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# CAPITULUM

THE INTERNATIONAL COMPOSITAE ALLIANCE NEWSLETTER

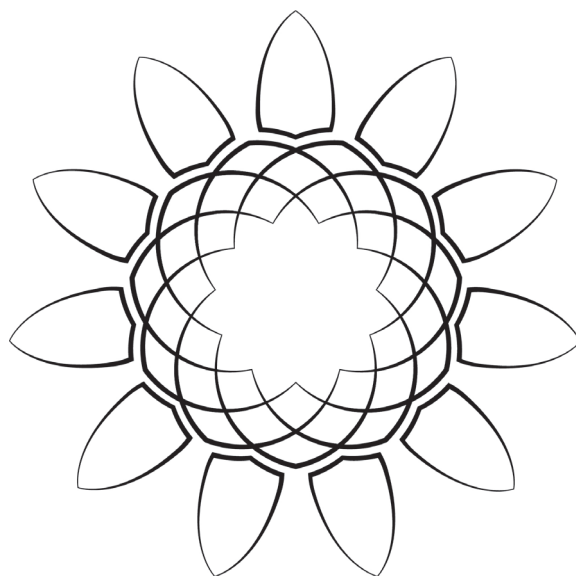


 **TICA**  
THE INTERNATIONAL COMPOSITAE ALLIANCE

VOLUME 2(1)- AUGUST 2022

# CAPITULUM

THE INTERNATIONAL COMPOSITAE ALLIANCE NEWSLETTER



**CAPITULUM**

*For the community & by the community.*



# CAPITULUM

THE INTERNATIONAL COMPOSITAE ALLIANCE NEWSLETTER

## CAPITULUM

CAPITULUM is the Newsletter of The International Compositae Alliance and is meant to be a venue for all things Compositae and welcomes all kinds of diversity in both its contributions and contributors. ISSN 2789-2786.

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Universidad de la República, Montevideo, URUGUAY  
*mbonifa@gmail.com*

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*b.loeuille@kew.org*

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*Alexander.S-L@csiro.au*

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University of Tennessee, USA  
*eschilling@utk.edu*

### **Alfonso Susanna**

Botanic Institute of Barcelona, SPAIN  
*asusanna@ibb.csic.es*

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**A NOTE FROM THE EDITORIAL BOARD**  
on the new series of the TICA Newsletter

Thank you for joining us for the third issue of CAPITULUM!

In this third issue, we bring to you two 'Head Topics' articles: J. Mauricio Bonifacino offers a window into the life and work of Jorge Crisci, an influential cladist, biogeographer and Compositae specialist from Argentina. Next, Alexander Schmidt-Lebuhn, Daniella Egli and Ben Gooden share with us a work that put taxonomy to direct use in efforts to control invasive species in Australia.

This issue hosts two articles in 'Brevia': one from Enrique Luengo, Juan M. Martínez Labarga, Rubén de Pablo, Alfonso Susanna and Roser Vilatersana where they report the rediscovery of a thistle presumed extinct from Spain and another from Oscar Hinojosa-Espinosa and Darío Javier Schiavinato on the phylogeny of marigolds. In 'The Cabinet', Gisela Sancho and Laura Iharlegui introduce us to the Compositae collection hosted at LP herbarium in the Museo de La Plata in Argentina. Finally, view the stunning images from three contributors to 'Style': Thorben Danke, Robert Dash, and Rainer W. Vogt.

Once again, we hope you enjoy reading our third issue of CAPITULUM.  
Please share the newsletter broadly with friends and colleagues!



J. Mauricio Bonifacino



Ilse Breitwieser



Benoit Loeuille



Jennifer R. Mandel



Abigail Moore




Erika R. Moore



Luis Palazzesi




Lizzie Roebke



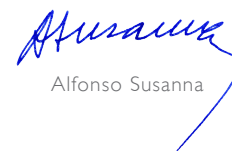
Gisela Sancho



Alexander Schmidt-Lebuhn



Ed Schilling



Alfonso Susanna

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## CONTENTS

### HEAD TOPICS

Jorge Víctor Crisci: Latin American champion of synantherology, phenetics, cladistics and biogeography | 1  
J. Mauricio Bonifacino

Invasive *Senecio madagascariensis* Poir. and the *Senecio pinnatifolius* A.Rich. complex (Senecioneae): Evolutionary relationships and their implications for biological control research | 20  
Alexander N. Schmidt-Lebuhn, Daniella Egli & Ben Gooden

Phylogeny of marigolds (*Tagetes* L., *Tageteae*) based on ITS sequences | 38  
Oscar Hinojosa-Espinosa & Darío Javier Schiavinato

### BREVIA

The people you kill are doing quite well: The rediscovery of an “extinct” species described from the outskirts of Madrid (Spain), *Carduncellus matritensis* Pau (Cardueae) | 50  
Enrique Luengo, Juan M. Martínez Labarga, Rubén de Pablo, Alfonso Susanna & Roser Vilatersana

### THE CABINET

The Compositae collection of LP Herbarium: past and present | 57  
Gisela Sancho & Laura Iharlegui

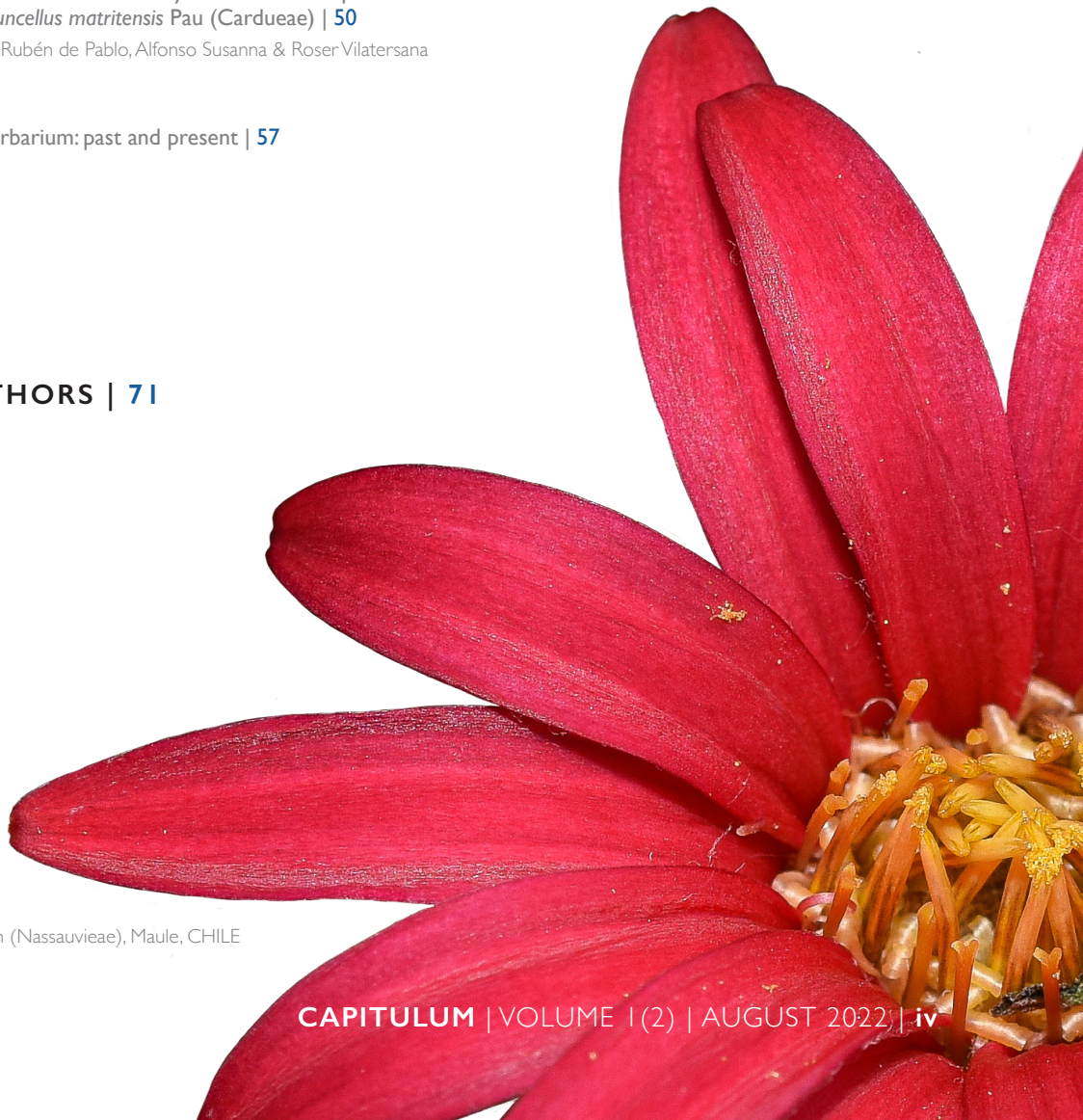
STYLE | 63

TICA TALKS | 66

TICA TIMES | 68

GUIDELINES FOR AUTHORS | 71

Cover photo: *Nassauvia pyramidalis* Meyen (Nassauvieae), Maule, CHILE  
Photo by J.M. Bonifacino



# Jorge Víctor Crisci:

## Latin American champion of synantherology, phenetics, cladistics and biogeography

Jose M. Bonifacino<sup>1</sup> 

<sup>1</sup> Laboratorio de Botánica, Facultad de Agronomía, Montevideo, URUGUAY, [mbonifa@gmail.com](mailto:mbonifa@gmail.com)

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### ABSTRACT

Jorge V. Crisci is a pheneticist, cladist, biogeographer, systematist, mentor, speaker, husband and father. Jorge is many things, hard to outline into a simple idea, a man of many talents which he claims are a reflection of his own teachers' and students' accomplishments. Throughout a career of more than 50 years dedicated to the study of Compositae and theoretical phenetics, cladistics and biogeography, he has had an extensive production in terms of published works, students mentored and courses taught across the five continents. One of Latin America's brightest systematists opens a door to his life and work so we could witness an amazing journey about the power of daring to learn more and the courage to follow one's dreams.

**Keywords:** *Biography, education, history*

On a March 2022 afternoon I sat down to talk with Jorge Víctor Crisci, one of the most influential botanists in the development of phenetics, cladistics and biogeography in Latin America, and who made a name for himself within the Compositae, where two genera have been dedicated to him: *Criscia* (Nassauvieae; Katinas, 1994; [Figure 1](#)) and *Criscianthus* (Eupatorieae; Grossi et al., 2013). In Compositae, Jorge followed the steps of one of his mentors, Angel Lulio Cabrera. The objective of this article is to offer a window to his life and academic career.

Jorge was born on March 22, 1945 in Ensenada, Argentina, a small coastal industrial city on the Rio de la Plata, located in the outskirts of La Plata, capital city of Buenos Aires province. La Plata is famous within the world of natural sciences for its internationally recognized Natural History Museum ("Museo de La Plata").

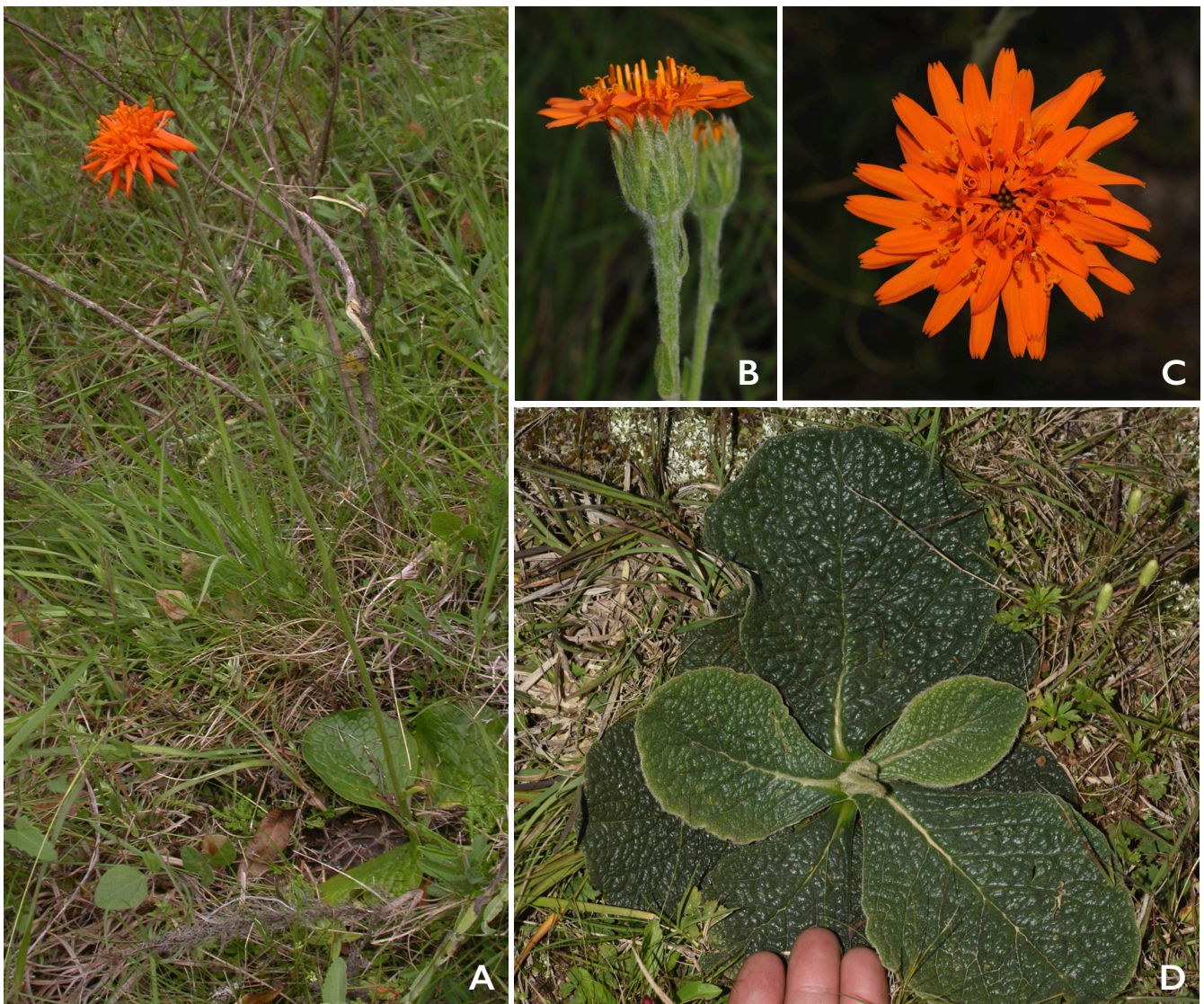
Through a series of sad family misfortunes Jorge lost his father early and then his mother, and was

raised by his maternal grandparents, who ensured that this young man from Ensenada could access a better education.

*"The activities that occupied most of the inhabitants of Ensenada were the shipyard and the oil refinery.*

*Since early age, and until I was 16 years old, I worked at my uncles' modest grocery-pub, located next to the shipyard gates. In this grocery-pub I had the opportunity to learn about life and how to overcome difficult situations. There I learned the value and meaning of responsibility with respect to the consequences of one's actions."*

*"In Ensenada, among refinery's workers, geologists were valued professionals. Under this influence, and excited about the idea of a future dedicated to geology, I decided to join the School of Natural Sciences and Museum of Universidad Nacional de La Plata (UNLP). Prior to entering the School, in the course of my last high school years (UNLP National School), I was able to access my first paid job at the University as a tutor for first-year students."*



**Figure 1.** *Criscia stricta* (Spreng.) Katinas. The emblematic species, endemic of the Pampas, had been placed in several genera. Jorge's early phenogram indicated its aberrant position that showed it didn't match any of them. It would be up to Liliana Katinas, Jorge's wife and partner in botany, to cast the new species in a monotypic genus honoring Jorge's long commitment to the study of the Nassauvieae. **A.** Habit. **B.** Head, lateral view. **C.** Head, top view. **D.** Detail of leaves.' Photos by J.M. Bonifacino.

Jorge entered the School of Natural Sciences in 1963, and there he took subjects common to all careers, which included chemistry, botany, geology, zoology and anthropology. Aida (Adita) Pontiroli, specialist in Apiaceae, was his first lab teacher on Botany 101 ("Fundamentos de Botánica").

*"In one of the many lab sessions, she said to me: 'I see that you and plants get along well, you should consider botany in your future'. Then, at the end of 1963, not without reservations, I decided to follow my career in botany... A geologist had good job prospects... but a botanist? It was not an easy decision."*

The lectures of Botany 101 were given by Humberto A. Fabris, who was a student of Cabrera. The charismatic personality of Fabris, together with his excellent teaching skills, and Adita's enthusiasm, spurred in Jorge a deep love for botany, sealing his academic destiny within the gentle science.

*"In December 1963, after passing the exams of four of the five subjects of the common cycle, Fabris summoned me to his desk at the La Plata Museum Herbarium, and told me about his collaboration with Cabrera in the Flora of Jujuy project, and made me a wonderful proposal for a young student: to join him on*

# Mine was not a time of selfies

Referring to the rather limited number of personal photos available. Jorge's frequent visits to the USA put him in close contact with researchers and discussions about the new and exciting methods and findings in the realm of plant systematics.

Jorge V. Crisci in a photo dated 1979,  
while visiting the National Museum of Natural History  
at the Smithsonian Institution in Washington DC  
*Photo by R. M. King*



*a month-long field trip to the mega-diverse province of Jujuy, traveling through a large part of northwestern Argentina. We were joined by Benno Schnack, professor of genetics at the Sciences School and already a distinguished scientist who had completed his postdoctoral work with G. Ledyard Stebbins in California.”*

*“I then was 18 years old and had scarcely ventured far from La Plata, and at any rate not out of Buenos Aires province, so for me this trip was a revealing experience, one that definitely cemented my fascination with plants and exposed me to a world of incredible diversity.”*

In March 1964, after returning from his first trip to Jujuy and while working on the labels of the plants collected in Jujuy, Jorge met Cabrera, who had just returned from a stay at Harvard where he had completed his review of the genus *Mutisia* L. (Cabrera, 1965).

Jorge's Science School years passed rapidly, with the added value of the trips to Jujuy that he repeated in the successive summers. In 1965, he obtained a post as a Teaching Assistant in Botany 101, starting a long and prolific academic career of 55 uninterrupted years at the Universidad Nacional de La Plata. During these years, and in different stages, he was professor of Introduction to Taxonomy, Systematics of Vascular Plants, Evolution, and Biogeography. His academic career has culminated with an Emeritus Professor position at the same university.

In 1967, he obtained his B.S. degree in Botany and decided to continue his education by entering the Ph.D. program, choosing Fabris as advisor and as a subject a taxonomic revision of Argentinean Araceae (Crisci, 1971). He completed his Ph.D. in a period of two years with the help of an initiation scholarship of the National Council for Scientific and Technical Investigations (CONICET after its Spanish acronym).

*“While working on my dissertation I had to make several collecting field trips, mostly to northern Argentina. When planning the first of them to northeastern Argentina, Cabrera, as Director of the herbarium, insisted that I should do it on my own and without a vehicle. At that moment in time, I would not describe myself as happy with that decision, but*

*in the end it turned into a very positive experience, Cabrera definitely knew what he was doing! The trip was not free from hardships and difficulties, but being alone and with limited mobility, forced me to interact with the locals and through them I was able to obtain data on the plants I collected. Coincidentally, on the same date I was defending my Ph.D., an anthropology student, Omar Gancedo, also was defending his on the Guayaquí ethnic group from Paraguay. In this thesis he talked about the “Güembé” (*Philodendron bipinnatifidum* Schott ex Kunth) a species I had also included in my thesis. Genoveva Dawson, the professor of Applied Botany, alerted me of this shared interest and urged me to meet Gancedo, which eventually led to the publication of a work on the systematics and ethnobotany of Güembé (Crisci & Gancedo, 1971).”*



**Figure 2.** *Moschardia solbrigii* Crisci. This species represents the starting point in a long career dedicated to the study of secondary heads in Compositae.  
Photo by J.M. Bonifacino.

Upon finishing his PhD in 1968, the new professor of Botany 101, Irma Gamundi (Fabris had moved on to Systematics of Vascular Plants) offered Jorge to lead Lab classes, a position he would hold for four years. During this period, he learned a lot about teaching, another of his passions.

The Araceae are not a diverse group in Argentina, but they proved very useful in exposing Jorge to the fundamentals of systematics. However, they presented limited research opportunity, as they were not diverse enough within the country, at a time when the logistics of studying them beyond Argentina was not easy. He needed to choose another group of plants that could offer a future of possibilities free from the financial hurdles of having to travel abroad. The presence of Cabrera and the vast Compositae collection in La Plata herbarium (LP) made that decision an easy one.

*“Cabrera was born in Spain and arrived in Argentina when he was 18 years old, accompanying his father, the famous zoologist Ángel Cabrera, who came to Argentina hired by the Museo de La Plata. Dealing with Cabrera was a real pleasure, he never lost his Spanish accent and had always a very gentle way of expressing himself. Cabrera had a way of conveying his infinite passion for Comps, a passion shared on weekends with his other love, sailing.”*

*“I met with Cabrera to choose the group to continue my career as a botanist and he suggested me the genus *Leucheria* Lag. (*Nassauvieae*).”*

*“At that moment I didn’t know it, but he really gave me a hard row to hoe [laughs]: *Leucheria* was an enormous constellation of scientific names in the midst of a fog of taxonomic confusion. In the end however, the challenge offered more pleasures than headaches. Once again, Cabrera’s wisdom at work.”*

Like Cabrera, Jorge shares his passion for Compositae with another activity, in his case it is not sailing, but something that marks his Argentine condition as it is his fervor for football [soccer]. His serenity as a teacher and composure as a seasoned botanist is in stark contrast with his passion for playing football (when younger) or his cheering on Gimnasia y Esgrima La Plata at the soccer stadium! But this is only part of who he is. Outside academia, he is also a cinephile and a bibliophile with a zealous inclination for Jorge Luis Borges and his fictions.

The interaction with Cabrera was especially beneficial for Jorge. Cabrera had a legendary knowledge of Compositae and even in that pre-globalization era, he was already a world famous botanist. This was a bygone era without the communication facilities of today, with limited access to literature and where the answers to questions sent by actual mail took weeks or months to return. Cabrera was known everywhere, and that unquestionably opened doors.

Cabrera's influence on Jorge was not limited to systematics per se, but included another of his great passions, biogeography.

*“In 1968, Cabrera said to me: ‘—I want to publish a new phytogeographic scheme, but I have doubts about some limits and ecotones between the Pampa, the Monte and Patagonia [biogeographic provinces]. Need to check this in the field, wanna come along? We go in my Citroën—’. The idea was to check the ecotones, write down the list of the species we found, collect them and mark the places where they occurred on a map. It was an extraordinary journey and a huge learning experience for me.”*

A few years later, Cabrera would finish publishing his classic biogeographic scheme, first including only the proposal for Argentina (Cabrera, 1971) and later extending it to the rest of Latin America (Cabrera & Willink, 1973). This scheme has withstood the test of time and methods and, with the exception of minor adjustments, remains intact today. Later biogeographic schemes, including maps of ecoregions of Argentina, were based on Cabrera's work. These achievements acquire more significance when one factors in that they were produced in a time without satellite images, in the absence of global positioning systems and without the help of computers. It was simply done by means of walking the land and marking points on paper maps.

The work in *Leucheria*, even with its many hurdles, gave Jorge a unique perspective for the most diverse early-diverging lineage in the Compositae, offering him a thorough understanding of its evolution. *Leucheria* is diverse on both sides of the Andes, which is what led Jorge into traveling to Chile. Several trips across the Andes resulted in a strong friendship with one of the most important botanists of Chile, Clodomiro Marticorena. With Clodomiro, Jorge not only learned about Chilean Compositae

# A cornucopia of diversity revealed

In december 1963, Humberto Fabris, Jorge's professor made him a wonderfull proposal, to join him on a one-month long fieldtrip to megadiverse Jujuy. That would change his life forever.



Jorge V. Crisci while collecting plants in Jujuy in 1966.  
Photo by Roberto Kiesling

and where they occurred, but he was also introduced to palynology (Marticorena & Crisci, 1972; Crisci & Marticorena, 1978).

In 1971 he entered the career of the Researcher at CONICET, whence in 1999 he reached the highest category of Senior Researcher.

The year 1972 was a turning point in Jorge's life. He won a position as Assistant Professor of Systematics of Vascular Plants. In that same year, and at the young age of 27 years, he obtained the prestigious John Simon Guggenheim scholarship that would allow him to continue his studies on *Leucheria* at Harvard University, following the steps of Cabrera himself.

*"I am convinced that to some extent it was the paper on *Philodendron* that opened the door to my stay at Harvard. One of the members of the committee that evaluated the proposals for this scholarship was the prestigious ethnobotanist Richard Schultes, and apparently he liked this article much, as I learned when I finally went to Harvard and got to know him personally. Many times the opportunities come from the least thought of places. The time at Harvard was for me equivalent to being in a botanical amusement park. It was there that my interest in the development and evolution of secondary heads arose. It all started with a few samples of *Moscharia* (Figure 2) that had been sent to me labeled as *Leucheria*."*

At Harvard Jorge worked with the Argentinean Otto Solbrig, who was a professor there and a well known specialist in population biology. Solbrig was a former student of Cabrera and he suggested a numerical and computational approach to tackle the complexity of *Leucheria* and the *Nassauvieae*.

Solbrig had been a professor at the University of Michigan in Ann Arbor, and had James Farris and Arnold Kluge as colleagues. Along with them, he had used the first computer programs for phylogenetic analysis. Especially the PRIM program (developed by telephone companies and used by biologists to implement a form of parsimony) and Wagner 72 (created by Farris to produce Wagner trees, an "ancestor" of the current phylogenetic programs that apply parsimony). This was a time when computer programs were "written" by punching holes on paper cards, as well as data and instructions. There

were no screens, and the results to the operations were visualized on printed paper about half a meter wide!

*"This year I was at Harvard, I met many key figures from the world of botany and biology who visited Harvard, such as the synantherologist Arthur Cronquist, the evolutionist G. Ledyard Stebbins and the anatomist Sherwin Carlquist. With them I discussed the subject of secondary heads in *Compositae*. These discussions were enormously beneficial for my research in the *Nassauvieae*. Stebbins was a truly inexhaustible source of ideas. We would remain in contact for many years to come. For Stebbins, the secondary heads were the result of a selection pressure to reduce the number of florets in the heads to avoid attracting phytophagous insects, and later to increase the number of florets again to achieve pollination success by means of grouping the many small heads, hence generating the so-called secondary heads."*

*"During that time at Harvard, I also met botanists Reed C. Rollins, Rolla M. Tryon, Bernice G. Schubert, Carroll E. Wood, paleontologist Stephen Jay Gould and evolutionist Ernst Mayr, who were all professors there. When I think retrospectively what they all had in common, apart from the greatness of intellect and the revolutionary and advanced ideas that each one of them imprinted in their fields, humility comes to mind as the ultimate common denominator."*

Just before returning to Argentina in 1973, Jorge had the opportunity to meet another Harvard visitor, Robert Sokal, who together with Peter Sneath was the architect of the development of numerical taxonomy. Talking with Sokal about his work with *Leucheria* and its closest relatives, Sokal mentioned a new program, the Numerical Taxonomy System (NTSYS) written by F. James Rohlf, with which all sorts of numerical analysis could be carried out. It was then that, at the suggestion of Sokal, and thanks to the insistence of Gould, he wrote to Rohlf who generously gave him a copy of the program to take back to Argentina (Figure 3).

On his return from the USA, several of the papers started during his stay at Harvard came to fruition, including a description of a new genus dedicated to Marticorena (Crisci, 1974a), the revision of *Moscharia* with a reinterpretation of its heads (Crisci,



**Figure 3.** Magnetic tape of one of Rohlf's earliest versions of NTSYS (Numerical Taxonomy System), a cornerstone of numerical taxonomy. *Photo by P. Marchionni*

1974b), the numerical analysis (Cluster Analysis and PRIM) of the Nassauvieae (Crisci, 1974c) and the revision of *Leucheria* (Crisci, 1976). In all of them, two distinctive elements are combined, the focus on the Compositae with an emphasis on the early-diverging lineages together with a detailed analysis of their morphology, and the application of emerging techniques of taxonomic analysis.

*“Back at the Museo de la Plata, the University had rented an IBM mainframe computer (at that time IBM did not sell computers, they rented them!). The NTSYS program was 200 kb and because of its size (figure that!) it could not be run during the day while the computer was being used by other researchers, so I punched the cards with the instructions and the data and left it with the technicians to be run through the night. The next day I would return and retrieve the results, in printed form. I used these programs while performing phenetic and cladistic analysis to different groups. Among these studies*

*were those done in collaboration with the botanist Bruno Petriella on Cycadales, for which we used NTSYS and Wagner 72 on the mainframe for a phenetic and phylogenetic analysis (Petriella & Crisci, 1975, 1977).”*

*“Thanks to the stay at Harvard, I also met another visitor, Tod Stuessy, with whom we shared the interest in secondary heads. In 1978, thanks to an invitation from Stuessy, I spent a year as visiting professor and Fulbright-Hays Fellow at Ohio State University. In that same visit I traveled to Ann Arbor and I met with James Farris (the great theorist of numerical cladism) who gave me his new version of the Wagner program (Wagner 78). During my stay at the Ohio State University, I used Wagner 72 to infer the relationships among the Nassauvieae (Crisci, 1980). Together with Stuessy, we analyzed *Melampodium* (Millerieae) using numerical and computational techniques (Stuessy & Crisci, 1984b).”*

# A model for evolutionary studies

*Leucheria diemii* Cabrera. One of the 29 currently recognized species of *Leucheria*. This genus shows an interesting diversity in terms of size and arrangement of heads, and internal organization of bracts in the head that helped to understand the evolution of secondary heads in the Nassauvieae.



*Leucheria diemii* in N. Santa Cruz, Argentina.  
Photo by J. M. Bonifacino

# We go in my Citroën

It was the summer of 1968 and Cabrera invited Jorge Crisci to tag along in a trip intended to adjust the limits of several biogeographic provinces, among which was Monte, an extense biogeographic province dominated by Zygophyllaceae.

Monte biogeographic province in San Juan  
Photo by J.M. Bonifacino

*“Numerical techniques were divided into two major areas, phenetics and cladistics, which differ on their philosophical basis. Phenetics is based on forming groups through the use of a large number of characters, all weighted equally. Cladistics is based on defining the groups by the evolutionary novelties or synapomorphies that support them. Both numerical methodologies hold much in common, so the meetings on the use of numerical techniques used to include contributions from both approaches. From the mid-1970s onwards, a great schism took place that set the two approaches apart, generating strong controversies that are reflected in the publications of the period. It is very interesting to note that with the appearance of molecular data, the phylogenetic analysis allowed the implementation of probabilistic models of evolution (maximum likelihood and bayesian). This division generated a sort of 21st century schism within phylogenetic methods (parsimony vs. probabilistic methods). I wonder what the next dichotomy would be, maximum likelihood vs. bayesian?”*

At Ohio State University, Jorge also met a Stuessy's graduate student, Bob Jansen, who would later be responsible together with Jeffrey Palmer for discovering the chloroplast inversion that would mark the basal split between the Barnadesieae and the rest of the Compositae.

*“During this visit I also met Vicki Funk, who was finishing her thesis on Montanoa (Heliantheae). That meeting made an everlasting impression on me. Vicki was an incredible person, overflowing with enthusiasm and energy, a tireless worker. Cladistics was at its height at that time, and Vicki, despite her youth, was an influential figure. My feeling is that she has rarely been credited with being one of the most important figures in the theoretical development of cladistics. Let us not forget that she was the one who co-edited the first books where the basis of the cladistic approach to the classification were laid out, something that still is central to our efforts to understand how organisms evolved and are classified (Funk & Brooks, 1981; Platnick & Funk, 1983).”*

*“In the early 1980s cladistics gained power among the systematists, especially after the theoretical contributions of Norman Platnick and Gareth Nelson from the American Museum of Natural History, which developed and improved the ideas proposed by Hennig (1950, 1966).”*

In the words of Dickens... *“It was the best of times, it was the worst of times, it was the age of wisdom, it was the age of foolishness, it was the epoch of belief, it was the epoch of incredulity, it was the season of Light, it was the season of Darkness...”*

*“It was a fascinating time full of discussions that sometimes became heated. I attended some of the scientific meetings of the society that brought together practitioners of these methods, and had the opportunity to get to know the majority of those who built the theoretical foundations of cladistic methods based on parsimony such as Bremer, Kluge, Carpenter, Platnick, and Nelson among others.”*

The end of the 1970s and the beginning of the 1980s were periods of much intellectual effervescence and methodological developments linked to cladistics, which eventually ended up being called “Phylogenetic Systematics”. Jorge was an active participant in this process, and made important contributions in the use of parsimony, taxonomic congruence, primitive states, character polarization, and species concepts (Crisci & Stuessy, 1980, 1982; Stuessy & Crisci, 1984a; Crisci, 1984a; Crisci, 1981, 1982, 1983, 1984). During this period, Jorge also continued with his interest in numerical taxonomy, which led him to publish in 1983 a book that would summarize the methods currently in use. The book, although mostly dealing with phenetic methods, also contains a chapter dedicated to phylogenetic reconstruction using the algorithms created by Farris for Wagner 72 and Wagner 78 (Crisci & López Armengol, 1983).

*“In 1986, I closed a deal with IBM, in which they gave us three personal computers and funded two IT positions for the development of an educational software on evolution (Crisci et al., 1989).*

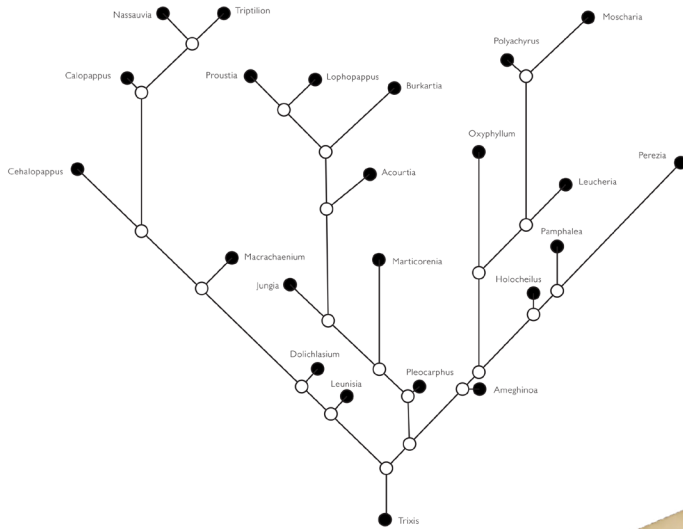
*Further adding to this, they also funded the visit of a specialist in computers and education, Ted Crovello, who had also worked on the systematics of Salicaceae using numerical and computational methods. With these computers that today would be outpowered by the simplest of the smartphones, but that back then were at the cutting edge, we began to work on phylogenetics, phenetics, and to perform evolutionary and biogeographical analyses. On the subject of education, I can't stress strongly enough the enormous influence that, from 1989 onwards, has had on me the great American educator Joseph McInerney. I met Joseph when we were*



# The mother of all numerical phylogenetic analyses

## Wagner tree

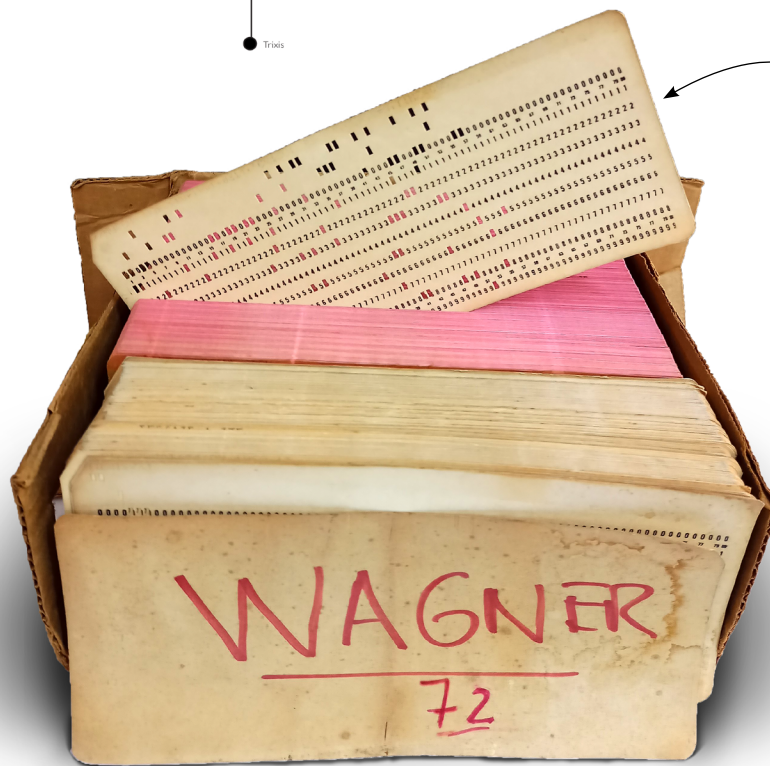
This diagram was published by Crisci in 1980 as part of his study on the evolution of Nassauvieae



Wagner 72 in punch-card format. This program, written by Farris, was the first ever to perform phylogenetic analysis in the shape of Wagner trees. The program in order to run had to be “written” by manually punching the cards using a machine, together with the instructions and data. The output was retrieved in printed form.

## Wagner 72

The “program” consisted of a whole deck of punched cards



## Punch-card

Each card had 80 lines of code capable of holding instructions or data

Photo by P. Marchionni

*both part of the Biological Education Committee of the International Union of Biological Sciences and from there we had several joint projects (Crisci et al., 2014; Apodaca et al., 2019) and a book on systematic teaching in primary schools sponsored by UNESCO (Crisci et al., 1993)."*

At the beginning of the 1990s, by invitation of Peter Raven, director of the Missouri Botanical Garden, Jorge traveled to Saint Louis, to participate with Raven's work group on Myrtales, with special emphasis on the Onagraceae. There he interacted with several researchers, especially Peter Hoch, that resulted in several contributions to understanding the evolution of that family (Boufford et al., 1990; Carr et al., 1990; Crisci & Berry, 1990; Crisci et al., 1990; Graam et al., 1993; Hoch et al., 1993a, b).

His visits to the Missouri Botanical Garden would repeat for several years, and he eventually was appointed an Honorary Curator of the institution. It is worth mentioning that these interactions with Raven further increased Jorge's interest in the conservation of biodiversity, and from then on, this topic would turn mainstream in Jorge's work.

Jorge's zeal for education is manifested in his published record (Crisci, 1994a, b; Crisci & Katinas, 2011; Apodaca et al., 2019; [Figure 4](#)) along with his efforts in the creation of educational software (Crisci et al., 1989; Andrews et al., 2002), but more importantly, it is reflected in the numerous courses taught in more than 20 countries, across the five continents. In this flurry of courses, he covered topics such as numerical taxonomy, phylogenetic systematics, biogeography, conservation of biodiversity, education, biological evolution, current state of systematics, comparative biology, collections of natural sciences, and scientific literacy and its relationship with democracy.

Jorge's presentations are charismatic and he invariably conveys his passion for the study of these disciplines. Literature and cinema always find a space in Jorge's talks, and allow him to present topics through the use of analogies and metaphors. Difficult topics and the latest advances are presented with wit and simplicity to make them accessible to diverse audiences.

The 1990s witnessed the creation in the Museo de la Plata of the Laboratory of Systematics and Evolutionary Biology (LASBE after its Spanish acronym), which represents the formalization of an eclectic group of systematists, led by Jorge, who seek to approach taxonomic and biogeographic problems from an evolutionary and multidisciplinary perspective (e.g., Crisci et al., 1991a, b; Crisci et al., 1994; Morrone et al., 1994; Semorile et al., 1994; Dewey et al., 1996). During this process, Jorge directed his efforts at another discipline, Biogeography, that had been introduced 20 years earlier by Cabrera himself. However, unlike Cabrera, who focused on the problem from a descriptive perspective, Jorge's approach to biogeography would be with a historical focus, facilitated by modern methodologies, including phenetics and phylogenetics.

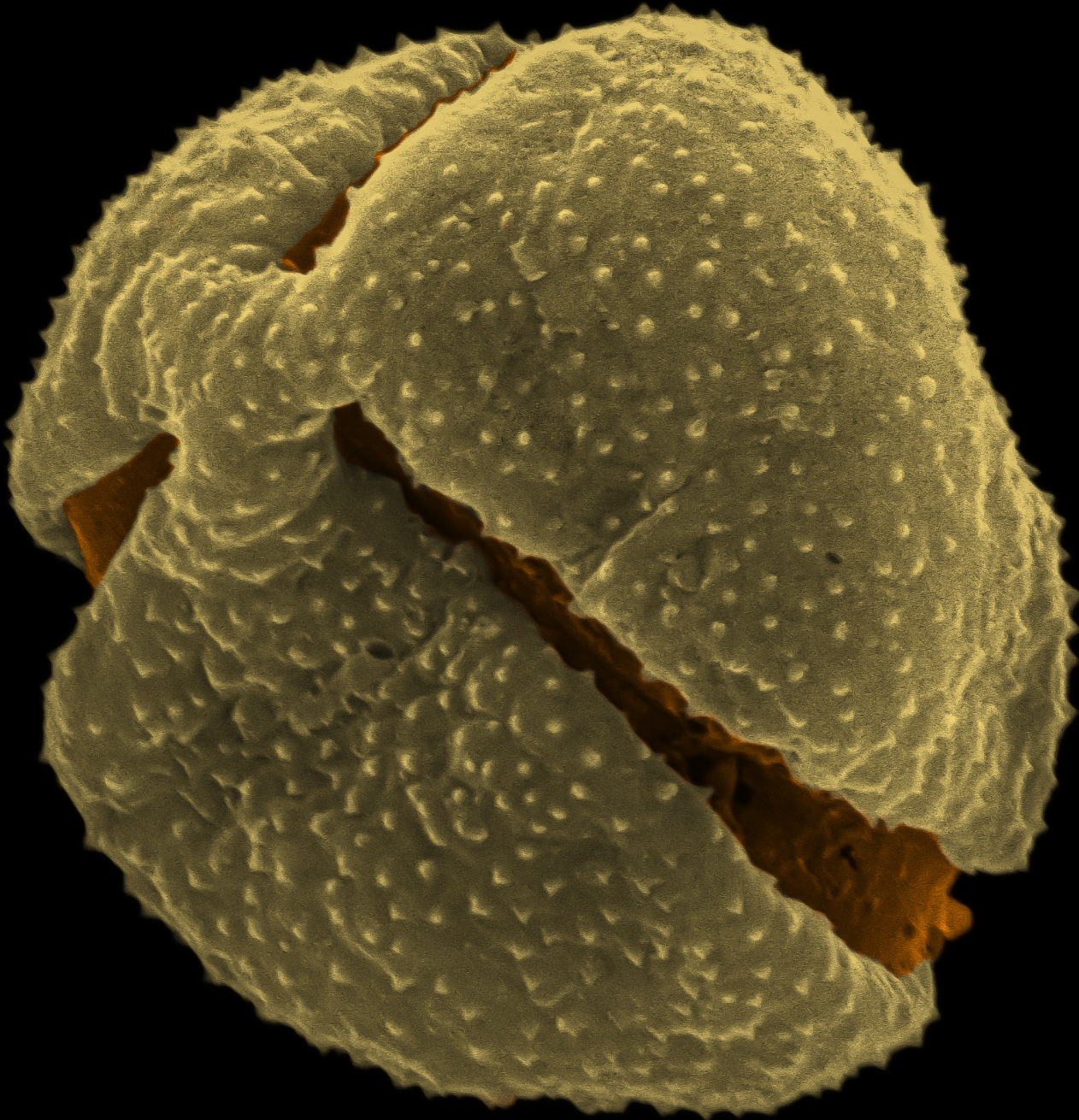
This is how Jorge produced a series of seminal works on the basic principles of historical biogeography (Crisci et al., 1991a, b; Crisci & Morrone, 1992a, b; Morrone & Crisci, 1990, 1992, 1995; Crisci, 2001a; Apodaca & Crisci, 2018) as well as several practical applications of these principles (Morrone et al., 1994, 1997; Katinas et al., 1999; Katinas & Crisci, 2000; Crisci et al., 2001; Roig-Juñent et al., 2002). Jorge dedicated much of the last years of the XX and the first years of the XXI century to this discipline, which eventually led to the production of two books entirely dedicated to biogeography (Crisci et al., 2000, 2003).

Four recurring themes have also found space in Jorge's recent years, including the conservation of biodiversity (Crisci et al., 1999; Crisci, 2001b, 2006c, 2008; Posadas et al., 2011), the teaching of biological evolution (Crisci et al., 2014; Apodaca et al., 2019), the importance of natural history collections (Crisci & Katinas, 2017a, 2017b) and scientific literacy (Crisci, 2011, 2014, 2015, 2016).

Finally, the most recent years have been a time of synthesis, the end result of a rich history that includes a broad spectrum of themes that range from science education to more philosophical approaches on the future of taxonomy (Crisci, 2006a, b; Crisci & Katinas, 2020; Crisci et al., 2020). Without forgetting his fascination with secondary heads in Compositae,

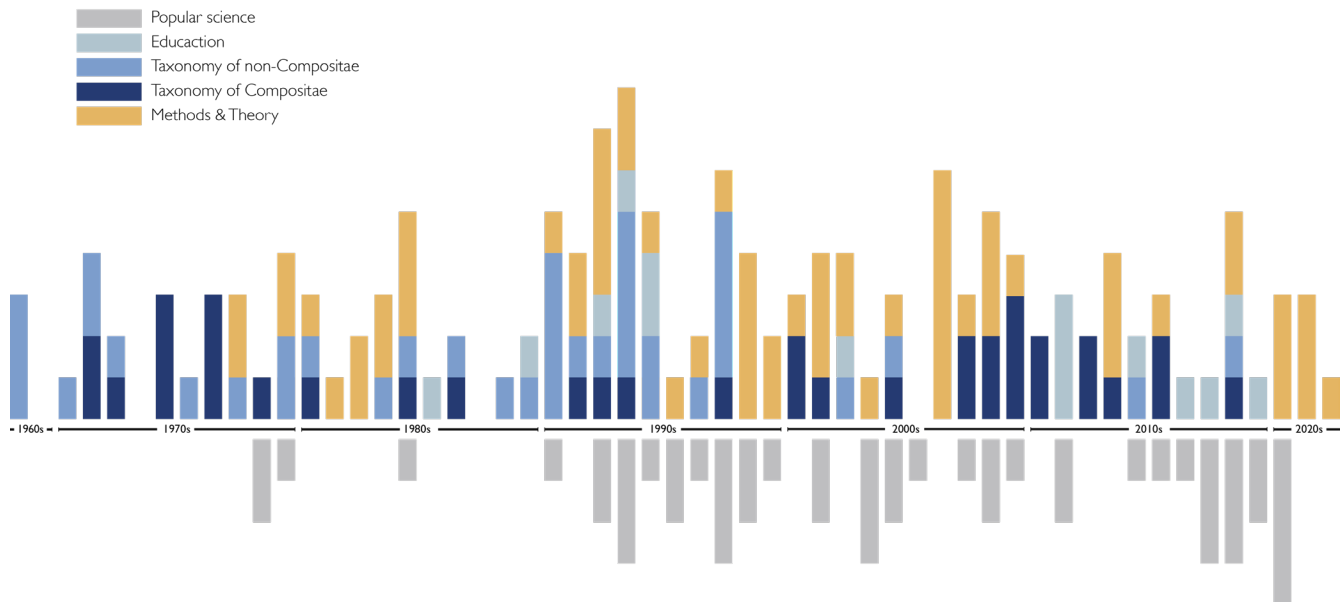
# SEM Miracles

*Huanilipollis criscii* Barreda & Palazzesi,  
Nassauvieae pollen, named in honor to Jorge Crisci.  
This morphospecies dated to the early Miocene, from  
the Chenque section, southeastern Chubut, Argentina,  
Chenque Formation (Barreda et al. 2008).



SEM of *Huanilipollis criscii* Barreda & Palazzesi  
Photo by V. Barreda

## Jorge V. Crisci's published record



**Figure 4.** Jorge V. Crisci published record. The infographic shows Jorge Crisci's continued involvement in Compositae, but also his significant dedication to methods and education.

in 2008 he revisited the concept, this time joined with other colleagues and approaching the subject from the molecular data perspective, in another take at the evolution of secondary heads in the Nassauvieae (Katinas et al., 2008).

In 2020 Jorge published, together with his colleagues Facundo Palacio and María José Apodaca, a book on multivariate analysis for biological data and its application using the language R. The book includes chapters on phylogenetic estimation (parsimony and probabilistic methods, cf. Palacio et al., 2020). As evidenced by the number of reads (currently more than 120000 on Research Gate), this book covered a strong need for a treatise in Spanish on the subject.

In 2022 Jorge has come around full circle, as he published with Liliana Katinas and María José Apodaca a synopsis of *Leucheria* (Katinas et al., 2022), a contribution where all the advances in the systematics of the genus since his original 1976 revision are presented.

*"I believe that one of the most challenging questions for synantherologists of the future is to find the morphological characters that support the main*

*nodes of the phylogenetic tree of Compositae. Bremer (1987) was a pioneer in this theme and created several hypotheses, but given the progress of knowledge of current relationships (Funk et al., 2009; Mandel et al., 2019) I believe that a re-evaluation of the morphological traits supporting the nodes may be in order."*

The moment is ripe for this type of work given the existence of robust and detailed phylogenies that show us the relationships between the different groups of Compositae. Knowing how these traits appear in the tree will not only satisfy our innate curiosity about the structures that define each group, but more importantly they will allow us to get closer to understanding the reasons that the Compositae are such a successful group of plants.

Now at 77, Jorge has been a witness and participant of one of the major revolutions in the history of biology, namely the development and maturation of modern systematic methods and biogeography. I am amazed by this rich history of experiences and contributions and was compelled to ask him about how he sees this journey, to which he gave a quintessential "Criscian" reply.

“I had always agreed with the vision that Spanish philosopher José Ortega y Gasset had on this very question:”

“Genuine vital integrity does not consist in satisfaction, in attainment, in arrival.  
As Cervantes said long since:  
The road is always better than the inn.”  
[Ortega y Gasset - *Revolt of the Masses*]

“It is highly likely that my ‘inn’ (i.e.: books, papers, courses, conferences, software) will not resist the test of time, but my ‘road’ — with its normal ups and downs — has been always marked by happiness because I simply love what I do. In this ‘road’ I feel like a fortunate and fortuitous link between two generations of brilliant biologists: my teachers (Cabrera, Fabris, Marticorena and Solbrig) and my students. I believe I have been a faithful mirror of other people’s talents. The ‘road’ has not only given me the happiness derived from the work I do, but it also led me to meet Liliana Katinas, my loving companion in life, but also a scientific collaborator so effective and brilliant that at the end of my life she has become the last of my teachers. The ‘road’ that brought us together with Liliana, awarded us with the arrival of Victoria, our daughter, the part of the road taken I am more proud of.”

## ACKNOWLEDGMENTS

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# Invasive *Senecio madagascariensis* Poir. and the *Senecio pinnatifolius* A.Rich. complex (Senecioneae):

## Evolutionary relationships and their implications for biological control research

Alexander N. Schmidt-Lebuhn<sup>1</sup> , Daniella Egli<sup>2</sup>  & Ben Gooden<sup>3</sup> 

<sup>1</sup> CSIRO, Australian National Herbarium, Clunies Ross Street, Canberra ACT 2601, Australia; alexander.s-l@csiro.au

<sup>2</sup> University of KwaZulu-Natal, School of Life Sciences, Carbis Road, Pietermaritzburg, 3209, South Africa; EgliD@ukzn.ac.za

<sup>3</sup> CSIRO Health & Biosecurity, Clunies Ross Street, Canberra ACT 2601, Australia; ben.gooden@csiro.au

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### ABSTRACT

Fireweed (*Senecio madagascariensis*, Senecioneae) is native to southern Africa and Madagascar but has become an invasive weed in southern South America, Japan, Australia, and Hawai'i. One strategy for reducing the impact of fireweed is classical biological control (biocontrol), i.e. the release of natural enemies of a weed such as pathogens or insects sourced from its home range. Before release, candidate agents are subjected to rigorous host specificity testing to minimise the risk of collateral damage to non-target species. It is important to include non-target species that are closely related to the target weed in these experiments, because candidate biocontrol agents are more likely to attack them than distantly related species. However, Australian biocontrol research on fireweed has for a long time suffered from confusion about the taxonomy and evolutionary relationships of fireweed and its presumed closest Australian relatives from the *Senecio pinnatifolius* complex. We provide an overview of the history of taxonomic and phylogenetic perceptions and relevant studies and illustrate that although *S. pinnatifolius* belongs to the Australasian clade of *Senecio* most closely related to fireweed, the two are not closely related in the context of the overall evolutionary history of the genus. We conducted a phylogenetic analysis of Senecioneae incorporating new sequence data for 38 specimens including all seven extant varieties of the *S. pinnatifolius* complex. The varieties were placed in different clades, suggesting that the species as currently circumscribed does not constitute a natural group, and that the varieties cannot be used interchangeably in biocontrol research. Further research into the complex is needed to arrive at a more appropriate taxonomy. *Senecio skirrhodon* was sequenced for the first time, confirming it to be closely related to fireweed, *S. harveianus*, and *S. inaequidens*.

**Keywords:** Australia, biological control, centrifugal phylogenetic method, fireweed, phylogenetics, *Senecio*

### INTRODUCTION

Fireweed, *Senecio madagascariensis* Poir. (Senecioneae), is a short-lived perennial herb native to southern Africa and Madagascar that has become successfully established as an invasive weed

in southern South America, Japan, Australia, and Hawai'i (Julien et al., 2012). In Australia, where it is widespread in open pastures across the south-eastern part of the continent, fireweed is recognised as one of 32 Weeds of National Significance (<https://weeds.org.au/weeds-profiles/>, accessed 22 April

2022) due to its adverse effects on pasture quality and toxicity to livestock, especially cattle, that reduce agricultural productivity (McFadyen & Morin, 2012).

Australia and Hawai'i have initiated research into the potential deployment of classical biological control (biocontrol) agents to help manage fireweed – i.e., the introduction of co-evolved 'enemies' (fungal pathogens, insects, mites) sourced from the weed's native range to reduce its competitive performance and invasion potential in the introduced range (Ramadan et al., 2011; Sheppard et al., 2011).

In weed biocontrol research, highly specialised biocontrol agents with native host ranges that are restricted to the target weed are prioritised for further host-specificity experimentation (Egli et al., 2020; Zuma et al., 2021), with the aim of minimising the risk of inadvertent, non-target damage to native or useful plants within the weed's introduced range. All else being equal, non-target plants that are closely related to the target weed are more at risk from candidate biocontrol agents, because herbivores or pathogens are more likely to find plants palatable that are similar to their co-evolved host (McFadyen, 1998; Thomas & Willis, 1998; Briese, 2003, 2005).

This observation has informed the Centrifugal Phylogenetic Method (Wapshere, 1974; Briese, 2003, 2005) that prescribes testing the biocontrol agent on a representative sample of non-target species drawn from lineages of increasing evolutionary distance to the target weed, with those closest to the target weed given highest priority. This means that an accurate understanding of the relationships between a target weed and other species in its introduced range is critical for robust and reliable risk assessment of biocontrol work, especially in the development of a 'host test list' of non-target plant species prioritised for host-specificity testing with the candidate biocontrol agent.

Unfortunately, research into the potential biocontrol of fireweed in Australia has often been impeded by taxonomic confusion around both fireweed itself and its presumed closest Australian relatives, and by misunderstandings of their phylogenetic relationships as discussed below. Uncertainty persists in the literature to this day (Wijayabandara et al., 2022).

In this contribution we summarise the history of taxonomic and phylogenetic (mis)understanding of fireweed and the species frequently considered most closely related to it in Australia, the *Senecio pinnatifolius* A.Rich. complex (previously *S. lautus* G.Forst. ex Willd.). We also comment on the phylogenetic position and status of another Australian species that has been of concern to biocontrol research in fireweed, *S. condylus* I.Thomps. Finally, we present new sequence data for all varieties of the *S. pinnatifolius* complex except one and incorporate these new sequences into a revised phylogenetic analysis of *Senecio* L. to inform the refinement of species selection for ongoing biocontrol risk assessment in Australia and weed management research on fireweed more generally.

## **TAXONOMIC PERCEPTION OF FIREWEED IN AUSTRALIA**

It is assumed that fireweed was introduced to Australia's southeast before 1918, but it was for decades considered to be a member of the native *Senecio pinnatifolius* complex (Julien et al., 2012). It was recognised as the South African and Madagascan *S. madagascariensis* only in 1980, when specimens were sent to the South African taxonomist O.M. Hilliard for identification (Michael, 1981). Chromosome counts confirmed the segregation, with fireweed having  $2n = 20$ , and *S. pinnatifolius*  $2n = 40$  (Radford et al., 1995), as did genetic data (Scott et al., 1998; Radford et al., 2000).

However, even as the evidence was accumulating, controversy and confusion persisted. Marohasy (1993) argued against the introduced status of fireweed in Australia, writing that "it appears the change of status, from native to exotic, was based essentially on a single identification by a foreign Compositae expert". Sindel (1986) and Radford & Cousens (2000) continued to assume that fireweed was "closely related" to Australian *Senecio pinnatifolius*. McFayden & Sparks (1996) cited then unpublished genetic data showing that fireweed was not part of the native Australian *S. pinnatifolius* complex but nonetheless stated that it was "closely related", that hybridisation between the two had been observed, and that the latter species should be prioritised for inclusion in a host test list for biocontrol research. Sheppard et al. (2011) considered the two species to be in "taxonomic close proximity". Most

# Fireweed

Southern African *Senecio madagascariensis* Poir. (fireweed) has been introduced in South America, Japan, Australia, and Hawai'i. It reduces agricultural productivity by invading pastures.

*Senecio madagascariensis*, Dunmore, New South Wales, Australia.  
Photo by Ben Gooden

recently, Wijayabandara et al. (2022) wrote that “the taxonomic position of Australian *S. madagascariensis* is undetermined”, thus underlining the need for a re-examination of the phylogenetic placement of fireweed in the context of native Australian *Senecio* species.

Confusingly, most of these publications cited one of the earliest genetic studies that demonstrated Australian fireweed to be part of the southern African *Senecio madagascariensis*/*Senecio inaequidens* DC. complex instead of the Australian *S. pinnatifolius* complex (Scott et al., 1998) in support of their close relatedness and/or continuing taxonomic uncertainty. That, however, appears to be a misreading of Scott et al.’s results and intentions, who only argued that the taxonomy inside the two complexes requires further work, not that the closeness of their relationship to each other remains unclear. Since that publication, formal phylogenetic studies have further clarified relationships, as discussed in the following section.

### **PHYLOGENETIC RELATIONSHIPS OF FIREWEED AND AUSTRALIAN SENECIOS**

*Senecio* is a large genus, with over 1,000 species distributed across all continents except Antarctica (Nordenstam et al., 2009), and because of changes in its taxonomic circumscription, it was even larger in the past (Pelser et al., 2007). This means that phylogeneticists needed to pick their battles, focusing either on shallow sampling across a large study group or deep sampling limited to a subgroup of the genus or tribe. This has complicated the interpretation of relevant phylogenetic studies by weed scientists, as partial phylogenies with few overlapping taxa were scattered across the literature without providing a comprehensive overview of all relationships.

As discussed in the previous section, two early genetic studies could have been expected to already have settled the question of a “close relationship”, in the absolute sense, between fireweed and Australian *Senecio* (Scott et al., 1998; Radford et al., 2000). A partial explanation of continuing confusion may be that the seminal phylogeny of Senecioneae produced by Pelser et al. (2007) showed the Australian clade 3, which included *Senecio pinnatifolius*, as, in a sense, “closest” to fireweed. However, that closeness is only relative. While Australian clade 3 was indeed topologically closest of all Australian *Senecio* to the

clade including fireweed, this latter clade including fireweed was itself not only very species-rich but also composed of southern African and New World subclades. This suggested a divergence very deep in time, followed by numerous speciation events, and consequently a very distant relationship between fireweed and Australian clade 3.

A subsequent study focused on Australasian species of *Senecio* related to *S. pinnatifolius*, sampling many more species and informally naming this group of species the Lautusoid group (Liew et al., 2018). The study resolved four distantly related lineages of Australian *Senecio* and identified several species potentially derived from hybridisation between different lineages. Three Australasian ribosomal sequence clades were found: clade 1 (Disciform group, Odoratus group), clade 2 (Quadridentatus group), clade 3 (Lautusoid group); as were three chloroplast clades: clade A (Odoratus group), clade B (Disciform group, Quadridentatus group), clade C (Lautusoid group). Liew et al. (2018) did not include fireweed in their analyses explicitly because they knew it to be unrelated to their study group. They did, however, include its close relative *S. inaequidens* DC., which was consistently placed outside of any of the Australasian groups.

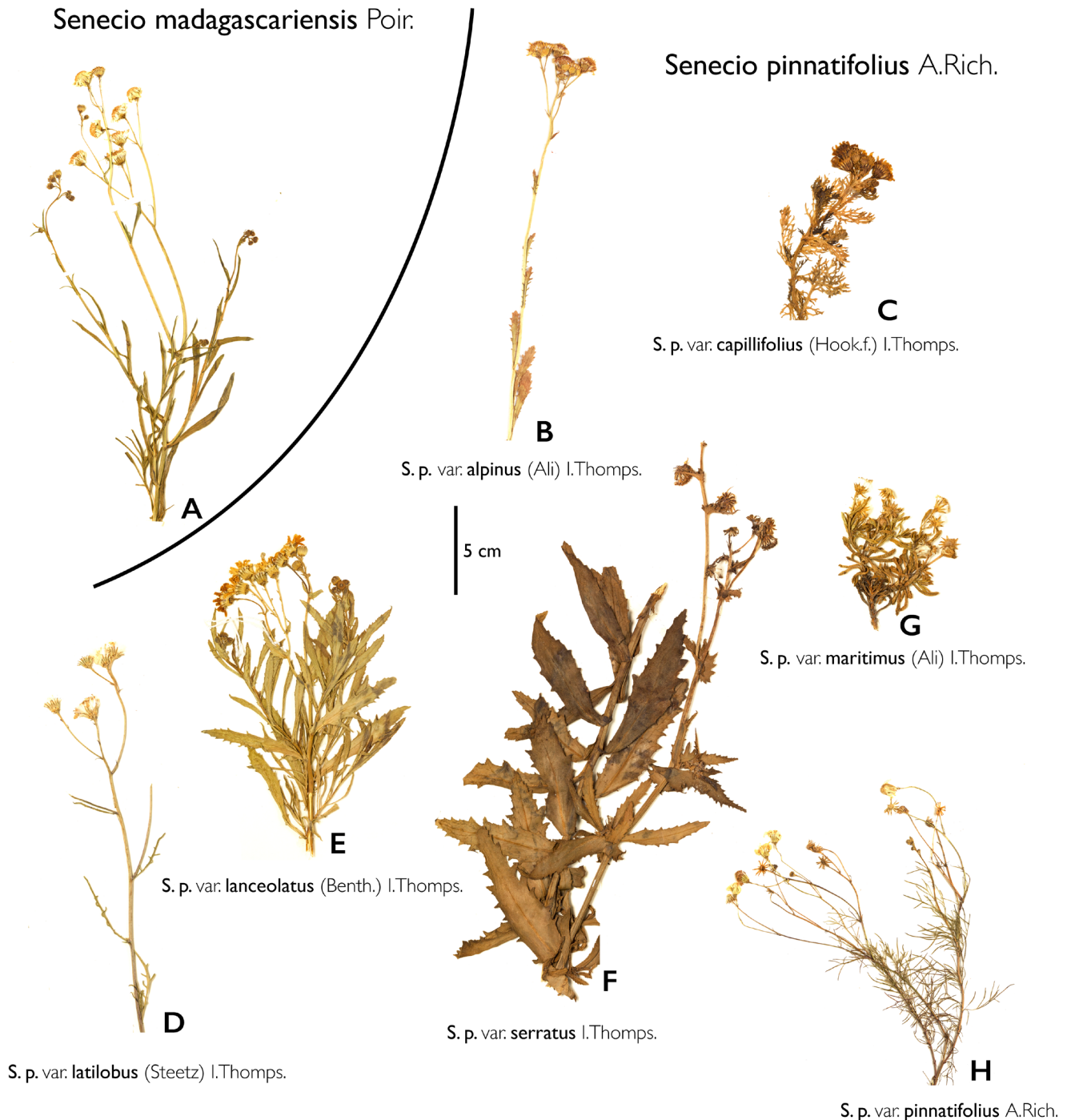
To assist in the prioritisation of native Australian *Senecio* species for inclusion on the biocontrol host test list and deployment in subsequent host-specificity experimentation, we recently conducted an analysis covering all species of Senecioneae for which ribosomal and chloroplast Sanger data were available, plus new data for previously neglected Australian species (Schmidt-Lebuhn et al., 2020). Our analysis therefore united both the broad backbone sampling of, e.g., Pelser et al. (2007) and deep sampling such as that of Liew et al. (2018). Our results confirmed the Australasian clades, including *S. pinnatifolius*, to be phylogenetically very distant from fireweed, and fireweed as part of a large African clade that also included *S. inaequidens* (Schmidt-Lebuhn et al., 2020).

### **THE *Senecio pinnatifolius* COMPLEX**

In addition to the changing status of fireweed itself in Australia, the taxonomic complexity of the *Senecio pinnatifolius* complex has contributed to confusion. For decades, this Australian taxon was named *S. lautus* G. Forst ex Willd., until Belcher

# MORE THAN A SINGLE ENTITY

a species complex with enormous morphological and ecological diversity



**Figure I.** Comparison of fireweed and the morphological diversity of the *Senecio pinnatifolius* complex. **A.** Fireweed, *S. madagascariensis*, C. Burgess s.n. (CBG). **B.** *S. pinnatifolius* var. *alpinus*, J. Pena 1 (CBG). **C.** *S. pinnatifolius* var. *capillifolius*, J.S. Whinray 488 (CANB). **D.** *S. pinnatifolius* var. *latilobus*, N.S. Lander 1025 (CANB). **E.** *S. pinnatifolius* var. *lanceolatus*, P.C. Heyligers 80012 (CANB). **F.** *S. pinnatifolius* var. *serratus*, I. Radford s.n. (CBG). **G.** *S. pinnatifolius* var. *maritimus*, P.C. Heyligers 79078 (CANB). **H.** *S. pinnatifolius* var. *pinnatifolius*, L.W. Cayzer 828 (CBG).

(1994) demonstrated it to be distinct from the New Zealand species of that name. Since then, weed researchers have shifted to using the name *S. pinnatifolius*, but the outdated name *S. lautus* is still used in some research fields, e.g. (Richards et al., 2019; James et al., 2021).

As implied by the term “complex”, *Senecio pinnatifolius* is a morphologically and ecologically diverse species of eight currently recognised varieties (Thompson, 2005b). *Senecio pinnatifolius* var. *alpinus* (Ali) I.Thomps. is an alpine taxon (Figure 1B); *Senecio p.* var. *capillifolius* (Hook. f.) I.Thomps. occurs on islands in the Bass Strait and has unusually finely divided leaves (Figure 1C); *Senecio p.* var. *lanceolatus* (Benth.) I.Thomps. occurs along the coasts of southeastern South Australia, Victoria, and northern Tasmania (Figure 1E); *Senecio p.* var. *latilobus* (Steetz) I.Thomps. occurs along the coast of southwestern Western Australia (Figure 1D); *Senecio p.* var. *leucocarpus* I. Thomps. is known from a single locality in Western Australia and presumed extinct; *Senecio p.* var. *maritimus* (Ali) I. Thomps. occurs along the southern coasts of Australia and Tasmania (Figure 1G); the most widespread and common *Senecio p.* var. *pinnatifolius* (Figure 1H) shares much of its distribution in eastern Australia with fireweed; *Senecio p.* and var. *serratus* I. Thomps. is found in southeastern Queensland and north-eastern New South Wales (Figure 1F) (Thompson, 2005b).

The delineation of varieties and the circumscription of the species complex as a whole remain controversial (Radford et al., 2004; Thompson, 2005b) and have never been comprehensively studied using genetic data, although some ecotypes serve as model organisms for research into incipient speciation (Roda et al., 2013). This means that if the complex is not a natural group but includes disparate lineages that potentially belong to different clades, the phylogenetic position of single samples may be misleading when preparing a host test list for fireweed biocontrol in Australia. Given the highly homoplasious nature of many characters traditionally used for species delimitation in *Senecio*, such a possibility should not be rejected out of hand, and indeed a recent study from New Zealand found what was previously treated as a single species of this genus

to fall into two different clades (Liew et al., 2021).

## HYBRIDISATION

Of particular interest in this context are claims that fireweed and *Senecio pinnatifolius* can be crossed. Although seemingly unlikely given the large phylogenetic distance between the two taxa, the possibility has been of great concern to invasion biology in Australia, sparking fears that hybridisation would drive native populations to genetic extinction (Johnston, 2008).

Claims of genetic intermediates observed in the field appear to trace back to an honours thesis (Scott, 1994), although no such claim was made in the subsequent publication of its results (Scott et al., 1998). Similarly, a Ph.D. thesis (Radford, 1997) is frequently cited as evidence for the risks of hybridisation, although it demonstrated artificially created hybrids to be sterile and did not find any hybrids in the field (Sindel et al., 1998).

The most widely cited study of hybridisation (Prentis et al., 2007) used Amplified Fragment Length Polymorphism markers to study gene flow and crossing experiments to test for hybrid formation. It was able to produce hybrid seed, which did not show reduced viability, but found no adult hybrid individuals in the wild, concluding possible selection against hybrids at later life stages. The main risk factor discussed by Prentis et al. was that fireweed was more successful in fathering hybrid seed than *Senecio pinnatifolius*, which may skew seed set towards fireweed in contact zones.

Dormontt et al. (2017), after clarifying that Prentis et al. (2007) had conducted their experiments on *Senecio pinnatifolius* var. *serratus*, repeated the experiment with *S. p.* var. *pinnatifolius*. They did not detect any adult hybrids in any population of *S. p.* var. *pinnatifolius* and found low hybrid seed set, concluding that the native taxon was unlikely to be at risk from introgression.

In summary, there is little concrete evidence to suggest that significant gene flow takes place between fireweed and *Senecio pinnatifolius*.

## *Senecio condylus*

Of all species presumed native to Australia, *Senecio condylus* was placed closest to fireweed in previous

# *Senecio pinnatifolius*

*Senecio pinnatifolius* A.Rich. has historically been considered the closest Australian native relative of fireweed. Its type variety and introduced fireweed share a large part of their ranges, and there have been concerns about the two species hybridizing.

*Senecio pinnatifolius*, Nerriga, New South Wales, Australia.  
Photo by Ben Gooden.

phylogenetic analyses (Liew et al., 2018; Schmidt-Lebuhn et al., 2020). It was described as new to science only as recently as 2005 and considered endemic to southwestern Western Australia (Thompson, 2005a). However, its placement as part of an otherwise entirely South African clade raised the question of whether it represented an isolated but natural introduction to Australia or whether it was a misunderstood invasive (Schmidt-Lebuhn et al., 2020). Independently, its occurrence in disturbed, near-urban areas has led to doubts about its status as a native species (Keighery & Keighery, 2017). The Western Australian Department of Biodiversity, Conservation and Attractions is conducting research into the provenance of *S. condylus* in collaboration with a South African taxonomist (Williamson & Balkwill, unpublished data).

## MATERIALS AND METHODS

To add to our understanding of the placement of taxa of relevance to fireweed biocontrol research, we generated new Sanger sequence data for 38 samples representing some taxa for which no data were previously available, species whose phylogenetic placement we wanted to confirm independently, and all taxonomic varieties of *Senecio pinnatifolius* except *S. pinnatifolius* var. *leucocarpus*, which is presumed extinct. The targeted sequence regions and primers used were the same as in our previous study (Schmidt-Lebuhn et al., 2020), i.e., the nuclear ETS and ITS as well as chloroplast psbA-trnH and trnL regions, so that the new data could be added to the existing dataset. For the purposes of the results presented here, we focus on ribosomal data (ETS, ITS), because they provide stronger phylogenetic resolution and confidence than the chloroplast regions.

DNA was extracted from herbarium specimens at CANB and NU. Laboratory work and sequencing were outsourced to the Australian Genome Research Facility. Contigs were produced using Geneious ([www.geneious.com](http://www.geneious.com)). Genbank accession numbers and voucher information for sequences newly generated for this study are listed in Appendix 1. We removed the sequences of *Senecio pinnatifolius* from the data matrices used in Schmidt-Lebuhn et al. (2020), because their varietal affiliation was not always known and may have been chimeric, and added the new sequences.

ETS and ITS sequences were concatenated using a custom Python script, and alignments were produced using MAFFT 7.453 (Kato & Standley, 2013). A Maximum Likelihood phylogeny was inferred with IQ-TREE 2.1.2 (Minh et al., 2020), with both gene partitions under the substitution model GTR+F+I+G4 chosen by automatic model and partition testing, and 1,000 UltraFast Bootstrap (UFB) replicates as branch support values (Minh et al., 2013). Chloroplast psbA-trnH and trnL sequences were likewise concatenated and analysed with the same approach; model testing favoured K3Pu+F+G4 for psbA-trnH and TIM+F+G4 for trnL. Concatenated data matrices and phylogenetic trees are available on the CSIRO Data Access Portal (<https://doi.org/10.25919/hf5f-6e62>).

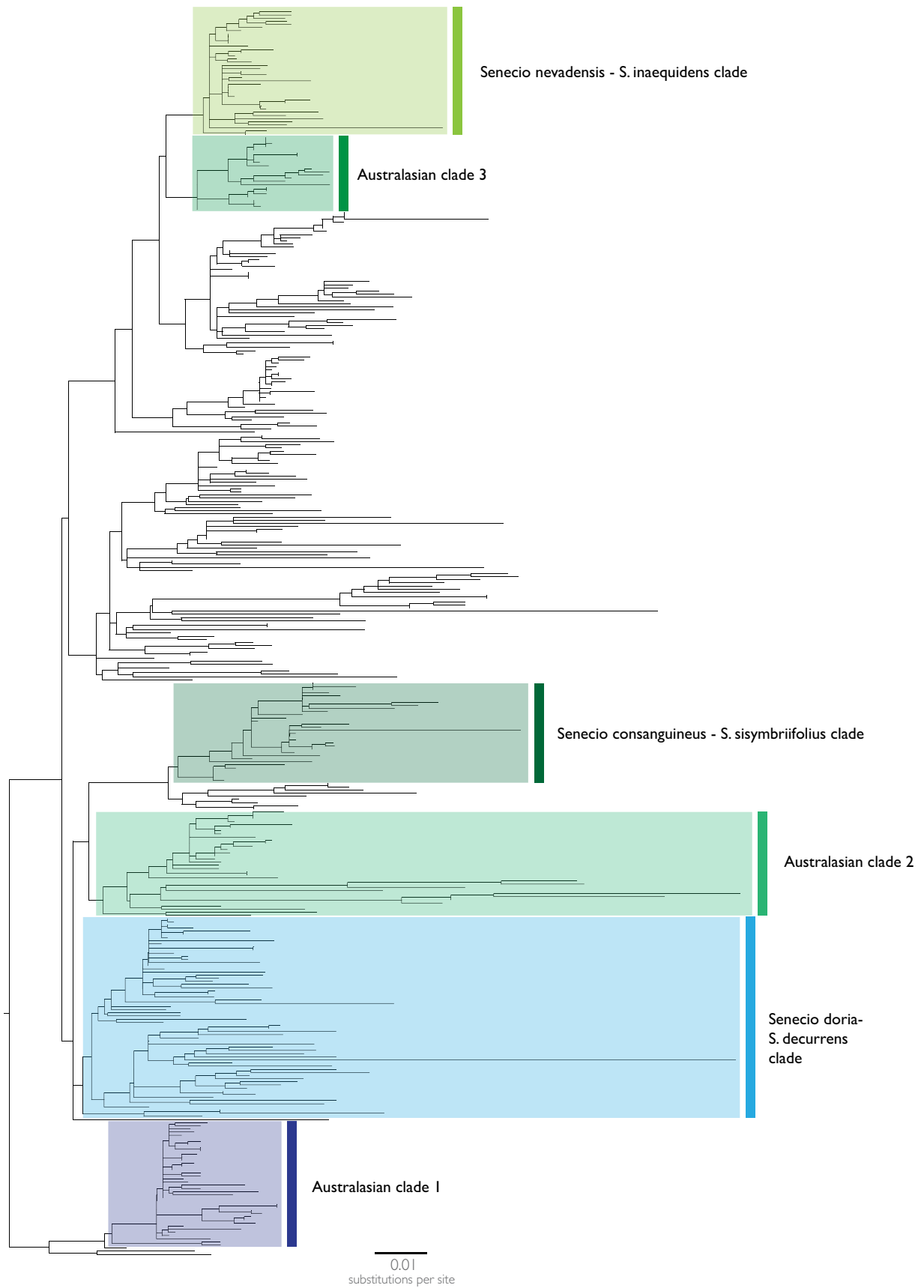
## RESULTS

We focus on the placement of fireweed and newly sequenced specimens, because the ribosomal phylogeny is otherwise not significantly different from Schmidt-Lebuhn et al. (2020). Where possible, clades are subsequently referred to by names used by Liew et al. (2018), as introduced above, Kandziora et al. (2017), and Pelsner et al. (2007) (Figure 2).

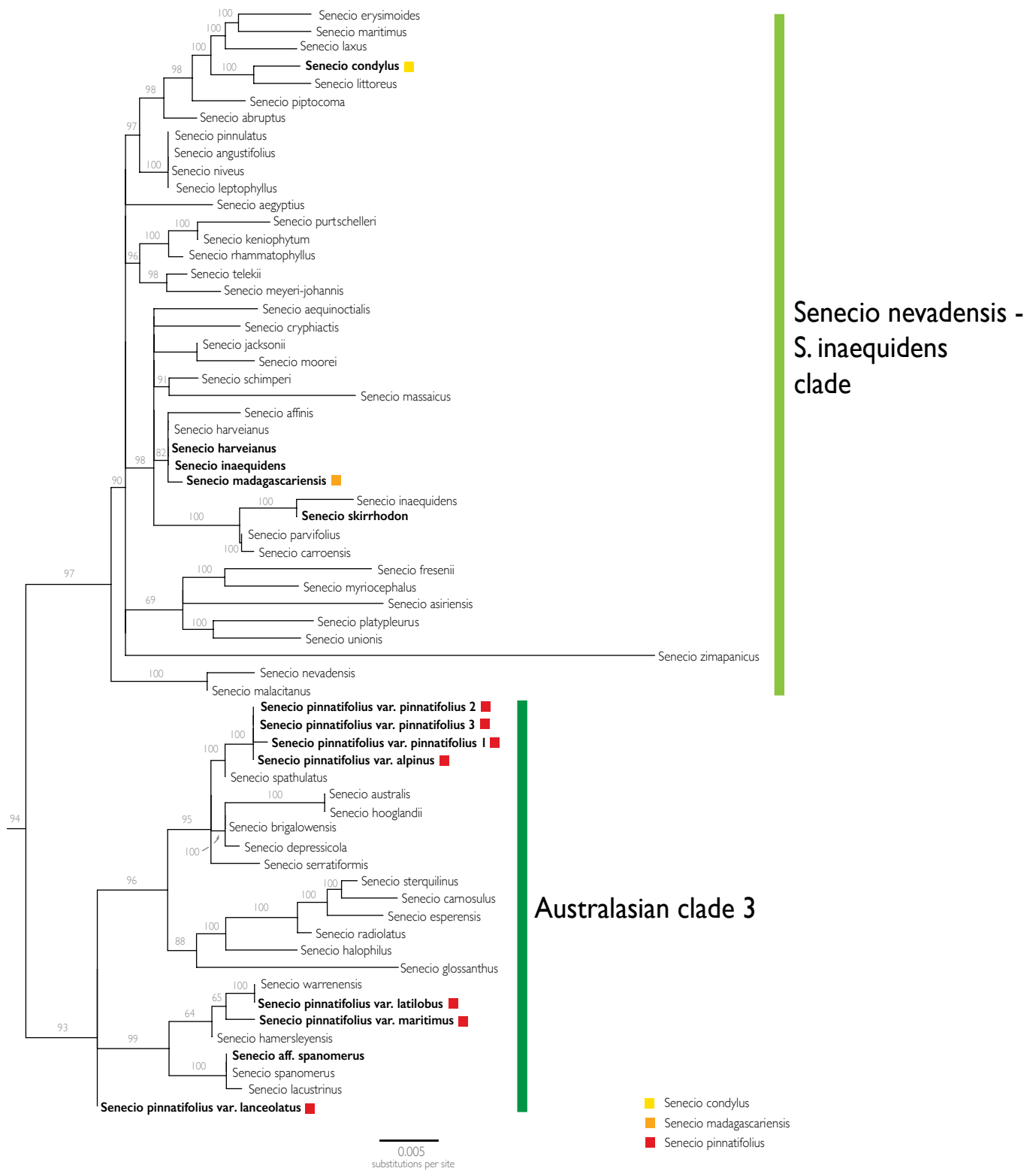
The phylogenetic position of several species we re-sequenced was confirmed, in that they were placed close to older sequence data ascribed to the relevant species. These included new samples of *Senecio inaequidens* and *S. harveyanus* MacOwan in the *S. nevadensis* Boiss. & Reut. – *S. inaequidens* clade that also contains fireweed (Figure 3); new samples of *S. coronatus* Harv., *S. inornatus* DC., and *S. panduriformis* Hillard in the *S. doria* L. – *S. decurrens* DC. clade; and a new sample of *S. distalilobatus* I.Thomps. in Australasian clade 1.

Other newly sequenced samples were placed in the expected clades but not necessarily close to older, conspecific sequences within those clades: new samples of *Senecio retrorsus* DC., *S. scitus* Hutch & Burt Davy, and of doubtful identification (*S. aff. adnatus* N.P.Balacr., *S. aff. conrathii* N.E.Br.) in the *Faujasia* Cass. – *Bethencourtia* Choisy clade outside of *Senecio* s.str.; a new sample of *S. polyodon* in the *S. consanguineus* DC. – *S. sisymbriifolius* DC. clade; and new samples of *S. prenanthoides* A.Rich. in Australasian clade 2. *Senecio skirrhodon* DC., for which no data were previously available, was part of the *S. nevadensis* – *S. inaequidens* clade (Figure 3).

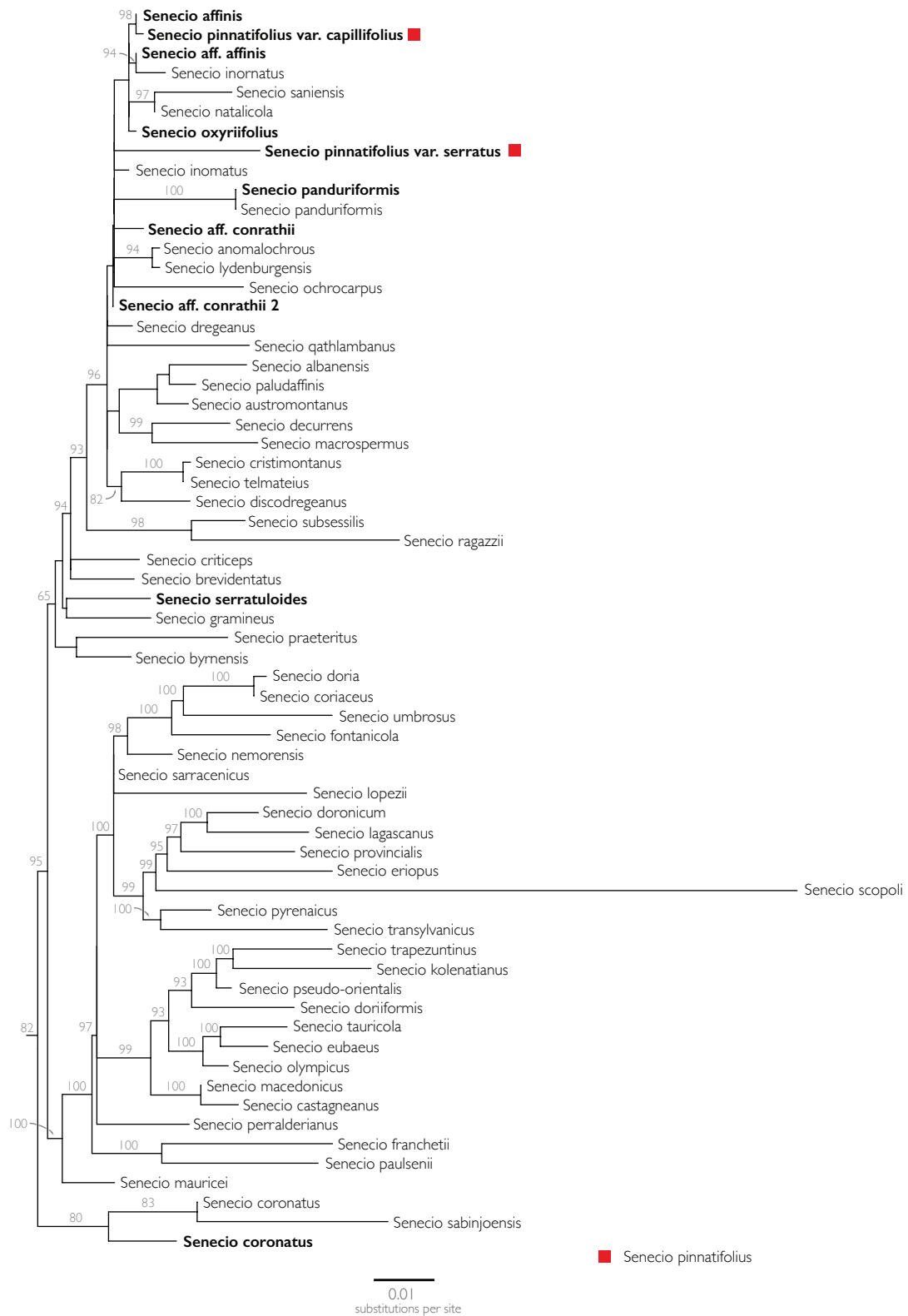




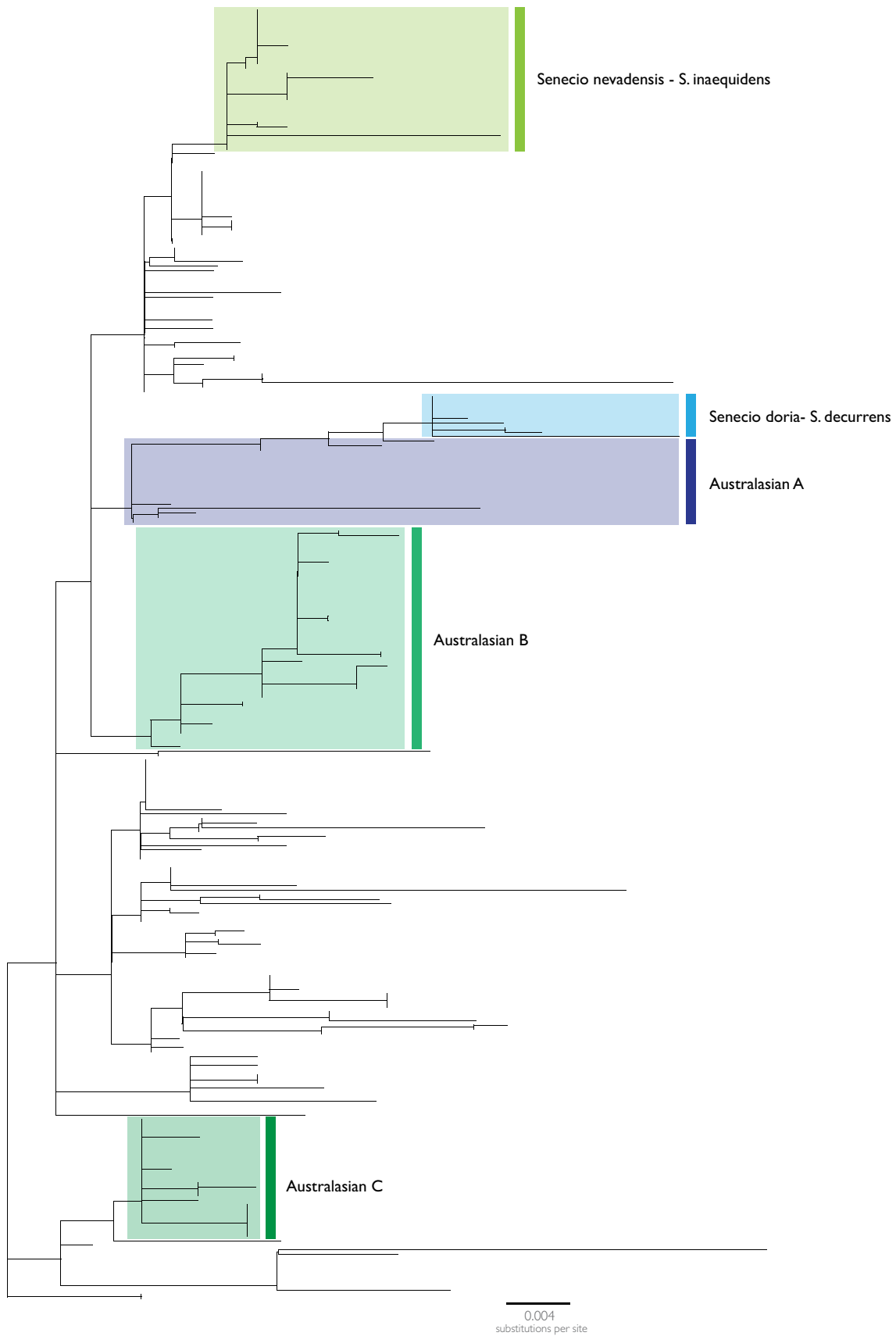
**Figure 2.** Part of ribosomal likelihood phylogeny showing the genus *Senecio* s.str. Coloured and labelled boxes indicate clades mentioned in main text.



**Figure 3.** Detail of ribosomal phylogeny showing *Senecio nevadensis* – *S. inaequidens* clade and Australasian clade 3. Terminals marked with bold font indicate new sequences produced for this study. Numbers above branches are UltraFast Bootstrap values.



**Figure 4.** Detail of ribosomal phylogeny showing *Senecio doria* – *S. decurrens* clade. Terminals marked with bold font indicate new sequences produced for this study. Numbers above branches are UltraFast Bootstrap values.



**Figure 5.** Part of chloroplast likelihood phylogeny showing the genus *Senecio* s.str. Coloured and labelled boxes indicate groups or clades mentioned in main text.

*Senecio pinnatifolius* var. *pinnatifolius*, *S. p.* var. *alpinus*, *S. p.* var. *lanceolatus*, *S. p.* var. *latilobus*, and *S. p.* var. *maritimus* formed part of Australasian clade 3 (Figure 3). Inside this clade they were, however, split into two groups: *S. p.* var. *pinnatifolius* and *S. p.* var. *alpinus* were placed as sister to *S. spathulatus* A.Rich., whereas *S. p.* var. *lanceolatus*, *S. p.* var. *latilobus*, and *S. p.* var. *maritimus* were grouped with *S. hamersleyensis* I.Thomps., *S. lacustrinus* I.Thomps., *S. spanomerus* I.Thomps., and *S. warrenensis* I.Thomps. In contrast, *S. pinnatifolius* var. *capillifolius* and *S. p.* var. *serratus* were unexpectedly placed in the non-Australasian *S. doria* – *S. decurrens* clade (Figure 4).

The chloroplast phylogeny presented in most cases the same placement of samples in clades, with the caveat that, as previously demonstrated (Liew et al., 2018; Schmidt-Lebuhn et al., 2020), its deeper topology was incongruent with that of the ribosomal phylogeny, with Australasian clade C containing *Senecio pinnatifolius* very distant from the *S. nevadensis* – *S. inaequidens* clade (Figure 5). Chloroplasts from species of the *S. doria* – *S. decurrens* clade and *S. pinnatifolius* var. *serratus* formed a clade nested inside Australasian clade A. *Senecio pinnatifolius* var. *capillifolius* was placed in the *S. nevadensis* – *S. inaequidens* clade, and varieties of *S. pinnatifolius* placed in Australasian clade C shared the same chloroplast sequences. However, the resolution provided by chloroplast sequences is overall low, with most species in any of the Australasian clades arranged on zero-branch-length polytomies.

## DISCUSSION

Our results have revealed that within Australasian clade 3, varieties of *Senecio pinnatifolius* did not form a clade and were not even all placed in the same subclade (Figure 3). These results strongly suggest that *S. pinnatifolius* as currently circumscribed is unlikely to be a natural unit, let alone a single species, as suggested by its enormous morphological heterogeneity (Figure 1B-H) and the uncertainty remaining after past studies (Radford et al., 2004; Thompson, 2005b). A dedicated research project with expanded sampling and considering morphology and nomenclature is needed to ascertain a more appropriate taxonomy.

One of the main implications of these results for biocontrol research is that the varieties of *Senecio pinnatifolius* cannot be used interchangeably on test lists, as they are placed at different phylogenetic distances to fireweed. For example, should the placement of *S. pinnatifolius* var. *serratus* be confirmed, it would also have implications for the interpretation of past research on invasive-native plant hybridisation using this variety (e.g. Prentis et al. 2007), and could raise similar questions about its potential status as an introduced species as for *S. condylus* (Keighery & Keighery, 2017). The incongruent position of *S. pinnatifolius* var. *capillifolius* in ribosomal and chloroplast phylogenies is even more unexpected and raises the question of a potential hybridogenic origin of the taxon, as demonstrated for members of the Lautusoid group (Liew et al., 2018).

As summarised in our literature review and reconfirmed in our analysis, the Australasian clade 3 containing (at least most of) *Senecio pinnatifolius* is closest to fireweed of all Australian *Senecio*, but it is nonetheless distantly related to fireweed in absolute terms, when placed in the broader phylogenetic context (Schmidt-Lebuhn et al., 2020). Indeed *S. pinnatifolius* is no more closely related to fireweed than the other members of its clade such as *S. spanomerus*. Contextualising the relatively large evolutionary distance between fireweed and *S. pinnatifolius* in this way reduces the probability that any candidate biocontrol agent will exert undesirable damage to non-target native species in the weed's introduced range. Despite this, the varieties of *S. pinnatifolius* remain important test plants, precisely because of their great diversity, morphological similarities, and overlapping distributions with fireweed across eastern Australia (Briese, 2005). If the candidate biocontrol agent is, for example, an endophagous insect, plants with stems that are too narrow, too short lived, too woody, or too succulent may not be suitable host plants, and therefore varieties of *S. pinnatifolius* morphologically similar to the target weed should be prioritised over those that are less morphologically and ecologically similar.

Conversely, the confirmation of close relationships between *Senecio inaequidens*, *S. harveyanus*, *S. madagascariensis*, and *S. skirrhodon* also has direct implications for ongoing biocontrol research. Candidate biocontrol agents *Gasteroclisus tricostalis*

(Thunberg) (Coleoptera: Curulionidae) and *Metamesia elegans* (Walsingham) (Lepidoptera: Tortricidae) were found on these four species in their native range across southern Africa (Egli & Olckers, 2020; Singh et al., 2022), which could in the absence of phylogenetic data be misinterpreted to mean that these insects have a broad host range and would be unsuitable for ongoing testing as candidate biocontrol agents. However, the very close relationship of these four *Senecio* species indicates that the insects' native host range may indeed be narrow, and that the likelihood of these insects exerting non-target damage to more distantly related native Australian *Senecio* species is low. Previously, a close relationship between these four species was hypothesised based on morphology (Hilliard, 1977) but had never been confirmed with genetic data.

Previous genetic studies have, however, struggled with the delimitation of *Senecio madagascariensis* from *S. inaequidens* (Le Roux et al., 2006), and there is uncertainty in several countries where members of the complex have been introduced about which species is, or are, present. Invasive plants from this complex are called *S. inaequidens* in Europe, *S. madagascariensis* in Australia, and *S. skirrhodon* in New Zealand. Additional research will be required to ascertain if these names are applied consistently across countries and which species have indeed become invasive in each jurisdiction.

Another consideration is that many insects and diseases investigated as candidate biocontrol agents for fireweed were shown to not be host-specific when exposed to *Senecio pinnatifolius* (Holtkamp & Hosking, 1993; McFadyen & Sparks, 1996). This suggests that many species of *Senecio* may have evolved through relatively recent diversification and are therefore biochemically similar.

Most newly sequenced or re-sequenced species were phylogenetically placed as expected. However, the results for the Australian *Senecio pinnatifolius* complex, in particular *Senecio pinnatifolius* var. *capillifolius* and *S. p.* var. *serratus*, and the South African species *S. adnatus* and *S. oxyriifolius* DC. were unexpected. Although not impossible, we currently consider it unlikely that laboratory errors such as sample mix-ups or cross-contamination have caused the observed relationships. In none of the cases would there be a partner for the mix-up, i.e., no species that would have been expected to be placed in the *Senecio dora* – *S. decurrens* clade was placed in Australasian clade 3 containing the other varieties of

*S. pinnatifolius* or in the Gynuroid clade containing older sequences of *S. oxyriifolius* DC. Furthermore, the quality of the sequences was much higher than we would expect contaminated Sanger reads to be.

Nonetheless, the placement of *S. pinnatifolius* var. *capillifolius* and *S. p.* var. *serratus* outside of the Australasian clade 3 should for now be interpreted with caution and requires confirmation. We are in the process of generating more data. Consultation of South African colleagues did not produce a match of *S. p.* var. *capillifolius* with African species (Marinda Koekemoer, pers. comm.).

The analysis presented here highlights the value of applied phylogenetics in weed biocontrol research. It has improved the efficiency of developing host test lists to inform experiments in Australia for a genus with high and phylogenetically disparate native species representation. It improves confidence that host testing is done in a deliberative, well-considered, robust and defensible manner by removing bias in sampling species of 'perceived' closeness (based on superficial morphological similarities) and reinforcing the use of the Centrifugal Phylogenetic Method of selecting species based on evolutionary relatedness (Wapshere, 1974).

Serendipitously, applied phylogenetics in biocontrol research has also thrown up interesting and unexpected taxonomic conundrums that may lead to revisions of accepted taxonomy from genus (Schmidt-Lebuhn et al., 2020) to species level (as potentially for *Senecio pinnatifolius*). Two different fields of research are thus cross-pollinating.

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## APPENDIX

Vouchers and GenBank accession numbers for sequence data newly generated for this study.

Taxon	Voucher	GenBank accession #			
		ETS	ITS	psbA-trnH	trnL
<i>Senecio</i> aff. <i>adnatus</i> DC. #1	D. Egli 142 (NU)	ON758992	ON759065	ON759004	ON759069
<i>Senecio</i> aff. <i>adnatus</i> DC. #2	D. Egli 146 (NU)	ON758991	ON759064	ON759002	ON759070
<i>Senecio</i> aff. <i>adnatus</i> DC. #3	D. Egli 170 (NU)	ON758986	ON759062	ON758999	ON759071
<i>Senecio adnatus</i> DC.	D. Egli 100 (NU)	ON758993	ON759063	ON759000	ON759072
<i>Senecio</i> aff. <i>affinis</i> DC.	D. Egli 188 (NU)	ON758973	ON759045	ON759012	ON759094
<i>Senecio affinis</i> DC.	D. Egli 55 (NU)	ON758970	ON759042	ON759011	ON759091
<i>Senecio bupleuroides</i> DC.	D. Egli 108 (NU)	ON758985	ON759060	ON758998	ON759073
<i>Senecio</i> aff. <i>conrathii</i> N.E. Br. #2	D. Egli 171 (NU)	ON758975	---	ON759013	ON759095
<i>Senecio</i> aff. <i>conrathii</i> N.E. Br.	D. Egli 99 (NU)	ON758976	ON759044	ON759008	ON759087
<i>Senecio coronatus</i> Harv.	D. Egli 128 (NU)	ON758978	ON759049	ON759029	ON759096
<i>Senecio distallobatus</i> I.Thomps.	B. Gooden s.n. (CANB952367) (CANB)	ON758982	ON759055	ON759006	ON759103
<i>Senecio glaberrimus</i> DC.	D. Egli 95 (NU)	ON758990	ON759059	ON758997	ON759077
<i>Senecio harveyanus</i> MacOwan	D. Egli 81 (NU)	ON758958	ON759033	ON759018	ON759098
<i>Senecio hygrophilus</i> Klatt	D. Egli 142 (NU)	ON758984	ON759056	ON758995	ON759076
<i>Senecio inaequidens</i> DC.	D. Egli 84 (NU)	ON758957	ON759032	ON759016	ON759099
<i>Senecio inornatus</i> DC.	D. Egli 53 (NU)	ON758974	ON759046	ON759007	ON759088
<i>Senecio minimus</i> Poir.	B. Gooden s.n. (CANB)	ON758981	ON759054	ON759028	ON759089
<i>Senecio oxyriifolius</i> DC.	D. Egli 90 (NU)	ON758972	ON759043	ON759010	ON759090
<i>Senecio panduriformis</i> Hilliard	D. Egli 198 (NU)	ON758977	ON759050	ON759009	ON759093
<i>Senecio phelleus</i> I.Thomps.	B. Gooden s.n. (CANB952366) (CANB)	ON758979	ON759052	ON759014	ON759101
<i>Senecio pinnatifolius</i> var. <i>alpinus</i> (Ali) I. Thomps.	B. Gooden s.n. (CANB952370) (CANB)	ON758965	ON759035	ON759027	ON759079
<i>S. p.</i> var. <i>capillifolius</i> (Hook. f.) I. Thomps.	J.S. Whinray 488 (CANB)	ON758971	ON759047	ON759030	---
<i>S. p.</i> var. <i>lanceolatus</i> (Benth.) I. Thomps.	P.C. Heyligers 80012 (CANB)	ON758966	---	ON759024	ON759081
<i>S. p.</i> var. <i>latilobus</i> (Steetz) I.Thomps.	N.S. Lander 1025 (CANB)	ON758960	ON759037	ON759026	ON759080
<i>S. p.</i> var. <i>maritimus</i> (Ali) I.Thomps.	M. Carter 155 (CANB)	ON758961	ON759036	ON759020	ON759078
<i>S. p.</i> A. Rich. var. <i>pinnatifolius</i> #1	B. Gooden s.n. (CANB952368) (CANB)	ON758964	ON759039	ON759023	ON759085
<i>S. p.</i> A. Rich. var. <i>pinnatifolius</i> #2	B. Gooden s.n. (CANB952369) (CANB)	ON758963	ON759038	ON759022	ON759084
<i>S. p.</i> A. Rich. var. <i>pinnatifolius</i> #3	B. Gooden s.n. (CANB952365) (CANB)	ON758962	ON759034	ON759025	ON759082
<i>S. p.</i> var. <i>serratus</i> I.Thomps.	I. Radford s.n. (CBG9308770) (CBG)	ON758968	ON759048	---	ON759086
<i>Senecio polyodon</i> DC.	D. Egli 113 (NU)	ON758983	ON759051	ON759019	ON759097
<i>Senecio</i> aff. <i>preanthoides</i> A. Rich.	B. Gooden s.n. (CANB952371) (CANB)	ON758980	ON759053	ON759015	ON759102
<i>Senecio retrorsus</i> DC.	D. Egli 49 (NU)	ON758987	ON759057	ON759003	ON759074
<i>Senecio</i> aff. <i>retrorsus</i> DC.	D. Egli 75 (NU)	ON758988	ON759061	ON759001	ON759068
<i>Senecio scitus</i> Hutch. & Burt Davy	D. Egli 146 (NU)	ON758989	ON759058	ON758996	ON759075
<i>Senecio serratuloides</i> DC.	D. Egli 192 (NU)	ON758969	ON759041	ON759005	ON759092
<i>Senecio</i> aff. <i>serratuloides</i> DC.	D. Egli 194 (NU)	---	ON759066	ON758994	ON759067
<i>Senecio skirrhodon</i> DC.	D. Egli 76 (NU)	ON758967	ON759031	ON759017	ON759100
<i>Senecio</i> aff. <i>spanomerus</i> I.Thomps.	B. Gooden s.n. (CANB952364) (CANB)	ON758959	ON759040	ON759021	ON759083

# Phylogeny of marigolds (*Tagetes* L., *Tageteae*) based on ITS sequences

Oscar Hinojosa-Espinosa<sup>1</sup>  & Darío Javier Schiavinato<sup>2,3</sup> 

<sup>1</sup> Plant Biology Graduate Group, University of California Davis, Shields Avenue, Davis, California 95616, USA; [ohinojosa@ucdavis.edu](mailto:ohinojosa@ucdavis.edu)

<sup>2</sup> Cátedra de Botánica Sistemática, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, C1417DSE, Ciudad Autónoma de Buenos Aires, Argentina; [schiavi@agro.uba.ar](mailto:schiavi@agro.uba.ar)

<sup>3</sup> Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), República Argentina

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## ABSTRACT

The genus *Tagetes* includes about 50 species, all native to the New World. Some species are widely cultivated, notably *T. erecta*, and many species are used as medicines, spices, and in rituals. These uses are related to the essential oils that the plants store in secretory cavities in their foliage. Despite several taxonomic contributions, there are still species complexes in need of much work. Moreover, comprehensive phylogenetic studies of *Tagetes* using molecular data have not been conducted yet. Here we present results of phylogenetic analysis of ITS sequences from almost 50% of the species of *Tagetes*. The genus is resolved as monophyletic and *Hydropectis* as sister to *Tagetes*. A wild form of *T. erecta* is resolved as sister to *T. patula*, a cultivated species with smaller heads that is often treated as a synonym of the former. *Tagetes lunulata*, often considered closely related to *T. erecta*, is resolved in a different clade. Some other clades are also strongly supported, such as Lucida clade, composed of mostly subaquatic and riparian species with an anise-like scent. It is necessary to sample species missing from these analyses to obtain a better understanding of the phylogeny of *Tagetes*, which will also allow us to postulate more robust evolutionary hypotheses, such as divergence times and character evolution, as well as to guide the search for medicines or other desirable traits from the closest wild relatives of the cultivated species.

**Keywords:** African marigold, Aztec marigold, French marigold, Heliantheae alliance, secretory cavities

## INTRODUCTION

With approximately 50 species, *Tagetes* L. is the second largest genus in the tribe *Tageteae* Cass. within the Heliantheae alliance clade (Panero, 2007; Baldwin, 2009). The species are distributed from the southwestern United States to central Argentina and central Chile (Figure 1), with the highest species richness recorded in Mexico and the second highest species diversity in western and northwestern Argentina, Bolivia, Peru, Ecuador, and Colombia (Schiavinato et al., 2017, 2021; Schiavinato & Bartoli, 2018). *Tagetes* includes terrestrial or subaquatic annuals or perennials, with entire or pinnately lobed to dissected leaves, radiate heads,

uniseriate connate involucre, and a pappus of short and truncated scales, long and subulate scales, or a combination of both (Figure 2). As most members of tribe *Tageteae*, the leaves and phyllaries in *Tagetes* have pellucid glands (secretory cavities) that contain fragrant essential oils (Figure 2B).

The most widely known species is the cultivated *Tagetes erecta* L., often known as French Marigold or African Marigold, although it is native to Mesoamerica (Figure 3A–C). *Tagetes erecta* is also known as Aztec marigold because it was cultivated and used as a medicinal and ritual plant by the Aztecs (Linares & Bye, 1997), who interestingly noticed that the capitula were inflorescences, not single flowers,



**Figure 1.** Native geographic range of *Tagetes* L. shaded with red (adapted from Soule, 1993)

as *cempoalxochitl*, Aztec's Nahuatl name meaning 20 flowers, clearly implies (Rzedowski, 1978). This species is one of the most important ceremonial plants of Mexico (Linares & Bye, 1997), where it is extensively used in Day of the Dead decorations. On this day, relatives and friends who have passed away are remembered by setting up colorful altars with pictures, candies, fruits, beverages, and dishes (Figure 3B–C). According to tradition, the souls of the departed come back to visit home and feed on the dishes in the altars, and they are guided by the intense orange color of the rays and the large globular capitula of *T. erecta*.

*Tagetes lucida* Cav. has also been used in Mesoamerica since pre-Columbian times (Figure 4). This species is known locally as *pericón* or *yerbanís* and is used as a medicinal plant or spice. Also, capitulescences of this anise-scented species are used to make religious crosses that are placed in gates, doors, and windows to repel evil spirits during a religious festivity (*Día de San Miguel Arcángel*) in south central Mexico

(Figure 4B). Several other species of *Tagetes* are used as ornamental plants, local medicines, and spices (e.g., *T. micrantha* Cav.).

*Tagetes* was first published by Linnaeus (1753) with three species: *Tagetes erecta*, *T. minuta* L., and *T. patula* L. During the following hundred years, the number of recognized *Tagetes* species increased with the contributions of different authors (e.g. Cavanilles, 1794; Lagasca, 1816; Candolle, 1836; etc.), who based their descriptions both on herbarium specimens sent from the American continent by the botanical expeditions of the time, as well as on plants grown in European botanical gardens from seeds collected on these journeys. The first comprehensive taxonomic revision of *Tagetes* was made by Neher (1966), who proposed two subgenera that were not effectively published: '*Tagetes* subgen. *Lucida*' included species with a distinctive anise-like scent, linear to lanceolate leaf laminae, and involucre with punctiform secretory cavities, while the typical subgenus contained species with a pungent odor, deeply pinnately lobed leaves, and involucre with linear secretory cavities. More recently, Soule (1993) conducted a cladistic analysis of *Tagetes* based on morphological data and performed a taxonomic revision. Soule (1993) recognized 55 species and proposed three subgenera, *Tagetes* subgen. *Hydrotagetes* Soule, *Tagetes* subgen. *Iya* Soule, and *Tagetes* subgen. *Tagetes*, the latter with two sections (i.e. *Tagetes* sect. *Filifoliae* Soule and *T. sect. Tagetes*) and 13 series (all of them included within section *Tagetes*). This infrageneric classification was effectively published by Soule (1996).

Despite the contributions of Neher (1966) and Soule (1993, 1996), there are some Mexican species complexes that require additional taxonomic work. One of them includes the cultivated species and several related wild taxa. Neher (1966) and Soule (1993) recognized two cultivated species, *Tagetes erecta*, the one with the largest heads and more numerous ray florets (Figure 3C) and *T. patula* with smaller heads and fewer ray florets. According to this interpretation, *T. erecta* and *T. patula* could be derived from wild species such as *T. lunulata* Ortega and *T. tenuifolia* Cav. On the other hand, Turner (1996) adopted a broader circumscription of *T. erecta* that included *T. patula* and a wild form of *T. erecta*, which is recognized by its fewer rays and red purplish disk corolla lobes (Figure 3A) and is



**Figure 2.** Diversity of *Tagetes* L. **A-C.** *Tagetes lemmonii*, one of the shrubby species. Also note secretory cavities filled with ethereal oils. **D.** *Tagetes micrantha*, an anise-like scented species with reduced capitula, which is used as spice. **E.** *Tagetes foetidissima*, a strongly pungent species. **F.** *Tagetes subulata*, a white-ray form (rays are usually yellow in this species). **G.** *Tagetes nelsonii*, used in traditional medicine in its native range (Chiapas, Mexico and adjacent Guatemala). **H.** *Tagetes filifolia*, another anise-like scented species, which is often found in wet soils. Photos by Oscar Hinojosa-Espinosa



**Figure 3.** **A.** Wild form of *Tagetes erecta* L., note purplish corolla lobes. **B–C.** Use of *T. erecta* during the Day of the Dead holiday. **D–E.** *Tagetes lunulata*, note acute capitulum in bud with apical hairs and red-orange spot at the base of the rays. Photos by Oscar Hinojosa-Espinosa.



**Figure 4.** A–B. *Tagetes lucida*, locally known as *pericón* or *yerbanís*, is mostly used as a medicine, and occasionally in religious festivities. C–E. *Tagetes tenuifolia* sensu Turner (1996). Note red-orange spot at the base of the rays and glabrous and round capitulum in bud. Photos by Oscar Hinojosa-Espinosa.

# Tagetes fields, Forever!

Every year plants of cempasúchil or flor de muerto (*Tagetes erecta*) are grown in many places in Mexico to use them during the holiday of Día de Muertos (Day of the Dead, usually, November 1-2). Seeds are planted in June so the blooming plants are ready to harvest in October. It is thought that the intense orange color of the rays guides the souls of the dead who, according to the tradition, come back to visit home in the night of Día de muertos.

Crop of *Tagetes erecta* in Oaxaca, México  
Photo by O. Hinojosa-Espinosa



the most probable source of the cultivated forms. According to Rzedowski (2005), *T. lunulata* belongs to this species complex and it is distinguished by its orange-reddish spot at the base of the rays (Figure 3E). In addition, Turner (1996) considered *T. tenuifolia* morphologically similar and closely related to *T. lunulata*, but it lacks the orange-reddish spot at the base of the rays and the capitulum in bud is round and glabrous (Figure 4E), whereas in *T. lunulata* the capitulum in bud is acute and provided with setulae (Figure 3D). However, we have seen populations in central Mexico whose individuals have the orange-reddish spot and round, glabrous capitula in bud (Figure 4C-E); these have been either recognized as *T. lunulata* (e.g.: Rzedowski, 2005) or *T. tenuifolia* (e.g.: Villaseñor, 2016).

In addition, the phylogenetic relationships of *Tagetes* have not been investigated using molecular data. The first hypothesis of relationships of the genus were based on morphology. Strother (1977) postulated that the Mexican genera *Gymnolaena* Rydb., *Adenopappus* Benth., and the South American genus *Vilobia* Strother were the closest relatives of *Tagetes*, as all share a uniseriate, connate involucre. However, in the molecular phylogenetic analyses of the tribe Tageteae (Loockerman et al., 2003), *Adenopappus* and *Vilobia* were nested within *Tagetes* and the small, aquatic genus *Hydropectis* Rydb. (including *Hydrodyssodia* B.L.Turner) was resolved as the sister group of those three genera. Moreover, the phylogenetic relationships within *Tagetes* have not been evaluated using molecular data, and the results of the cladistic analyses based on morphology of Soule (1993) were not published. In this study we estimate the most densely sampled phylogeny to-date of *Tagetes* using ITS sequences aiming to 1) investigate the sister group to *Tagetes*; 2) corroborate the phylogenetic position of *Adenopappus* and *Vilobia* within *Tagetes*; 3) investigate species relationships within *Tagetes*.

## **MATERIALS AND METHODS**

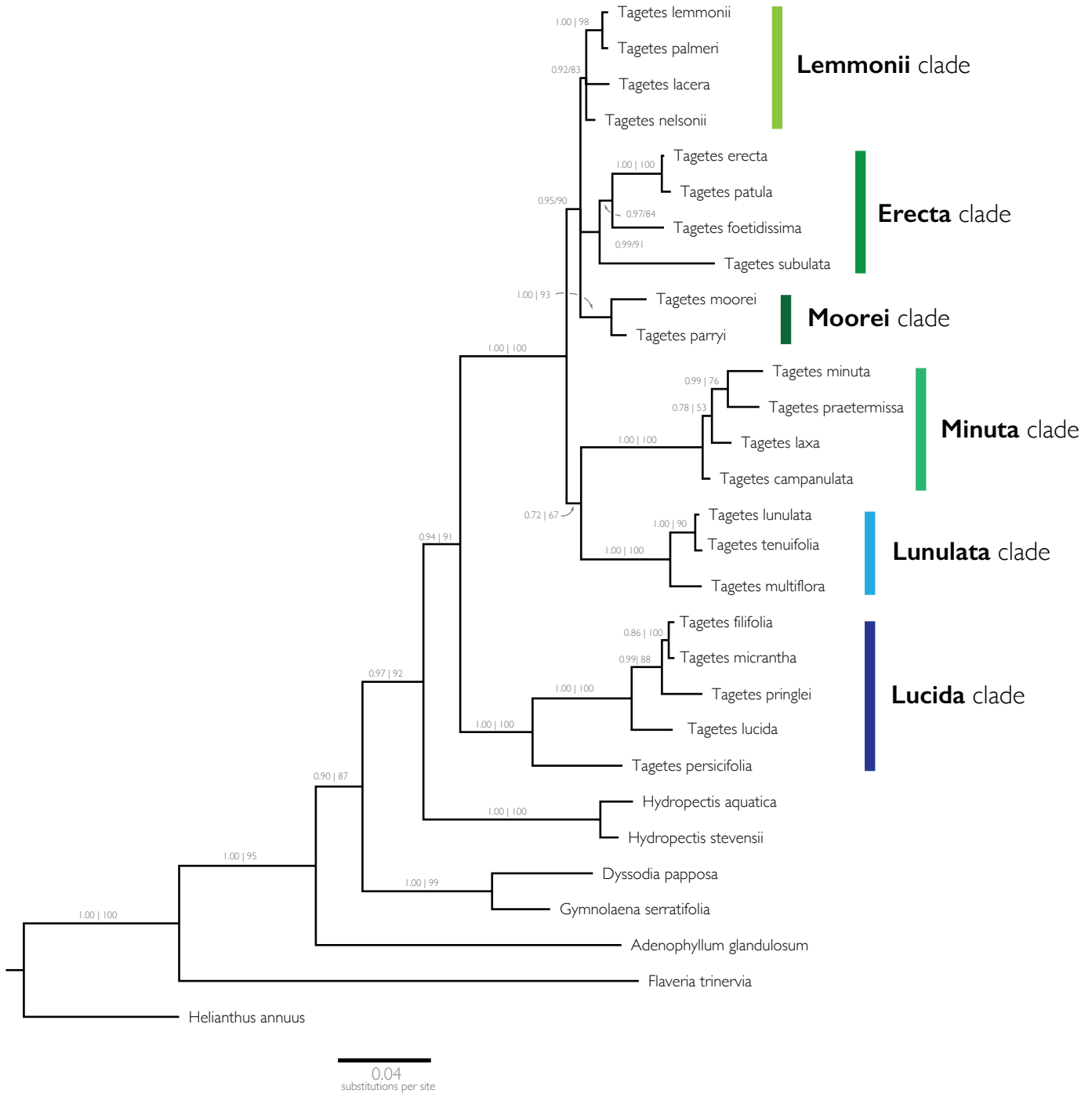
We sampled 22 species of *Tagetes*, including a wild form of *T. erecta*, the cultivated *T. patula*, *T. persicifolia* (Benth.) B.L.Turner ( $\equiv$  *Adenopappus persicifolius* Benth.), and *T. praetermissa* (Strother) H.Rob. ( $\equiv$  *Vilobia praetermissa* Strother). We also sampled

the type species of *Adenophyllum* Pers., *Dyssodia* Cav., *Gymnolaena* (DC.) Rydb., and two out of the three species of *Hydropectis*. *Adenophyllum glandulosum* (Cav.) Strother was considered intermediate between *Dyssodia* and *Tagetes* (Strother, 1969) and *Gymnolaena* was regarded as closely related to *Tagetes* (Turner, 1996). These genera are classified in the subtribe Tagetinae Dumort. Moreover, we included two more outgroups, *Flaveria trinervia* (Spreng.) C.Mohr, from the subtribe Flaveriinae (tribe Tageteae), and *Helianthus annuus* L., from tribe Heliantheae. The latter was used to root the trees. Leaves and voucher specimens were collected during fieldwork in Mexico. The leaves were preserved in silica gel and vouchers were imported to the University of California Davis (DAV) herbarium with the appropriate valid permits. Leaf samples were also removed from herbarium specimens with permission from curators from the following herbaria: CH, DAV, HCIB, MEXU, SD, TEX (Thiers, 2022). Moreover, additional 15 ITS sequences were extracted from GenBank. A list of voucher specimens and GenBank accession numbers is presented in the Appendix.

We used the DNeasy Plant Kit (Qiagen, Valencia, California) for DNA extraction and amplified the ITS region using the ITS5 and ITS4 primers from White et al. (1990). Taq PCR Core Kits (Qiagen, Valencia, California) were used to amplify the ITS region following the protocol of Rivera et al. (2016) with minor modifications. PCR products were checked and separated by agarose gel electrophoresis. The amplified ITS was extracted from gel slices using the QIAquick Gel Extraction Kit (Qiagen, Valencia, California) and submitted for sequencing at the UC Davis College of Biological Sciences DNA Sequencing Facility.

Sequencher 5.4.6 (Gene Codes Corporation) was used to assemble contigs and edit the sequences. MUSCLE (Edgar, 2004) implemented in MEGA 7.0 (Kumar et al., 2016) was used to align the sequences followed by minor manual adjustments. Gaps range from 1 to 5 base pairs in length and were treated as missing data. Both Bayesian inference and maximum likelihood approaches were conducted. MrBayes 3.2.7 (Huelsenbeck & Ronquist, 2001) was used to perform the Bayesian phylogenetic analyses. The nucleotide substitution models were assessed by implementing Reversible Jump-Markov Chain Monte Carlo (RJ-MCMC). As implemented in

# PHYLOGENY OF TAGETES



**Figure 5.** Majority rule consensus tree of 10,000 sampled trees from the Bayesian analysis of *Tagetes* using ITS performed in MrBayes. Posterior probabilities annotated next to the nodes followed by bootstrap values from the maximum likelihood and bootstrap analyses (1000 replications) of the same data conducted in RaxMLGUI.

MrBayes 3.2.7, all possible time-reversible substitution models (i.e., 203 models) are evaluated during the MCMC. According to the RJ-MCMC analysis, the four-parameter GTR submodel [122341] best fit the data with a posterior probability (PP) of 0.36. Two simultaneous independent runs of 1 million generations using four chains were applied. The runs were compared every 1000 generations and sampled every 100, discarding the first 25% samples as burn-in. Tracer 1.7.1 (Rambaut et al., 2018) was used to assess mixing and convergence. One million generations were more than enough for the two independent runs to converge, as our data set was relatively small. FigTree v1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/>) was used to edit the majority rule consensus tree that MrBayes uses to summarize the sampled phylogenetic trees.

Maximum likelihood and bootstrap analyses were conducted on RaxMLGUI 2.0 (Edler et al., 2020). The GTR substitution model was used since it is closer to the model identified using RJ-MCMC. Ten independent runs and 1000 bootstrap replications were performed and summarized as a majority rule consensus tree.

## RESULTS

The ITS region ranged from 640 base pairs (bp) in *Tagetes campanulata* Griseb. to 651 bp in *T. pringlei* S. Watson, and the aligned data set included 29 species and 678 characters. The majority rule consensus tree from the Bayesian and maximum likelihood analyses were totally congruent (Figure 5). *Tagetes* (including *Adenopappus* and *Vilobia*), was resolved as a monophyletic group (PP=0.94, bootstrap=91) with *Hydropectis* as its sister genus (PP=0.97, bootstrap=92) (Figure 5). Two strongly supported clades were resolved within *Tagetes*: 1) the Lucida clade, which is composed of *T. persicifolia*, *T. lucida*, *T. pringlei*, *T. micrantha*, and *T. filifolia* Lag.; and 2) a larger clade that is composed of five smaller clades (Lemmonii, Erecta, Moorei, Minuta, and Lunulata). The Lemmonii clade includes *T. lacera* Brandegee, *T. nelsonii* Greenm., and the sister species *T. lemmonii* A. Gray and *T. palmeri* A. Gray. The Erecta clade contains *T. erecta* resolved as sister to *T. patula*, with *T. foetidissima* as sister to both, and *T. subulata* as sister to all three. The Moorei clade includes *T. moorei* H. Rob. and *T. parryi* A. Gray. The Minuta clade contains

*T. minuta* L., resolved as sister to *T. praetermissa*, with *T. laxa* Cabrera sister to both, and *T. campanulata* sister to all three. Finally, the Lunulata clade includes *T. lunulata* resolved as sister to *T. tenuifolia*, with *T. multiflora* as sister to both.

## DISCUSSION

Our results corroborate that *Hydropectis* is the closest relative of *Tagetes* (Loockerman et al., 2003), and further sampling may show that *Hydropectis* is nested within *Tagetes*. The *Tagetes* clade is weakly supported (PP=0.94), as usually a posterior probability value of at least 0.95 is considered statistically robust (Wilcox et al., 2002), however, the *Tagetes* clade is strongly supported by the bootstrap analyses (Figure 5). The sister relationship of *Tagetes* and *Hydropectis* is strongly supported (PP=0.97, bootstrap=92). *Hydropectis* is a small genus of three aquatic annuals endemic to Mexico (Turner, 1995). It shows similarities to some species of *Tagetes*, such as *T. micrantha*, in having small heads with very reduced rays, but it differs from all species of *Tagetes* by having a base chromosome number of  $x=9$  (Keil & Stuessy, 1977; Zhao & Turner, 1993), whereas in *Tagetes* the base chromosome number is  $x=11$  or  $12$  (Soule, 1993; Turner, 1996). Our results also corroborate that *Adenopappus persicifolius* (= *Tagetes persicifolia*) and *Vilobia praetermissa* (= *Tagetes praetermissa*) belong to *Tagetes*, and that the genera *Dyssodia*, *Gymnolaena*, and *Adenophyllum* are distantly related to *Tagetes* only.

Since *Tagetes erecta* and *T. patula* were resolved as sister taxa these are perhaps best treated as a single species as proposed by Turner (1996), but it is necessary to sample the cultivated form of *T. erecta*. It is also notable that our results suggest that *T. foetidissima* and *T. subulata* are the nearest relatives of *T. erecta*, but not *T. lunulata* as previously thought (Soule, 1996). Moreover, our results support Rzedowski (2005) treatment of *Tagetes* populations from central Mexico that have an orange-reddish spot near the base of the ray as *T. lunulata*, regardless of the morphology of the head in bud. However, at least the populations from Mexico City and adjacent regions that we have seen in the field have glabrous, round capitula in bud (Figure 4C-E), while the populations of *T. lunulata* from Western and north-central Mexico have acute, setulaceous capitula in bud (Figure 3D-E), and perhaps it is best to treat all of these as a single species with two varieties.

Some of the resolved clades are composed of species that are similar in ecology, morphology or geography. For instance, the *Lucida* clade includes *Tagetes persicifolia*, a riparian species, and it is also composed of species that are common in wet soils (*T. micrantha* and *T. filifolia*) or are subaquatic (*T. pringlei*). Moreover, the species in this clade have mostly a sweet anise-like aroma, and appear to correspond to the subgenus *Lucida* proposed by Neher (1966). We would expect that *T. epapposa* B.L.Turner, another subaquatic species that is similar in morphology to *T. pringlei*, is a member of this clade. Another example is the *Minuta* clade, which in this case is composed of South American species only. This group loosely matches Soule's series *Minutae* (1996); however, Soule (1996) placed *T. campanulata* in its own series (ser. *Campanulatae*), which is not supported by our preliminary results. Another example is the *Lemmonii* clade, which is composed of species that are suffruticose and occur in northern Mexico and Southwest USA, except of *T. nelsonii*, which is confined to Chiapas in Southern Mexico and Guatemala.

To estimate phylogenetic relationships more accurately, it is necessary to sample the missing species of *Tagetes* and to use additional molecular markers, such as ETS, plastid markers, and/or low-copy targeted nuclear genes. A more robust phylogeny will be useful to investigate evolutionary processes, such as divergence times and character evolution, and to guide the search for new potential medicines or spices. Furthermore, knowing the closest relatives of the cultivated form of *Tagetes erecta* will facilitate the search for desirable traits in the wild species.

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## APPENDIX

Species, vouchers of plant material from which DNA was extracted and GenBank accession numbers.

Species	Voucher	GenBank accession #
<i>Adenophyllum glandulosum</i> (Cav.) Strother	Hinojosa-Espinosa 630 (MEXU)	ON695767
<i>Dyssodia papposa</i> (Vent.) Hitchc.	Hinojosa-Espinosa 684 (DAV, MEXU)	ON798518
<i>Flaveria trinervia</i> (Spreng.) C.Mohr	Huffman s.n. (DAV)	ON695768
<i>Gymnolaena serratifolia</i> Rydb.	Cronquist 11219 (MEXU)	ON695769
<i>Helianthus annuus</i> L.	Schilling 660	KX671853
<i>Hydropectis aquatica</i> Rydb.	Soule 2796 (DAV)	ON695770
<i>Hydropectis stevensii</i> McVaugh	Perez-Calix 4706 (TEX)	ON695771
<i>Tagetes campanulata</i> Griseb.	Soule 3553 (TEX)	AF413574
<i>Tagetes erecta</i> L.	Hansen 126 (TEX)	KJ525046.1
<i>Tagetes filifolia</i> Lag.	*****	DQ862118.1
<i>Tagetes foetidissima</i> DC.	*****	DQ862119.1
<i>Tagetes lacera</i> Brandegee	Medel 2014-03 (HCIB)	ON695774
<i>Tagetes laxa</i> Cabrera	*****	KC800431.1
<i>Tagetes lemmonii</i> A.Gray	Reina 1120 (HCIB)	ON695775
<i>Tagetes lucida</i> Cav.	Hinojosa-Espinosa 676 (DAV, MEXU)	ON695772
<i>Tagetes lunulata</i> Ortega	Hinojosa-Espinosa 723 (DAV, MEXU)	ON695776
<i>Tagetes micrantha</i> Cav.	Hinojosa-Espinosa 724 (DAV, MEXU)	ON695773
<i>Tagetes multiflora</i> Kunth	*****	KC800434.1
<i>Tagetes minuta</i> L.	*****	AF413576
<i>Tagetes moorei</i> H.Rob.	*****	KC800433.1
<i>Tagetes nelsonii</i> Greenm,	Hinojosa-Espinosa 731 (CH, DAV, MEXU)	ON695777
<i>Tagetes palmeri</i> A.Gray	Soule 3362 (TEX)	AF413577
<i>Tagetes parryi</i> A.Gray	*****	KC800427.1
<i>Tagetes patula</i> L.	*****	DQ862121.1
<i>Tagetes persicifolia</i> (Benth.) B.L.Turner	Sundberg 2954 (TEX)	AF413580
<i>Tagetes praetermissa</i> (Strother) H.Rob.	Balls 6183 (UC)	AF413581
<i>Tagetes pringlei</i> S.Watson	Soule 2798 (TEX)	AF413578
<i>Tagetes subulata</i> Cerv.	Rebman 30705 (SD)	ON695778
<i>Tagetes tenuifolia</i> Cav.*	Hinojosa-Espinosa 677 (DAV)	ON695779

\* (sensu Turner 1996, *T. lunulata* Ortega sensu Rzedowski 2005)

\*\* Information not available in GenBank

# The people you kill are doing quite well:

## The rediscovery of an “extinct” species described from the outskirts of Madrid (Spain), *Carduncellus matritensis* Pau (Cardueae)

Enrique Luengo<sup>1</sup>, Juan M. Martínez Labarga<sup>2</sup> , Rubén de Pablo<sup>3</sup>, Alfonso Susanna<sup>4</sup>  & Roser Vilatersana<sup>4</sup> 

<sup>1</sup> Asociación para la Recuperación del Bosque Autóctono del Bajo Jarama - ARBA BJ; [kikeluengo2@gmail.com](mailto:kikeluengo2@gmail.com)

<sup>2</sup> Depto. de Sist. y RRNN, E.T.S. de Ingeniería de Montes, Forestal y del Medio Natural, Universidad Politécnica de Madrid, Spain; [juanmanuel.martinez@upm.es](mailto:juanmanuel.martinez@upm.es)

<sup>3</sup> Instituto de Educación Secundaria el Carrascal, Av. del Instituto s/n, 28500 Arganda del Rey, Madrid, Spain; [rubendepablo1@gmail.com](mailto:rubendepablo1@gmail.com)

<sup>4</sup> Botanic Institute of Barcelona (IBB, CSIC- Ajuntament de Barcelona), Pg. del Migdia s/n, 08038 Barcelona, Spain; [asusanna@ibb.csic.es](mailto:asusanna@ibb.csic.es), [vilaterana@ibb.csic.es](mailto:vilaterana@ibb.csic.es)

DOI: <http://dx.doi.org/10.53875/capitulum.02.1.04>

### ABSTRACT

The fate of the enigmatic species *Carduncellus matritensis* looked clear when the type locality in Cerro Negro was razed by the growing of Madrid at the beginning of the XX century: it was officially listed as one of the six extinct species in the Red Book of the Spanish flora. The controversy on the identity of the taxon continued on the basis of the scarce and undeveloped samples gathered before the purported extinction and the species was not accepted by some specialists in the genus. One year ago, some relictic populations of an unknown species of *Carduncellus* were located in the surroundings of the Gran Madrid, 50 km south of the type locality. After careful review of the available materials and new gatherings, we conclude that *Carduncellus matritensis* did escape extinction and can be found on the same expansive clay soils that characterize the Cerro Negro. On morphological basis, we also conclude that it is a distinct species that cannot be reduced to any of the extant species of the genus.

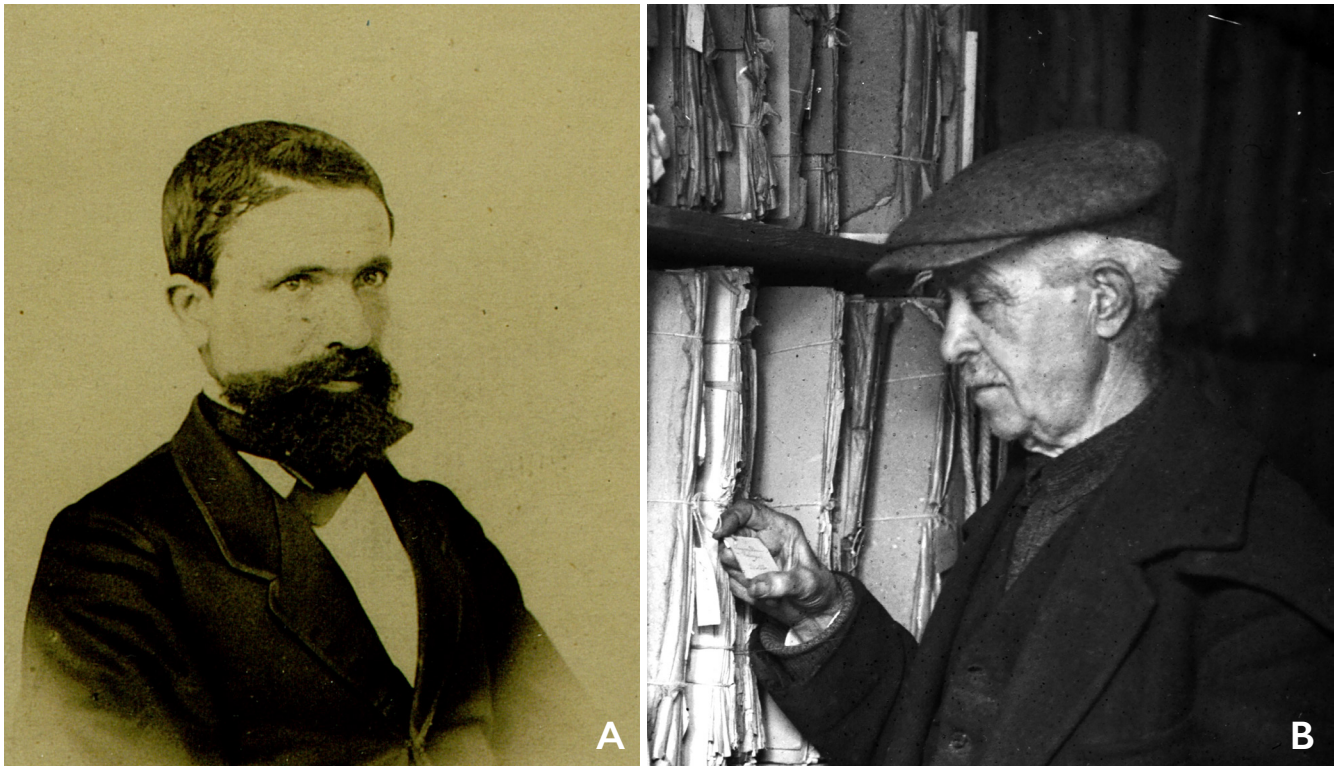
**Keywords:** Compositae, thistle

### INTRODUCTION

We have titled this short note with a quote from French dramatist Pierre Corneille (1606-1684): “les gens que vous tuez se portent assez bien” (*Le Menteur*, IV, 2, p 81, 1644) [the people you kill are doing quite well] that expresses our surprise and our delight for a striking botanical discovery in Spain: the reappearance of a supposedly extinct species.

Somewhere between 1851 and 1862 (the exact date is unknown), the Spanish botanist Joan Isern ([Figure 1A](#)) collected a species of the genus *Carduncellus* Adans. (Compositae) from the Cerro Negro hill, one of the many clay and gypsum knolls located in the south-east outskirts of Madrid ([Figure 4B](#)). Later on,

the specimen was described as a new species by Carlos Pau ([Figure 1B](#)), as *Carduncellus matritensis* (Pau, 1904; [Figure 2A](#), [Figure 3](#)). Some exemplars were collected in the years following the discovery, all of them incomplete. Unfortunately, the only known locality was engulfed by the fast-growing capital of Spain. Between 1917 and 1926, the Cerro Negro railroad station was built (Domínguez López, 1987) exactly on the spot ([Figure 4B](#)). Domínguez Lozano & al. (2000) listed the species as extinct, and Bañares et al. (2004) suggested that the species vanished in the thirties. However, the plant was still there albeit extremely rare: our investigations have dated the last collection in 1972 by José Borja, as demonstrated by the herbarium sheet kept at MAF (MAF 179908). This was the last time the species was seen and the extinction was considered definitive.



**Figure 1. A.** Joan Isern (1821-1866), who collected the species for the first time. Anonymous calotype, 1850-1855; courtesy of the Royal Botanic Garden of Madrid. **B.** Carlos Pau (1857-1937), who described Isern's gathering as *Carduncellus matritensis*. Photo: J. Cuatrecasas, 1933; archive of the Botanic Institute of Barcelona.

We have summarized this history in [Figure 2](#).

Cerro Negro is located in one of the northern limits of a wide plain formed by expansive clays (magnesian smectites or green clay). The flora of this very peculiar type of soils was known and well studied exclusively through this locality, and many rare species seemed to be restricted to Cerro Negro and the immediate localities of Vallecas or Vicálvaro. However, the study of the flora of the whole area has shown that they have a wider distribution in the center of the Iberian Peninsula (Luengo et al., 2017). Anyway, Cerro Negro and its very rich flora was an obligated point to visit for botanic travelers in Spain in the XIX and XX centuries. The list of great names exploring the place includes P. Löffling (who sent plants from Cerro Negro to Linnaeus according to López González, 2003), E. Boissier (Boissier & Reuter, 1842), G. Rouy (Rouy, 1883), J. Lange (Lange, 1860), C. Pau (Pau, 1904) and P. Font Quer in 1911 and 1924 (Font Quer, 1934). Besides *C. matritensis*, other species were also described from Cerro Negro: *Astragalus scorpioides* Pourr., *Cynara tournefortii* Boiss. & Reut., *Hippocrepis commutata* Pau, *Minuartia dichotoma* Loefl. ex L., and

*Queria hispanica* Loefl. ex L. Unfortunately, only a few heavily disturbed and anthropized patches of the hills were saved from the constructions and the crisscross of highways and railroads, and are today part of the Entrevías urban park ([Figure 4B](#)).

In 2021, a team working in the limits of the provinces of Madrid and Toledo ca. 50 km south of Madrid discovered a thriving population of 130 individuals of a species of *Carduncellus* on green clay soils. After careful examination by the team that found the population in the field and also by the specialists in the genus at the Botanic Institute of Barcelona, it was unambiguously identified as the defunct *C. matritensis* from Cerro Negro. The taxonomic status of the species has been disputed (see López-González, 2014) partly because of the poor quality of the gatherings ([Figure 3](#)). However, a careful examination of the new samples and the living plants does not leave any doubt in our opinion: *C. matritensis* is a good species that cannot be reduced to any other species of the genus, whether Iberian or North-African. Preliminary results of an ongoing molecular survey support morphological evidence. Our team is also working on more urgent tasks:



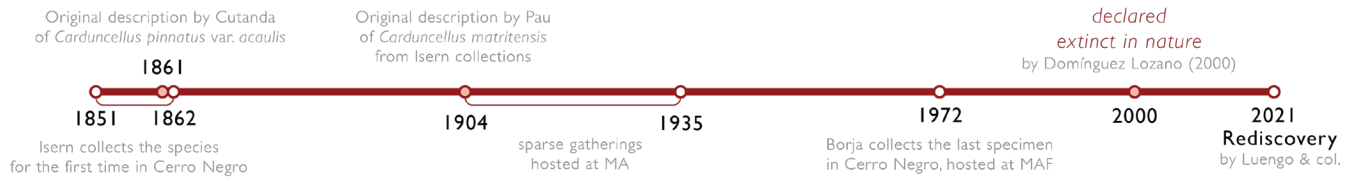
# *Carduncellus matritensis*

The disputed and purportedly extinct species that miraculously survived in the worst dumping grounds and waste places of Spain capital's hinterland



*Carduncellus matritensis*, from Illescas  
Photo by R. de Pablo

## CHRONICLE of the REDISCOVERY of *Carduncellus matritensis* Pau or the thistle that returned from the list of extinct plants



**Figure 2.** Chronicle of the rediscovery of *Carduncellus matritensis* Pau. **A** *Carduncellus matritensis*, habit showing distinctive involucre phyllaries. **B**. Vilatersana and Luengo making a census of a population of *C. matritensis* in an abandoned olive grove; in the back, an industrial dumping ground showcasing the fragility of the populations. Photos by R. de Pablo (A) and A. Susanna (B).



**Figure 3.** Herbarium sheet of *Carduncellus matritensis* Pau collected by Joan Isern, probably the holotype. Manuscript labels (from bottom to top) by Isern, Pau, Cutanda and Vicioso. Image courtesy of the Royal Botanic Garden of Madrid.

described from Cerro Negro, in the north-east of Madrid (Martínez-Labarga et al., in prep.).

## SYSTEMATIC TREATMENT

**Carduncellus matritensis** Pau, Bol. Soc. Aragonesa Ci. Nat. 3: 291 (1904)  $\equiv$  *Carduncellus pinnatus* (Desf.)DC. subsp. *matritensis* (Pau) Rivas Goday & Rivas Mart. In Anales Inst. Bot. Cavanilles 25: 192 (1969)  $\equiv$  *Carthamus matritensis* (Pau) Greuter in Willdenowia 33: 53. (2003)  $\equiv$  *Carduncellus monspelliensium* subsp. *matritensis* (Pau) Mateo & M. B. Crespo, Fl. Montiber. 59: 88 (2015). **Type:** Cerro Negro (Madrid), Isern s.n. (MA136760, holotype?)

= *Carduncellus pinnatus* (Desf.)DC. var. *acaulis* Cutanda, Fl. Matrit.: 421 (1861). **Type:** unknown.

The species is different from all the other species of the genus and especially from the two taxa to which it was subordinated as a subspecies. It can be distinguished from both *C. monspelliensium* and *C. pinnatus* by the appendages of the bracts that are much larger and cucullate in *C. matritensis*.

**Note:** Type of *Carduncellus pinnatus* (Desf.)DC. var. *acaulis* Cutanda. Cutanda did not indicate collector or date, only the locality: "Cerro Negro". It is possible that the type is the same as that of *Carduncellus matritensis* (Figure 3), because there is a label by Cutanda identifying the plant as *Carduncellus pinnatus*.

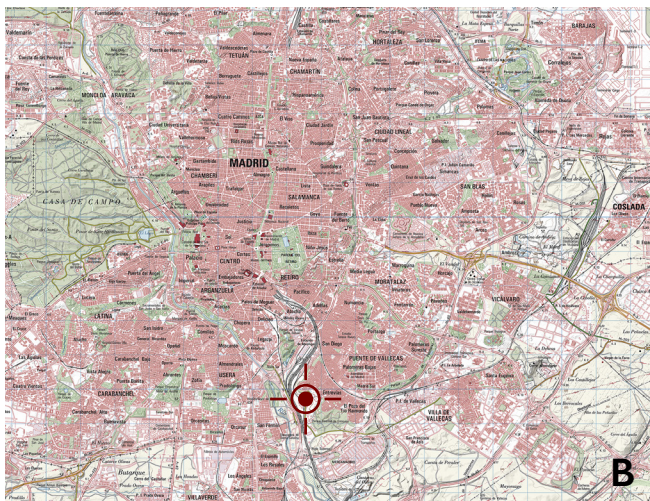
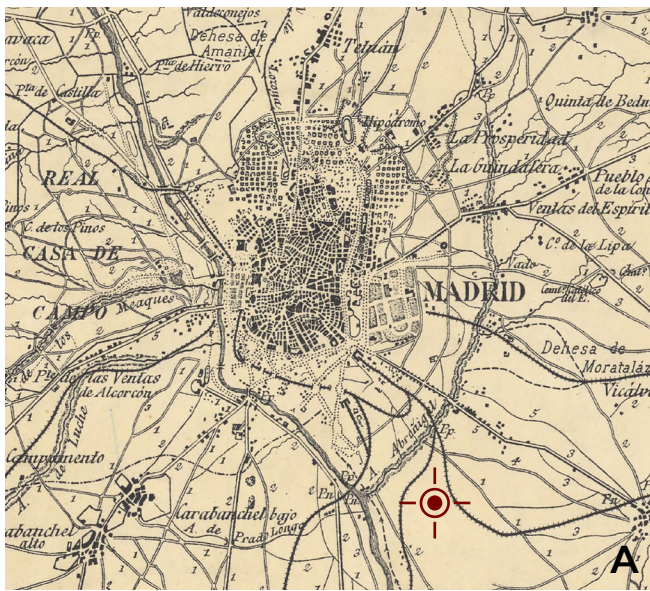
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Cutanda, V. 1861. *Flora compendiada de Madrid y su provincia*. Madrid: Imprenta Nacional.

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**Figure 4.** Type locality of *Carduncellus matritensis* Pau as seen in the maps through history. **A.** Map of 1890s Madrid. **B.** Current map of Madrid; notice type locality deeply inside the limits of the city.

elaborating detailed censuses of the three known populations, fine-combing the surroundings for new ones, and promoting the immediate protection of the species, which will be surely catalogued as critically endangered.

It is unusual that an extinct species, and one that vanished long ago from its only single population, reappears in relatively good conditions in an area so profusely explored as the hinterland of Madrid, a region of great botanical value despite intense anthropization (Martínez-Labarga et al., 2005). The good news of the resurrection of *C. matritensis* adds more joy to the discovery of new populations of the rare Iberian endemic *Cynara tournefortii*, also

estación histórica, paso a paso. *Vía Libre* 279: 26–31.

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# The Compositae collection of LP Herbarium: past and present

Gisela Sancho<sup>1</sup>  & Laura Iharlegui<sup>1</sup> 

<sup>1</sup> División Plantas Vasculares, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad de La Plata, La Plata, Buenos Aires, Argentina; [sancho@fcnym.unlp.edu.ar](mailto:sancho@fcnym.unlp.edu.ar).

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## ABSTRACT

The Herbarium LP (Museum of La Plata, National University of La Plata) holds nearly 300,000 specimens representing a rich history of challenging collecting journeys to uncharted lands and a deep love for plants. Specifically, for Compositae, the LP herbarium holds about 50,000 non-type specimens and 2,415 type specimens. From these types, the tribes Senecioneae, Astereae, Nassauvieae, and Mutisieae are, in decreasing order, the best represented. The legacy of Angel Lulio Cabrera is especially noteworthy by representing nearly 44% of the total type specimens. This essential collection makes the LP herbarium a reference institution for South American Compositae knowledge.

**Keywords:** Asteraceae, type specimens

## INTRODUCTION

The Herbarium LP belongs to the Division of Vascular Plants, Museum of La Plata, Faculty of Natural Sciences, National University of La Plata (UNLP), Argentina.

The Museum of La Plata is a symbol of the city of La Plata and has been declared a national monument since 1997. This Museum was founded during a period with a complicated social, political, and economic context. Despite this, the enthusiasm of its founder, Francisco Pascasio Moreno (1852-1919), an explorer, collector, and politician, managed in 1884 to get the government of that time to decree its foundation and construction, thus fulfilling one of his old dreams (Editorial Board Revista Museo, 1997). The indelible mark that F. P. Moreno left on Argentine science at the time was not limited to his management as director of the Museum of La Plata. The explorations that he carried out in his

early youth, as well as those that he carried out as Expert (“Perito”) on behalf of Argentina (1896-1903) commanding commissions of topographical engineers and traveling naturalists, made it possible to explore and resolve the regions in dispute with Chile that extended along of the Andes Mountains (Editorial Board Revista Museo, 1998). It is in this context of scientific effervescence and exploration at the end of the 19th and beginning of the 20th centuries that two enthusiastic naturalists, Carlo Luigi Spegazzini (1858-1926), born in Italy, and Nikolai Mikhailovich Alboff (1866-1897), born in Russia carried out collection expeditions that would forever change the destiny of the collections of the Museum of La Plata.

Shortly after the museum was founded and by indication of F. P. Moreno, C. L. Spegazzini was appointed head of the botanical section (Crisci et al. 1997). Spegazzini had a great enthusiasm to learn about the flora of the New World and his



**Figure 1.** Angel Lulio Cabrera collecting in Paso del Agua Negra, San Juan province, Argentina. *Photo by Roberto Kiesling.*

collections in remote lands were the cornerstone of the LP herbarium. Although he carried out several field campaigns to gather botanical specimens in Argentina and Chile between the years 1880 and 1926 (Katinas et al., 2000), the most remarkable trips were carried out in the lost land, Patagonia, at that time almost unexplored. Spegazzini, as well as Alboff, were pioneers in the explorations, for example, of Tierra del Fuego and Isla de los Estados, being among the first botanists in Argentina to collect vascular plants from those confines (Sancho and Iharlegui, 2017). Their specimens, together with those of other important contemporaneous collectors like C. Ameghino (Argentinian paleontologist), C. Berg (German naturalist), C. Burmeister (German naturalist), J. Molfino (Argentinian collector), C. Moyano (Argentinian botanist), T. Stuckert (Swedish collector), F. Tonini del Furia (Italian collector), among others, shaped the historical collection held nowadays at LP.

The Herbarium LP also houses other important historical specimens gathered by, for instance, C. E. O. Kuntze, in the 1890s, G. H. E. M. Hieronymus in

the 1870s and 1880s, and R. A. Philippi in Chile in the second half of the nineteenth century.

## **A. L. CABRERA'S LEGACY**

By 1946, the Spanish botanist Angel Lulio Cabrera (1908-1999) (Figure 1) would start, as the new Director of the LP herbarium, the most important transformation of the institution. His scientific work would begin many years before, after falling in love with the Patagonian Compositae while helping his zoologist father in the field. His work continued until he turned 90 years old. Cabrera, during his life, produced an impressive amount of 250 articles mostly on Compositae and phytogeography of Argentina. Cabrera deeply knew the plants and the ecological characteristics in which they lived. This allowed him to establish the phytogeographic limits of the vegetation units in Argentina (e.g., Cabrera 1971; Cabrera and Willink, 1973), a scheme that remains solid and valid despite the years and the new biogeographic perspectives.



**Figure 2.** Type specimen designated by A. L. Cabrera to describe his first new species, *Grindelia aegialitis* (Cabrera, 1931, pp. 234). Image courtesy of LP herbarium.





**Figure 3.** *Grindelia aegialitis* Cabrera, the first species described by this author.  
Photo by Cintia Celsi, Proyecto Costas Bonaerenses, Fundación Azara.

With his work, Cabrera, together with other South American synantherologists such as J. Cuatrecasas (1903-1993) and G. Barroso (1912-2003), among others, changed, forever, the knowledge about the South American Compositae.

For the LP herbarium, Cabrera's contribution had the same overwhelming effect as for the knowledge of South American Compositae. Under his direction, the herbarium increased the number of its specimens to more or less its present number. His collections, about 36000 specimens, together with those obtained during the completion of several of the INTA Projects on regional floras, and a regular exchange of specimens with other South American herbaria, highly increased the value of the collection at LP. Cabrera also left 957 type specimens of Compositae that gave rise to 508 new taxa, mainly in the Eupatorieae, Gochnatieae, Mutisieae, Nassauvieae, Senecioneae, and Vernonieae (Freire and Iharlegui, 2000) (Figs. 2 and 3). Most synantherologists working with South American species have surely come across or relied on Cabrera's publications while conducting their

research or have consulted his collections. Cabrera's contributions transcend time, and the words of this article humbly attempt to honor his work.

## **THE HERBARIUM LP TODAY**

The collection at LP now numbers about 300,000 specimens (Figure 4). The type collection is also important by including 4818 type specimens. Specifically, for Compositae, the LP herbarium holds about 50000 non-type specimens (Figure 5) and 2415 type specimens (Figure 6) from which nearly 44% are Cabrera's types (Figure 7). This essential collection makes the LP herbarium a reference institution for the South American Compositae knowledge.

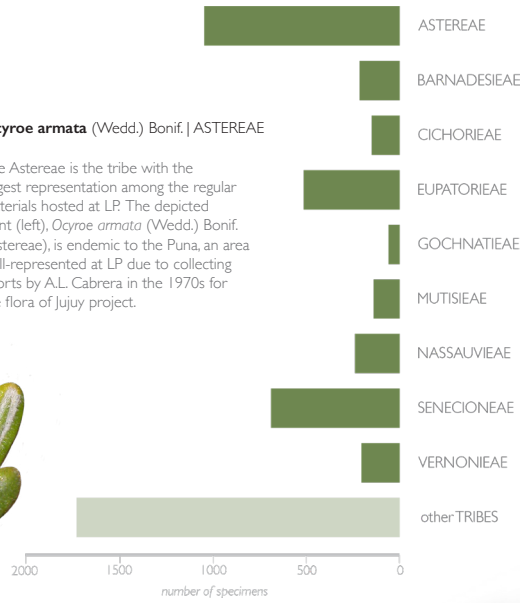
As for most similar institutions, one of the current main challenges in Herbarium LP is to compile the specimen information in a database and make

# COMPOSITAE in LP

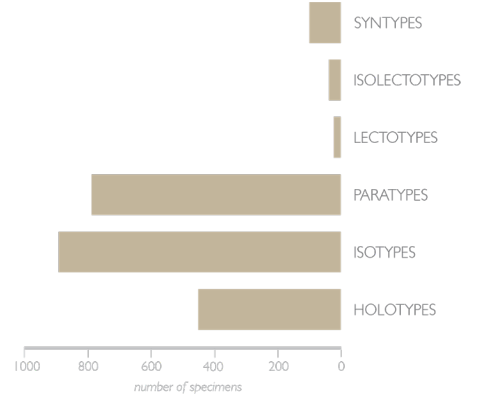


**Ocyroe armata** (Wedd.) Bonif. | ASTEREAE

The Astereae is the tribe with the largest representation among the regular materials hosted at LP. The depicted plant (left), *Ocyroe armata* (Wedd.) Bonif. (Astereae), is endemic to the Puna, an area well-represented at LP due to collecting efforts by A.L. Cabrera in the 1970s for the flora of Jujuy project.



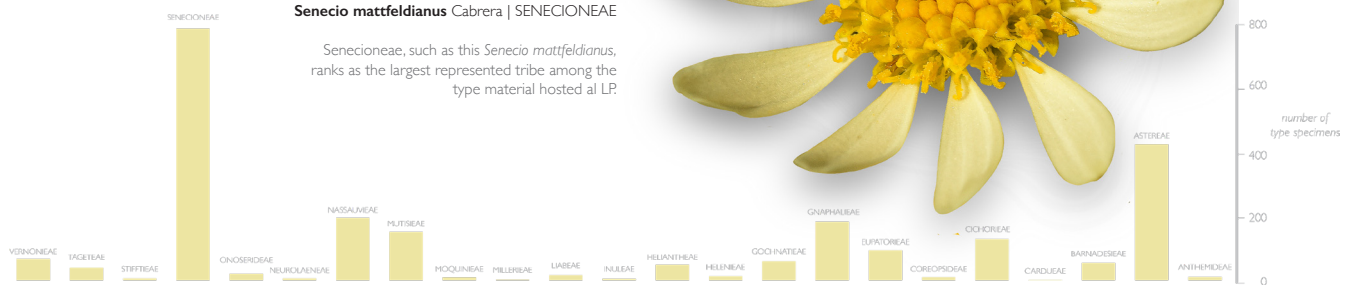
## TYPES of TYPES



## TYPE SPECIMENS by TRIBE

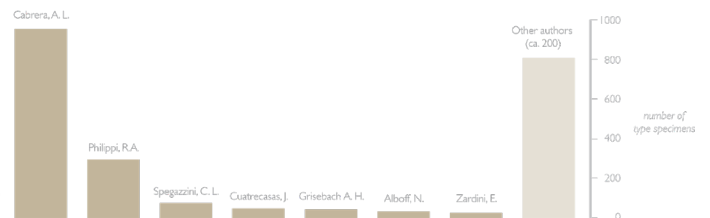
**Senecio mattfeldianus** Cabrera | SENECIONEAE

Senecioneae, such as this *Senecio mattfeldianus*, ranks as the largest represented tribe among the type material hosted at LP.



## Angel Lulio Cabrera (1908-1999)

A leading figure of Compositae research, Cabrera not only broke ground studying this family across the whole phylogenetic spectrum, but also contributed significantly to biogeography and formed a school of taxonomists in southern South America.





**Figure 4.** Specimen cabinets of the Herbarium LP.

it available to the scientific community. The first efforts to digitize the specimen data began about 2007. Not without quite a few rocks in the way, the database operation is being progressively carried out. Nowadays, the platform Specify 7 is used to hold the LP specimen data.

In addition to providing information about the specimens, the database also has created a network where university students forge their first tools with the botanical collections and, at the same time, develop their love for plants. This has resulted in the training of about 70 interns who have been a fundamental link in the development of the database.

Up to the present, we have digitized 85,000 specimens including all of the type collection. Some of the LP records are available at Global Plants on JSTOR (<https://plants.jstor.org>), Portal de Datos del Sistema Nacional de Datos Biológicos (<https://datos.sndb.mincyt.gob.ar>), GBIF (<https://www.gbif.org>) and, soon, they will be at the Museum of La Plata webpage (<https://www.museo.fcnym.unlp.edu.ar>). Indeed, the main objective is to include in the institutional database all the Compositae of the LP herbarium to make available to the botanical world the treasures that our predecessors bequeathed to us. Slowly but surely, and with the help of our students, we are on that path.

## ACKNOWLEDGEMENTS

We thank M. Bonifacino for the valuable comments on the manuscript and help with preparation of the figures. We are grateful to Adriana Bartoli and Cintia Celsi for providing pictures of *Grindelia aegialitis* Cabrera.

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# STYLE

Where art and science converge



## SUNRISE

A pollen grain of the Asteroideae subfamily on the wingscale of *Vanessa cardui* "painted lady" (Insecta: Nymphalidae). The bright pollen grain on white scales resembles a sunrise scenery. Magnification at 60:1 with 0.4  $\mu\text{m}$  step-size.

*Thorben Danke*



### RIDERS ON THE STORM

This micrograph of a *Helianthus* (HELIANTHEAE) floret features pollen grains at 30 microns. This image is part of my Food for Thought exhibition, which explores food and climate change. Sunflowers are especially interesting due to their resilience to drought and heat. Researchers collect crop wild relative specimens and look for ways that relevant genes could help contemporary crops.

*Robert Dash*



### VEGETABLE- SHEEP

*Haastia pulvinaris* Hook.f., Mt Terako, South Island, New Zealand.

The capitula are heterogamous and disciform, with numerous outer and central florets. The corollas of the outer florets are very short and narrowly tubular, sometimes with an uneven apex. The style- branches are long, far-exserted. The corollas of the central florets are tubular and 5-lobed. The style-branches are not so long. The style-branches of *Haastia pulvinaris* have a tuft of trichomes projecting beyond the apex. The pappus is composed by numerous rigid bristles, thickened at the tips. In the photo, only a few florets are open, the ones in the centre are still closed and hidden by the pappus.

Cockayne in *New Zealand Plants and Their Story* (1910) wrote that "the great hummocks of *Haastia pulvinaris* are not inaptly named "vegetable-sheep", for at a distance a shepherd might be misled". However, *Haastia* Hook.f. also misled us botanists: about 100 years after Cockayne wrote his book we finally established its tribal position in the Senecioneae . (see Breitwieser and Ward <https://doi.org/10.1080/0028825X.2005.9512989>)

Rainer W. Vogt



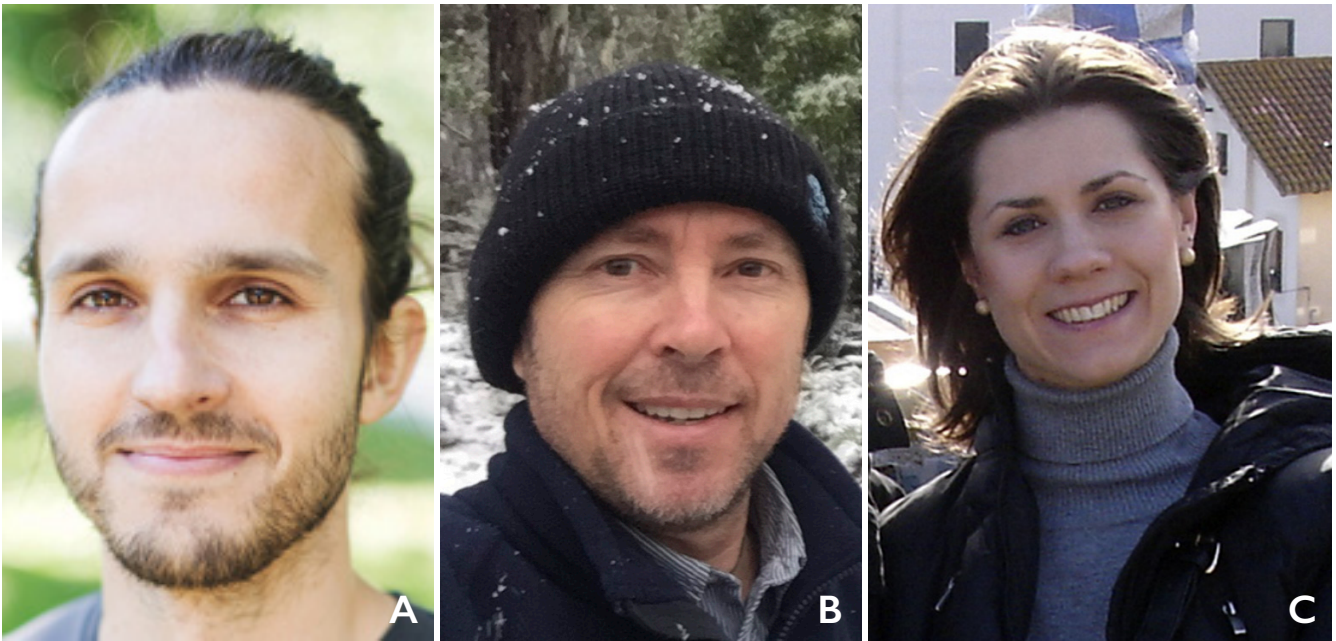
After a very successful first year of TICATalks, we came back in 2022 with a shorter but excellent program.

In March, we welcomed Dr. Marco Todesco from the University of British Columbia, Canada, who gave the talk titled “Hidden in plain sight: the role of ultraviolet colors in sunflower adaptation”, about his most recent paper. We learned about the invisible ultraviolet patterns of sunflower heads and how the genetic mechanisms that lead to this diversity are regulated.

In May, Dr. Tim Collins joined us all the way from Australia to give the talk “Taxonomy, systematics, and polyploidy in *Xerochrysum*, *Coronidium* and *Helichrysum leucopsideum* (Asteraceae: Gnaphalieae)”. In this beautifully illustrated talk, we got to know more about the amazing diversity of Gnaphalieae in Australia.

In June, we received Dr. Makeli Garibotti Lusa, who gave us a comprehensive overview of phytomelanin, in the talk “Melanin in Asteraceae shoot systems: what we know about this pigment, its occurrence and synthesis”. We learned about the possible functions and the occurrence of this mysterious pigment in Asteraceae.

We are planning a few more talks for the rest of this year and we still have open spots. If you are interested in presenting, please contact us at [ticaseminarseries@gmail.com](mailto:ticaseminarseries@gmail.com). All our previous sessions are recorded and available online, at [compositae.org](http://compositae.org).



**Speakers at TICATALKS. A.** Marco Todesco (University of British Columbia, Canada). **B.** Tim Collins (NSW Department of Planning, Industry and Environment, New South Wales, Australia). **C.** Makeli Garibotti Lusa (Universidade Federal de Santa Catarina, Brazil).



# TICATIMES

selected Compositae news and updates from  
THE INTERNATIONAL COMPOSITAE ALLIANCE

*Edited by Jennifer R. Mandel*



**JULY 2022**

## **VICKI FUNK SYMPOSIUM**

The 2022 Botany Conference took place from July 24-27 in spruce-filled Anchorage, Alaska. Members of TICA held a symposium to honor the late Vicki A.

Funk, an American botanist and one of the leading figures studying the taxonomy and biogeography of the Compositae. She was famously known for bringing together botanists from different countries, disciplines, and career stages and thus the symposium honored her spirit of collaboration. Seven leading plant researchers from multiple disciplines whose work is centered in Compositae gave talks at the symposium:

The Reinvention of Compositae: Vicki Funk's legacy in the systematics of the largest plant family on Earth  
**Jennifer Mandel & Mauricio Bonifacio**

Exploring two mysteries of chromosomal evolution in plants  
**Loren Rieseberg**

Putting our heads together: utilizing comparative genomics to understand capitulum  
**Daniel Jones**

Diversification of *Cirsium* (Carduoideae: Compositae) in North America—Insights into a continental-scale radiation  
**Jennifer Ackerfield**

Explosive adaptive radiation of *Bidens* (Compositae) across the most isolated archipelagos in the world  
**Matt Knope**

Vicki Funk, an influential botanist  
**Warren Wagner**

Next year these authors and other Compositae researchers will publish their work in a special issue, a Festschrift, in the International Journal of Plant Sciences.

MORPHOLOGY & CLASSIFICATION OF  
**COMPOSITAE**  
COMPS AT THE EXTREME EDITION



**JULY 2022**  
**COMPS AT THE EXTREME WORKSHOP**

Following the Botany meeting, Mauricio Bonifacio, Gustavo Heiden, and Jennifer Mandel hosted a two-day workshop entitled: Morphology and Classification of Compositae: Comps at the extreme edition. On the first day, 16 participants learned the key characteristics of most of the family's largest tribes through a series of short lectures that awed and inspired even the non-synantherologists of the group. On the second day, participants received hands-on experience recognizing the main features of the most relevant groups in the family by analyzing plant material under the stereoscope.

**AUGUST 2022****PLANT GENOME RESEARCH IN COMPOSITAE**

Jennifer Mandel at the University of Memphis and a collaborative team comprising researchers Daniel Jones at Auburn University and John Burke of the University of Georgia, were awarded a \$2.2M grant from the United States National Science Foundation Division of Integrative Organismal Systems – Plant Genome Research Project to study the genomics of inflorescence development and evolution in the sunflower family.

The project, entitled: “Comparative genomics of the capitulum: deciphering the molecular basis of a key floral innovation” will use the latest genomic technologies to discover the genes that control how the sunflower head inflorescence, or capitulum, develops and evolved.

The work will increase available genomic resources for the sunflower family and result in the development of novel tools for gene editing in the family, as well as provide educational opportunities for diverse students and researchers at multiple training levels, through directed efforts to recruit individuals from traditionally underrepresented groups.

# CAPITULUM

THE INTERNATIONAL COMPOSITAE ALLIANCE NEWSLETTER

## GUIDELINES FOR AUTHORS

### HEAD TOPICS

Section to showcase current research on Compositae. It could be a digest of a paper recently published or a description of a research project among other things. Length of articles could be up to 3000 words.

### PIPET & PRESS

Articles about methods and techniques. Length of articles up to 1000 words.

### BREVIA

Same scope as in HEAD TOPICS section but not as long. Length of articles could be up to 1500 words.

### THE HANDLENS

A close up look to a given species or morphological structure. Length of article up to 1500 words

### THE CABINET

A window to the stories behind ancient or recent herbarium samples and the botanists behind them. Length of articles up to 1500 words

### FROM THE FIELD

The place where the bold and the adventurous share their latest finds in their eternal pursuit of the more recalcitrant comps. Length of articles up to 2000 words

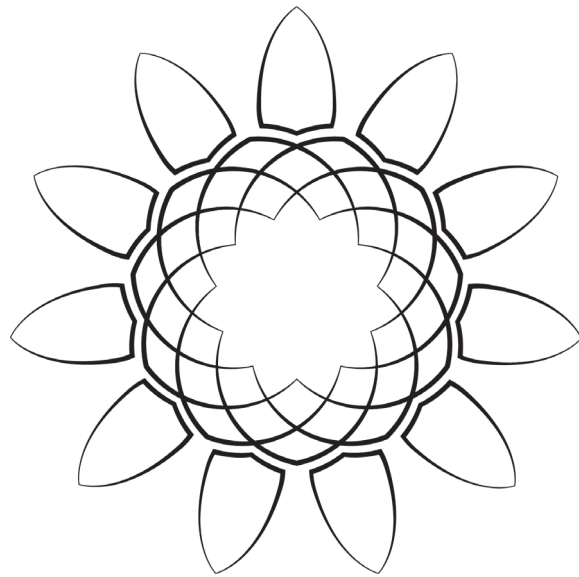
### STYLE

Where science and art converge, artistic photography, botanical illustration or creative infographics. All is welcome if it comes with style.

### PREPARATION OF TEXT

Consult a recent issue of CAPITULUM and follow these instructions. Language for submission is English. Contributions are sent to two external reviewers. Use Times New Roman/Arial typography. Provide a title and if needed, a subtitle. Include names of all authors, their Orcid IDs, their professional affiliations and emails. Include a list of 5–6 keywords in alphabetical order. Provide an abstract of up to 250 words. There is no set structure on how to organize your text; however you may include the classic I-M&M-R-D or none of these, but you should include Acknowledgements and Literature Cited. Up to two subheading categories are accepted. Keep title and subheadings short and informative. All scientific names at the rank of tribe or inferior should include authorship the first time they appear in the text, following Brummitt & Powell, Authors of Plant Names (Kew, 1992; info included in the International Plant Names Index [IPNI]). In text, a single space must follow a period, colon, semi-colon, or comma. Tables must be prepared using MS Excel, please include different tables as different spreadsheets on the same file. Figures should be provided in either TIFF format (for photos) or as vector graphics such as AI or EPS for diagrams, illustrations, or phylogenetic trees. Maps should be provided as shape files when possible or as vector graphics. You may send the photos and other graphics ordered and arranged following your preference, but you are advised that we could edit them to adjust them to CAPITULUM style. All figures must be uploaded as individual original files. Photos should be at least 300 dpi in resolution. Literature citation: please check that all your references are cited and vice versa. For the style of references check a recent issue of CAPITULUM.

Manuscripts or photos intended for publication in CAPITULUM  
are to be submitted at [www.compositae.org](http://www.compositae.org)



*Magno amore in familiam Synantherearum captus*  
Lessing, 1829

