldwork to be carried out in the Fiji Archipelago (funded by our DFG grants). Guillaume did not shy away from rope-climbing trees, then hanging in a harness to reach his epiphytic study plants with their ant-housing tubers, which of course were aggressively defended by the ants. He was as ingenious in the lab as in the field, for example, applying computer-tomography to study the inside of the ant-housing tubers, and just a fantastic student.

Guillaume’s work led to the discovery of obligate insect agriculture, involving the symbiosis between the ant *Philidris nagasau* and epiphytes in the genus

Squamellaria (Rubiaceae), which the ants plant, fertilize, defend, harvest, and depend on for nesting. Before our project, farming systems (outside human agriculture) had only been known to involve fungi cultivated by social insects, but never plants obligately depending on ants throughout their life cycle (Chomicki and Renner 2016, 2017a, b). The relationships between *P. nagasau* and several *Squamellaria* are reciprocally obligate and evolved about 5 million years ago, as we inferred from clock-dating a phylogeny for the ants and another for the plants. Guillaume and I have explored many aspects of the ants' and plants' mutual adaptations, such as the flowers' concealed nectar, exclusively available to *P. nagasau* (Chomicki et al. 2016) or the different trade-offs in the symbiosis in sun or shade environments (Chomicki et al. 2020a), and we are continuing to collaborate. Now in his own lab at the University of Sheffield, Guillaume is asking more general questions about the evolution of mutualistic dependence and its role in diversification (e.g., Chomicki et al. 2020b, c).

6 Bee Phylogeny and Behaviour, and a Botanical Garden as a Terrarium

I had originally wanted to study animal behaviour, especially in bees, probably because of Karl von Frisch's work on bee communication (von Frisch 1965; Sect. 1), and my first-ever paper was on pollen-stealing bees-stealing because the thieves do not pollinate the flowers whose pollen they steal (Renner 1983; Fig. 6). This topic – deception in mutualisms, with one partner gaining a benefit without 'paying' the other – is fascinating, but requires mathematical modelling for a deeper understanding, and for lacking this skill, my forays into deception and ecological (phenological) mismatch have mostly remained meta-analyses or reviews (Renner 2006; Renner and Zohner 2018; Chomicki et al. 2020b).

An opportunity to again work on bees came when Hanno Schaefer visited to discuss possible postdoctoral projects in late 2004. Hanno, now a professor at the Technical University in Munich, has an incredible knowledge of the diversity and ecology of temperate and tropical bees, birds, and plants, and since we both were fans of the work of Stefan Vogel (Sect. 1) on oil bees and the oil-offering flowering flowers, we settled on this topic and got a DFG grant. Among the results of this work was a phylogeny of the Ctenoplectrini bees, a clade of 20 species in Africa, Asia, and Australia that has coevolved in space and time with oil-offering Cucurbitaceae (Schaefer and Renner 2008) and a study of how the various mutualistic systems of oil-collecting bees and oil-offering flowers in South America, Africa, Asia, and Europe originated and diversified, using other plant/bee interactions as stepping stones (Renner and Schaefer 2010). Many of our insights were due to Hanno's field work, my molecular-clock expertise, and the ground-breaking work of Stefan Vogel (Sect. 1).



Fig. 6 Examples of the pollen-robbing behaviour discovered during the fieldwork for my dissertation (Renner 1983). A. *Trigona williana* cutting into an anther of *Rhynchanthera grandiflora*. B. A bud of *R. grandiflora* damaged by *Trigona* bees trying to get at its pollen before the flower even opened. C. *Tococa longisepala* flower with 9 of its 10 anthers completely cut off by *Trigona* bees. D. *T. fulviventris* destroying the anthers of *Tibouchina maximiliana* to get at the pollen grains. All Photos: S. S. Renner

Further work on oil bees, this time from South America, was possible when Aline Martins, a sandwich Ph.D. student from Brazil joined the lab for a year (2013/2014). We investigated the coevolution and geographic range overlap between various oil bee subgroups and South American plant families (Martins et al. 2014, 2015).

My last doctoral student, Michaela Hofmann (2017–2020), also worked on bees, this time, bees in Germany, with a focus on niche occupation, food competition between wild bees and honeybees, and experiments in the Munich botanical garden. One of our discoveries was that in Germany (with 445 species for which we had data), bee species that forage in the spring are less extinction prone than species that forage later in the year and that bees capable of living in urban environments (82 species) are less extinction prone than the 346 species specialized to live in various non-urban habitats (Hofmann et al. 2019). We were able to quantify local extinction because of Germany’s ‘Red List’ assessments, which have been carried out regularly for the past 40 years, usually by the same few experts (for different taxa).

With Andreas Fleischmann, my colleague in Munich and another bee expert, we took advantage of the Munich botanical garden being a kind of terrarium, that is, a

system whose components are known and change in pretty well-understood ways, for example, due to climate warming. The garden, which covers 21 ha and opened in 1914, has not changed its basic lay-out and for the past 100 years and is home to 110 species of bees that are well monitored. This permitted us to attribute the strong increase in warm-habitat loving bee species since 1997 to climate warming rather than increase in food or nesting sites (Hofmann et al. 2018). Michaela and Andreas also taught several cohorts of bachelor students how to label tiny bees with numbers or colour codes, so we could study foraging distances. Foraging distances are well studied for bumble bees (and of course the honey bee), but 92% of the 561 species that occur in Germany are only 4.5–13.5 mm long, and by studying the foraging distances in six species with body lengths of 6–15 mm, we developed a 150-m-rule-of-thumb for flower strip distances (Hofmann et al. 2020). With another two cohorts of bachelor students, Andreas and I also studied food competition between honey bees and wild bees, discovering a clear displacement effect in a year when honey bees were more abundant than in a previous year (Renner et al. 2021a, b).

7 Plant Sexual Systems and Molecular Cytogenetics

The evolution and function of unisexual flowers has been one of my main topics (Sect. 2), with a focus on dioecy and monoecy, the distribution of unisexual flowers on separate individuals or on each individual (in populations). My first forays into the field were reviews of the distribution of dioecy and monoecy in the flowering plants, pollinators of tropical dioecious angiosperms – most dioecy is found in long-lived tropical plants – and the occurrence of heteromorphic sex chromosomes in land plants (Renner and Feil 1993; Renner and Ricklefs 1995; Ming et al. 2011; Renner 2014). A step forward came with the doctoral research of Stefanie Volz, who studied monoecy, dioecy, and chromosomes in *Bryonia*, the Cucurbitaceae genus in which Carl Correns in 1903 discovered the Mendelian inheritance of sex by counting the male and female offspring from crossings that he carried out between monoecious and dioecious species. Among my many adventurous students, Stefanie stands out by traveling to the deserts of Uzbekistan to dig for *Bryonia* tubers so as to bring them into cultivation in the Munich botanical garden for chromosome counts.

An insight emerging from our phylogenetic studies was how often monoecy and dioecy have gone back and forth during evolution. This finding gradually became a leitmotif in my understanding of sexual system evolution: The biggest hurdle for flowering plants is to achieve reliable pollination with unisexual flowers, after which switches between monoecy and dioecy are evolutionarily easy (Renner and Won 2001; Renner et al. 2007a, b; Volz and Renner 2008; Schaefer and Renner 2010; Renner 2016b; Renner and Müller 2021). My persistent stressing of the ‘monoecy pathway’ to dioecy, which arose from the taxa I was working on (Laurales and Cucurbitaceae), became a much-cited contribution to the field.

The advent of NGS resulted in the easy amplification of repetitive DNA (Sect. 4), which when labelled with fluorescent molecules and hybridized onto chromosomes

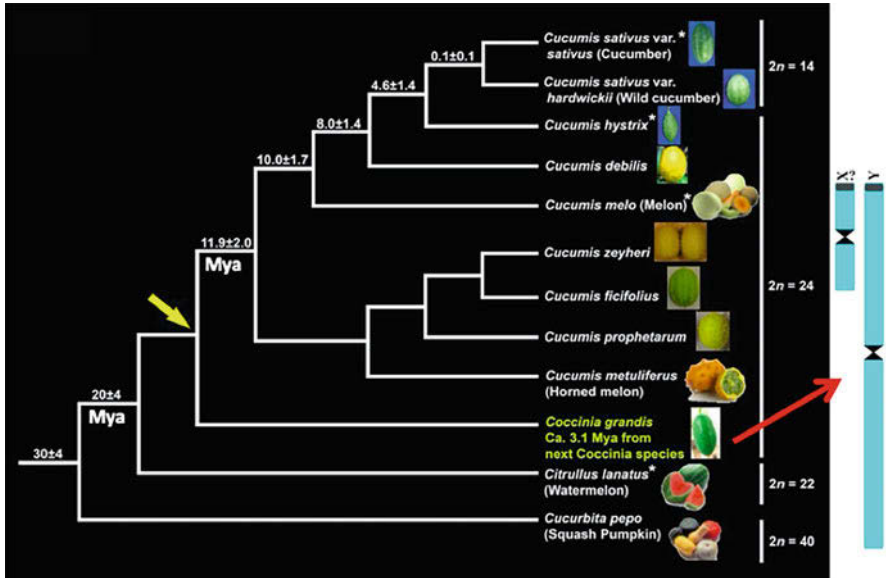


Fig. 7 A partial phylogeny for the Cucurbitaceae showing some of the family’s many crop species and the placement of the genus *Coccinia*, all species of which are strictly dioecious, with at least two of them having an extremely large Y chromosome (image created by A. Sousa in 2013)

can serve to distinguish individual chromosomes (under fluorescent light). This molecular-cytogenetic technique, called FISH, was developed in the 1980s, but in plants applied only from 1989 onwards because plant cell walls make it hard to obtain good chromosome preparations, which are the sine qua non for successfully ‘painting’ chromosomes. Chromosome researchers in Poland, Vienna, and the former East Germany were leaders in this field, and they trained students in molecular cytogenetics. One of them started his own cytogenetic lab in Brazil, and by sheer luck, a M.Sc. student from his lab, Aretuza Sousa, applied to work with me. She opened up an entire field not only for me, but also for several graduate students and one of my colleagues, who all enlisted her help for cytogenetic studies on their groups of interest.

With Aretuza’s molecular-cytogenetic know-how, we studied fusion of chromosomes during evolution (inferred when telomeric fluorescent markers suddenly appear in the middle of chromosomes), changes in chromosome numbers during evolution using a new maximum-likelihood model (Cusimano et al. 2012), the UUV sex chromosomes of liverworts (Renner et al. 2017; Sousa et al. 2021), and the sex chromosomes of species of *Coccinia* (Sousa et al. 2016, 2017; Fig. 7). This last topic continues to fill my days, with ongoing collaborative work on the evolution of the huge Y chromosome of *C. grandis* by now based on a chromosome-level assembled and annotated genome of this species. The annotation of the function of many of the genes was possible because the cucurbit family contains so many vegetable and fruit crops (Fig. 7) with much research on fruit yield, appearance, and taste.

8 Phenology and Botanical Gardens as Common Gardens

The species-specific flowering times of trees growing near the equator, which in some species are precisely synchronized among thousands of individuals across large geographic regions, have long been noted by tropical botanists. However, the environmental signals used by these plants have not yet been figured out. In my doctoral research, I had documented such synchronized annually repeated flowering in species of *Miconia*, using my own observations and herbarium material to acquire data for earlier years. This brought me in contact with the plant physiologist Rolf Borchert (1933–2017) from the University of Kansas in Lawrence, and we worked together from 1995 until 2009, with mutual visits in Mainz, Saint Louis, Lawrence, and Munich during which we discussed possible experiments to try and figure out the environmental cues. However, even though our collaboration resulted in a paper in *Nature* (Borchert et al. 2005), it ended in frustration because I remained unconvinced that our proposed explanation was completely right. The controversial discussions with Rolf about whether air temperature, precipitation, or the annual day length cycle was the external signal against which tropical plants are calibrating their internal clocks, however, stuck in my mind.

In the spring of 2012, Constantin Zohner came to my office asking about a possible topic for his M.Sc. thesis (in Germany still the obligatory precondition for starting on any doctoral research). I suggested that he should study leaf-out times in the Munich Botanical Garden, observing as many trees and shrubs as possible and relating their leaf-out to the region where they came from. Constantin is an exceptional experimentalist and, equally important, interested in statistics and analytical methods; he is now at the ETH in Zurich, with his own state-of-the-art climate chambers. In Munich, Constantin ended up studying almost 500 woody species (permanently outdoors) from numerous genera, families, with 85% of them not native in Central Europe. The results revealed, for the first time, the permanent footprint that adaptation to local climate leaves on the phenology of tree species (Zohner and Renner 2014). We titled our paper ‘common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change’ because we realized that for long-lived species, botanical gardens are equivalent to common garden experiments in giving us the power to separate genotype and phenotype, an experimental approach first developed in the 1930s by one of the fathers of the study of plant adaptation, Göte Turesson, working on bud burst and autumn leaf senescence in Sweden, and Clausen et al. (1940), working in California. Amazingly, nobody had ever applied the concept to the arboreta of botanical gardens.

The insight that botanical gardens, for long-lived plants that are not allowed to reproduce within the gardens, constitute ‘common garden experiments’ led to many further studies, all carried out in the Munich botanical garden. Constantin, for example, cut off many species’ branches to study their leaf-out under controlled conditions (in the greenhouse) and shaded branches outdoors by covering and uncovering them daily, which involved him living in the gardeners’ building on