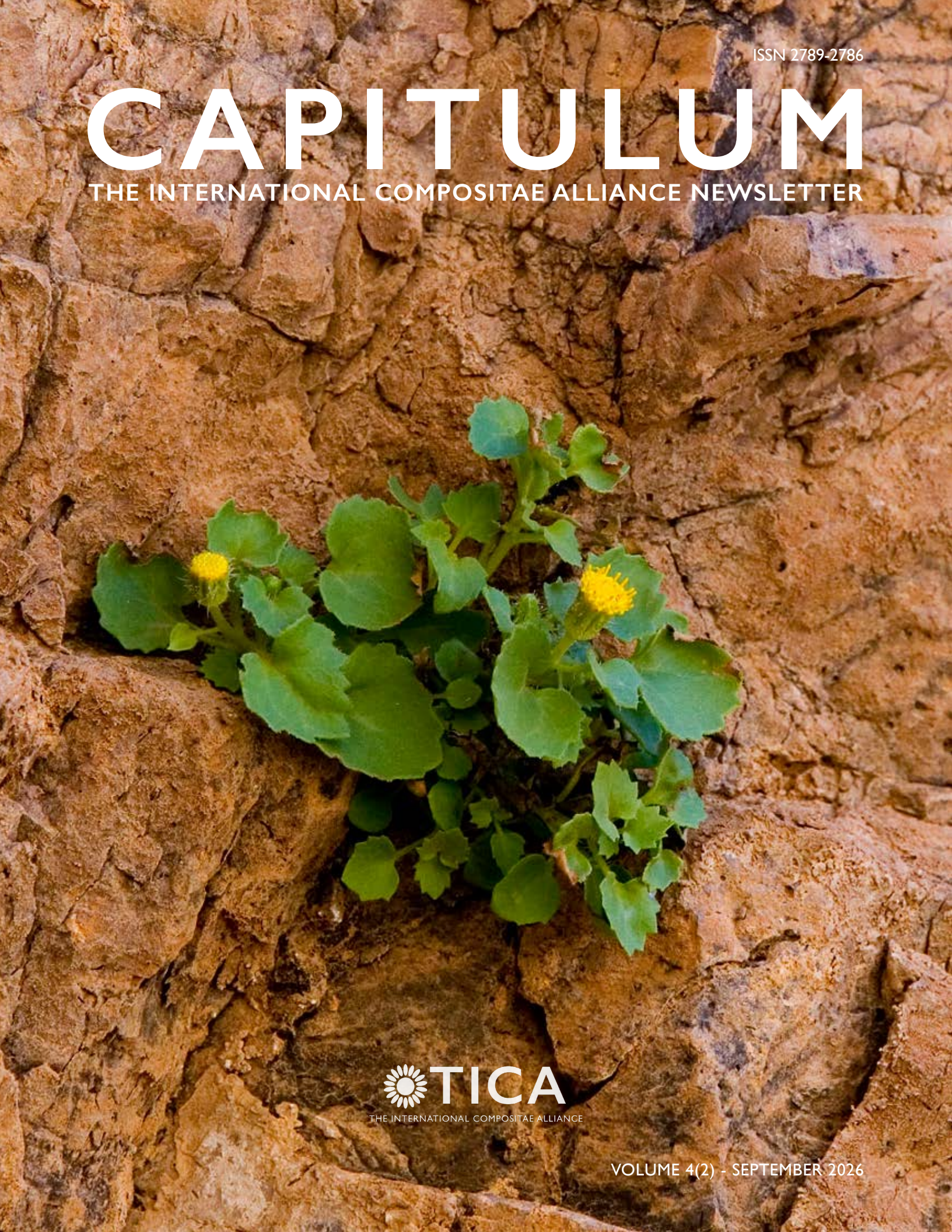
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# CAPITULUM

## THE INTERNATIONAL COMPOSITAE ALLIANCE NEWSLETTER

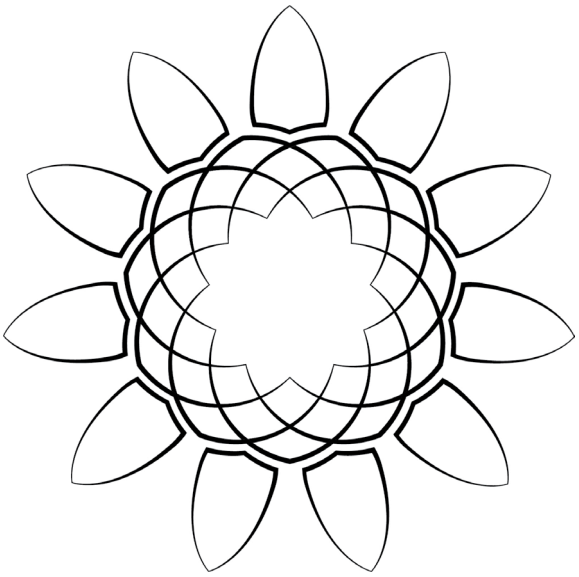


TICA
THE INTERNATIONAL COMPOSITAE ALLIANCE

VOLUME 4(2) - SEPTEMBER 2026

# CAPITULUM

## THE INTERNATIONAL COMPOSITAE ALLIANCE NEWSLETTER



**CAPITULUM**

*For the community, by the community.*

TICA

THE INTERNATIONAL COMPOSITAE ALLIANCE

# 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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# CAPITULUM

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**Cover photo:** rare *Laphamia cernua* Greene in the Organ Mountains of southern New Mexico where it grows on difficult to reach, bare, rhyolitic cliffs.

*Photo by C. Alexander*

*Tilesia baccata* (L.) Pruski ▶

# Kåre Bremer:
## Synantherologist, Pioneer of Cladistics and Co-Architect of APG

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## ABSTRACT

Swedish botanist Kåre Bremer (b.1948) reshaped modern botany across three interconnected domains: the systematics of Compositae, the theory and practice of cladistics, and the phylogenetic classification of flowering plants. As a synantherologist, he produced foundational revisions of South African Gnaphalieae and Anthemideae, conducted the first comprehensive cladistic analysis of the entire Compositae family, and edited Asteraceae: Cladistics and Classification (1994), the first encyclopedic global treatment of the family in nearly a century, which remains a cornerstone of Compositae research. As a pioneer of cladistics in botany, he co-authored the landmark 1978 article "Phylogenetic systematics in botany," helped introduce rigorous phylogenetic reasoning into a discipline long resistant to explicit methodology, and served as President of the Willi Hennig Society from 1985 to 1988. James S. Farris applied Bremer's name to the measure of clade robustness now known as Bremer support, which became an important measure of robustness in phylogenetic analysis. He contributed to our understanding of angiosperm phylogeny and attempted to clarify the evolution of asterids and monocots in space and time, equipped with methods for ancestral area identification and phylogenetic dating, methods he had devised for that purpose. Separately, he served as one of the coordinators of the Angiosperm Phylogeny Group through three successive installments, APG I (1998), APG II (2003), and APG III (2009), the classification framework that now defines global plant systematics. Beyond his research, Bremer mentored fifteen doctoral students and served as President of Stockholm University from 2004 to 2013.

**Keywords:** Asteraceae, Asterales, APG classification, Compositae, phylogenetic systematics, Swedish botany

## INTRODUCTION

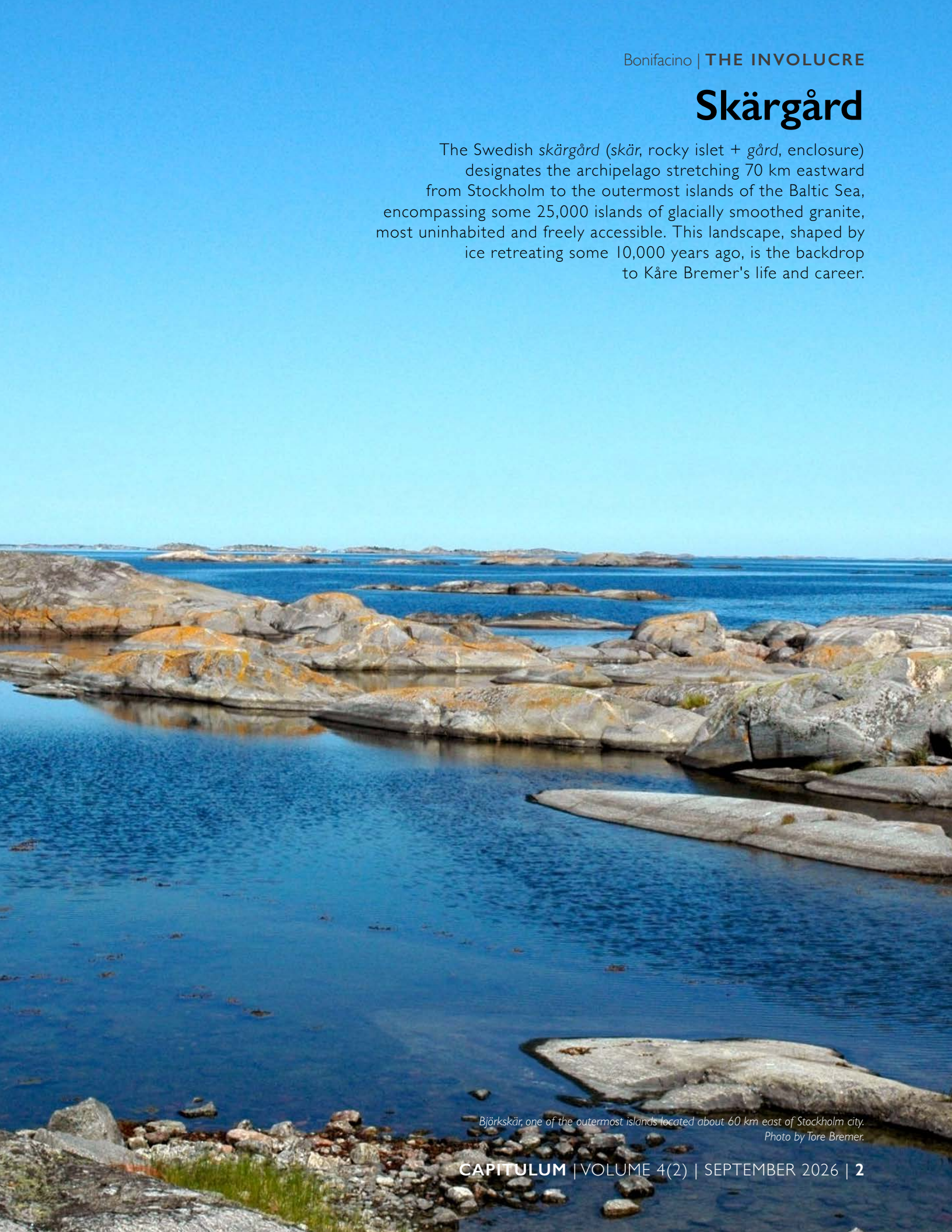
Kåre Bremer is one of the most influential botanists of the late twentieth and early twenty-first centuries, with a career that spans systematics, phylogenetics, cladistic theory, and academic leadership. Born on 17 January 1948 at Lidingö, an island municipality adjacent to Stockholm, he grew up amid the lakes and islands of the Stockholm archipelago, a landscape he would never quite leave behind.

He was raised in an academic household. His father, Georg Bremer, born Georg Hansson, before adopting the less common family name, had grown up on a farm in southern Sweden, studied at Lund University, and gone on to a career in medicine and dentistry, earning a Ph.D. at Uppsala and eventually becoming professor of dental surgery. His mother, Dagmar Bremer (née Lidén), held an M.Sc. in English and German from the Stockholm University College and taught both languages at the high school level. The Bremers married in 1946 and had two sons; the younger, Tore, born in 1949, would become a medical doctor.

Kåre Bremer attended school in Lidingö, completing the standard eight years of compulsory schooling followed by four years in a high school with an emphasis on the natural sciences. Beyond his coursework

# Skärgård

The Swedish *skärgård* (*skär*, rocky islet + *gård*, enclosure) designates the archipelago stretching 70 km eastward from Stockholm to the outermost islands of the Baltic Sea, encompassing some 25,000 islands of glacially smoothed granite, most uninhabited and freely accessible. This landscape, shaped by ice retreating some 10,000 years ago, is the backdrop to Kåre Bremer's life and career.



*Björkskär, one of the outermost islands located about 60 km east of Stockholm city. Photo by Tore Bremer.*

he was active in a student science club, organizing visits to research institutions and expeditions to the islands of the Stockholm archipelago, early evidence of an inclination toward fieldwork and scientific community that would mark his later career. He matriculated in 1967.

His first contact with botany came in his early teens, as part of a long-standing Swedish school tradition requiring students to learn 100 native plant species over the summer. What he initially viewed as an unwelcome imposition quickly became something else entirely.

*"I regarded this as a particularly mean attack on my holidays in the Stockholm archipelago. To my great surprise, however, I immediately became fascinated by searching for the plants and when school started again, I knew many more than the required 100 species."*

Even while still at school, Bremer had begun to spend time at the Swedish Museum of Natural History (SMNH) in Stockholm, where he was occasionally hired to label and sort specimens in the herbarium. After matriculation he studied chemistry, genetics, and other foundational subjects in preparation for graduate work in botany, beginning at Uppsala University and continuing at Stockholm University, where his earlier friendships drew him back.

The decisive intellectual turn had come earlier still. In January 1968, between school and university, Bremer approached Tycho Norlindh (then professor and director of the SMNH's botanical department) for advice on a future B.Sc. thesis. Norlindh, who had himself worked on the tribe Calenduleae of the Compositae, surprised him by suggesting a small South African genus rather than something from the Swedish flora.

*"I had Swedish plants in mind and was therefore surprised when Tycho suggested revisions of plant genera in South Africa and other exotic countries; but I became curious, and eventually chose a South African genus of the Compositae."*

Bremer began work on the genus *Osmitopsis* Cass. (then *Osmites* L., Anthemideae) almost immediately, in 1968, two years before he would formally take up botany at the university. Specimens were loaned from Kew, Kirstenbosch and other herbaria, and he taught himself to read and write botanical Latin with the help of William T. Stearn's *Botanical Latin* (Stearn himself became a personal acquaintance through his visits to Stockholm). Bertil Nordenstam, recently arrived at SMNH from Lund University, guided him through the considerable nomenclatural complications. The completed manuscript was accepted as his B.Sc. thesis in 1971 and published the following year in *Botaniska Notiser* (Bremer, 1972).

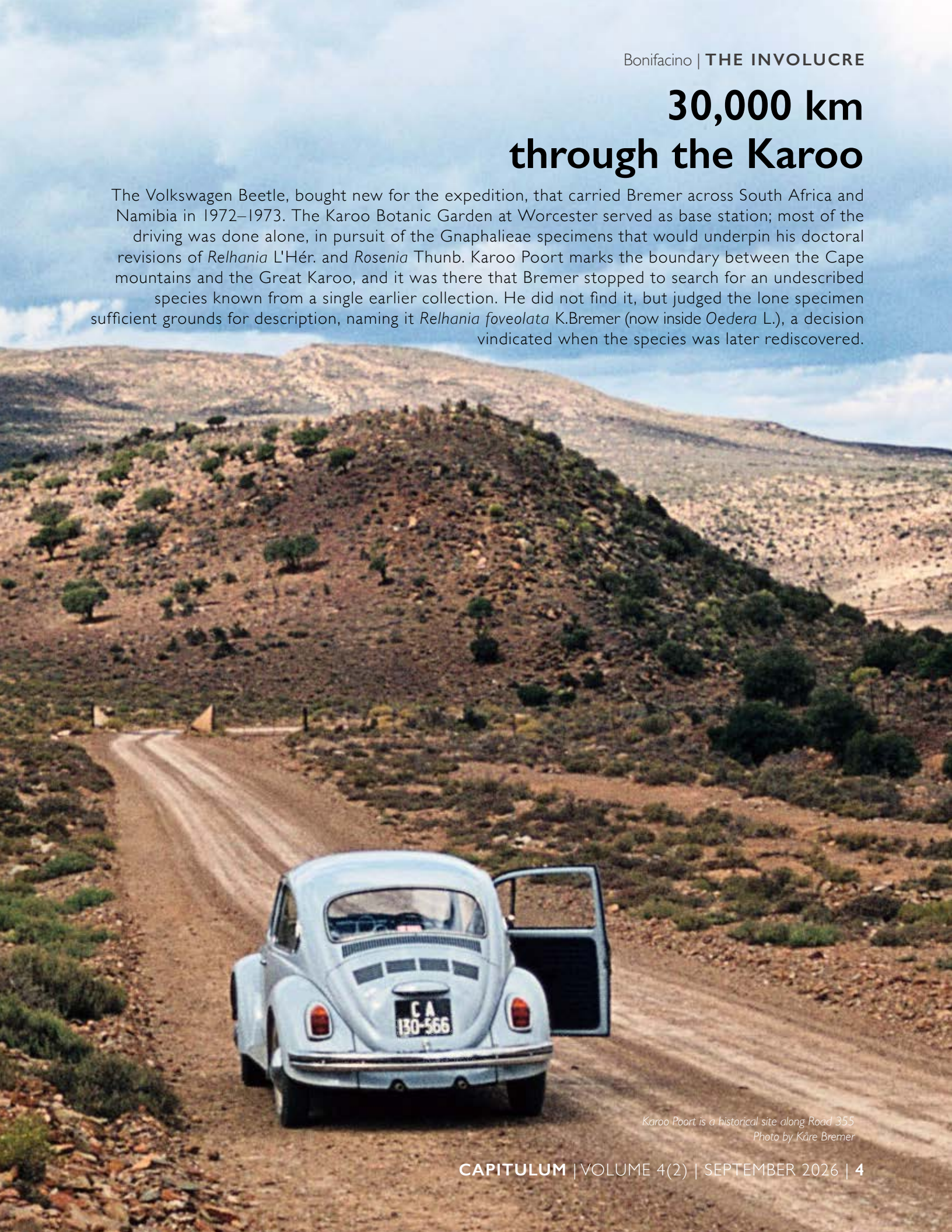
His formal botanical training had begun a year earlier, in the summer of 1970, with a five-week field course on the Swedish flora. Of the nearly 800 vascular plants encountered during the course he already knew roughly half, and the teaching staff made a point of finding and showing him as many of the remainder as possible. He completed his M.Sc. in 1972, the same year he was admitted to the Ph.D. program in systematic botany at Stockholm University. From 1972 he held part-time positions as an assistant teacher at Stockholm University, leading many field courses on the Swedish flora himself, and as an assistant curator at SMNH; the professor of botany, Folke Fagerlind, also supported him through several university funds.

For his doctoral dissertation Bremer shifted from the Anthemideae to the Gnaphalieae, undertaking a revision of *Relhania* L'Hér. and *Rosenia* Thunb. that he completed in 1976 (Bremer, 1976a, b, c). He continued to regard the species-level taxonomy of this work as solid, even if the generic concepts inherited from earlier literature later proved artificial.

Material for that project came in part from a six-month collecting expedition to South Africa and Namibia (1972–1973), undertaken in the early months of his doctoral work. Through Nordenstam's connections, Bremer became affiliated with the National Botanic Gardens at Kirstenbosch and the Department of Botany at the University of Cape Town. He bought a new Volkswagen Beetle (sold back to the dealer upon his departure) and used the Karoo Botanic Garden in Worcester as his base station, traveling nearly 30,000 km across South Africa and Namibia. He was occasionally accompanied by local specialists, including Ted Oliver, an expert on the large genus *Erica* L. (Ericaceae), and Elsie Esterhuysen, described by those who knew her as one of South Africa's most energetic plant collectors. At Kirstenbosch, John Rourke (who took over as director that same year) took special care of him in the herbarium.

# 30,000 km through the Karoo

The Volkswagen Beetle, bought new for the expedition, that carried Bremer across South Africa and Namibia in 1972–1973. The Karoo Botanic Garden at Worcester served as base station; most of the driving was done alone, in pursuit of the Gnaphalieae specimens that would underpin his doctoral revisions of *Relhania* L'Hér. and *Rosenia* Thunb. Karoo Poort marks the boundary between the Cape mountains and the Great Karoo, and it was there that Bremer stopped to search for an undescribed species known from a single earlier collection. He did not find it, but judged the lone specimen sufficient grounds for description, naming it *Relhania foveolata* K.Bremer (now inside *Oedera* L.), a decision vindicated when the species was later rediscovered.




*Karoo Poort is a historical site along Road 355*
*Photo by Kåre Bremer*



**Figure 1.** The Wemmershoek Mountains, Western Cape, South Africa. In 1972 Bremer climbed Wemmershoek Peak in search of an undescribed *Osmitopsis*. The two-day ascent ended on the steep southern face, where he collected the specimens later described as *Osmitopsis pinnatifida* subsp. *serrata*. *Photograph by Kåre Bremer.*

*"I travelled all over South Africa and Namibia… most of the time I was alone, sometimes accompanied by local botanists. The search for my species was overall successful, I found most of them, including some undescribed ones."*

One ascent in particular stayed with Bremer. Elsie Esterhuysen had collected an undescribed *Osmitopsis* high on Wemmershoek Peak, accessible by a long path that required no technical climbing but a full two-day return on foot (Figure 1). Bremer drove with her to the top of Franschhoek Pass, walked until dark, slept on the ground, and reached the peak the next morning, where Esterhuysen showed him the plants flowering in rock crevices on the steep southern face. Terrified of the height, he crawled forward to the vertical drop and collected several specimens. He eventually described the plant as *Osmitopsis pinnatifida* subsp. *serrata* K.Bremer.

From 1980 to 1990 Bremer served as Head Curator of Phanerogamic Botany at SMNH. Already in the late 1970s, however, he had embarked on a significant parallel research project on the palaeotropical rain-forest tree genus *Memecylon* L. (Melastomataceae) — a deliberate broadening of his systematic experience beyond the Compositae as he prepared for a future university or museum position. The project came about by an accident of funding. Bremer had originally hoped to do fieldwork in South America with support from the Royal Swedish Academy of Sciences' Regnell fund, but the next call had been cancelled and the available money reserved for a senior colleague's expedition at Göteborg. He pivoted to tropical Asia, where F. Raymond Fosberg, at the Smithsonian Institution, agreed to assign him the Melastomataceae for the Revised Handbook to the Flora of Ceylon, and covered travel, vehicle, field assistant, and prepaid airline tickets. Sri Lanka was traversed by Land Rover in early 1977; a more demanding expedition to peninsular Malaysia and Sarawak followed in 1978–79, the latter including days of river travel by longboat, operated by Iban boatmen, deep into the interior of Borneo. His treatment of the Melastomataceae appeared in volume 6 of the Revised Handbook to the Flora of Ceylon (Bremer, 1987a). Bremer eventually abandoned the wider project — *Memecylon*, he concluded, was simply too difficult and too poorly known — but the experience had served its broadening purpose, and the Compositae would in any case prove to be his true home.

Both of those journeys had been undertaken together with his wife, Birgitta Bremer (Figure 2), who he

# The Daily Press

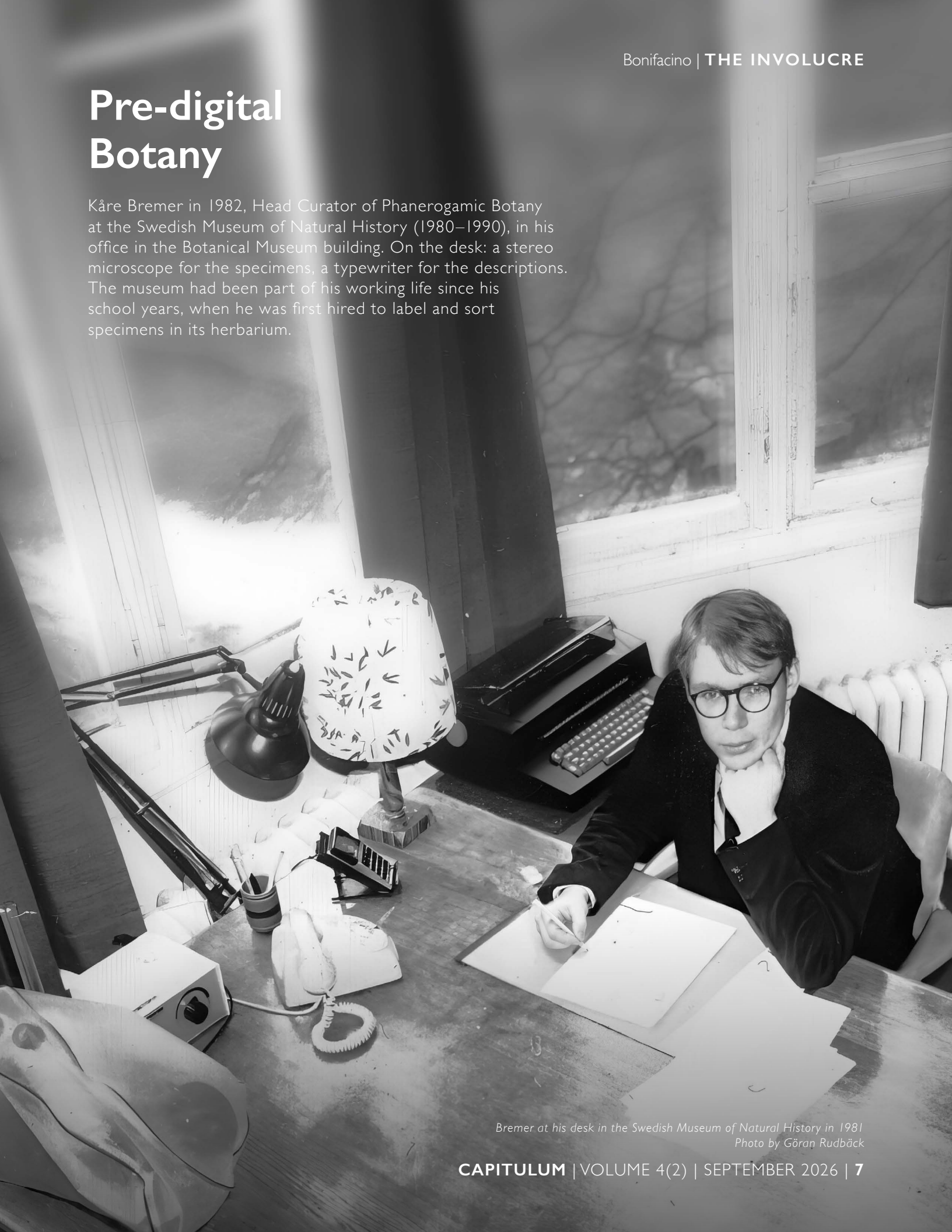
Kåre Bremer at the National Botanic Gardens at Kirstenbosch, Cape Town, 1972 —checking specimens after drying during his six-month collecting expedition through South Africa and Namibia.



*Bremer in National Botanic Gardens at Kirstenbosch in 1972*
*Photo by Kåre Bremer*

# Pre-digital Botany

Kåre Bremer in 1982, Head Curator of Phanerogamic Botany at the Swedish Museum of Natural History (1980–1990), in his office in the Botanical Museum building. On the desk: a stereo microscope for the specimens, a typewriter for the descriptions. The museum had been part of his working life since his school years, when he was first hired to label and sort specimens in its herbarium.



*Bremer at his desk in the Swedish Museum of Natural History in 1981*
*Photo by Göran Rudbäck*



**Figure 2.** Birgitta and Kåre Bremer in the Stockholm archipelago, 2007, aboard their 24-foot Coronet, one of the Danish-built motorboats of the 1960s and 1970s on which Bremer is a self-taught authority. The same archipelago supplied the hundred-plus islands that he and Birgitta surveyed, from 1990 onwards, for the regional Floras of Södermanland and Uppland.

had met as a fellow doctoral student and married in 1976; they have a son, Oscar (born 1981), and a daughter, Hanna (born 1983). Birgitta had used those same expeditions to begin her own work on the Rubiaceae, the family on which she would later become a world expert; she went on to become a pioneer of molecular systematics in Sweden, and is well known for her work on the Rubiaceae and other asterids, later holding the position of Professor Bergianus at the Royal Swedish Academy of Sciences and serving as director of the Bergius Botanical Garden in Stockholm.

The network around the Swedish Museum of Natural History and Stockholm University produced several generations of synantherologists. Bremer identifies Norlindh, Nordenstam, and himself as the first three "generations," followed by a fourth (Figure 3) comprising Arne Anderberg, Annette Wiklund, Mari Källersjö, Per Ola Karis, Mats Gustafsson, Ulf Swenson, and Johannes Lundberg (the last three graduated at Uppsala University), and a fifth represented by Anderberg's students. This scientific lineage reflects the deep collaborative environment between SMNH and Stockholm University, where curators and professors could serve interchangeably as doctoral supervisors. Over the course of his career, Bremer supervised a total of fifteen doctoral students, including Jens Klackenberg and Barbro Axelius at Stockholm University, as well as Mariette Manktelow, Anders Backlund, Elisabeth Långström, Jesper Kårehed, Annika Vinnersten, and Cajsa L. Anderson at Uppsala University, in addition to those already mentioned.

In 1989 Bremer became Professor of Systematic Botany at Uppsala University, where he expanded his research into deep phylogenetic structure within the asterids, historical biogeography of Gondwanan lineages, and the limits of molecular and morphological evidence in reconstructing major clades. His work also extended beyond the Asterales

# A botanist's wonderland

Desert vegetation beneath a mountain horizon, featuring a species named in honor of Bertil Nordenstam, Bremer's mentor, and evoking the field landscapes that supplied the Gnaphalieae material for his doctoral revisions.



*Gedera nordenstamii* (K.Bremer) Anderb. & K.Bremer in its limestone habitat, with a close-up of the capitulum. Summit southeast of Numeesberg, Richtersveld, South Africa.
*Photos by Nicola Bergh*

# Taxonomists who are serious enough about the plants they study should make their own illustrations

Elements of a plate illustrated by Bremer of *Oedera speciosa* (DC.) N.G.Bergh, a species in the Gnaphalieae complex of which he produced his doctoral revision, and which his former students Anderberg and Källersjö, and later Bentley and colleagues would reorganize on morphological and molecular evidence, respectively. Making one's own illustrations compels a close looking that nothing else replaces: every detail must be seen, and the form of every structure pinned down, decision by decision, in line and shading — so that the finished illustration carries not only what was observed but how it was understood.

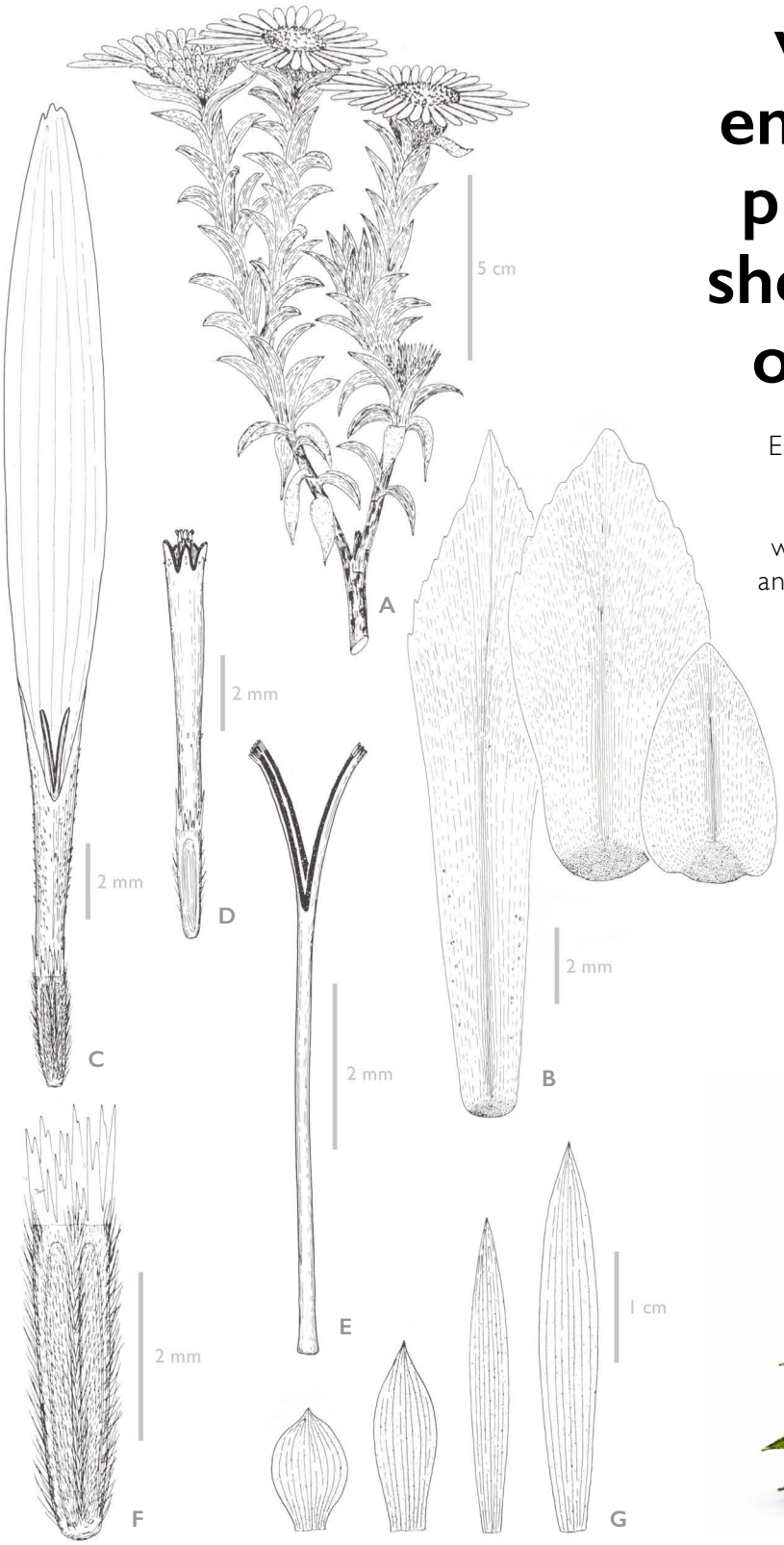





*Photo of* Oedera speciosa *taken by Bremer in 1972*

**Oedera speciosa. A.** *Habit.* **B.** *Phyllaries (left to right, inner to outer phyllaries).* **C.** *Ray floret.* **D.** *Disk floret.* **E.** *Disk floret style.* **F.** *Achene and pappus of ray floret.* **G.** *Leaves.* Illustrations taken from Bremer 1976a



**Figure 3.** Bremer with five members of the "fourth generation" of Swedish synantherologists in 2022, the lineage that runs from Tycho Norlindh through Bertil Nordenstam to Bremer himself, and onward through students who have since trained their own. From left: Arne Anderberg, Ulf Swenson, Kåre Bremer, Johannes Lundberg, Per Ola Karis, Mari Källersjö. All professors and curators; all, except Johannes, now retired.

to the monocots, including a study of the Poales, though this line of research was eventually set aside as administrative responsibilities grew. Considerable unexplored territory remained, particularly regarding Gondwanan biogeography in both monocots and eudicots. He served as Dean of Biology at Uppsala from 1993 to 1999, overseeing the construction of the Evolutionary Biology Centre — a major facility housing 400 scientists and doctoral students in evolutionary biology, completed in January 2000.

Bremer's later career transitioned increasingly toward high-level administration. From 2000 he served as Secretary-General for Natural and Engineering Sciences at the Swedish Research Council, where he oversaw the amalgamation of basic-science and engineering research communities that had previously regarded one another with suspicion. From February 2004 he was President of Stockholm University — a role he held until January 2013 — during which he led the implementation of the Bologna system in undergraduate education, pushed for greater internationalisation in research, and oversaw the absorption of Stockholm's separate teacher-education college into the University in 2008. He served under eight ministers of education from across the political spectrum during these years.

*"There is simply no time for research in that position… but I say this without regret. My time as president of Stockholm University was fantastic and I liked it all the time."*

After stepping down, he continued to serve in national capacities. From 2013 to 2021 he sat on the board of the Knut and Alice Wallenberg Foundation — one of Europe's largest private funders of research — as well as on the boards of other Wallenberg foundations. From 2014 to 2020 he served as founding chair of the board of the newly established Stockholm University of the Arts, formed by the merger of four schools covering theatre, film, dance, opera, and circus. In 2015 he led a government commission on university management and governance whose 500-page report informed subsequent revisions to Swedish higher-education regulations.

In 2006 he received His Majesty the King's Medal — 12th size, in gold, with the ribbon of the Order of the Seraphim — for exceptional service to science. Three plant species have been named in his honour:



**Figure 4.** Kåre Bremer in 2017 at the helm of the 1925 Forslund mahogany runabout he restored, a boat originally owned by his father and a counterpart, in family history, to the Stockholm archipelago itself. Both have been part of his life since boyhood; the same restored boat appeared, with Bremer aboard, on the cover of Rudder, the magazine of the American Antique and Classic Boat Society (Rudder 2018 volume 27, no. 3). *Photos by Georg Oppermann Moe.*

*Athanasia bremeri* Källersjö (Anthemideae, South Africa), *Memecylon bremeri* M.B.Viswan (Melastomataceae, India), and *Pseudoblepharispermum bremeri* J.-P.Lebrun & Stork (Inuleae, Ethiopia). In retirement, Bremer returned to the Stockholm archipelago, botanizing in the landscapes where his fascination with plants first began.

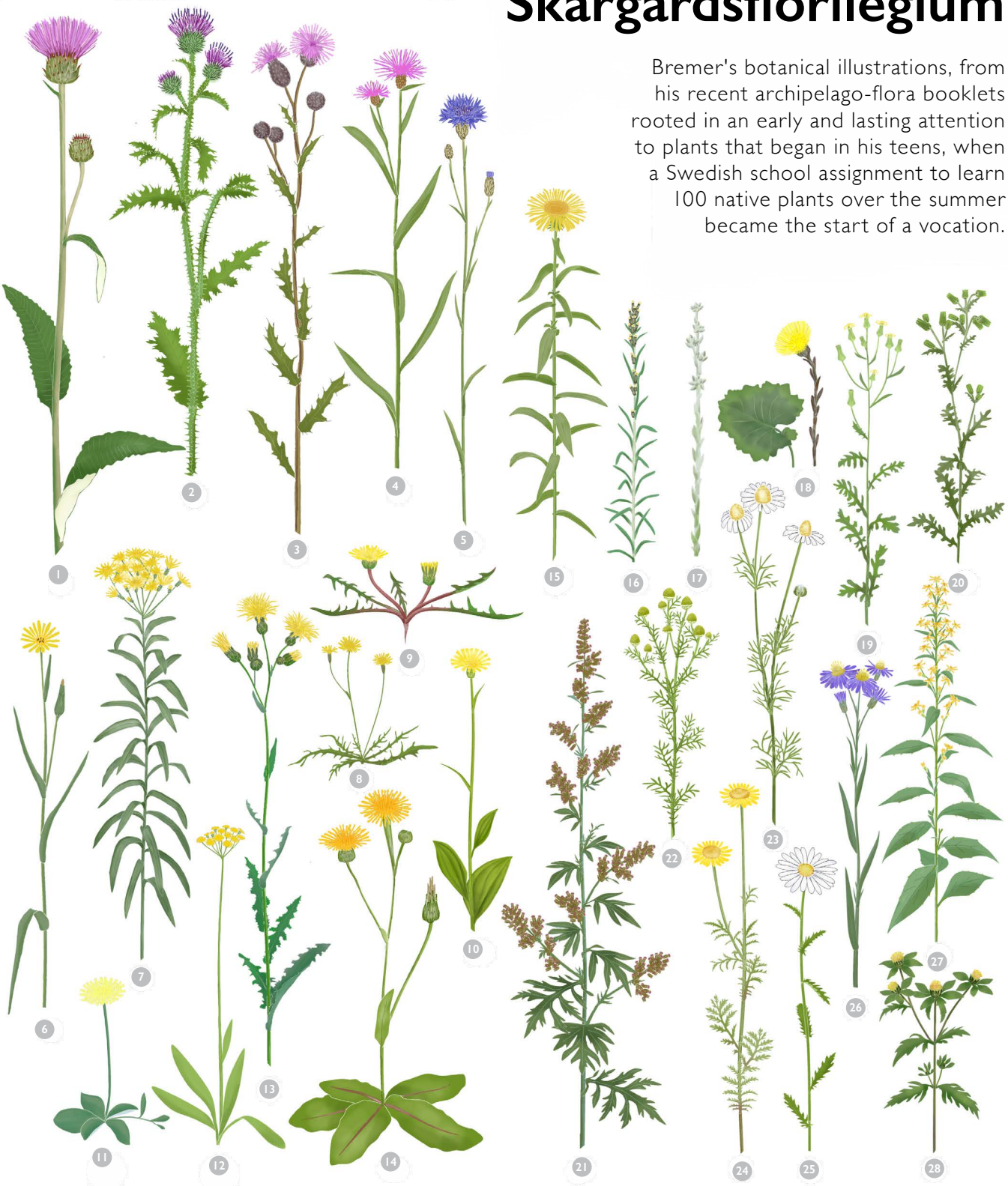
The archipelago itself had been a constant presence in Bremer's life since childhood. His parents had owned a summer house on one of the larger islands, and each year, when his father closed his dental surgery in mid-June, the family moved there for the next two months. Bremer and his brother were trusted with their own outboard motorboat as boys and could reach much of the archipelago all the way to its outermost islands; they explored countless of them, often searching for plants. The archipelago has remained Bremer's preferred summer landscape ever since, and he is also a longstanding motorboat enthusiast — a self-taught authority on the Danish-built Coronet boats of the 1960s and 1970s, on which he has written for boating magazines, and the restorer of a 1925 Forslund mahogany runabout originally owned by his father, which appeared, with Bremer at the helm, on the cover of Rudder (volume 27, No 3, 2018), the magazine of the American Antique and Classic Boat Society (Figure 4).

For roughly two decades from 1990 onwards (overlapping with his career at Uppsala and at Stockholm University) Bremer and his wife Birgitta took part in the long-running surveys that produced the Flora of Södermanland and Flora of Uppland, accepting responsibility for a large part of the Stockholm archipelago and visiting more than a hundred islands in the course of the work. He continues to monitor populations of rare species and report them to the national flora and fauna database. In recent years he has developed his own technique for producing line drawings of archipelago plants — based on cell-phone photographs and rendered in vector graphics in Microsoft PowerPoint — for small booklets that he gives away or sells to a local botanical public (Figure 5). On 25 September 2026, after having hosted many of Stockholm University's academic ceremonies as president, Bremer returned to Stockholm City Hall to be conferred *jubeldoktor* (jubilee doctor), a traditional Swedish and Finnish designation marking fifty years since the original doctoral conferment.

A scientific life may be evaluated in many ways, by the students trained, the institutions shaped, the research questions persistently asked. But the truest measure of a career, and among the rarest, is whether it has produced work that permanently advances how a

# Skärgårdsflorilegium

Bremer's botanical illustrations, from his recent archipelago-flora booklets rooted in an early and lasting attention to plants that began in his teens, when a Swedish school assignment to learn 100 native plants over the summer became the start of a vocation.




**1**. *Cirsium heterophyllum* (L.) Hill, **2**. *Carduus crispus* L., **3**. *Cirsium arvense* (L.) Scop., **4**. *Centaurea jacea* L., **5**. *Centaurea cyanus* L., **6**. *Tragopogon pratensis* L., **7**. *Hieracium umbellatum* L., **8**. *Scorzoneroides autumnalis* (L.) Moench, **9**. *Taraxacum balticum* Dahlst., **10**. *Scorzonera humilis* L., **11**. *Pilosella officinarum* F.W.Schultz & Sch.Bip., **12**. *Pilosella cymosa* (L.) F.W.Schultz & Sch.Bip., **13**. *Sonchus arvensis* L., **14**. *Hypochaeris maculata* L., **15**. *Pentanema salicinum* (L.) D.Gut.Larr., Santos-Vicente, Anderb., E.Rico & M.M.Mart.Ort., **16**. *Gnaphalium sylvaticum* L., **17**. *Filago arvensis* L., **18**. *Tussilago farfara* L., **19**. *Senecio viscosus* L., **20**. *Senecio vulgaris* L., **21**. *Artemisia vulgaris* L., **22**. *Matricaria discoidea* DC., **23**. *Matricaria chamomilla* L., **24**. *Cota tinctoria* (L.) J.Gay ex Guss., **25.** *Leucanthemum vulgare* Lam., **26**. *Tripolium pannonicum* (Jacq.) Dobrocz., **27**. *Solidago virgaurea* L., **28**. *Bidens tripartita* L. Illustrations by Bremer made in Microsoft PowerPoint.



**Figure 5.** Kåre Bremer in 2025, explaining the morphology of *Pilosella cymosa* (L.) F.W.Schultz & Sch.Bip. (Cichorieae) to a local botanical audience on Gällnö, the island in the Stockholm archipelago where he and his family have their summer house, and one of the landscapes that has shaped his botanical eye since youth. *Photo by Kina Robberts.*

community understands the natural world. To achieve one such contribution is more than most researchers manage; to produce several, in different domains and at different moments across a long career, is something rarer still — the mark of a mind that does not merely participate in the history of a science but helps determine its direction. Bremer's career produced at least three contributions of that kind. The first was a methodological declaration that brought an entirely new epistemological standard into botanical classification, one that has shaped every plant cladistic and phylogenetic study that followed. The second was a phylogenetic synthesis of the Compositae—approached through a 1987 proof of concept and completed in the 1994 monograph that gave the family a rigorous phylogenetic framework for the first time. The third was a collective enterprise that replaced prior angiosperm classification systems with a single, phylogenetically grounded framework, an effort by the Angiosperm Phylogeny Group, of which Bremer was one of the coordinators. The sections that follow trace each of these contributions in depth, interleaved within the narrative of the career that produced them.

## CLADISTICS AND ITS INTRODUCTION TO BOTANY

The intellectual catalyst for Bremer's engagement with cladistics was Hans-Erik Wanntorp (Figure 6), a colleague at Stockholm University who had been following the cladistics debate in the journal Systematic Zoology (now Systematic Biology). Wanntorp (born 1940) had been assistant and lecturer at the Department of Botany, Stockholm University since the mid-1960s, where he held a position in systematic botany and was widely regarded as an enthusiastic and dedicated teacher. He earned his Ph.D. for a monograph of the Southern African genus *Microloma* R.Br. (Asclepiadaceae), and his breadth of knowledge — extending well beyond botany into zoology — made him a natural reader of the zoological systematics literature. It was on Wanntorp's advice that Bremer first began to study cladistic principles, and the two decided to write a joint paper to make the case for their adoption in botany (Bremer & Wanntorp, 1978).

Its occasion was a provocation: at a major Hamburg symposium on flowering plant classification held two years earlier, Hennig's phylogenetic systematics — by then nearly thirty years old and an expanding yet still controversial framework in zoological taxonomy — had gone entirely unmentioned. Bremer and Wanntorp took that silence as a diagnosis of the discipline's condition and set out to remedy it. Their paper was, in effect, the manifesto for cladistics in botany: a clear, systematic exposition of Hennig's principles translated into botanical terms, followed by a demonstration of what those principles, rigorously applied, would do to some of the most firmly established certainties in plant classification.



**Figure 6.** Kåre Bremer (left) and Hans-Erik Wanntorp in 1974, examining plants during one of the numerous excursions and field courses they had together with students his Stockholm University. It was Wanntorp who first drew Bremer into cladistics debate. Their 1978 paper in Taxon set out the case for phylogenetic systematics in botany and reshaped the methodological standards of the discipline. *Photo by Birgitta Bremer.*

The core argument was simple but its implications were profound. Phylogenetic reconstruction must be based exclusively on synapomorphies and any group defined by plesiomorphies, or by overall similarity, is not a natural group but a convenience of the taxonomist's making. Two requirements follow for any classification that claims to reflect evolutionary history: all taxa must be strictly monophyletic, and sister groups must always be given equal rank. A system violating either rule encodes information that cannot be recovered or tested from the system itself — it is, Bremer and Wanntorp wrote, not falsifiable in Popper's sense, and therefore more a work of art than a scientific statement.

The paper's two examples were not only illustrative but strategic. At the higher level, Bremer and Wanntorp took Takhtajan's angiosperm system — then among the most authoritative and admired in the world — and showed that it harboured at least four major paraphyletic groupings, of which the most consequential was the dicotyledons themselves. Since Takhtajan's own dendrogram placed the monocotyledons as the sister group of Nymphaeales rather than as the coordinate of all dicotyledons, the class Magnoliatae was paraphyletic by Takhtajan's own evidence: it excluded some of its own descendants. The monocotyledons, far from constituting one half of the angiosperm world, were a single nested branch within what was being called the dicotyledons. At the generic level, the paper turned to Iltis's work on the Cleomoideae — an admirable study, Bremer and Wanntorp said, chosen precisely because it was a lucid and representative example of traditional evolutionary systematics at its best. Yet even there, when specialized derivative genera were segregated from *Cleome* L. (Cleomaceae), the residual genus became paraphyletic, defined not by any character it possessed but merely by the absence of the characters used to circumscribe the



**Figure 7.** Christopher J. Humphries (left, 1947–2009) and Kåre Bremer during a coffee break at the Willi Hennig Society meeting in Miami, November 1985. Bremer was at the time on sabbatical at the Missouri Botanical Garden (as the MBG tie attests) and it was at this meeting that he was elected President of the Society, succeeding James S. Farris; he would in turn be succeeded by Humphries in 1988.

segregates. The practical implication was one that every working taxonomist would recognize and find uncomfortable: the common habit of carving morphologically distinctive groups out of larger genera almost inevitably renders the remainder incoherent. The only phylogenetically defensible solutions were either to absorb the segregates back into a broadly circumscribed monophyletic *Cleome*, or to subdivide all the way down until every recognized genus was defined by its own synapomorphies — a thoroughgoing reorganization that the traditional approach had no tools to accomplish.

The paper greatly affected Bremer's subsequent career, and its influence on botanical systematics was, in time, transformative. What the 1978 paper established was not merely a method but an epistemological standard: that a classification is only as good as its explicitness, its falsifiability, and its freedom from the subjective weighting of characters that made traditional systems, however erudite, ultimately personal and therefore unrepeatable. Bremer would spend the rest of his career demonstrating that this standard could be met — first with morphological characters alone, then with the early molecular data, and finally with the genomic approaches that would only become available in the last decade of his active research. Bremer and Wanntorp's paper provoked an initial hostility.

*"We were quite outspoken… Some established professors completely condemned what we had to say. It spurred us even more."*

The reaction was not without historical precedent. Linnaeus's own reforming publications had met fierce resistance from the botanical establishment of his day before being almost universally adopted and then left behind. Bremer and Wanntorp's paper provoked a similar initial hostility, but with a crucial difference: where the Linnaean sexual system was ultimately a convenience that nature did not ratify, the phylogenetic principles Bremer and Wanntorp championed have become the permanent methodological foundation of all modern biological classification. The paper became widely read and instrumental in shifting botanical systematics toward cladistic methodology. Bremer regards it as probably his most important single contribution, even though, as is typical of methodological papers, its influence is difficult to gauge through citation counts.

In 1979, Bremer and Wanntorp attended a symposium on historical biogeography at the American Museum of Natural History in New York, where they encountered the leading cladists in zoology — Gareth Nelson, Donn Rosen, Norman Platnick, Ed Wiley, and others — and were warmly received. The contrast with the resistance they had encountered in European botany was marked, and their involvement placed them at the center of an international network driving phylogenetic systematics forward. When Ed Wiley organized an early cladistics meeting in Kansas, the Willi Hennig Society was founded with James S. Farris as its first president. Bremer soon became an active participant, and in 1985 he succeeded Farris as President of the

Society, a position he held until 1988, organizing two landmark meetings in Stockholm: an open cladistics conference and, following it, the Nobel Symposium "The Hierarchy of Life — Molecules and Morphology in Phylogenetic Analysis" (Fernholm, Bremer & Jörnvall 1989). Because Nobel symposia are limited to 50 or 60 invited participants, two parallel events were necessary. The symposium brought together leading molecular and morphological systematists at a pivotal moment in phylogenetic research.

Before chloroplast DNA revolutionized plant phylogenetics, researchers had explored amino acid sequences as phylogenetic markers. Bremer evaluated these early datasets with skepticism, recognizing that they required numerous homoplasy-based auxiliary hypotheses. In a 1988 paper he demonstrated that the apparent phylogenetic structure collapsed progressively as one allowed more auxiliary hypotheses (Bremer, 1988).

> *"The branches started to collapse one by one in the consensus tree when the number of allowed auxiliary hypotheses increased."*

The 1988 paper did not propose a metric in any formal sense. What Bremer offered was a methodological criterion for working with protein-sequence based cladograms: groups that appeared in the most parsimonious tree but failed to survive in the consensus of slightly suboptimal trees should not be regarded as confidently monophyletic. James S. Farris recognized the significance of this observation immediately. He called Bremer to say: "*What an extraordinarily good idea!*", and went on to coin the metric Bremer support, using the number of extra steps needed to collapse a clade as a measure of its robustness. Bremer later elaborated the concept formally in "Branch support and tree stability" (Bremer, 1994a), now among his most cited papers.

The 10-page paper published in *Cladistics* in September 1994 — appearing in the same year as the Asteraceae book — was, in one sense, an act of methodological housekeeping. The measure it formalized had already been in use since Bremer had applied it in his 1988 paper, where he had introduced the idea of examining how many additional steps were required before a branch present in the most parsimonious tree was lost in the consensus of suboptimal trees. In the years between 1988 and 1994 other workers had picked up the concept and given it various names: Faith called it simply "length difference," (Faith, 1991), Källersjö and colleagues called it "Bremer support," (Källersjö et al., 1992), Donoghue and colleagues and several *rbcL* analysts called it the "decay index" (Donoghue et al., 1992), Eernisse and Kluge (1993) called it the "support index." The 1994 paper was Bremer's consolidation of this scattered usage into a single, precisely defined measure — branch support, or b — and his extension of it in two directions that the earlier informal applications had not fully developed. What the paper clarified, above all, was the conceptual distinction between branch support and the bootstrap. The bootstrap, Felsenstein's 1985 procedure then becoming ubiquitous in phylogenetics, works by resampling characters from the original data matrix to create a new one — effectively simulating what would happen if some characters were deleted and others doubled. Branch support, by contrast, asks a different and more direct question: how strongly does the actual data, unchanged, require a given node? A bootstrap value tells you how the tree behaves under hypothetical perturbation of the evidence; branch support tells you how deep into suboptimality you must go before the evidence as it stands is no longer sufficient to sustain the node. The difference, Bremer argued, was not merely technical but epistemological.

The paper's second contribution — in some respects more original — was the introduction of the total support index (ti). Källersjö and colleagues had already defined total support as the sum of all branch support values across a tree; Bremer's addition was to observe that this sum has a natural upper bound, namely the length of the most parsimonious tree itself, since branch support for any individual branch cannot exceed its length. Dividing total support by tree length therefore yields a normalized index, the ti, that runs from zero, when the consensus of near-most-parsimonious trees is completely unresolved, to one, when there is no homoplasy and the data unambiguously support every node. What ti measures is not the fraction of characters consistent with the tree, which is what the consistency index expresses, nor the fraction retained on it, which is what the retention index expresses, but something distinct and complementary: the fraction of tree length dedicated to supported resolution, as opposed to resolution that collapses under any relaxation of

parsimony. Bremer demonstrated the index across 12 angiosperm datasets drawn from the contemporary literature and showed that ti varied widely and independently of the consistency and retention indices, confirming that it was capturing a genuine property of the data not previously quantified.

The 1980s had brought new pressures to cladistic practice. Parsimony searches grew computationally challenging as character matrices expanded, and the equally parsimonious trees they produced often yielded strict consensus trees that were poorly resolved — an unsatisfactory outcome for workers seeking to communicate clear phylogenetic conclusions. Methods for assessing nodal support emerged in part as a response, providing a way to distinguish nodes well supported by the data from those vulnerable to small perturbations of the evidence. Bremer support became one of the standard measures, alongside the bootstrap (a resampling procedure, which asks how often a node persists when the character matrix is perturbed by sampling characters with replacement; Felsenstein, 1985), the jackknife (a related method that deletes a randomly chosen subset of characters and asks the same question; Farris et al., 1996), and, with the later rise of Bayesian phylogenetics, posterior probabilities (the probability of a node given the data and an explicit model of character evolution; Rannala & Yang, 1996), now the dominant support measure in molecular work. The relative merits of these measures, and the question of when to prefer one over another, became a recurring topic in methodological discussion for the following two decades.

The appeal of Bremer support was its directness: it required no data manipulation, no resampling, no simulation, and no probability model; it simply asked how far the data had to be degraded before a conclusion dissolved. For workers applying parsimony to morphological matrices — where characters were few and resampling procedures of uncertain validity — branch support offered a way to communicate the robustness of individual nodes without the statistical apparatus that the alternatives appeared to require.

Bremer's latest research agenda – Gondwanan ancestry in angiosperms – took shape when Mats Gustafsson's and Johannes Lundberg's work on circumscribing the order Asterales revealed numerous Southern hemisphere distributions. The Gondwanan research program necessitated methods for estimating the age and distribution of ancestors represented by the nodes of phylogenies. Not satisfied with standard area-character optimization Bremer devised Ancestral Areas (AA) analysis, a simple procedure for estimating ancestral areas. Dating large phylogenies with many terminals was not always possible with existing methods and hence Bremer proposed the mean path length (MPL) method, formalized with the help of mathematician Tom Britton, and implemented in the PATHd8 program, which delivered age estimates for large trees when alternative methods were computationally impractical. Both methods were deployed together in the founding paper on East Gondwanan ancestry of the Asterales (Bremer & Gustafsson, 1997). Later Bremer replaced AA analysis with Fredrik Ronquist's dispersal-vicariance analysis (DIVA), a method of finding the most parsimonious solution to ancestral distributions considering relevant biogeographical processes, dispersal, extinction, and vicariance. Bremer adopted it — judging it epistemologically superior — for his subsequent biogeographical work on the Poales (Bremer, 2002) and broader monocot origins (Bremer & Janssen, 2006), building upon the phylogenetic dating foundations established in his earlier work (Bremer, 2000; Janssen & Bremer, 2004). A planned extension to the eudicots was cut short when Bremer's appointment to the presidency of Stockholm University in 2004 effectively ended the program. The whole effort reflected his lifelong interest in Gondwanan biogeography — an interest that traced back to his school days, when he first heard the entomologist Lars Brundin speak about Gondwanaland

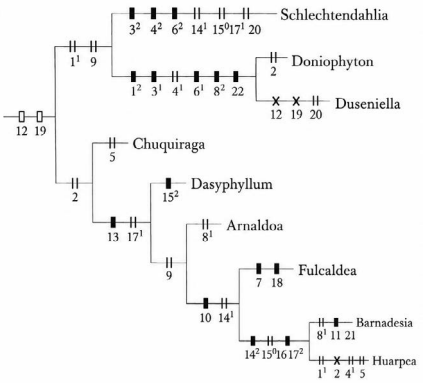
## THE COMPOSITAE

Bremer's most extensive empirical work concerns the Compositae, where he made foundational contributions to taxonomy, phylogeny, biogeography, and classification across four decades.

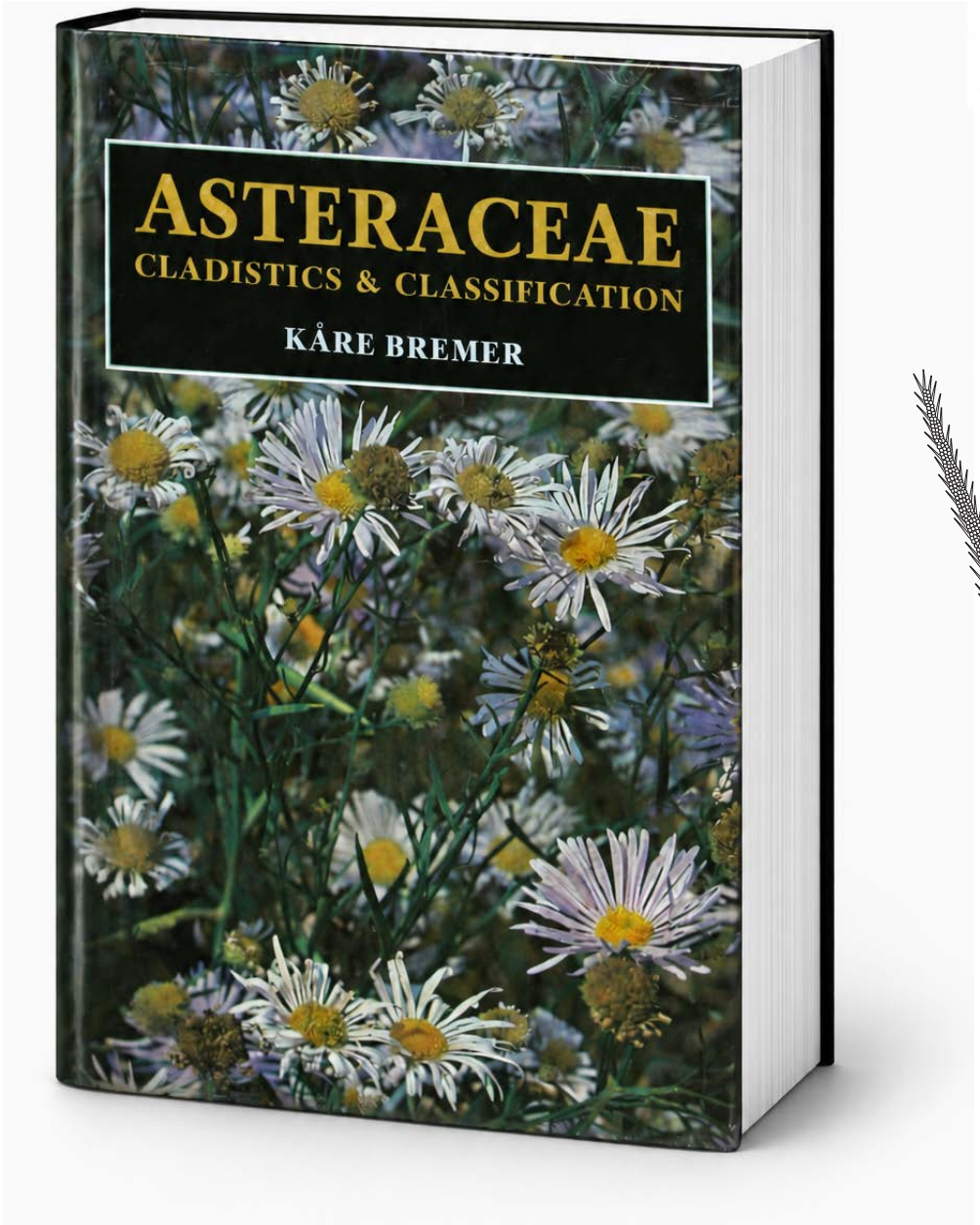
His earliest systematic research focused on South African lineages of the Gnaphalieae and Anthemideae, leading to revisions of *Osmitopsis*, *Relhania*, and *Rosenia*. His former students Arne

# An epoch making publication

Seven years in the making, with five collaborators, this 766-page monograph treats all 1,535 genera of the Compositae, across the three subfamilies and 17 tribes recognized in 1994. It was the first encyclopedic synthesis of the family in nearly a century, and the first to apply a cladistic framework throughout.




*Central to Bremer's 1994 monograph was the systematic inclusion of cladograms for each of the 17 tribes and their subgroups, with the supporting morphological characters mapped directly onto the branches, a choice that made the phylogenetic reasoning of the book explicit and reproducible at every taxonomic level, from subfamily to subtribe.*






*The book is illustrated throughout with original plates commissioned for the volume, covering everything from general morphology and diagnostic character complexes to the habit and aspect of representative genera across the 17 tribes in the family.*

Anderberg and Mari Källersjö later demonstrated that *Oedera* L. actually formed a subgroup within *Relhania* in the Gnaphalieae (Anderberg & Källersjö, 1988) prompting a revision of Bremer's original generic circumscription. The correction required renaming most of the species Bremer had treated in his doctoral thesis — an outcome he accepted with equanimity, noting that the species-level work remained sound even as the generic framework required major revision. Bremer and Anderberg made a provisional cladistic analysis of the enlarged group of genera to establish a working hypothesis before molecular data became available. In time, Joanne Bentley, a student of Nicola Bergh at Kirstenbosch, sequenced all species in the complex and established two monophyletic groups, with the larger group now renamed as *Oedera* (Bentley et al., 2017).

Participating in the 1975 Reading Symposium (Heywood et al., 1977) exposed Bremer to the full range of debate on Compositae classification. The symposium's stated premise was conservative: Bentham's tribal classification had, in the words repeatedly invoked by participants, "stood the test of time," and what was needed was only to relocate misplaced genera and establish new tribes where unavoidable — not to question the basic framework. The ancestral tribe of the family was openly debated, with Cronquist arguing forcefully for Heliantheae and Turner arguing for Mutisieae; the sister group of the family was equally contested, with most participants favouring Campanulaceae, Cronquist favouring Rubiaceae, the phytochemists under Ferdinand Bohlmann favouring Apiaceae, and Turner — alone among the major voices — arguing for Calyceraceae. On both counts, as subsequent molecular work would confirm, Turner was right. Bremer, then a doctoral student, was already skeptical of the conservative consensus but held his reservations back, sensing that the moment was not right to introduce cladistic principles to that audience.

*"I had already learned enough about cladistics to realize that Bentham's classification surely suffered from the same defects as plant classification in general."*

The symposium also marked the beginning of his long collaboration with Christopher J. Humphries (1947–2009), then a doctoral student working on *Argyranthemum* Webb under Vernon Heywood — and, like Bremer, among the systematists who came to cladistics through the daisy family. Based at the Department of Botany of the Natural History Museum in London, Humphries (Figure 7) would become one of the foremost figures in cladistic biogeography, co-authoring with Lynne Parenti Cladistic Biogeography, the field's standard textbook (Humphries & Parenti, 1986), and a central figure in the international network that carried the cladistic program from its Hennigian origins into plant systematics. Humphries had encountered cladistic thinking through Colin Patterson and others at the Natural History Museum, and when he later saw Bremer's thesis — which contained a cladogram — he recognized their common interest and initiated a correspondence that grew into a lasting collaboration and close friendship. In the spring of 1982, Humphries sat at Bremer's dining room table and compiled their first provisional cladogram of the Anthemideae on a large sheet of paper — a document Bremer kept, had framed, and eventually presented as a gift to Humphries.

Their monograph on the Anthemideae appeared in 1993 (Bremer & Humphries, 1993): a generic-level treatment of all 108 genera of the tribe. Each genus receives a diagnostic description, general distribution, taxonomic commentary, and a list of its constituent species, while cladistic analyses of generic relationships are provided for each subgroup of the tribe, with the supporting morphological characters mapped onto the branches. Humphries did not live to see the full fruits of the phylogenetic revolution he had helped initiate. Colleagues organized a symposium in London in 2008 to celebrate his contributions — at which Bremer presented the framed 1982 cladogram — but Humphries died the following year, in 2009.

Bremer's large-scale studies of Compositae tribal relationships culminated during his sabbatical (September 1985 to March 1986) at the Missouri Botanical Garden, where he held the title of B.A. Krukoff Curator of African Botany, arranged through Peter Raven, and examined extensive herbarium collections with the explicit goal of testing Cronquist's hypothesis about Heliantheae.

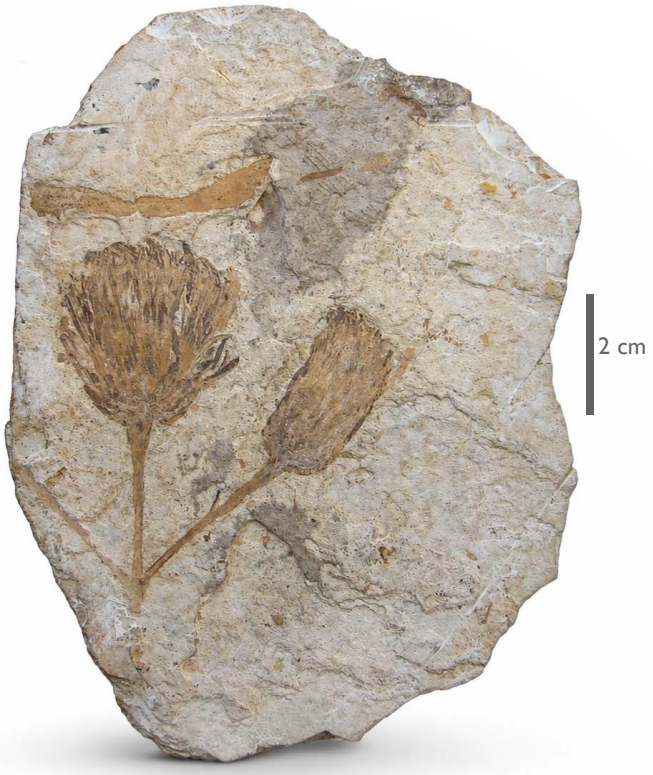
*"After grinding on with the Heliantheae for a few months I started to doubt Cronquist's hypothesis. I found nothing to indicate that the Heliantheae were the ancestral group."*

# A Patagonian witness

A cladistic prediction made entirely from living taxa, and the fossil that arrived fifteen years later to confirm it. Together they offer one of the most striking convergences between phylogenetic reasoning and the palaeontological record in flowering-plant systematics.



*Kerstin Thunberg's 1994 reconstruction in Bremer's Asteraceae: Cladistics and Classification, the predicted ancestor of the family, a woody plant with discoid capitula and a short bilobed style, derived entirely from outgroup comparison and character optimisation across living taxa.*




*Eocene capitulum fossil from Patagonia (Barreda et al. 2010, Science; 2012, Annals of Botany), the first fossil evidence of early Compositae, vindicating the cladistic prediction made fifteen years earlier.*

*Image of fossil courtesy of Asociación Paleontológica Bariloche*

He switched to examining Mutisieae and quickly concluded that it represented a collection of early branches in the family phylogeny — arriving at this conclusion independently of and simultaneously with the molecular work then being done by Robert Jansen and Jeffrey Palmer. It was Peter Raven who, at the end of 1985, told Bremer that he had heard at a recent ASPT meeting about Jansen's discovery of a chloroplast DNA inversion present in all Compositae except *Barnadesia* Mutis ex L.f. — the molecular evidence that placed the *Barnadesia* group as sister to all remaining tribes (Jansen & Palmer, 1987a, 1987b). Bremer wrote to Jansen and attached his preliminary cladogram, which had the *Barnadesia* group as one of several unresolved branches at the base of the cladogram, but not explicitly as sister group to the rest of the family. Bremer and Jansen met on one occasion and published some articles together (Bremer & Jansen, 1992; Bremer et al., 1992a, 1992b) but did not pursue any further collaboration.

Bremer completed his cladistic analysis and published it as "Tribal interrelationships of the Asteraceae" in 1987 (Bremer 1987b), presenting the results at the International Botanical Congress in Berlin the same year. The formal establishment of Barnadesioideae as a distinct subfamily, separating the basal lineage from the rest of Mutisieae, followed in 1992 (Bremer & Jansen 1992). Christopher Humphries moderated the Berlin session. At the back of the large lecture hall sat Cronquist, who after Bremer's talk, rose and delivered a public condemnation of both the results and cladistics in general. Before Bremer could respond, Humphries intervened: *"Kåre, you don't have to respond to that, it's a statement, not a question."* The moment has since been remembered as a symbolic hinge in the transition from traditional to phylogenetic systematics.

The 1987 paper (Bremer 1987b) and the 1994 book (Bremer 1994b) constitute the most sustained and consequential contribution Bremer made to Compositae science. The 1987 paper in *Cladistics* was the moment Bremer turned the methodology he had argued for in 1978 onto the family that had always been his primary subject. Where the *TAXON* paper had argued, in principle, for what cladistic reasoning could do to botanical systematics, the *Cladistics* paper showed what it actually did to the Compositae. The analysis assembled 81 characters drawn from every available source: corolla types, style morphology, stamen anatomy, pollen structure, cypsela and pappus characters, chromosomal data, chemistry, and notably the chloroplast DNA inversion that Jansen and Palmer had detected while the paper was still being prepared. That molecular character, reported in the paper as forthcoming, was central to the argument: a large inversion present in every investigated member of the Compositae except the Barnadesieae, a group of South American shrubs then placed obscurely within tribe Mutisieae. Its absence from Barnadesieae could only mean that this group had diverged before the inversion occurred and thus indicated the earliest diverging lineage of the family. The heliocentric hypothesis that had dominated Compositae systematics since Bentham — and which Cronquist had defended at Reading twelve years earlier — was structurally inverted: what had been regarded as a peripheral oddity was instead the family's deepest root.

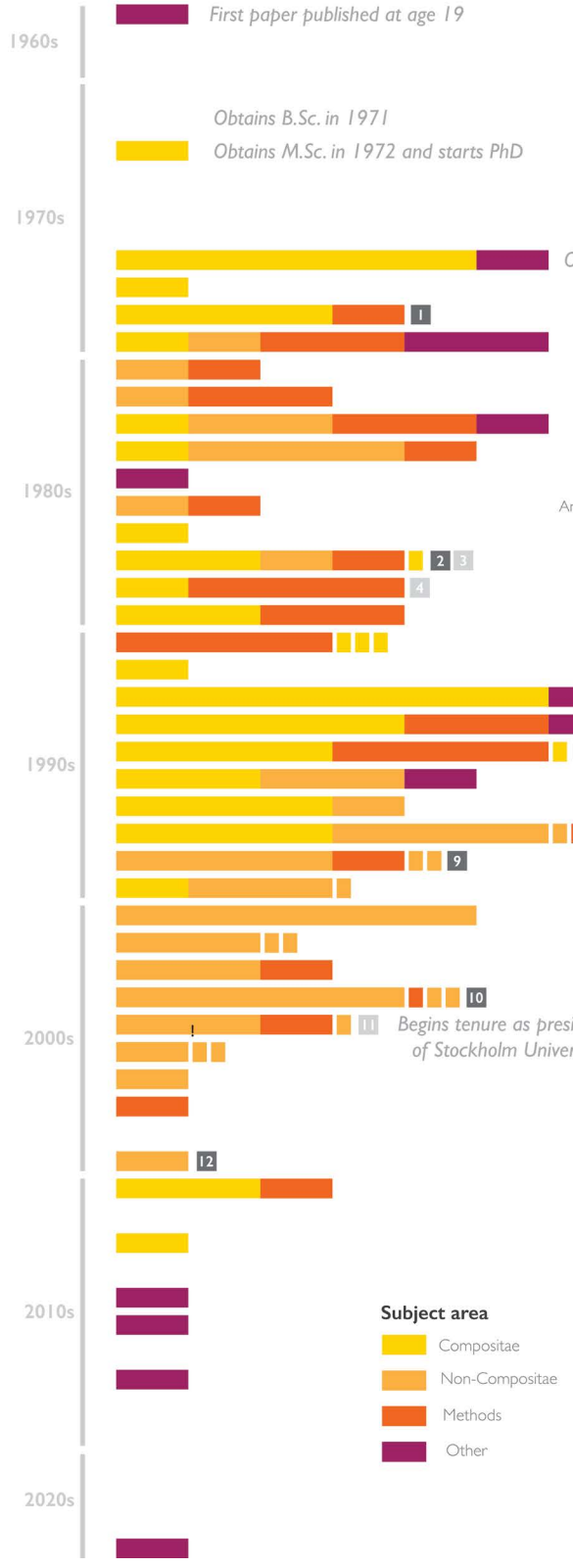
The cladogram that emerged from the analysis — a working hypothesis of tribal interrelationships based on 27 terminal taxa and run through Swofford's *PAUP* package — was the first explicit, reproducible phylogenetic reconstruction of the entire family. Its conclusions were in several respects as destabilizing as the Barnadesieae finding. The two-subfamily system — Cichorioideae and Asteroideae — which had been gaining acceptance as the natural primary division of the family was shown to be only partially right: Asteroideae was confirmed as monophyletic, supported by a coherent set of synapomorphies, but Cichorioideae was paraphyletic, a residual grade rather than a clade. The Mutisieae, long classified as a single tribe on the basis of bilabiate corollas, were shown to be a paraphyletic assemblage forming a basal grade at the stem of the family. Within Asteroideae, the analysis proposed sister-group relationships: Anthemideae with Heliantheae sensu lato, Astereae with Eupatorieae. The paper was candid about its limits: 576 equally parsimonious trees lay beneath the consensus, interrelationships among the cichorioid tribes remained largely unresolved, and Bremer stated plainly that much progress would require smaller, more clearly monophyletic terminal taxa and more precisely defined characters.

When *Asteraceae: Cladistics and Classification* appeared in 1994, it was the first book devoted

# Kåre Bremer published record

*Numbered boxes indicate key publications. Dark grey denotes works discussed in full in the text*

1 publication  1 abstract at meeting




**1**

Bremer, K. and Wanntorp, H.-E. 1978
**Phylogenetic systematics in botany.**
*TAXON 27: 317–329.*

This paper introduced cladistic principles to a botanical community long resistant to explicit phylogenetic methodology. It became a landmark paper for a generation of plant systematists.

**2**

Bremer, K. 1987
**Tribal interrelationships of the Asteraceae.**
*Cladistics 3: 210–253.*

The first comprehensive cladistic analysis of the entire Compositae family, establishing tribal relationships through rigorous parsimony analysis. It laid the groundwork for the global monograph that followed seven years later.

**3**

Bremer, K. 1987
**Melastomataceae.**
*In Dassanayake and Fosberg (eds.), Flora of Ceylon 6: 157–240.*

This family treatment for the Flora of Ceylon represented a deliberate broadening of Bremer's systematic experience beyond Compositae, demonstrating his command of an entirely different plant group. It remains the authoritative treatment of the family for the region.

**4**

Bremer, K. 1988
**The limits of amino acid sequence data in angiosperm phylogenetic reconstruction.**
*Evolution 42: 795–803.*

An early and prescient critical assessment of the potential and limitations of molecular data in phylogenetic analysis, published at a moment when such data were just beginning to transform systematics. It showed Bremer's methodological rigour extended well beyond morphological approaches.

**5**

Bremer, K. & Humphries, C. J. 1993
**Generic monograph of the Asteraceae-Anthemideae.**
*Bull. Brit. Mus. (Nat. Hist.), Bot 23: 73–179.*

Co-authored with Christopher Humphries, this monograph provided a comprehensive cladistic revision of one of the largest and most complex tribes of Compositae. It stands as one of the most thorough tribal treatments in the family's literature.

**6**

Bremer, K. (ed.) 1994
**Asteraceae: Cladistics and Classification.**
*Timber Press, Portland, Oregon. 752 pp.*

The first encyclopedic global treatment of the Compositae in nearly a century, covering all tribes and genera through a cladistic framework.

**7**

Bremer, K. 1994
**Branch support and tree stability.**
*Cladistics 10: 295–304.*

This paper formally introduced the measure of clade robustness that James S. Farris would name Bremer support.

**8**

Bremer, K. & Gustafsson, M. H. G. 1997
**East Gondwana ancestry of the sunflower alliance of families.**
*Proc. Natl. Acad. Sci. U.S.A. 94: 9188–9190.*

This paper established the deep biogeographic origins of the Asterales alliance of families.

**9 10 12**

Angiosperm Phylogeny Group, 1998, 2003, 2009
**APG I, APG II & APG III**
*Ann. Missouri Bot. Gard. 85: 531–553*
*Bot. J. Linn. Soc. 141: 399–436.*
*Bot. J. Linn. Soc. 161: 105–121.*

These three successive publications, produced by the Angiosperm Phylogeny Group where Bremer was one of the coordinators, established the consensual phylogenetic classification of all flowering plant families and orders setting a worldwide standard.

**11**

Bremer, K., Friis, E. M. & Bremer, B. 2004
**Molecular phylogenetic dating of asterid flowering plants shows Early Cretaceous diversification.**
*Syst. Biol. 53: 496–505.*

This paper used molecular clock methods to date the diversification of asterid flowering plants to the Early Cretaceous. It anchored the APG classification in deep evolutionary time.

entirely to the Compositae to apply a fully cladistic framework to the entire family. Bremer decided to write it the moment he finished the 1987 paper and the result, produced with five collaborators and seven years of sustained collective effort, is a 766-page monograph covering 1,535 genera arranged in three subfamilies and seventeen tribes. The book opens with three introductory chapters that establish the foundations for everything that follows. and a critical evaluation of which characters are reliable at the suprageneric level, which are convergent or homoplastic, and which require cautious coding.

The body of the book is the tribal treatment, where each of the seventeen tribes receives a chapter structured on the same principles: a morphological characterization of the tribe, a discussion of its history and the problems of its classification, a data matrix coding morphological characters across representative genera, a cladistic analysis, and a rigorous evaluation of which groups within the tribe are monophyletic, which are paraphyletic, and — with equal candour — which cannot yet be resolved at all. The cladograms cover every significant taxonomic level from subfamily to subtribe, and at the level of individual genera, all 1,535 genera of the family receive a standardized treatment: author citation and date, habit and foliage, capitulum type and arrangement, floret morphology, anther and style characters, cypsela and pappus, distribution, and approximate species count. The cumulative effect of reading through these chapters is to encounter a family from a new perspective with classification issues from paraphyletic groups pointed out as problems to be solved. And scattered through the tribal cladograms is the continuous evidence for the important findings of 1987 — Cichorioideae as a grade, Mutisieae as a paraphyletic stem, Asteroideae as a well-supported clade —demonstrated at a resolution that the 1987 paper could only anticipate.

The book's synthesis arrives in Chapter 4 on evolution, where the accumulated evidence of the tribal cladograms is brought to bear on the deepest questions about the family. The sister group of the Compositae is resolved in favour of Calyceraceae, on the strength of shared embryological features and a pump-mechanism of secondary pollen presentation. The geographic origin of the family is traced through an ancestral areas analysis to South America, with Brazil south of the Amazon and the Andes as the most probable core of origin. And the ancestral morphology of the family is reconstructed as a woody plant with alternate entire leaves, solitary or laxly cymose discoid capitula, calcarate and caudate anthers, and a short bilobed glabrous style: the precise opposite of what Cronquist had argued, and a hypothesis rendered visual in a drawing by Kerstin Thunberg, a woody bush with thistle-like capitula, looking nothing like a sunflower or anything extant.

For the student opening the book for the first time, the effect is striking. Every one of the 1,535 genera receives the same standardized treatment and the consistency with which the information is laid out makes the entire family, for perhaps the first time in its bibliography, fully and immediately comparable across tribes and subtribes. Three decades on, that same combination of conciseness and comprehensiveness keeps the volume on the working desks of both beginning and advanced synantherologists: a reference few in the family can do without.

Several years after concluding his major Compositae research, Bremer received an email from Jorge Crisci in La Plata, Argentina,reporting a fossil Compositae capitulum discovered by local paleontologists in southern South America. The fossil bore a striking resemblance to Thunberg's drawing (Bremer, 1994b) of the primordial composite — an unexpected confirmation of a hypothesis built entirely from living taxa and their relatives. After substantial contributions to the manuscript, Bremer joined the author team. The resulting article, published in Science (Barreda et al. 2010) with a more detailed account in Annals of Botany (Barreda et al. 2012), provided the first fossil evidence for early Compositae evolution and offered in Bremer's own words *"a fitting coda to forty years of work on the family."*

*"While working on the fossil paper I visited Jorge Crisci and his colleagues in La Plata where I had a great time and I am grateful to him, Liliana Katinas, Viviana Barreda and the other co-authors for a very suitable ending of my four decades of research efforts in the Compositae."*

## ANGIOSPERM PHYLOGENY AND THE APG SYSTEM

By the early 1990s, large *rbcL* datasets (particularly those assembled by Mark W. Chase) were revealing deep patterns in flowering plant phylogeny.

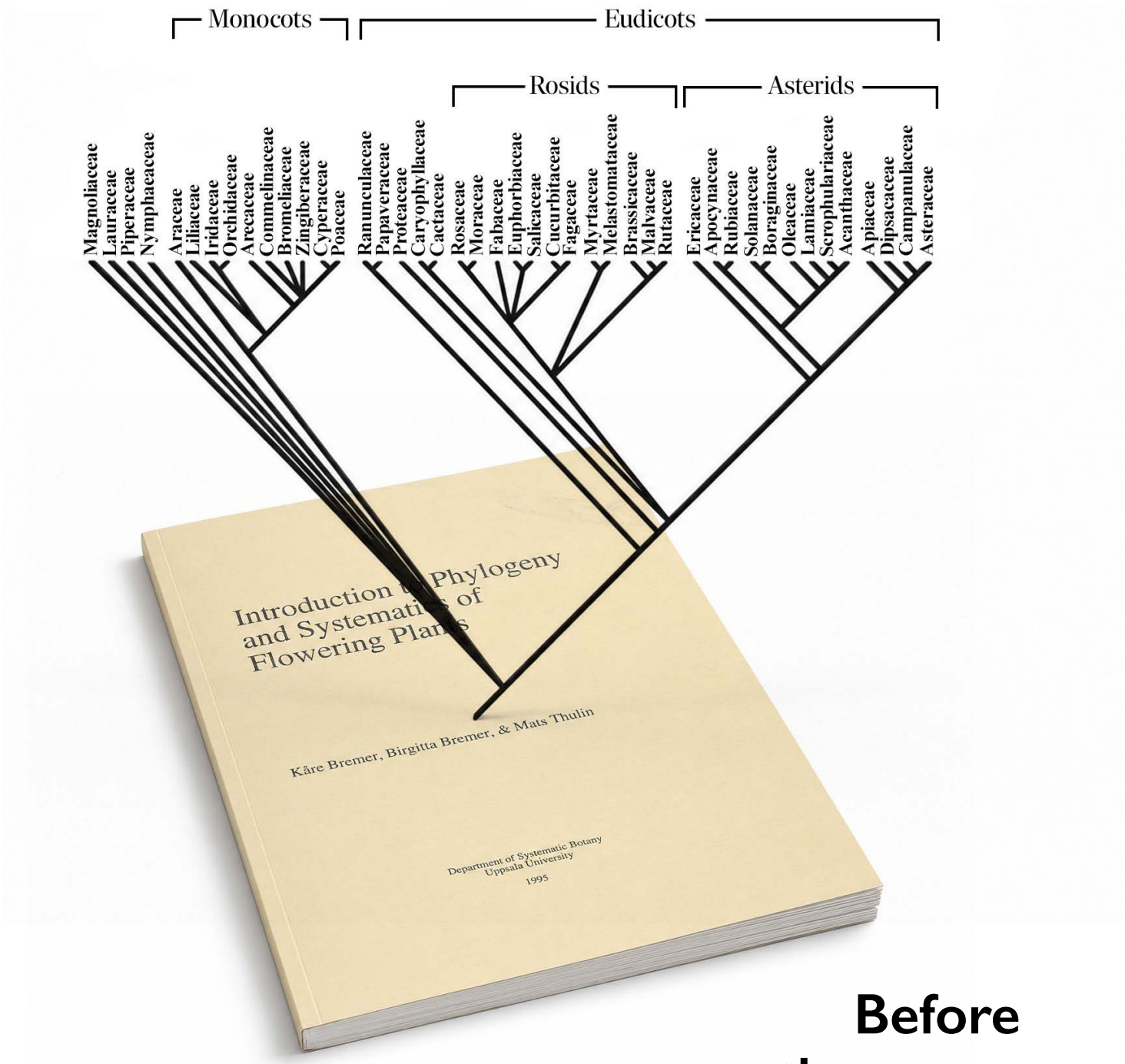
Bremer was present at Chase's influential presentation at the 1993 International Botanical Congress in Yokohama, where Chase displayed a compound tree assembled from sequences contributed by multiple laboratories — a status report rather than a finished phylogeny, but the first large-scale molecular view of the angiosperms to be shown publicly, and one that already refuted many of the groupings of Cronquist and Takhtajan. The same body of work appeared in print that year as Chase et al. (1993) with forty-two authors representing the laboratories whose sequences had been pooled into the analysis.

In the years following Yokohama, the rapidly improving *rbcL* phylogeny made the older morphology-based classifications increasingly difficult to teach, and provisional reclassifications began to appear at several institutions. In Uppsala, Bremer, Birgitta Bremer, and their colleague Mats Thulin produced an annually updated compendium that arranged the families of flowering plants into putatively monophyletic orders compatible with the emerging consensus. Mark Chase, who visited Uppsala on several occasions during this period proposed that the active workers in angiosperm phylogeny should produce a single jointly authored classification. The group was to be known as the Angiosperm Phylogeny Group (APG), and by deliberate decision no individual or subgroup would be identified as its leader: the classification, and any future publications, would be the work of APG as a collective.

The 1998 paper published in the Annals of the Missouri Botanical Garden under the authorship of APG was, in its form as much as its content, a document unlike anything that had appeared before in botanical systematics. Its authorship was itself a statement: not a single taxonomist's name but a collective — twenty-nine contributors listed alphabetically, coordinated by Bremer, Mark Chase, and Peter Stevens — assembled from institutions across North America, Europe, and beyond. Within this collective, Chase tracked the increasingly detailed overall phylogeny as molecular sequences accumulated; Stevens, drawing on an encyclopedic knowledge of obscure angiosperms, handled the placement of groups not yet represented in molecular datasets and the treatment of families left *incertae sedis*; and Bremer prepared the successive drafts and coordinated the voluminous e-mail exchanges through which the group's positions converged. The three were nonetheless careful to insist that they were compilers rather than constructors of a community consensus, built from the convergence of multiple independent molecular datasets and submitted to the discipline as a shared reference tool. What APG produced was 462 families organized into 40 putatively monophyletic orders, supported at most nodes by jackknife values from analyses of hundreds to thousands of sequences.

The APG I (1998) classification introduced a set of informal higher-level groupings — monocots, eudicots, core eudicots, commelinoids, rosids, asterids, and their subdivisions into eurosids I and II and euasterids I and II — that were deliberately left unranked. Within the asterids, the order Asterales — encompassing the Compositae, their sister group, the small South American Calyceraceae, and several families of East Gondwanan ancestry such as Goodeniaceae, Stylidiaceae, Argophyllaceae, Alseuosmiaceae, Phellinaceae, Carpodetaceae and Pentaphragmataceae — had been circumscribed by Bremer's doctoral students Mats Gustafsson and Johannes Lundberg, with an East Gondwanan ancestry established through Bremer's collaboration with Gustafsson (Gustafsson & Bremer 1995; Bremer & Gustafsson 1997); it was one example of the kind of family- and order-level work that fed into the larger collective project. The systematic use of informal names for major clades, while reserving Linnaean ranks for orders and families, marked a clear break from the conventions of comprehensive angiosperm classifications such as Cronquist's or Takhtajan's, and it reflected a deeper shift in how systematists were being asked to think about classification — as a tool for communicating evolutionary relationships rather than as an independent hierarchy with its own logic. The paper was explicit about its incompleteness: families of uncertain position were listed separately at the end, and the authors explicitly anticipated that additional orders would have to be recognized as unplaced families found their positions.

Bremer continued among the coordinators through APG II (2003) and APG III (2009), a stewardship




# Before there was an APG

A course compendium for PhD students at Uppsala University, first printed in 1995 by Kåre Bremer, Birgitta Bremer, and Mats Thulin, presented the new angiosperm phylogeny three years before APG I appeared. Six editions followed between 1995 and 2000, each an unformatted text of 70–80 A4 pages closing with relevant publications, a classification overview, and the overall phylogeny conceived from the cited publications. It was this work that Mark Chase encountered during his visits to Uppsala, prompting the international collaboration that culminated in the landmark 1998 publication.

# Rektor

Kåre Bremer as President (Rektor) of Stockholm University, 2004–2013. During his nine-year tenure he led the implementation of the Bologna reform of undergraduate education, oversaw the absorption of Stockholm's teacher-education college into the University in 2008, and served under eight ministers of education across the Swedish political spectrum. Two subtle details in the portrait register the scientific life that ran beneath the administrative one: the *Gerbera* L. on the table is an unmistakable allusion to his work on Compositae, while a cladogram, almost hidden within the wooden frame in the upper left corner, bears quiet witness to the methods he developed, and to his lifelong advocacy for cladistics as the foundation of systematic biology.

*Portrait of Kåre Bremer. Oil on canvas by Olle Hamngren, 2012, Stockholm University.*

spanning more than a decade. By the time APG IV (2016) appeared he and Birgitta had retired and were no longer involved, but each successive instalment refined and extended the 1998 framework with successively fewer changes. An APG V (2026) is now published, and like its predecessors it still closely resembles the 1998 original. The APG system received global attention — news of its publication appeared on *CNN* and on the front page of the *New York Times* — and shifted the botanical world from morphology-based classifications to a fully phylogenetic framework, now the global standard.

## LEGACY

Kåre Bremer's scientific legacy is both broad and deep, tracing a remarkable arc, from learning Swedish wildflowers in the Stockholm archipelago, to exploring the mountains and semi-deserts of southern Africa, to reshaping global plant systematics and leading one of Scandinavia's premier universities. The 1978 paper with Wanntorp helped introduce phylogenetic reasoning into botany; Bremer support became a new standard for evaluating clade robustness; and his role as one of the coordinators of the APG helped create the classification framework that now defines global plant systematics. Through revisions, tribal analyses, and a global monograph, he shaped modern understanding of the Compositae, the family that first seized his attention through Norlindh's unexpected suggestion and gave him the material for his most consequential phylogenetic analyses. Fifteen doctoral students carry forward his intellectual lineage, constituting what he himself describes as five generations of Swedish synantherologists. His influence endures through his students, his methods, his publications, and the scientific frameworks he helped build.

## ACKNOWLEDGMENTS

I am deeply grateful to Kåre Bremer himself, who generously provided biographical materials, anecdotes, and personal recollections that form the backbone of this article; as a student of the Compositae, this has been a particularly rewarding article to write. Our email exchanges proved a remarkably efficient and enjoyable means of collaboration. I also thank Mark Chase for sharing his recollections on the origins of the Angiosperm Phylogeny Group, Nicola Bergh for supplying photographs of *Oedera nordenstamii* (K.Bremer) Anderb. & K.Bremer, and the Asociación Paleontológica Bariloche for providing a photograph of the Patagonian fossil. Jorge Crisci and Ken Wurdack are thanked for their comments on early versions of the manuscript, and Linda Watson and Bruce Baldwin for their thorough and constructive reviews.

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# Perityleae B.G.Baldwin (Asteroideae):
## A catalogue of natural history, taxonomy, and morphology of the rock daisy tribe

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## ABSTRACT

Tribe Perityleae includes eight genera and 90 taxa of rock daisies distributed in arid to semi-arid environments in North and South America, many of which grow on steep, vertical cliffs and bare, rocky outcrops in canyons and sky islands. Due in part to their diversity, morphological complexity, and growth in difficult-to-access terrain, rock daisy taxonomy has been in flux for over a century. Recent molecular studies and extensive fieldwork have helped to resolve much uncertainty in this group, but the process of formalizing new insights into codified nomenclatural changes has only begun. As a first step towards an updated monograph of the rock daisies, we present a comprehensive account of all validly published taxonomic names applied to tribe Perityleae in the form of a nomenclator and annotated checklist, and for each taxon we summarize recent discoveries from the field. In total, 273 names are accounted for here, including 81 accepted species, 10 varieties, 125 homotypic synonyms, 53 heterotypic synonyms, and 5 names that apply to taxa in other tribes of Compositae. We also elevate two infraspecific taxa to species level (*Perityle cuneata* and *Perityle marginata*), place five names in synonymy (*Galinsogeopsis stevensii* [a synonym of *G. canescens*], *G. pennellii* [a synonym of *G. hofmeisteria*], *G. scopulorum* and *G. pseudociliata* [both synonyms of *G. coronopifolia*], and *Perityle trichodonta* [a synonym of *P. rosei*], and we reinstate basionyms with nomenclatural priority in four cases (*Galinsogeopsis microglossa*, *G. microglossa* var. *saxosa*, *Laphamia toumeyi*, and *Villanova anemonifolia*). Our review of recent discoveries from the field uncovers ten cases where rock daisies were recently rediscovered by field botanists following many decades of being "lost" and 16 cases where taxa have recently been photographed for the first time. Despite abundant efforts on the part of field biologists to relocate populations of rock daisies, there are still at least ten "lost" rock daisy taxa for which knowledge of current population persistence in the wild is unconfirmed.

**Keywords:** cliff plants; collaborative monography; Compositae; field work; Heliantheae alliance; nomenclator; taxonomy.

## INTRODUCTION

Rock daisies (Perityleae) are an enigmatic tribe of Compositae comprising 81 currently recognized species and ten varieties in eight genera distributed in mostly arid, rocky environments from western North America south to the Atacama Desert in Peru and Chile (Lichter-Marck & Baldwin, 2022; see map on page 33). Most species of rock daisies are extreme habitat specialists that grow on bare, rocky outcrops and cliffs in mountains and canyons; however, this group also includes seasonally-abundant herbaceous

annuals, shrubs, and rhizomatous perennials (Lichter-Marck & Baldwin, 2023). Botanical collections from steep, rough terrain in recent decades have led to new insights into rock daisy diversity, including new species, new collections, and the first photographs of many rock daisies previously known only from type specimens. Recent molecular phylogenetic studies have also illuminated the evolutionary history of rock daisies and resolved long-standing uncertainty in their classification (Lichter-Marck et al., 2020; see page 36). Here, we synthesize the latest knowledge about rock daisy natural history and taxonomy to provide a panorama of this fascinating group of composites and a taxonomic framework for upcoming new species descriptions and detailed monographic studies.

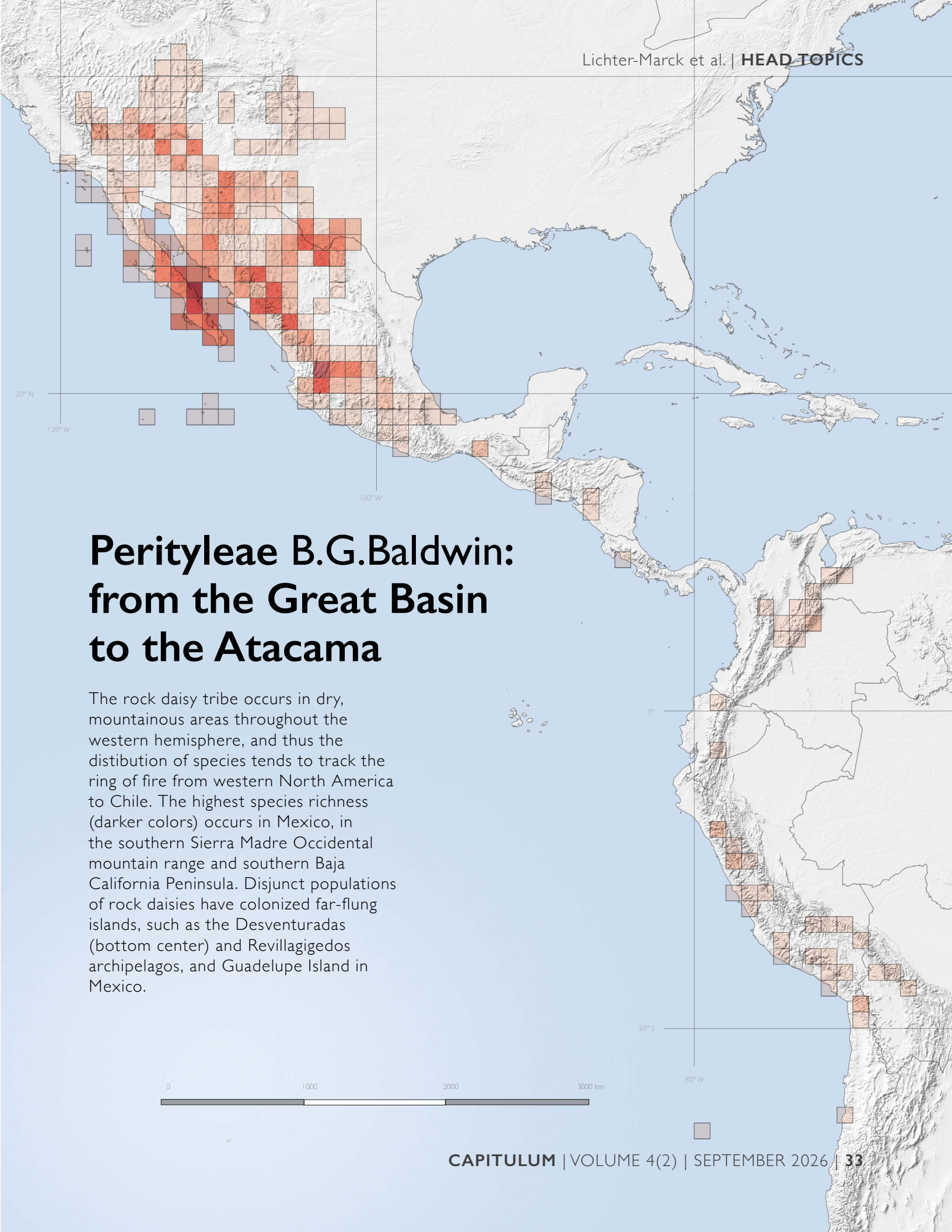
As currently recognized, tribe Perityleae mostly conforms to subtribe Peritylinae (sensu Robinson (1981), ca. 77 species), a group which had long been acknowledged based on distinctive morphological traits (Figure 1 & Figure 2; see also page 37-43), including epaleate heads, four-lobed disc corollas, and one or two series of subequal, naviculate (boat-shaped) phyllaries (Baldwin, 2009). Early molecular studies (Baldwin et al., 2002; Panero and Funk, 2008; Schilling et al., 2013, 2015) supported the monophyly of Peritylinae with the minor expansion of tribe Perityleae to encompass two additional subtribes, Lycapsinae H.Robinson, with only 1 species, *Perityle tenuifolius* (Phil.) Lichter-Marck, endemic to the desolate Desventuradas Archipelago in Chile, and Galeaninae Panero & B.G.Baldwin, which includes two genera, *Galeana* La Llave and *Villanova* Lag., with ca. four species (Panero, 2007). Perityleae occupy a prominent phylogenetic position among the epaleate tribes of the Heliantheae alliance (Helenieae sensu Bentham), because it is the sister lineage to the hyper-diverse, mostly tropical boneset tribe Eupatorieae (~2,500 spp.) (Baldwin, 2008). Perityleae and Eupatorieae in turn belong to a clade of mostly temperate epaleate tribes within the Heliantheae alliance that includes Madieae, Bahieae, and Chaenactideae (Baldwin et al., 2002, Mandel et al. 2019, Zhang et al. 2024).

Uncertainty surrounding the delimitation of genera within subtribe Peritylinae has been a perennial theme of rock daisy classification over the past 150 years (Shinners, 1959; Niles, 1970; Powell, 1968, 1973b, 1973c; Powell & Turner, 1974; Lichter-Marck & Baldwin, 2022; see page 34). First, as western botanists explored the vast roadless terrain of western North America that rock daisies call home, new species were described in the taxonomic literature, and successive taxonomists proposed new genera to accommodate their growing diversity (Niles, 1968). Then, Shinners (1959) boldly lumped most rock daisies into the single, drastically expanded, heterogeneous genus *Perityle* Benth. Niles (1970) did not initially adopt this radically expanded concept of *Perityle* when a few years later, he monographed cliff-endemic rock daisies in genus *Laphamia* A.Gray sensu Rydberg. However, A. Michael Powell did adopt Shinners' broader circumscription of *Perityle* when he monographed the rock daisies in the early 1970s (Powell, 1969, 1973a, 1974). To account for the clear polyphyletic nature of *Perityle* sensu Shinners, Powell proposed three subgeneric sections, *Perityle* sect. *Perityle*, *Perityle* sect. *Laphamia* (A.Gray) A.M.Powell, and *Perityle* sect. *Pappothrix* (A.Gray) A.M.Powell, and created informal groupings of related species (Powell, 1974). Powell's insightful phylogenetic inferences were based on artificial hybridizations, chemotaxonomy, cytology, morphology, and ecological observations made during his exhaustive field work. In recent years, whole-genome scale DNA sequence data has been used to test, and in most cases substantiate Powell's hypotheses, including the polyphyly of *Perityle* sensu Shinners (Lichter-Marck et al., 2020; Lichter-Marck & Baldwin, 2023). With phylogenomic-scale data in hand, a stable generic taxonomy based on natural groups for Perityleae has finally been proposed (Lichter-Marck & Baldwin, 2022; see page 36). This classification of rock daisies recognizes a much narrower circumscription of *Perityle* (~12 taxa) incorporating the three taxa of the Baja California-endemic genus *Amauria* Benth. and the single species of the Desventuradas Islands-endemic genus *Lycapsus* Phil. The recent classification also reinstates the monotypic Guadalupe Island-endemic genus *Nesothamnus* (A.Gray) Rydb. and restores the genera *Galinsogeopsis* Sch.Bip. and *Laphamia* to accommodate two independent radiations of sky island rock daisies found in the Sierra Madre Occidental of Mexico and the Basin and Range province of western North America, respectively (Lichter-Marck & Baldwin, 2022).

Most species of rock daisies are extreme ecological specialists that grow exclusively on vertical, bare rocky cliffs in arid environments (see page 43). As in many other diverse groups of plants where

*Continues in page 44*

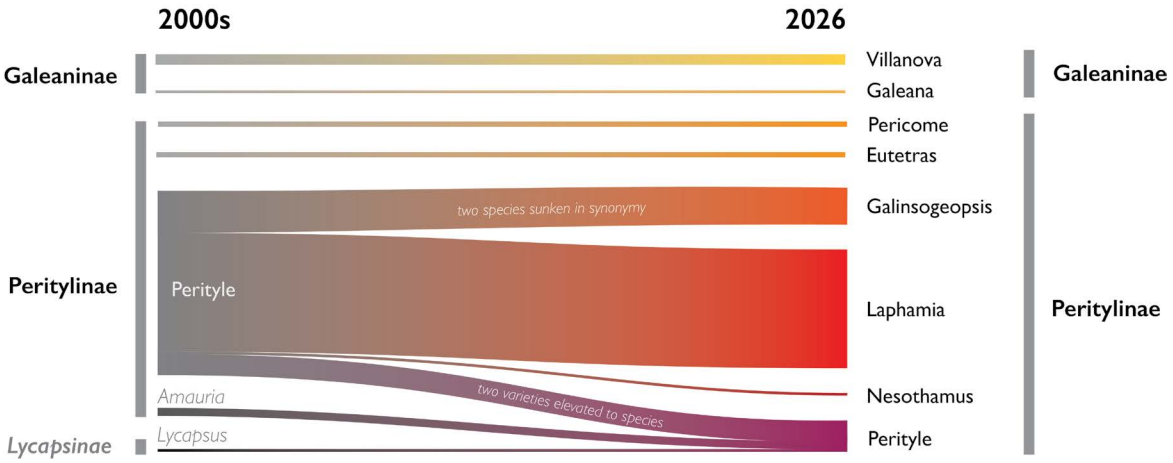
# Perityleae B.G.Baldwin: from the Great Basin to the Atacama




The rock daisy tribe occurs in dry, mountainous areas throughout the western hemisphere, and thus the distibution of species tends to track the ring of fire from western North America to Chile. The highest species richness (darker colors) occurs in Mexico, in the southern Sierra Madre Occidental mountain range and southern Baja California Peninsula. Disjunct populations of rock daisies have colonized far-flung islands, such as the Desventuradas (bottom center) and Revillagigedos archipelagos, and Guadelupe Island in Mexico.

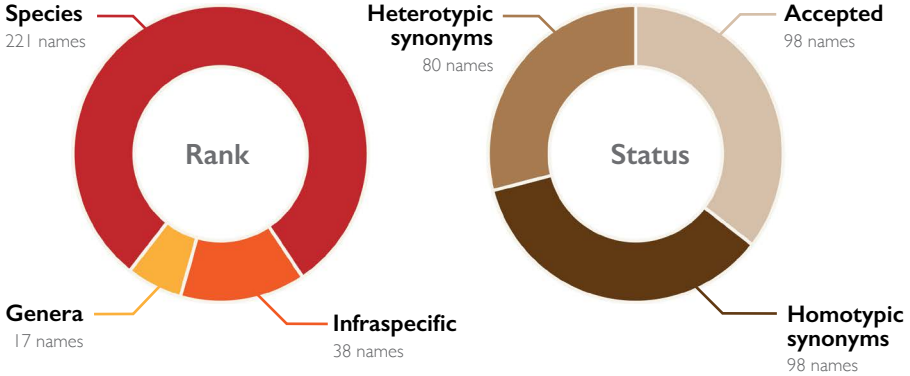
# Recent changes in the classification of Perityleae

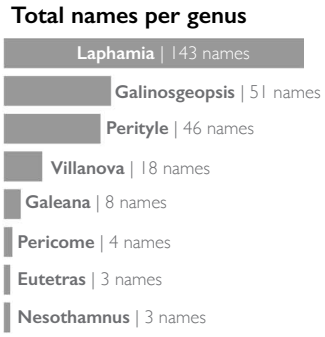
Prior to 2022, the vast majority (72) of rock daisy species were classified within heterogeneous *Perityle*, with the remaining species split among a constellation of distinctive smaller rock daisy genera. Molecular phylogenetic analyses revealed *Perityle* to be non-monophyletic with respect to *Amauria*, *Eutetras*, *Lycapsus* and *Pericome*, prompting a reclassification of tribe Perityleae at the generic level.




## Nomenclator of Perityleae

**276** total names treated (see page 109-107)



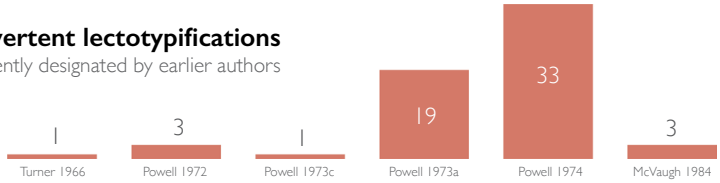




## Lectotypifications

**20 lectotypes** designated here for the first time; this includes 3 second step lectotypifications.

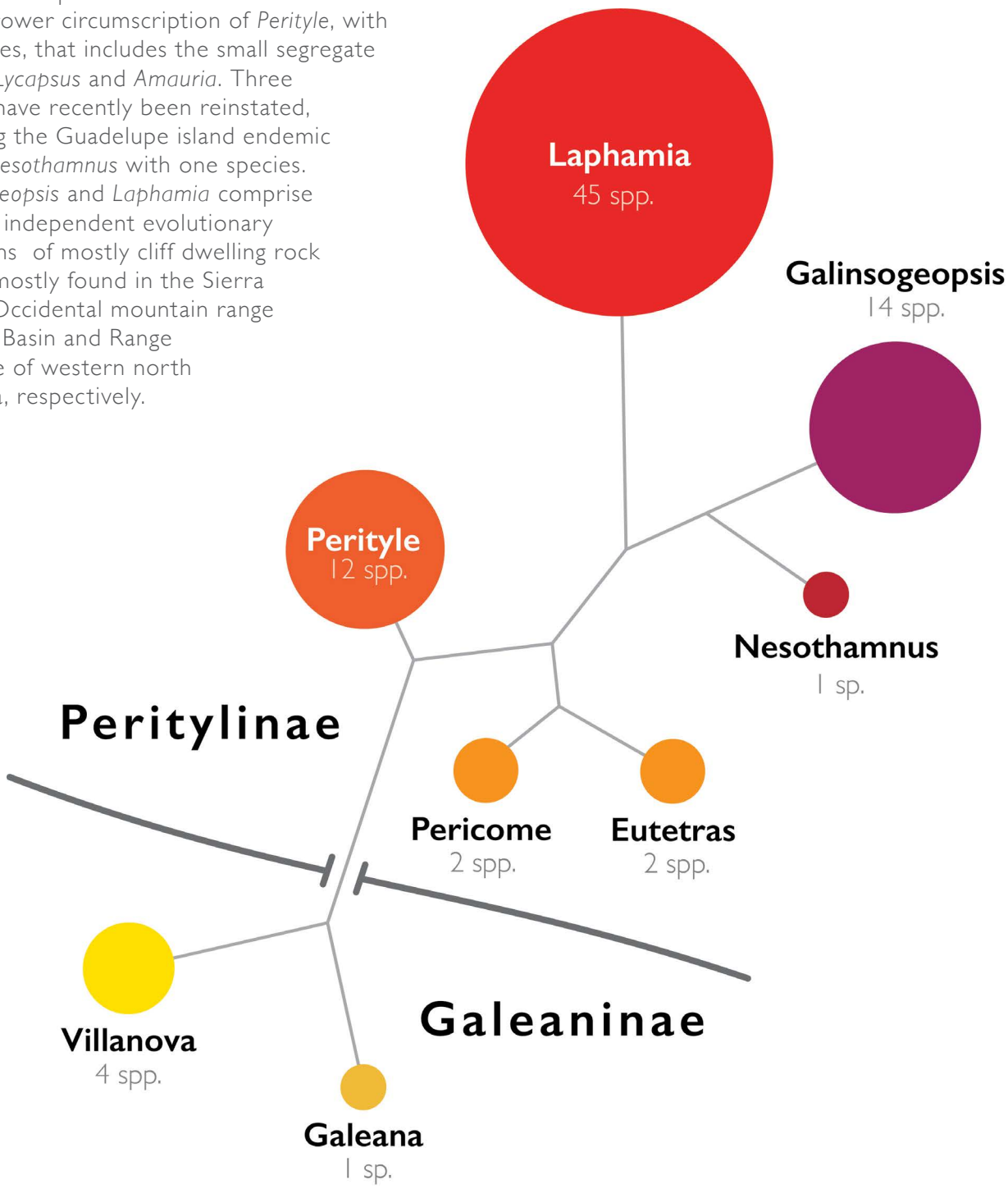
### Inadvertent lectotypifications

**62 lectotypes** inadvertently designated by earlier authors



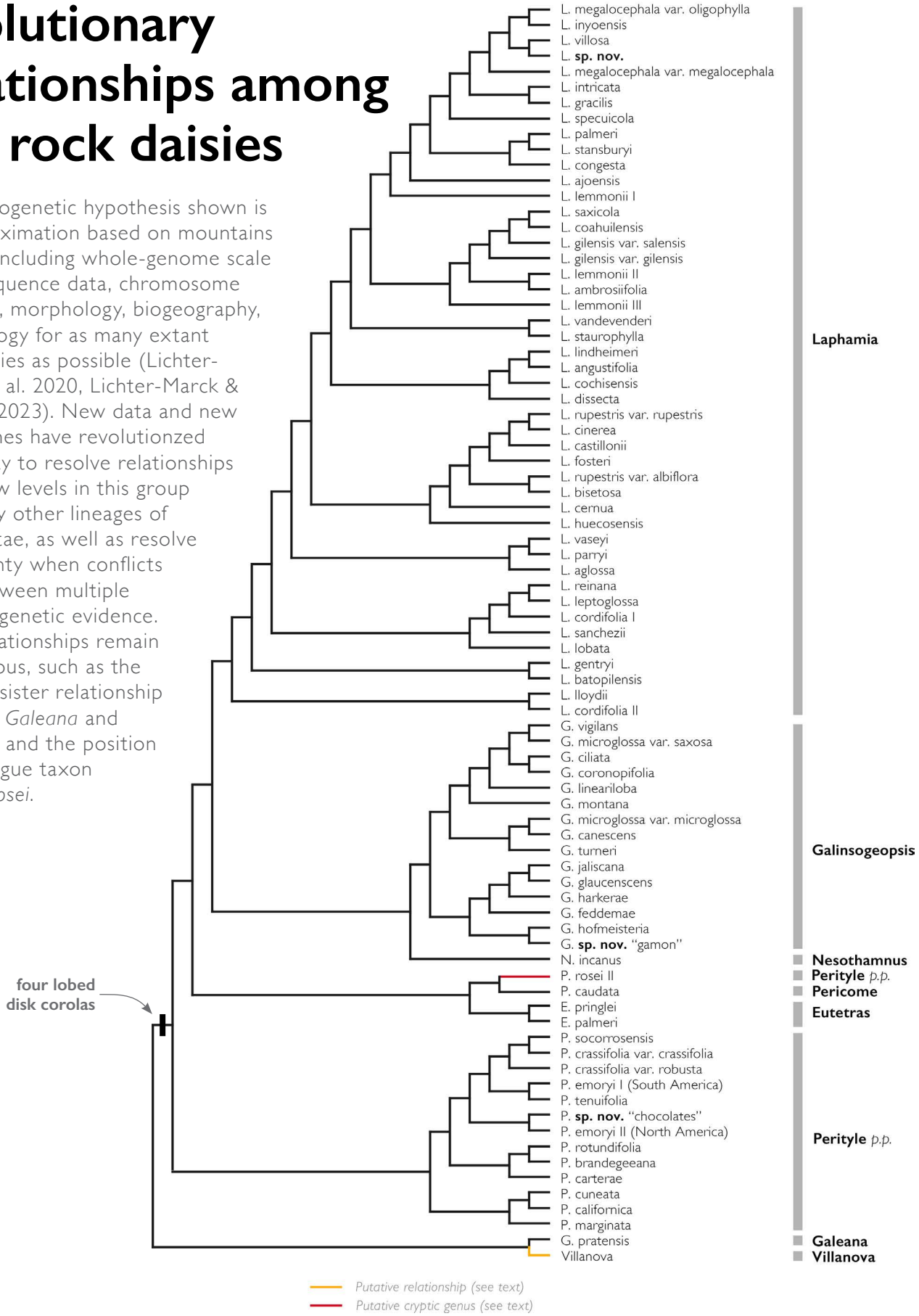
# Classification of Perityleae

The updated classification of the rock daisies recognizes six genera within the heterogeneous and diverse subtribe Peritylinae. A key change compared to previous classification schemes is a narrower circumscription of *Perityle*, with 12 species, that includes the small segregate genera *Lycapsus* and *Amauria*. Three genera have recently been reinstated, including the Guadelupe island endemic genus *Nesothamnus* with one species. *Galinsogeopsis* and *Laphamia* comprise diverse, independent evolutionary radiations of mostly cliff dwelling rock daisies mostly found in the Sierra Madre Occidental mountain range and the Basin and Range province of western north America, respectively.



# Evolutionary relationships among the rock daisies

The phylogenetic hypothesis shown is an approximation based on mountains of data, including whole-genome scale DNA sequence data, chromosome numbers, morphology, biogeography, and ecology for as many extant rock daisies as possible (Lichter-Marck et al. 2020, Lichter-Marck & Baldwin 2023). New data and new approaches have revolutionized our ability to resolve relationships at shallow levels in this group and many other lineages of compositae, as well as resolve uncertainty when conflicts arise between multiple types of genetic evidence. Many relationships remain contentious, such as the putative sister relationship between *Galeana* and *Villanova*, and the position of the rogue taxon *Perityle rosei*.



## Morphology of Perityleae

# Fruit and Pappus

### Pappus scales

Hyaline scales vary in number and when present, form a crown at the fruit apex

### Pappus awns

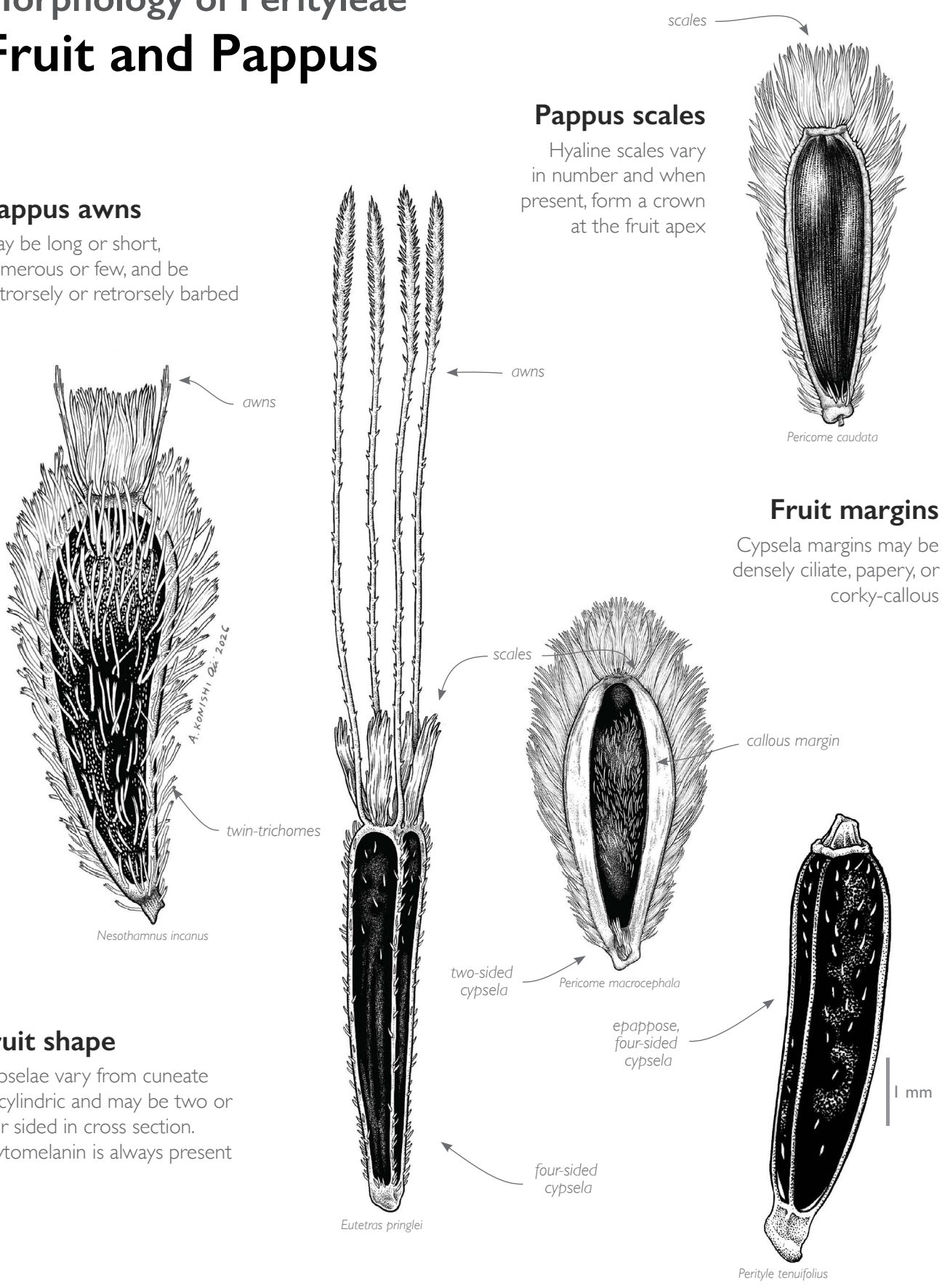
May be long or short, numerous or few, and be antrorsely or retrorsely barbed

### Fruit margins

Cypsela margins may be densely ciliate, papery, or corky-callous

### Fruit shape

Cypselae vary from cuneate to cylindric and may be two or four sided in cross section. Phytomelanin is always present



## Morphology of Perityleae

# Habit and capitulescences

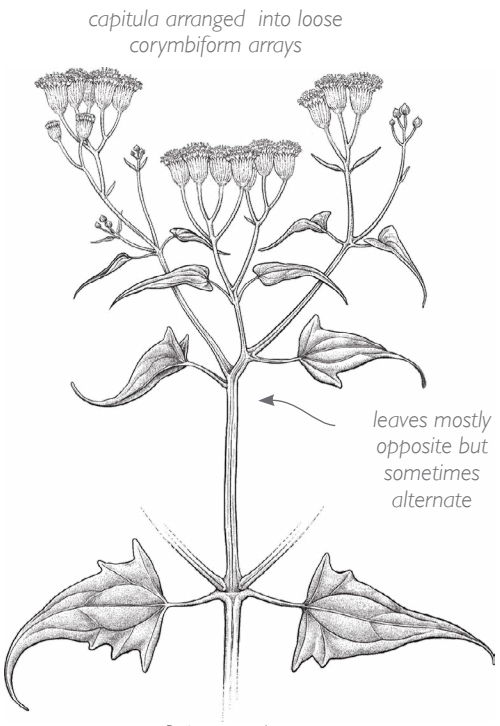
### Habit

Rock daisies can be woody shrubs, suffrutices, perennial or annual herbs with slender herbaceous stems

### Capitula

Capitula are often borne solitary but may be arranged into loose or dense corymbiform capitulescences





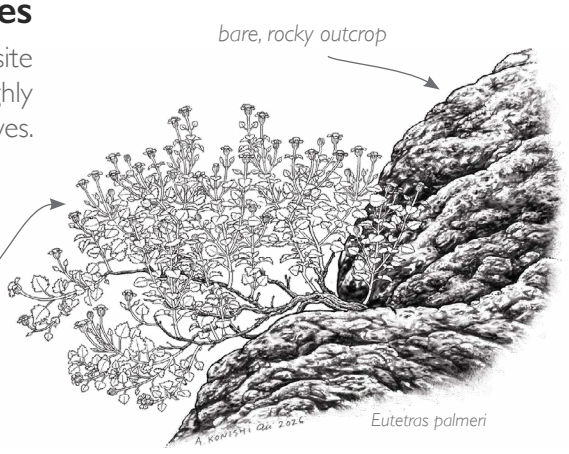


### Cliff dwellers

The vast majority of rock daisies occur as extreme ecological specialists on vertical cliffs of consolidated bedrock

### Leaves

Most rock daisies have opposite or sub-opposite entire or highly dissected leaves.




### Wood

A gnarled woody caudex occurs in many species, acting both as a grappling hook for cliffy rock faces and as a site to form adventitious shoots after the long desert dry season.



## Morphology of Perityleae

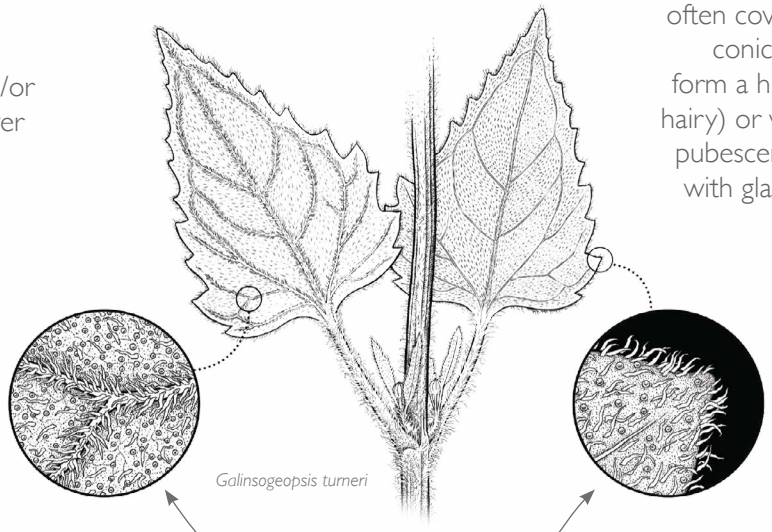
# Indument

### Trichomes

An abundance of glandular and/or non-glandular trichomes are ever present in Perityleae on leaves, stems, florets, and fruits

### Simple conical trichomes

Leaves and stems are often covered with simple conical trichomes that form a hirtellous (coarse-hairy) or villous (long-soft) pubescence, interspersed with glandular trichomes

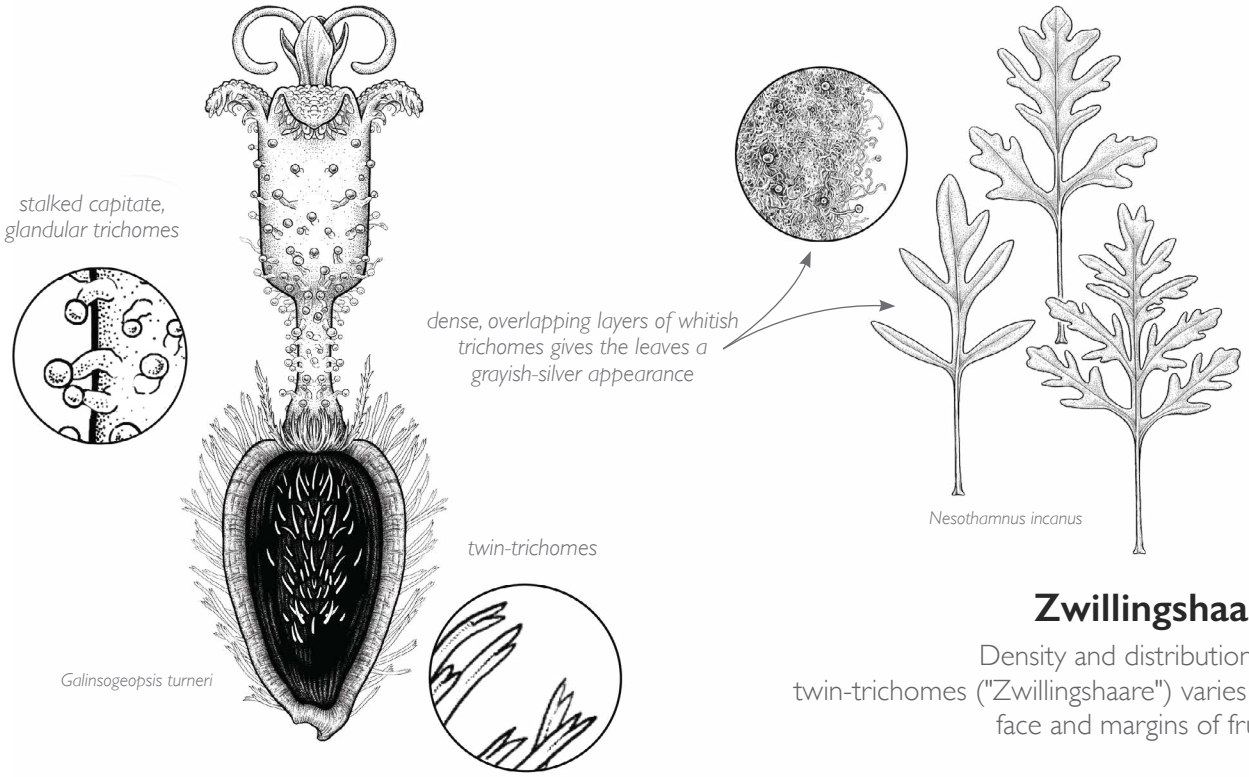



### Glandular trichomes

Simple, biseriate glandular trichomes, with a clearly differentiated stalk and head, often densely cover corollas.

### Flagellate trichomes

Some rock daisies have a more densely tomentose-canescent appearence that comes from having long and twisted unicellular flagellate trichomes densely matted on the surface




### Zwillingshaare

Density and distribution of twin-trichomes ("Zwillingshaare") varies on face and margins of fruits

## Morphology of Perityleae

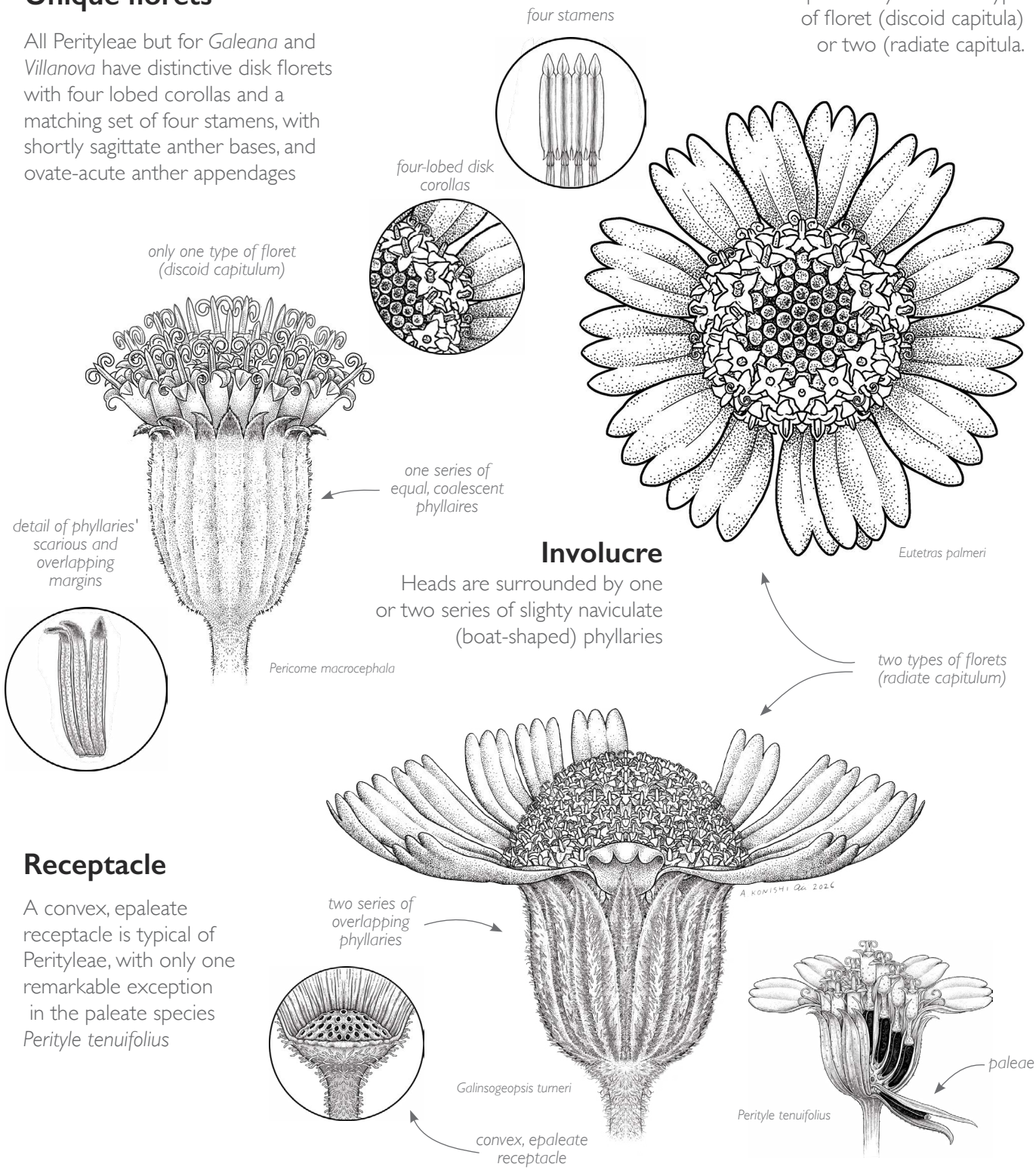
# Florets and capitula

### Unique florets

All Perityleae but for *Galeana* and *Villanova* have distinctive disk florets with four lobed corollas and a matching set of four stamens, with shortly sagittate anther bases, and ovate-acute anther appendages

### Capitula

Capitula may have one type of floret (discoid capitula) or two (radiate capitula.




### Involucre

Heads are surrounded by one or two series of slighty naviculate (boat-shaped) phyllaries

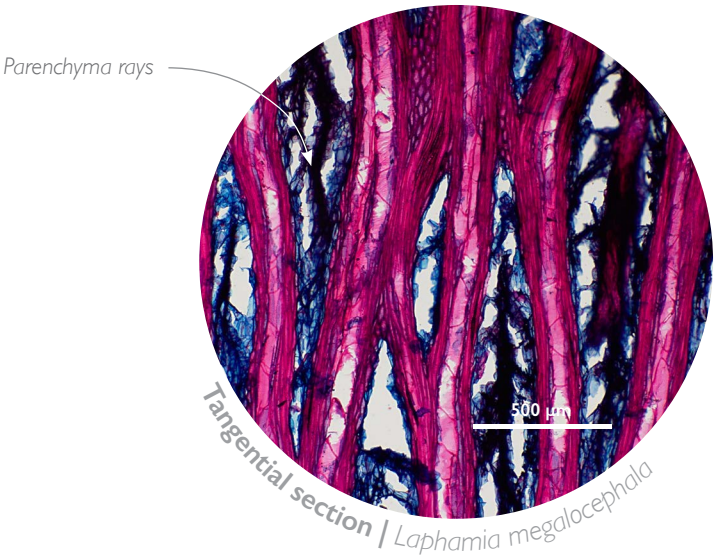
### Receptacle

A convex, epaleate receptacle is typical of Perityleae, with only one remarkable exception in the paleate species *Perityle tenuifolius*

# Anatomy of Perityleae
# Stem wood

## A specialized stem

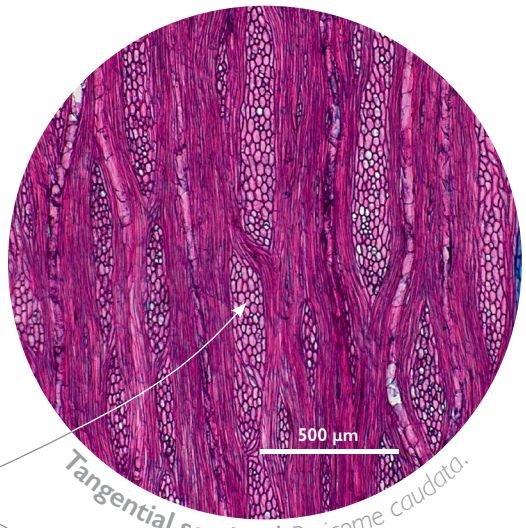
The gnarled, woody base present in most species of rock daisies serves both for rooting in minute cracks or crevices of vertical cliffs and as a site to form adventitious shoots after the long desert dry season.



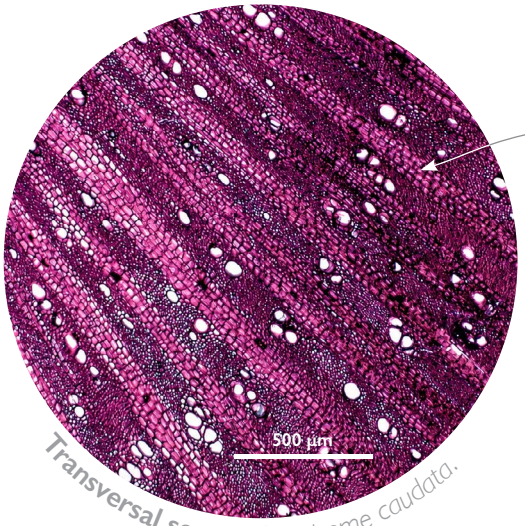

**Tangential section** | *Laphamia megalocephala*

## Fishnet Stockings

The convoluted wood anatomy of the caudex is the result of massive parenchyma rays. These structures may offer an ecological advantage under water stress conditions by acting as water reservoirs.




**Tangential section** | *Pericome caudata.*




**Transversal section** | *Pericome caudata.*



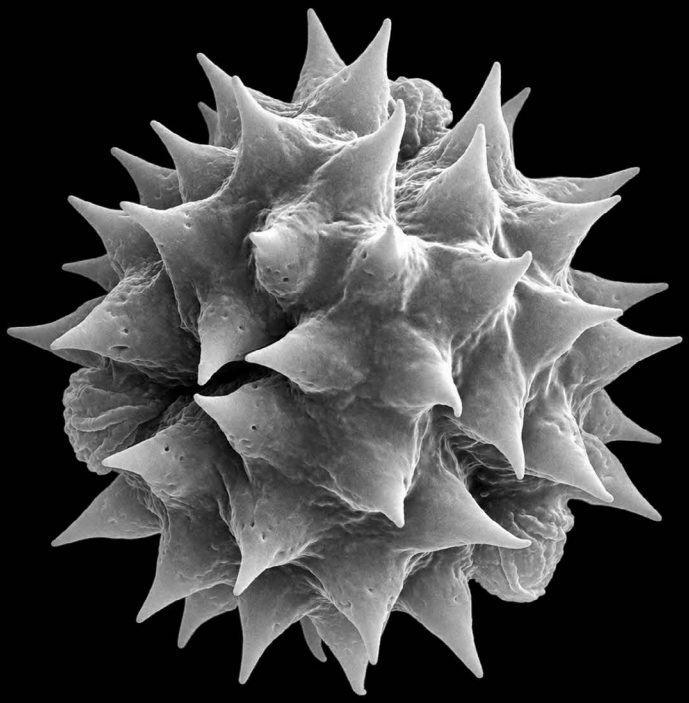

**Radial section** | *Pericome caudata.*



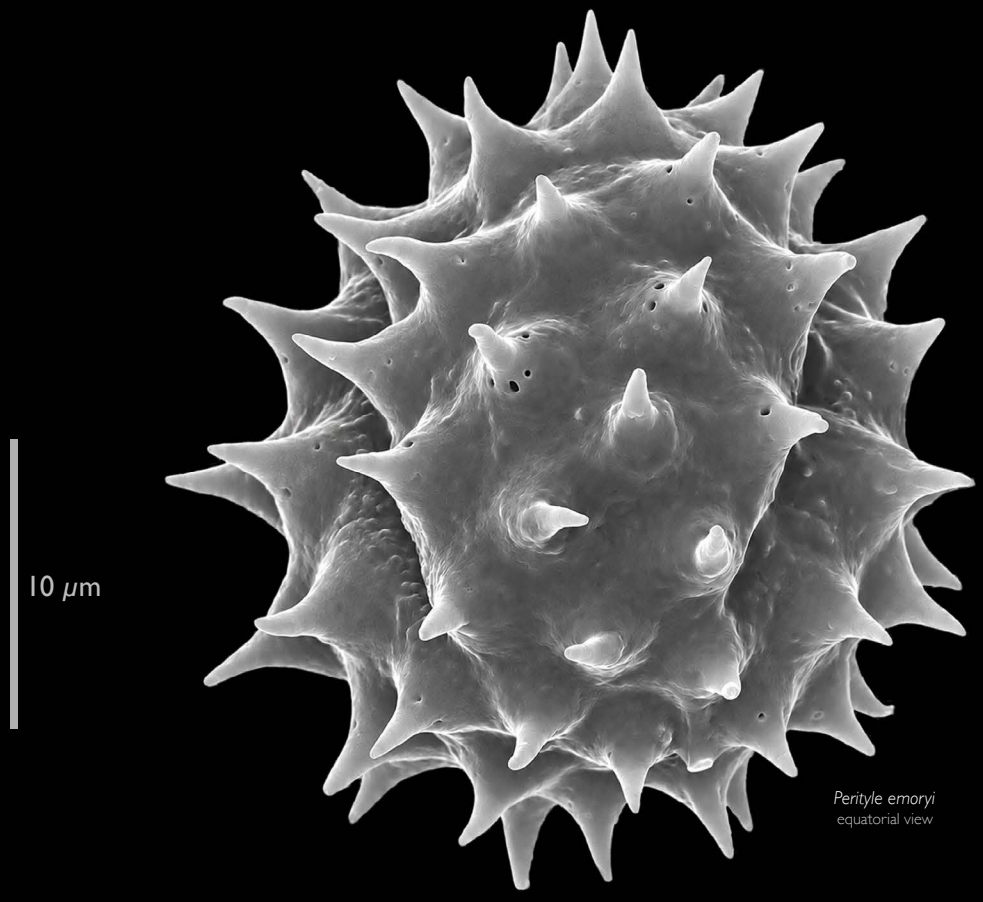

*Photos by Fabio Andrés Avila.*

# A closer look at Perityleae pollen

SEM images of rock daisy pollen reveal the typical shape and ornamentation of Asteroideae. The grains are generally spherical and tricolporate, with the apertures arranged equidistantly into three furrows. As in most other members of the subfamily, the outer layer of the pollen wall is covered in spike-like projections called echinae. These sculpture elements function as hooks, helping the pollen hitch a ride on animals to a distant stigma.



*Perityle emoryi*
polar view




*Perityle emoryi*
equatorial view

*Photos by Ciara Casas.*



# The ecosystem that doesn't exist

Cliffs are an ecosystem that doesn't exist. Invisible on any map. They are the boundaries of ecosystems, not ecosystems themselves. Geological processes are paused there. Physical laws are defied. A cliff is a paradox. It is both a dynamic, eroding fell-field and a static, stable refugium. At the end of our imagination of what a viable home for a food web would be is a cliff. Who would want to live and reproduce and evolve there?

*Big Hatchet Mountains, New Mexico, USA. Photo by Isaac Lichter-Marck*

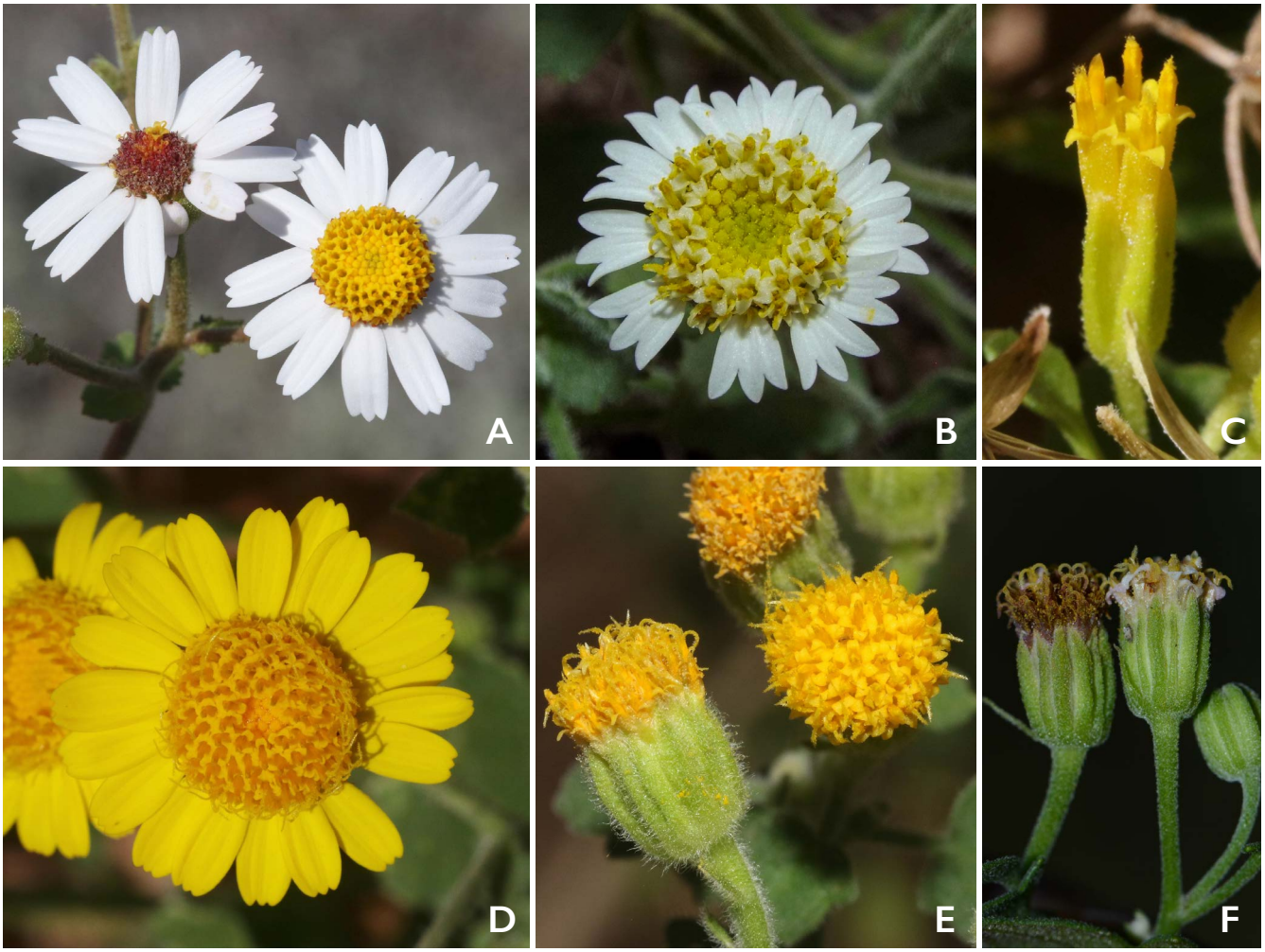



**Figure 1.** Floret number and corolla color varies among Perityleae and can be useful characteristic for distinguishing between groups. **A.** *Perityle brandegeeana* Rose, with white ray corollas and yellow tubular ones that fade to dark red. **B.** *Eutetras pringlei* Greenm., white ray corollas and cream-white tubular ones. **C.** *Laphamia quinqueflora* Steyerm. has discoid heads with 4 to 5 (-8) florets with bright yellow tubular corollas. **D.** *Laphamia parryi* (A.Gray) Benth & Hook. ex. Hemsl., with both ray and and tubular corollas yellow. **E.** *Laphamia ajoensis* (Todsen) Lichter-Marck, has discoid heads with florets with yellow corollas. **F.** *Galinsogeopsis glaucescens* (B.L.Turner) Lichter-Marck, has discoid heads with florets with white tubular corollas that fade to lilac. *Photos by James Bailey (A–E), Pablo Carrillo Reyes (F).*

ecological specialization is common, we still know little about the life history and ecology of rock daisies beyond what can be gleaned from a few, often old and fragmented specimens stored in natural history museums. The value of these specimens, especially for taxa that cannot be relocated in the field or may have gone extinct, is incalculable. Yet new collections and new observations of rock daisies made during field work, often as part of regionally focused floristic studies, have incredible potential to illuminate key aspects of rock daisy biology that cannot be gleaned from herbaria. The accomplishments and discoveries of field botanists often go overlooked. In recognition of the new understanding of rock daisy natural history provided by these recent field discoveries and of the cascading consequences that changes in taxonomy will have on collections and online databases, here we compile a comprehensive nomenclator as a reference guide to Perityleae taxonomy and present an annotated checklist in which we summarize notable recent records, ecological observations, and novel phylogenetic insights. We also include photographs of enigmatic rock daisies known previously only from specimens. This nomenclator is the result of intensive review of taxonomic publications, specimens in herbaria, and online databases, especially the Global Biodiversity Information Facility (GBIF), the Southwest Environmental Information Network (SEINet), iNaturalist, and the Global Compositae Database (GCD) as well as extensive collaborative fieldwork by a diffuse informal network of field

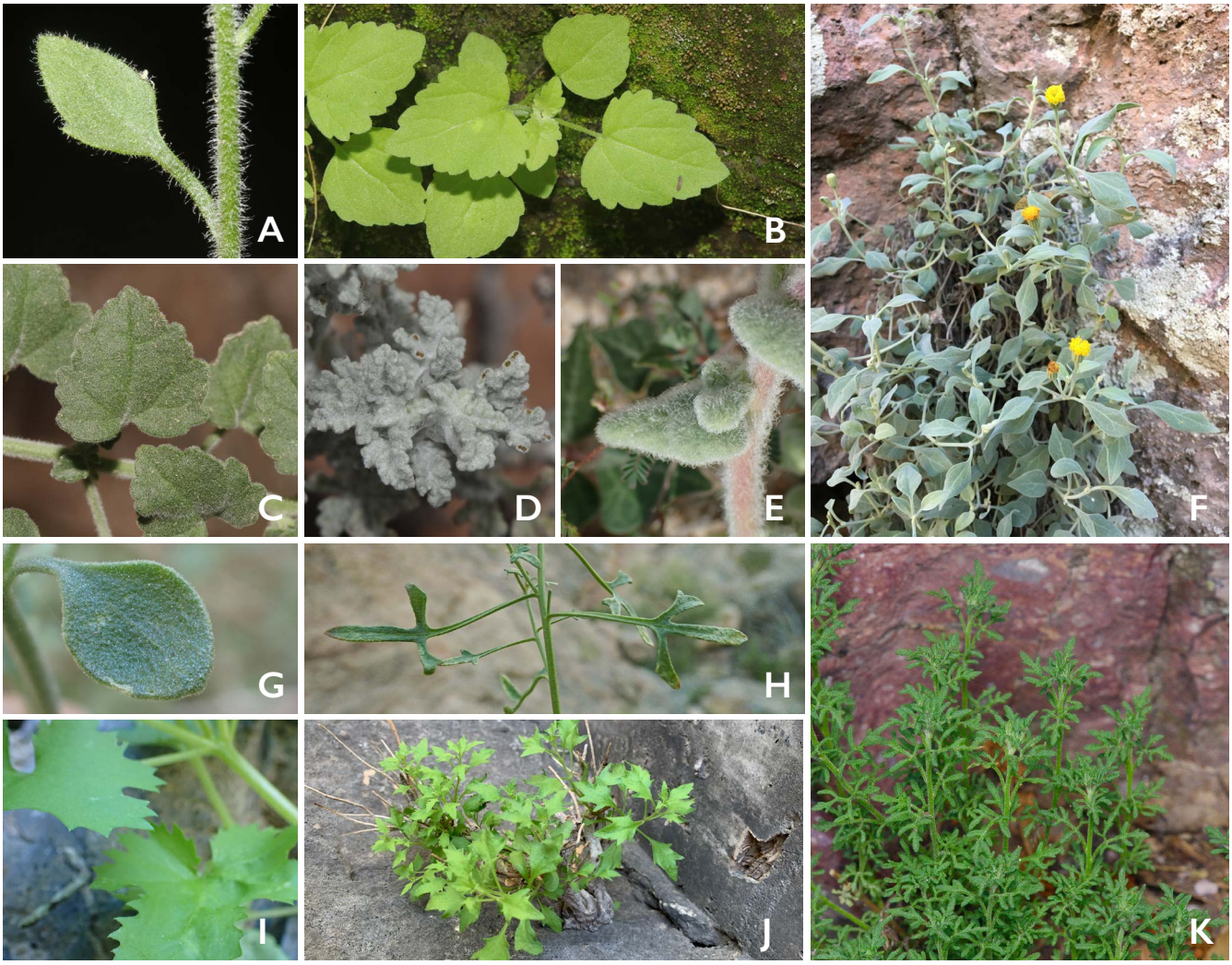



**Figure 2.** Leaf morphology varies widely in Perityleae and can be a informative trait to identify species. **A.** Simple, long-spatulate leaf of *Laphamia inyoensis* Ferris. **B.** Membraneous deltate leaves with crenate margins of *Galinsogeopsis microglossa* (Benth.) Lichter-Marck var. *microglossa*. **C.** Waxy, delatet leaves with crenate margins in *Laphamia ajoensis* Todsen. **D.** Dissected, white-tomentose leaves of *Laphamia vandevenderi* (B.L.Turner) Lichter-Marck. **E.** Pilose-villous, cordate leaves of *Perityle crassifolia* Brandegee. **F.** Ovate, densely white-pubescent leaves of *Galinsogeopsis harkerae* (P.Carrillo) Lichter-Marck. **G.** Simple elliptic leaf of *Laphamia megalocephala* S.Watson. **H.** Cruciform leaf of *Laphamia staurophylla* Steyerm. **I.** Glabrous, 3-lobed, cordate leaves of *Laphamia lobata* (Rydb.)Lichter-Marck. **J.** lanceolate, 3- or 5-lobed leaves of *Laphamia angustifolia* A.Gray. **K.** Simple, pinnately lobed leaves of *Galinsogeopsis coronopifolia* (A.gray) Lichter-marck. *Photos by James Bailey (A-C), Sue Carnahan (D), Isaac Lichter-Marck (E-J), Michelle Wong (K):*

biologists, herbarium staff, and community scientists throughout western North America and Chile. Bibliographic information for all valid names is listed according to the format used by the International Plant Names Index (IPNI). Type information with localities and notes have been gleaned from the literature and when possible, from scouring herbarium collections or digitized images available on JSTOR Global Plants. As part of this effort we have updated the GCD, a living taxonomic resource for Compositae, where one can stay up to date with rock daisy taxonomy (Gostel & Bonifacino, 2020).

In the process of compiling the checklist and nomenclator, several taxonomic issues in need of resolution were recognized. These include corrections to new combinations presented in Lichter-Marck & Baldwin (2022), as well as cases where older basionyms were placed incorrectly in synonymy and need to be reinstated according to nomenclatural rules of priority. After evaluating the status of each accepted name in Perityleae, we found several cases where taxa are clearly conspecific. In these cases, we make the necessary taxonomic adjustments and provide a detailed justification.

# ANNOTATED CHECKLIST

**Perityleae** B.G.Baldwin, Syst. Bot. 27(1): 192-193, 2002. **TYPE: Perityle** Benth.

**Annuals, perennial herbs, shrubs, mostly rupicolous suffrutices.** Herbage viscid or hirsute with stipitate or sessile glandular and non-glandular trichomes. **Leaves** opposite, subopposite, or alternate, usually petiolate, blades entire or lobed, linear, ovate, deltate, or hastate, rarely dissected, usually petiolate, often with simple conical trichomes interspersed with capitate or sessile glandular trichomes, occasionally densely covered with unicellular flagellate trichomes. **Capitula** discoid or radiate, solitary or loosely to tightly arranged in paniculiform or corymbiform arrays. **Involucres** cylindrical, obconic, urceolate, campanulate, or hemispheric. **Phyllaries** in 1–2 series, bracts linear to ovate, naviculate, fused or free. **Receptacles** flat to convex, epaleate or, rarely, paleate. **Ray florets** pistillate, fertile, corollas white or yellow, sometimes fading to red or lilac. **Disc florets** monoclinous, corollas tubulose, lobes 4 (5), yellow, white or cream, often fading to red or lilac, corolla throats typically covered in sessile or stipitate glandular trichomes and short cylindrical trichomes. **Athers** 4(5) fused, ecalcarate and ecaudate, appendages ovate to acute, eglandular, not blackened, anther bases shortly sagittate, filament with a collar at the apex. **Style** branch appendages when present shorter than the stigmatic lines, rarely fusing at apices, apices tapered to acute or round, adaxial surface with a dense covering of papillae. **Cypselae** carbonized, without striations, compressed, tetramerous, or obpyramidal, with 2-4 angles separated by thick, callous margins, sometimes corky, or winged, or tuburculate, often ciliate. **Pappus** present or absent, made of 1 to 30 erose, non-costate scales and/or awns, often reduced to a crown.

Perityleae comprise 8 genera, 81 species and 10 varieties. Distributed throughout western North America (United States and Mexico), South America (Ecuador, Chile, Colombia, and Peru), and Hawai'i (introduced). Most of Perityleae can be distinguished by four lobed disc corollas. Most are also subshrubby edaphic specialists that inhabit bare, rocky outcrops and cliff faces in arid and subtropical regions. Populations isolated onto sky islands in the Basin and Range Province follow a pattern of geographic speciation. Widespread annuals of *Perityle* may be among the most abundant annuals during a good rain year in low deserts.

## Key to the genera of Perityleae

**1a.** Disc corollas pentamerous

**2a.** Ray cypselae with corky wings; Mexico..... **Galeana**

**2b.** Ray cypselae without wings; Mexico & South America..... **Villanova**

**1b.** Disc corollas tetramerous

**3a.** Capitula in congested corymbiform cymes, multi-stemmed woody shrubs

**4a.** Leaves dissected; Guadelupe Island, Mexico..... **Nesothamnus**

**4b.** Leaves hastate; western North America ..... **Pericome**

**3b.** Capitula solitary, or in loose corymbiform arrays; annuals perennials, woody shrubs, or suffrutices

**5a.** Cypselae four-angled in cross section

**6a.** Pappus of four scales alternating with awns; mainland Mexico. ..... **Eutetras**

**6b.** Pappus absent; baja California and Chile ..... **Perityle**

**5b.** Cypselae two-angled in cross section

**7a.** Heads discoid

**9a.** Cypselae with a well-defined crown of fused or free squamellae (scales); Jalisco & Zacatecas states, Mexico ..... **Galinsogeopsis (p.p.)**

**9b.** Cypselae without a crown of squamellae (scales) or with only a weakly defined, vestigial crown of free scales; Sonora, Sinaloa, Baja California and southwestern U.S..... **Laphamia (p.p.)**

**7b.** Heads radiate

**10a.** Ray corollas white

**11a.** Sub-shrubby suffrutices of rock cliffs ..... **Galinsogeopsis (p.p.)**

**11b.** Delicate to robust annuals or perennial herbs with thin or fleshy taproots

**12a.** Cypselae with a well-defined crown of fused or free squamellae (scales) and 2(1) robust awns with antrorse barbs along their entire length ..... **Galinsogeopsis (p.p.)**

**12b.** Cypselae without a well-defined crown of squamellae (scales) or only weakly defined, and 1(2) delicate awns, irregularly or retrorsely barbed at the apex. ..... **Perityle (p.p.)**

**10b.** Ray corollas yellow

**13a.** Sub-shrubby suffrutices of rock cliffs ..... **Laphamia (p.p.)**

**13b.** Delicate to robust annuals or perennial herbs with thin or fleshy taproots

**14a.** Pedicel recurving upon maturity of the fruits, cypselae narrowly oblong, the margins nearly parallel ..... **Laphamia (p.p.)**

**14b.** Pedicel not recurving upon maturity of the fruits, cypselae obovate, wider at the apex than at the base ..... **Perityle (p.p.)**

**Galeaninae** B.G.Baldwin & Panero, Fam. Gen. Vasc. Pl. [Kubitzki] 8: 508 (2007). **TYPE: Galeana** La Llave. Map on page 48.

***Notes:*** The genera *Galeana* and *Villanova* constitute subtribe Galeaninae, one of two subtribes of Perityleae. These two genera are outliers within tribe Perityleae as they lack a four-lobed disc floret corolla and show inflorescence and fruit characteristics that are not present elsewhere in the group. Together they form what is informally known as the "Villanova clade," which has been sometimes been treated as *incertae sedis* within the Heliantheae alliance. Molecular studies based on nuclear ribosomal and chloroplast genes resolved the *Villanova* clade as the earliest diverging lineage within the rock daisy tribe and an important evolutionary link to its hyper-diverse sister group, the Eupatorieae (ca. 2500 spp.) (Baldwin et al., 2002; Panero and Funk, 2008; Schilling et al., 2013; Schilling et al., 2015). However, morphology and recent phylogenomic datasets suggests other possible, more robust links between this group and other epaleate tribes of the Heliantheae alliance, such as Bahieae and Eupatorieae.

**1** **Galeana** La Llave, Nov. Veg. Descr. [La Llave & Lexarza] 1:12 (1824). **TYPE: Galeana hastata** La Llave.

*Chlamysperma* Less. Syn. Comp. 256 (1832). **TYPE:** *Chlamysperma pratense* Less.

**1.1** **Galeana pratensis** (Kunth) Rydb., N. Amer. Fl. 34: 42, 1914. *Unxia pratensis* Kunth Nov. Gen. Sp. [H.B.K.] 4: 279, 1820. *Chlamysperma pratense* (Kunth) Less., Syn. Comp. 256, 1832. *Villanova pratensis* (Kunth) Benth. & Hook.f., Gen. Pl. 2: 405, 1873. **TYPE:** Mexico, Michoacan, Pazcuaro. *Bonpland A.J.A, F.W.H.A. Humboldt s.n.* (lectotype: P00320270 [photo!] [designated by McVaugh 1984]). Figure 3; map on page 48.

*Galeana hastata* La Llave, Nov. Veg. Descr. [La Llave & Lexarza] 1: 12, 1824. **TYPE:** Mexico, Veracruz, S. Jose de Corral, *La Llave s.n.* (lectotype: G00300001 [photo!] [**here designated**]).

*Chlamysperma arenarioides* Hook. & Arn., Bot. Beech. Voy. P. 300, 1838. *Galeana arenarioides* (Hook. & Arn.) Rydb., N. Amer. Fl. 34(1): 43, 1914. **TYPE:** Mexico, Nayarit, Tepic, *T. Beechey s.n.* (lectotype: K000502329 [photo!] [designated by McVaugh 1984], isolectotype: E00369141 [photo!]).

*Melampodium minutiflorum* M.E.Jones, Cont. W. Bot. 18: 72, 1933. **TYPE:** Mexico, Jalisco, Guadalajara, La Barranca, 17 November 1930, *M.E.Jones s.n.* (lectotype: POM [RSA0001418] [photo!][designated by McVaugh 1984], isolectotypes: GH00002557 [photo!], LL00373910 [photo!], UC522228!, US00128445!).




**Figure 3.** *Galeana pratensis* (H.B.K) Rydb. **A.** Capitula with dense indumentum of soft-hairy, glandular trichomes and boat shaped phyllaries. **B.** Mature capitululm showing slightly reflexed phyllaries and the tuburculate, carbonized cypselae. *Photos by Isaac Lichter-Marck.*

# The *Villanova* clade: to be or nor to be

Two genera of annuals, *Galeana* La Llave and *Villanova* Lag. comprise subtribe Galeaninae, also known as the *Villanova* clade. This clade is an outlier in tribe Perityleae and its position within the Heliantheae Alliance has been a topic of debate in the past. Both genera occur in Mexico, but *Villanova* also occurs in western South America, where it is both a common weed in urban centers such as Bogota, Colombia, and a rare annual in arid environments in Peru, Bolivia, and Chile.



**2** **Villanova** Lag., Gen. Sp. Pl. [Lagasca] 31, 1816. **TYPE: Villanova oppositifolia** Lag. Figure 4; map on page 48.

*Vasquezia* Phil. Fl. Atacam. 31, 1860. **TYPE:** *Vazquezia biternata* Phil.

**2.1** **Villanova anemonifolia** (Kunth) Less., Syn. Gen. Compos. 256, 1832. *Unxia anemonifolia* Kunth, Nov. Gen. Sp. [H.B.K.] 4(18): 219, t. 402 (ed. fol.), 1818. *Vasquezia anemonifolia* (Kunth) S.F.Blake, Contr. U.S. Natl. Herb. 26: 261, 1930. **TYPE:** Mexico, *A.J.A. Bonpland & F.W.H.A. von Humboldt s.n.* (lectotype: P00320271 [photo!] [**here designated**]).

*Villanova achilleoides* (Less.) Less, Syn. Gen. Compos. 256, 1832. *Unxia achilleoides* Less., Linnaea 5(1): 159, 1830. *Melampodium achilleoides* (Less.) Hemsl. Biol. Centr.-Amer., Bot. 2(8) 145, 1881. **TYPE:** Mexico, Veracruz, Llanos de Perote, *C.J.W. Scheide 354* (lectotype: HAL0017700 [photo!] [**here designated**], isolectotypes: HAL0111590 [photo!], GH00014050 [fragment] [photo!]).

***Notes:*** *Villanova anemonifolia* is accepted here over *V. achilleoides* because its basionym, *Unxia anemonifolia,* is older, dating to 1818, whereas *Unxia achilleoides* was named in 1830 (Govaerts, pers. comm., senior content editor of the Plants of the World Online [POWO] database). *Villanova* (4 taxa) and *Galeana* (1 taxon) make up the subtribe Galeaninae, which possess a five-lobed disk corolla (rather than four-lobed as in all other Perityleae). Although the fruits and floral features clearly set this species apart, the single series of boat-shaped phyllaries is like other members of Perityleae. The four taxa of *Villanova* are distributed in Mexico and western South America.

**2.2** **Villanova oppositifolia** Lag., Gen. Sp. Pl. [Lagasca] 31, 1816. *Vasquezia oppositifolia* (Lag.) S.F.Blake, J. Wash. Acad. Sci. 27: 387, 1937. **TYPE:** Peru, Lima, *H. Cuming 1082* (lectotype: K000502237 [photo! [**here designated**], isolectotypes: E00312229 [photo!], E00335060 [photo!]).

*Villanova perpusilla* Phil., Anales Mus. Nac., Santiago de Chile 1891: 47, 1891. **TYPE:** Chile, Lima, *Phillipi s.n.* (syntypes: SGO [pending lectotypification once a closer examination is possible]).

*Villanova alternifolia* Lag., Gen. Sp. Pl. [Lagasca] 31, 1816. *Unxia alternifolia* (Lag.) Spreng., Syst. Veg. ed. 16 [Sprengel] 3: 620, 1826. **TYPE:** Peru, "cerca Limam" (type: unknown).

***Notes:*** *Villanova oppositifolia* is a widespread annual in western South America and even occurs within the city limits of Bogota, Colombia, where it was seen growing in a moist habitat in an urban park with ferns and moss by Felipe Zapata in 2023.

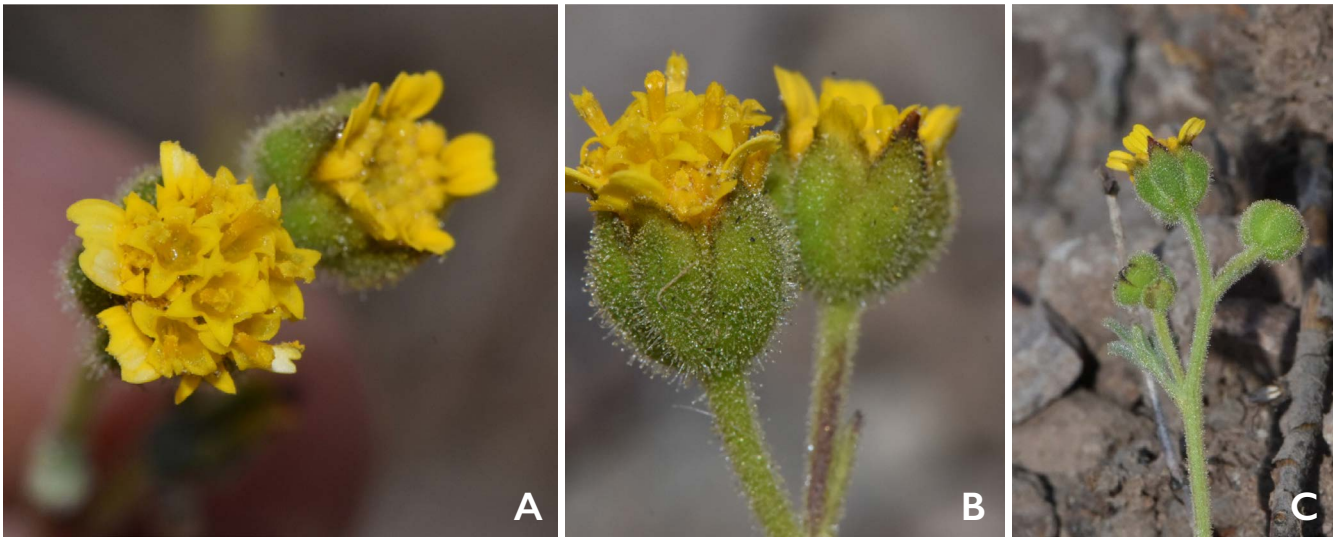



**Figure 4.** *Villanova robusta* Phil. is a rare annual species that occurs in semi-arid canyon of the high andes in northern Chile. **A.** Superior view of capitulum showing the five lobed disc floret corollas and short limbs of ray corollas. **B.** Lateral view of capitulum showing the single series of mostly coalescent phyllaries covered in a dense glandular indumentum. **C.** Capitulescence in lateral view, showing capitula organized into loose corymbiform arrays. *Photos by Joey Santore.*

Based on photos taken by Zapata, the phyllaries appear to partially enclose the ray fruit ovary and bend back upon maturity, which is a trait that we have observed in several species of genus *Perityle,* including *P. californica*, *P. crassifolia*, and *P. rotundifolia*. *Villanova alternifolia* is tentatively recognized as a heterotypic synonym here because the type locality listed is identical to that of *V. oppositifolia*, but we have so far not been able to locate the type.

**2.3** **Villanova robusta** Phil., Anales Mus. Nac., Santiago de Chile 1891: 47, 1891. **TYPE:** Chile, Tarapaca, Jaina, *A.R. Philipi s.n.* (syntypes: SGO [pending lectotypification once a closer examination is possible]). Figure 4.

***Notes:*** *Villanova robusta* is a scarce annual found in mid to high elevation arid sites in the north of Chile. It is the only species of *Villanova* endemic to Chile.

**2.4** **Villanova titicacensis** (Meyen & Walp.) Walp., Nov. Actorum Acad. Caes. Leop.-Carol Nat. Cur. 19 (Suppl. 1): 296, 1843. *Wedelia titicacensis* Meyen & Walp., Nov. Actorum Acad. Caes. Leop.-Carol Nat. Cur. 19(Suppl. 1): 296, 1843. *Vasquezia titicacensis* (Meyen & Walp.) S.F.Blake ex Herrera, Proc. Soc. Biol. Washington 27(9): 387, 1937. **TYPE:** Peru, *Meyen s.n.* (lectotype: B[F0BN015423] [photo!] [**here designated**]).

***Notes:*** *Villanova titicacensis* is an annual found in high elevation sites in Peru. As with other species of *Villanova*, its phylogenetic relationships and distinctness as a taxon separate from other *species* of *Villanova* has yet to be evaluated using morphological or phylogenetic data.

**Peritylinae** Rydb., N. Amer. Fl. 34: 11, 1914. **TYPE: Perityle** Benth.

Amauriinae Rydb., N. Amer. Fl. 34: 11. 1914. **TYPE:** *Amauria* Rydb.

Lycapsinae H. Rob. Phytologia 46(2): 120 (1980). **TYPE:** *Lycapsus* Phil.

***Notes:*** Subtribe Peritylinae includes the majority of species in tribe Perityleae and is comprised by six currently recognized genera, *Eutetras*, *Galinsogeopsis*, *Laphamia*, *Nesothamnus*, *Pericome*, and *Perityle*. This group differs from Galeaninae in having a four-lobed disc corolla, two or four-sided cypseleae, and a single series of typically linear-oblong, naviculate (boat-shaped) phyllaries. Subtribes Amauriinae and Lycapsinae are included in Peritylinae here, as the type genera for those subtribes, *Amauria* and *Lycapsus* respectively, are now subsumed into the genus *Perityle*.

**3** **Eutetras** A.Gray, Proc. Amer. Acad. Arts 15: 39, 1800. **TYPE: Eutetras palmeri** A.Gray. Figure 5 & Figure 6.

***Notes:*** *Eutetras* is a genus of two allopatric species endemic to the southern portion of the Mexican Plateau. Its distribution follows a series of scattered peaks and small *sierras*, especially along the southern transition of the Mexican Plateau into the more rugged neighboring regions of the Sierra Madre Oriental, the Trans-Mexican Volcanic Belt and the Sierra Madre Occidental. *Eutetras* grows directly out of emergent bare, rocky outcrops and cliffs of volcanic substrates within a heterogeneous matrix of semi-arid oak/pine forest and xerophilous scrub. The genus is closely related to *Pericome* and to an anomalous lineage (*Perityle rosei* Greenm.) that is currently retained tentatively in *Perityle* pending further study. Large capitula and tetramerous cypselae with an erect crown of four alternating pappus scales and barbs are diagnostic for *Eutetras*.




**Figure 5.** Geographic distribution and species richness in *Eutetras* A.Gray. Darker colors indicate areas of overlap between the two extant species, *Eutetras palmeri* and *Eutetras pringlei.*

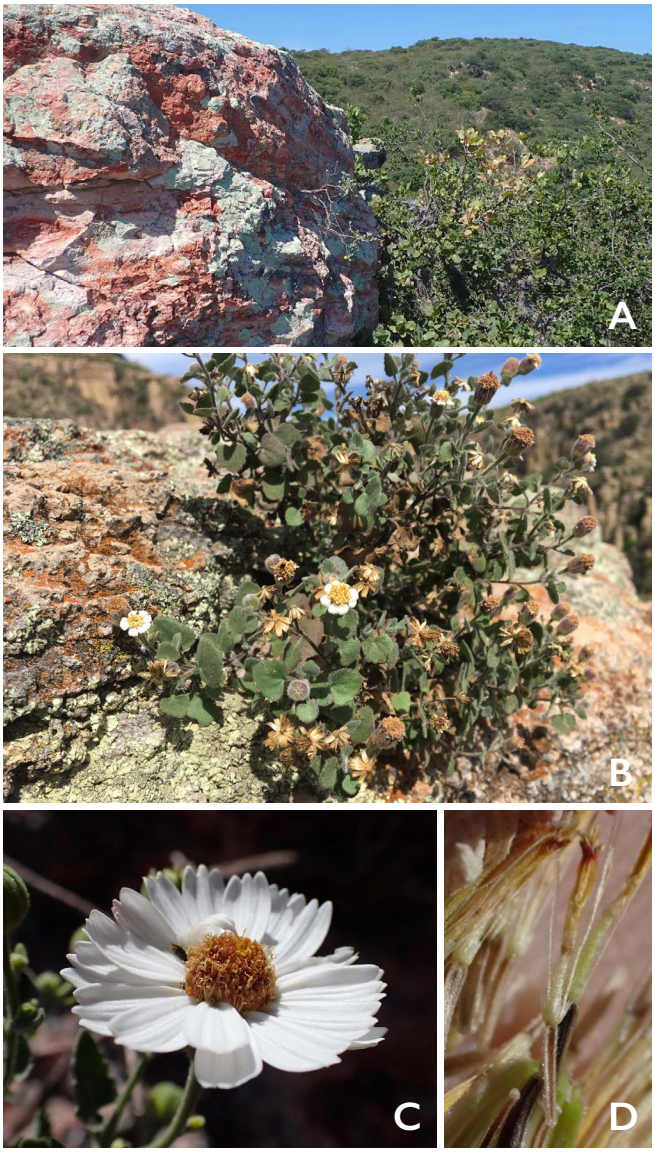



**Figure 6.** *Eutetras* A.Gray. **A.** The long-recognized *Eutetras* includes two distinctive species of rock daisies that grow exclusively on mostly volcanic rocky outcrops and cliffs surrounded by a matrix of *Quercus* L. (Fagaceae) and *Ipomoea* L. (Convolvulaceae) forests in central Mexico. **B.** *Eutetras palmeri* A.Gray, shown here growing out of a solid slab of igneous rock, has short ray corollas and cream white disc corollas. **C.** *Eutetras pringlei* Greenm. has long ray corollas and yellow disc corollas that fade to orange or red. **D.** The cypselae of *Eutetras* are square in cross section, and crowned by a set of four alternating squamellae (scales) and awns. *Photos by Isaac Lichter-Marck.*

**3.1** **Eutetras palmeri** A.Gray, Proc. Amer. Acad. Arts 15: 40, 1880. **TYPE:** Mexico, San Luis Potosi, near Angostura, 100 miles east of San Luis Potosi, 1878, *C.C. Parry & E. Palmer 520 ½* (lectotype: GH00008092 [photo!], [designated by Turner 1966], isolectotypes: K000502204 [photo!], ISC0000112 [photo!]). Figure 6A & 6B.

***Notes:*** *Eutetras palmeri* represents the northern half of the distribution of the genus. It is found southwards from central Zacatecas, towards neighboring regions in Aguascalientes, Jalisco and San Luis Potosí to the north of Guanajuato at elevations between 1,700 and 2,800 m. Morphological features that clearly distinguish *E. palmeri* are fewer (40 to 60) and white disk florets (instead of more than 100 and yellow florets in *E. pringlei*); sometimes absent rays of no more than 4 mm long (instead of ever present rays of 6 to 15 mm length in *E. pringlei*); and an involucre of less than 14 mm wide (instead of an involucre of more than 14 mm wide in *E. pringlei*) (Turner, 1966; Villarreal Q. *et al*., 2006). This plant is common around its distribution area where it grows along a wide variety of rock associated plants, including Asparagaceae, Cactaceae, Pteridaceae and Crassulaceae as well as Fagaceae, Pinaceae, Fabaceae and Poaceae which dominate the most common plant associations in the landscape. Collections from recent decades have expanded our knowledge of the distribution area of *E. palmeri* towards western Zacatecas along the limits of the Mexican Plateau with the Sierra Madre Occidental. This species harbors variation in vegetative and reproductive characters throughout its distribution that are especially evident in western populations. For example, longer and much denser foliar tomentum (HUAA – *G. García R. 2485*), cypselae with glandular trichomes (HZAC – *E. J. Rodríguez P. 3297*), and yellow disk florets (CHAPA - *L. Hurtado R. 186*). Further study is needed to determine if these represent localized environmental responses or new taxa.

**3.2** **Eutetras pringlei** Greenm., Proc. Amer. Acad. Arts 41: 266, 1905. **TYPE:** Mexico, Guanajuato, about basaltic cliffs near Acambaro, 6 October 1904, *C.G. Pringle 8813* (holotype: GH00008093 [photo!], isotypes: CM2388 [photo!], E00433208 [photo!], E00433209 [photo!], E00433210 [photo!], F0050214 [photo!], GOET001542 [photo!], K000502203 [photo!], LL00374162 [photo!], M0030102 [photo!], MEXU01220321 [photo!], MEXU01220319 [photo!], MEXU01220320 [photo!], MIN1001158 [photo!], NY00169288 [photo!], PH00013960 [photo!], S08-596 [photo!], UC84199!, US00124702!, US00931231!, UVMVT027525 [photo!]). Figure 6C & 6D.

***Notes:*** *Eutetras pringlei* is found from the east of Guanajuato through Querétaro to the west of Hidalgo, Mexico, at elevations between 1,600 and

2,200 m. This species exhibits variation regarding leaf size and indument between populations but is distinct from *E. palmeri* (Turner, 1966). The habitat of *E. pringlei* is like that of *E. palmeri* with the exceptions of a few collections which were found on sedimentary instead of volcanic rock outcrops (e.g., MEXU – *L. Paray 2969*). Representing the southern half of the distribution of the genus, it is separated from *E. palmeri* by the Sierra de Guanajuato and the Río Laja basin. The Sierra de Guanajuato has been cited as central in understanding tectonics of Central Mexico as it is considered the limit between the Mexican Plateau and the Trans-Mexican Volcanic belt. It experienced its most recent uplift event, relative to the surrounding basin, from the Late Miocene to the Quaternary (del Río Varela *et al.*, 2020). This overlaps with the onset of aridification of the Late Miocene which is recognized as a driver of evolution within the Perityleae tribe (Lichter-Marck & Baldwin, 2023). This raises questions regarding how the interplay of orogeny and climate change may influence population differentiation in *Eutetras* as well as in other rupicolous plant lineages of the Mexican Plateau and similar areas.

**4 Galinsogeopsis** Sch.Bip. Bot. Voy. Herald [Seemann] 7-8: 307 (1856). **TYPE:** *Galinsogeopsis spilanthoides* Sch.Bip. Figure 7-17.

*Correllia* A.M.Powell, Brittonia 25: 226 (1973). **TYPE:** *Correllia montana* A.M.Powell

**4.1 Galinsogeopsis canescens** (Everly) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. *Perityle canescens* Everly, Contr. Dudley Herb. 3: 393, tab. 71, figs. 7 & 8, 1947. **TYPE:** Mexico, Sinaloa, Capadero, Sierra Tacuichamona, 12 February 1940, *H.S. Gentry 5588* (holotype: DS[CAS0003923]! , isotypes: ARIZ0004460 [photo!], 0004461 [photo!], ARIZ0004462 [PHOTO!], GH00011104 [photo!], MEXU00138033 [photo!], NY00231053 [photo!], RSA0001473 [photo!], UC651747!, US00124595!).

*Galinsogeopsis stevensii* (B.L.Turner) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. *Perityle stevensii* B.L.Turner, Phytologia 69: 298, 1990. **TYPE:** Mexico, Sinaloa, Municipio San Ignacio, 2.6 km from Highway 15 on road to microwave tower, ca. 17 mi. E of Emcosa, 10 September 1973, *W.D. Stevens & M. Fairhurst 2040* (holotype: NY00231074 [photo!], isotype: TEX00374417 [photo!]).

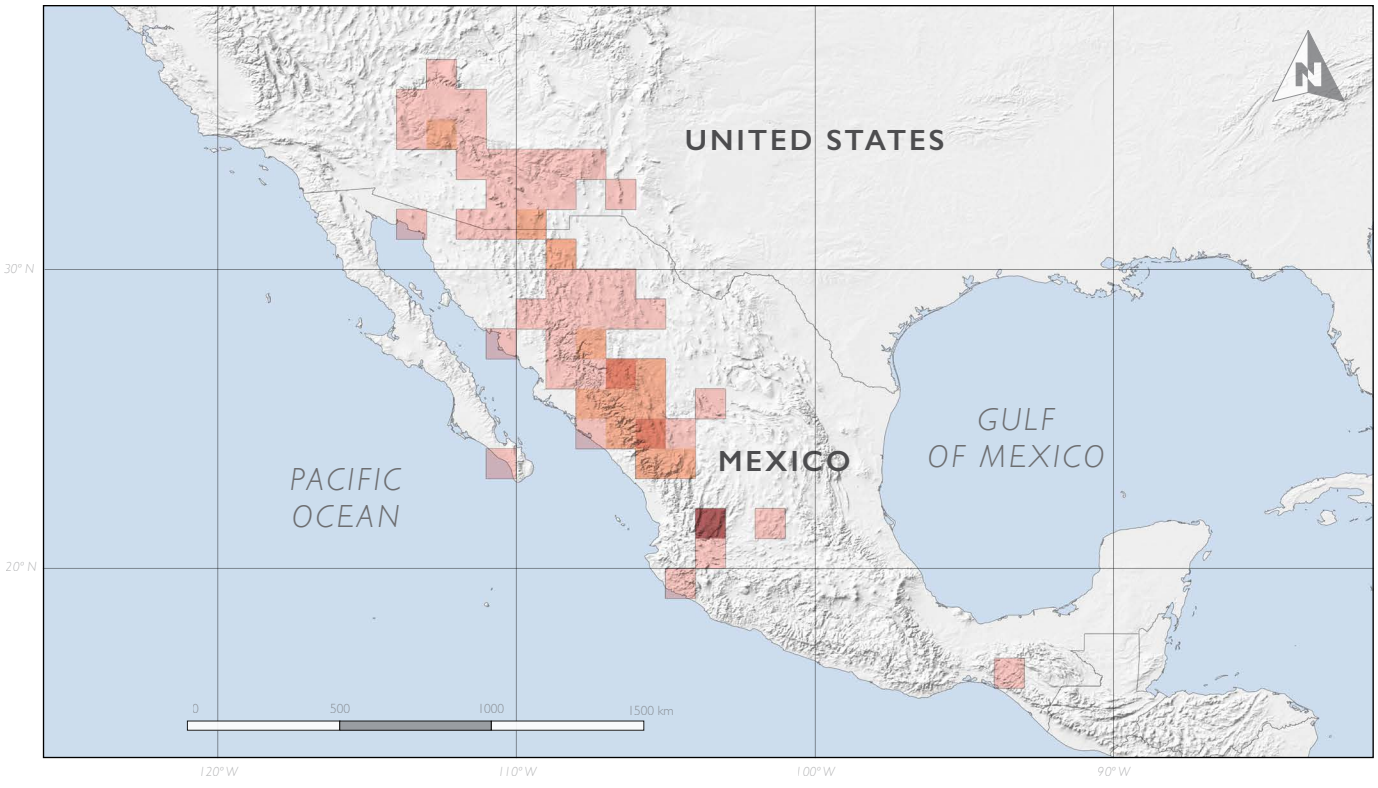



**Figure 7.** Geographic distribution and species richness in *Galinsogeopsis* Sch. Bip. Peak diversity (darkest colors) occur in near the southern extent of the genus in the Sierra Madre Occidental, but the range reaches as far north as Arizona, in the U.S. and as far south as Chiapas state, Mexico.

***Notes:*** *Galinsogeopsis canescens* and *G. stevensii* are here treated as conspecific for the first time. Until recently both taxa were known only from type specimens, collected in 1940 and 1973 in the western foothills of the Sierra Madre Occidental in Sinaloa. Collections made by Rito Vega and deposited in the herbarium in Culiacán, and more recently, photographs taken by J.F. Pio León and uploaded to *iNaturalist* show overlapping leaf morphological variation displayed by the two taxa. In addition, the type location described by Turner (1990) for *G. stevensii,* "Mpio. San Ignacio, ca. 2.6 mi. from highway 15 along road to microwave tower, ca. 17 mi S of Emcosa," was in error, as the locality mentioned is in Culiacán not San Ignacio. This updated locality places the only known location for *G. stevensii* only 17 km to the east of the type locality for *G. canescens* (Pío-León et al., 2023).

**4.2** **Galinsogeopsis ciliata** (L.H.Dewey) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. *Laphamia ciliata* L.H.Dewey, Bot. Gaz. 20: 425, 1895. *Perityle ciliata* (L.H.Dewey) Rydb., N. Amer. Fl. 34: 23, 1914. **TYPE:** USA, Arizona, rocks along Pine Creek near Pine, 26 August 1891, *D.T. MacDougal 676* (lectotype: US00124597! [**here designated**], isolectotype: US01105962!). Figure 8.

***Notes:*** *Galinsogeopsis ciliata* is one of two species of *Galinsogeopsis* found in the southwest U.S. (along with *Galinsogeopsis coronopifolia*), where they sometimes co-occur with *Laphamia*. *Galinsogeopsis ciliata* and *G. coronopifolia* are obligately associated with bare, rocky outcrops, but unlike most species of cliff dwelling *Laphamia*, they can be found on minor outcrops, such as boulder fields or barrens, and thrive on diverse substrates, including sandstone, limestone, and granite.




**Figure 8.** *Galinsogeopsis ciliata* (L.H.Dewey) Lichter-Marck is one of the most common rock daisies on cliffs at mid to high elevations in Arizona, U.S.A. **A.** side view of capitula showing the sparse pubescence, and single series of linear, naviculate (boat-shaped) phyllaries. **B.** Abaxial view of ray floret corolla. **C.** Cypsela, showing the elongated shape, long twin-trichomes on face and margin and 2(1) pappus awns. *Photos by Isaac Lichter-Marck.*

**4.3** **Galinsogeopsis coronopifolia** (A.Gray) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. *Perityle coronopifolia* A.Gray, Smithsonian Contr. Knowl. 5(6): 82–83, 1853. *Laphamia coronopifolia* (A.Gray) Hemsl., Biol. Cent.Amer. Bot. 2: 210, 1881. **TYPE:** USA, New Mexico, Grant Co., copper mines of Santa Rita del Cobre, September 1851, *C. Wright 1196* (lectotype: GH00011072 [photo!] [designated by Powell 1974], isolectotypes: GH00011073 [photo!], GH00011074 [photo!], K001079926 [photo!], K001079927 [photo!], NY00231038 [photo!], PH00021253 [photo!], TCD0090359 [photo!], US00124601 [photo!]). Figure 9.

*Laphamia scopulorum* M.E.Jones, Contr. W. Bot. 12: 48, 1908. *Perityle scopulorum* (M.E.Jones) A.M.Powell & B.L.Turner, Phytologia 66: 505, 1989. *Galinsogeopsis scopulorum* (M.E.Jones) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. **TYPE:** Mexico, Chihuahua: Colonia Juarez. Sierra Madre mts. 12 September 1903, *M.E. Jones s.n.*, (lectotype: POM [RSA0001355]! [designated by Powell 1974], isolectotype: US00124653!).

*Perityle pseudociliata* A.M.Powell & Yarborough, Phytologia 82: 326, fig. 1, 1998. *Galinsogeopsis pseudociliata* (A.M.Powell & Yarborough) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. **TYPE:** Mexico, Chihuahua: 26 km NW of Colonia Juarez in the "Tinaja", a canyon thru the foothills of the Sierra Madre Occidental, 30°22' N, 108°12', 28 July, 1972, *W. Wilson, M.; Wilson, E; Johnston, L.A.; Johnston, M.C., 8480* (holotype: TEX00031083 [photo!], isotype: MEXU00479519 [photo!]).

***Notes:*** Phylogenetic data supports the synonymy of *G. pseudociliata* and *G. scopulorum* with *G. coronopifolia* (Lichter-Marck & Baldwin 2023). Both species are known only from their type localities, about 26 km from each other near Colonia Juárez in Chihuahua, Mexico. *Galinsogeopsis coronopifolia* is a widespread taxon found throughout the southwest United States. *G. scopulorum* has bounced in and out of synonymy multiple times. Originally described by Marcus Jones as *Laphamia scopulorum*, it was considered a synonym of *Laphamia coronopifolia* by Rydberg (1914). Blake (1945) then reinstated *L. scopulorum* as a distinct taxon from *L. coronopifolia*. Powell (1973a) however, placed *L. scopulorum* back in synonymy with *Perityle coronopifolia*. Turner (1989) again recognized the species and made the necessary transfer to *Perityle*. Both *G. scopulorum* and *G. pseudociliata* have been understood to be geographically disjunct, from the remainder of *G. coronopifolia* with reduced marginal cypsela cilia, but more field research in northern Chihuahua will likely infill the geographic disjunctions and morphological gradations between these former taxa and other members of the widespread *G. coronopifolia*.

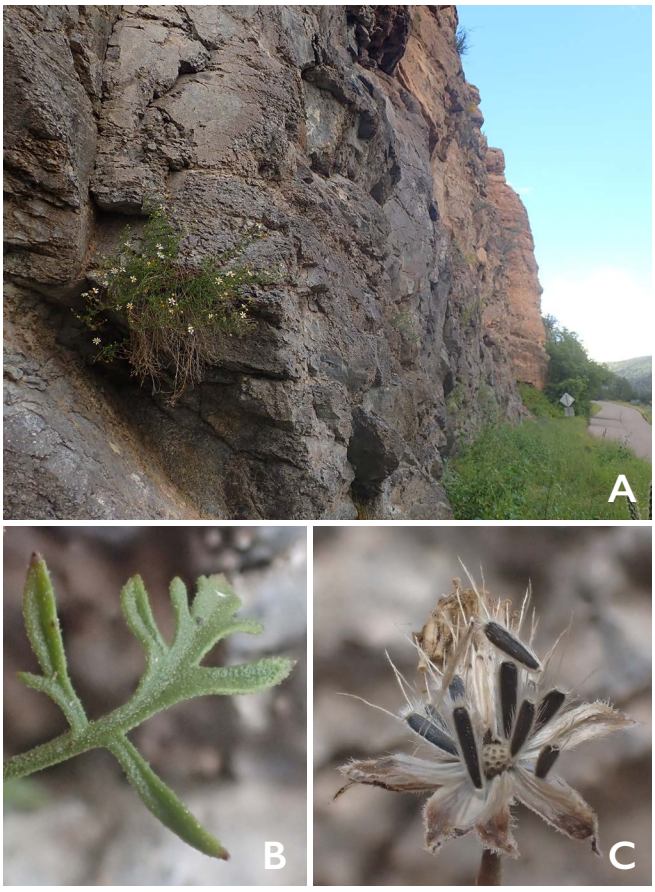



**Figure 9.** *Galinsogeopsis coronopifolia* (A.Gray) Lichter-Marck is a widespread rock daisy that grows on boulders, cliffs, and canyons in sky island mountain ranges of southeast Arizona and New Mexico. **A.** This species is a suffrutescent perennial with a woody caudex that roots into minute cracks and crevices in rock faces of various lithologies. **B.** The leaf is pinnately dissected and covered in a short-hirsute pubescence. **C.** The cypselae spill out of the capitula upon maturity, and disperse to far flung rock faces by virtue of a pappus that consists of a crown of scales and two pappus awns. *Photos by Isaac Lichter-Marck.*

**4.4** **Galinsogeopsis feddemae** (McVaugh) Lichter-Marck, Lichter-Marck, Syst. Bot. 47(3): 807, 2022. *Perityle feddemae* McVaugh, Contr. Univ. Michigan Herb. 9: 431, fig. 35, 1972. **TYPE:** Mexico, Jalisco, Rancho Viejo, 10 km ENE of Huejuquilla el Alto, rock crevices, open oak-woodland, 1900 m, 31 October 1963, *C. Feddema 2278* (holotype: MICH1107599 [photo!], isotypes: CAS0003924!, LL00208159 [photo!], NY00231057 [photo!], PH00021279 [photo!], TEX00374219 [photo!]). Figure 10.



**Figure 10.** *Galinsogeopsis feddemae* (McVaugh) Lichter-Marck is a rare rock daisy with discoid, cream white disc corollas that fade lilac and trilobed leaves that occurs on rocky mesas at two known points in the southern Sierra Madre Occidental. Shown here is an individual growing out of a boulder on Mesa de Caballos in Zacatecas state. *Photo by Isaac Lichter-Marck.*

***Notes:*** In 1963 and 1969 this species was collected at two localities, the type location near Huejuquilla el Alto, Jalisco and from approximately 50 km to the west in Zacatecas state near the town of Valparaiso. This species was not collected again for over thirty years until the initiation of Pablo Carrillo-Reyes floristic inventory of the Cuixtla-Patitos river basin, in Jalisco and Zacatecas, in which a disjunct population of *G. feddemae* was discovered approximately 350 km south of the type on the ledge of an emergent mesa near the hamlet of San Cristóbal de la Barranca. These disjunct plants conform to McVaugh's (1984) description of *G. feddemae* in that they possess leaves that are glabrate (not canescent) with oblong lobes. Molecular phylogenetic data suggests that these recently discovered plants are more closely related to distinctive species of rock daisies found in the southern Sierra Madre Occidental than to conspecific populations to the north; therefore, closer study of morphological characters is warranted to see if these constitute a new species.

**4.5** **Galinsogeopsis glaucescens** (B.L.Turner) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. *Perityle glaucescens* B.L.Turner, Phytologia 75: 176, 1993. **TYPE:** Mexico, Zacatecas, km 8 along the road to El Teul and Florencia, "Rupícola, en acantilado de exposición oeste", 2000 m, 17 October 1992, *J.A. Lomelí-Sención s.n.* (holotype: TEX00208144 [photo!]).

***Notes:*** *G. glaucescens* is a micro-endemic species known from only two neighboring locations, Teúl de González Ortega and Pueblo Viejo, in the southern Sierra Madre Occidental, where it grows on ledges and cliffs surrounded by a matrix of pine-oak forest.

**4.6** **Galinsogeopsis harkerae** (P.Carrillo) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. *Perityle harkerae* P.Carrillo, Syst. Bot. 33: 459 (461, fig. 1), 2008. **TYPE:** Mexico, Zacatecas, Municipio de Teúl de González Ortega, puente sobre el Río Patitos, camino de El Conejo a Milpillas Allende, 21°21'06"N, 103°33'55"W, 1580 m, 26 December 2004, *P. Carrillo-Reyes & R. Ramírez-Delgadillo 4462* (holotype: IBUG0180698, isotypes: IEB000204867 [photo!], KANU369177 [photo!], MEXU01262019, MU000065559 [photo!], NY00888423 [photo!], TEX00208662 [photo!], UAMIZ0067921 [photo!], WIS0262865 [photo!], XAL). Figure 11.

***Notes:*** An attractive micro-endemic described in 2008 by Pablo Carrillo-Reyes and still known only from the type locality in the municipality of Teúl de González Ortega,

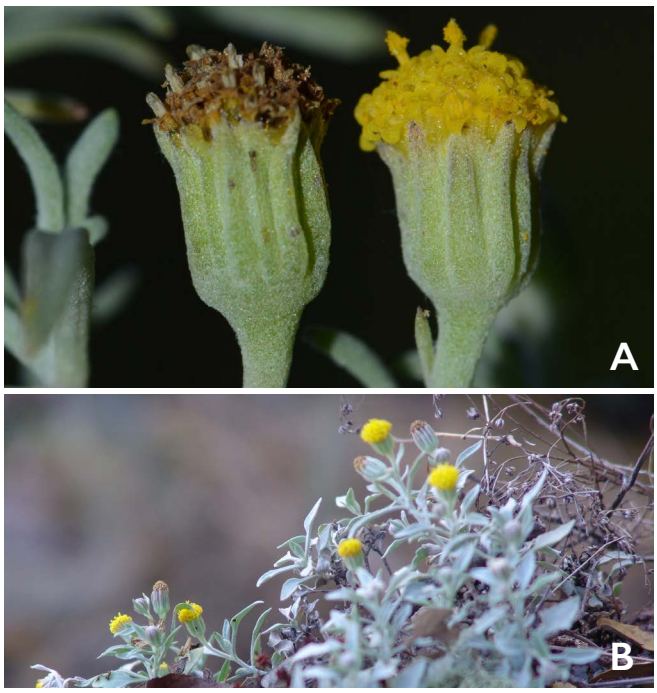



**Figure 11.** *Galinsogeopsis harkerae* (P. Carrillo) Lichter-Marck is a rare rock daisy known from only one location in the southern Sierra Madre Occidental, where it grows on rocky outcrops along with a diverse cliff flora of lichens, succulents, orchids, agaves and many other plants. **A.** Lateral view of head. **B.** The leaves and stems of this species are densely covered in a white indumentum that makes the yellow discoid heads stand out with added contrast. *Photos by Pablo Carrillo-Reyes.*

Zacatecas, and two additional locations, close by and across the border in Jalisco (*P. Carrillo-Reyes 8570*), and in the Municipality of Arandas, ca. 140 km southeast (*Puga 15963*).

**4.7** **Galinsogeopsis hofmeisteria** (Rydb.) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. *Perityle hofmeisteria* Rydb., N. Amer. Fl. 34(1): 18, 1914. **TYPE:** Mexico, Durango, vicinity of Durango, April–November 1896, *E. Palmer 28* (holotype: NY00231058 [photo!], isotypes: GH00011123 [photo!], K000502190 [photo!], US00124618!). Figure 12.

*Galinsogeopsis pennellii* (B.L.Turner) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. *Perityle pennellii* B.L.Turner, Phytologia 69: 298, 1990. **TYPE:** Mexico, Durango, Cerro de Mercado, N of Cd. Durango, crevices of ferruginous rocks, 2000–2100 m, 24–25 August 1934, *F. W. Pennell 18160* (holotype: NY00231074 [photo!], isotype: TEX00374417 [photo!]).

***Notes:*** The type specimens of *G. hofmeisteria* (*Palmer 28*) and *G. pennellii* (*Pennell 18160*) are similar and were probably collected at the same location, therefore *G. pennellii* is here recognized as a heterotypic synonym of *G. hofmeisteria*. Pennell lists the collecting locality as Cerro Mercado, the prominent rocky hill to the immediate north of Ciudad Durango, while Palmer's much earlier specimen states only "city of Durango and vicinity." Many of Palmer's types were likely collected on Cerro Mercado, which was an accessible cliffy habitat within the city's limits. The growing city of Durango now engulfs Cerro Mercado, which has been severely impacted, as it was developed for mineral resources.



**Figure 12.** *Galinsogeopsis hofmeisteria* (Rydb.) Lichter-Marck is a rare species known from only a handful of occurrences in Durango, Mexico, where it grows on igneous rock outcrops and cliffs at mid elevations in scattered sky island mountains. *Photo by Isaac Lichter-Marck.*

New records for *G. hofmeisteria* have surfaced since this taxon was last treated by Powell (1974). New populations have been found for example in limestone mountains to the southwest of Mapimi (*Wendt, Chiang, & Johnston 10017* and @idlegrraphics 38850112 (iNaturalist)) and metamorphic cliffs along the route to Nombre de Dios (*Pinkava 9598*). These populations share the vestiture of the type collections but reveal greater variation in leaf margin lobing than mentioned in the original descriptions of either *G. hofmeisteria* or *G. pennellii*. Atypical plants collected by Arturo Castro-Castro in the isolated Sierra de Gamón, Durango likely constitute an undescribed taxon of rock daisy and are currently under further study.

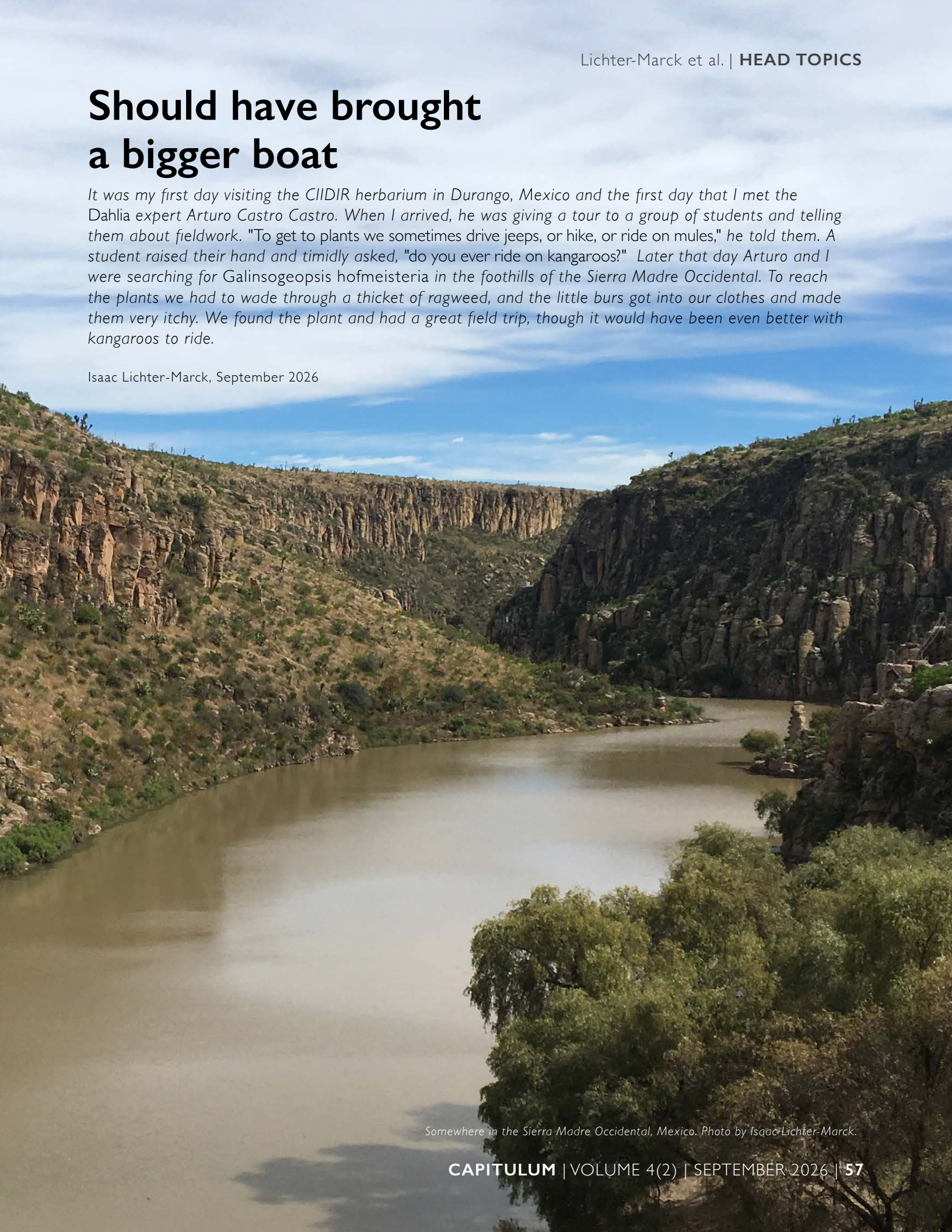
**4.8** **Galinsogeopsis jaliscana** (A.Gray) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. *Perityle jaliscana* A.Gray, Proc. Amer. Acad. Arts 22: 431, 1887. **TYPE:** Mexico, Jalisco, Río Blanco, ca. 10 mi. NW of Guadalajara, 17–23 September 1886, *E. Palmer 554* (lectotype: GH00011125 [photo!] [designated by Powell 1974] , isolectotypes: MEXU01220286 [photo!], MO934172 [photo!], NY00231065 [photo!], PH00021282 [photo!], US00124623!, YU002284 [photo!]). Figure 13.

***Notes:*** *Galinsogeopsis jaliscana* has been collected more frequently than most other cliff-dwelling rock daisies in the southern Sierra Madre Occidental due to its proximity to an urban area (Guadalajara) with an active herbarium (IBUG). Nevertheless, it has only been found within a relatively narrow range along the banks of the Río San Isidro on rock outcrops and ledges in the Sierra de San Esteban. An easy place to see *G. jaliscana* is on bare, rocky outcrops at a popular recreational climbing site on the outskirts of Guadalajara known as "El Diente," where it grows on granodiorite chimneys in a matrix of oak forest.

# Should have brought a bigger boat

*It was my first day visiting the CIIDIR herbarium in Durango, Mexico and the first day that I met the* Dahlia *expert Arturo Castro Castro. When I arrived, he was giving a tour to a group of students and telling them about fieldwork.* "To get to plants we sometimes drive jeeps, or hike, or ride on mules," *he told them. A student raised their hand and timidly asked,* "do you ever ride on kangaroos?" *Later that day Arturo and I were searching for* Galinsogeopsis hofmeisteria *in the foothills of the Sierra Madre Occidental. To reach the plants we had to wade through a thicket of ragweed, and the little burs got into our clothes and made them very itchy. We found the plant and had a great field trip, though it would have been even better with kangaroos to ride.*

Isaac Lichter-Marck, September 2026



*Somewhere in the Sierra Madre Occidental, Mexico. Photo by Isaac Lichter-Marck.*




**Figure 13.** *Galinsogeopsis jaliscana* (A.Gray) Lichter-Marck. **A.** Habit and habitat: plant growing from a minute crack in a rock face at a popular climbing destination outside of Guadalajara known as el Diente. It is a suffrutescent perennial with a woody caudex that roots in minute cracks in vertical rock outcrops in the mountains of Jalisco, Mexico. **B.** Sideview of discoid capitula showing the linear, naviculate (boat-shaped) phyllaries and white disc corollas that fade to dark lilac. *Photos by Isaac Lichter-Marck (A) and Pablo Carrillo Reyes (B).*

**4.9 Galinsogeopsis lineariloba** (Rydb.) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. *Perityle lineariloba* Rydb., N. Amer. Fl. 34(1): 18, 1914. **TYPE:** Mexico, Durango, San Ramon, 21 April–18 May 1906, *E. Palmer 89* (holotype: NY00231067 [photo!], isotypes: CM2490 [photo!], GH00011126 [photo!], K000502197 [photo!], K000502196 [photo!], UC298455!, UC145620!, US00124627!).

***Notes:*** This species, previously only known from the type collection made by Palmer in the state of Durango, at San Ramón in 1906, was recently rediscovered and photographed for the first time by Jesús Sánchez-Escalante in Sonora, near the town of Nacozari de García. This new locality is over 700 kilometers north of Palmer's collecting locality; however, additional collecting in the Sierra Madre Occidental may show that its distribution is continuous throughout low to mid elevations around the mountain range. Other rock daisies show similar disjunctions in the Sierra Madre Occidental (e.g. *Galinsogeopsis feddemae, Pericome macrocephala* B.L.Rob.) and it is too soon to tell whether these disjunctions merely reflect collecting bias.

**4.10 Galinsogeopsis microcephala** (A.Gray) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. *Perityle microcephala* A.Gray. Proc. Amer. Acad. Arts 21: 391, 1886. **TYPE:** Mexico, Chihuahua, rocky hills near Chihuahua, 8 October 1885, *C.G. Pringle 571* (lectotype: GH00011132 [photo!] [designated by Powell 1974], isolectotypes: US00124635!, UVMVT027699 [photo!]).

***Notes:*** Some uncertainty surrounding disc corolla color in *G. microcephala*, a character that does not preserve well in specimens, has been resolved by photographs from across the range of this species in the northern Sierra Madre Occidental. Disc corollas appear cream to cream-yellow and show deeper hues of lilac, red, and blue as they age. This disc corolla color occurs in other *Galinsogeopsis,* such as *G. jaliscana, G. feddemae*, as well as other rock daisies (e.g. *Eutetras palmeri, Laphamia rupestris* var. *albiflora,* and *Perityle rosei*).

**4.11 Galinsogeopsis microglossa** (Benth.) Lichter-Marck **comb. nov.** *Perityle microglossa* Benth. Bot. Voy. Sulphur [Bentham] 119, 1845. **TYPE:** Nicaragua, Realejo, 1844, *D. Sinclair s.n.* (lectotype: K000502195 [photo!] [**here designated**]). Figure 14.

*Galinsogeopsis spilanthoides* Sch.Bip., Bot. Voy. Herald [Seemann] 7-8: 307, 1856. *Pericome spilanthoides* (Sch.Bip.) Benth. & Hook.f. ex. Hemsl., Biol. Centr.-Amer., Bot. 2(9): 215, 1881. *Perityle spilanthoides* (Sch.Bip.) Rydb., N. Amer. Fl. 34: 23, 1914. **TYPE:** Mexico, Sinaloa, Sierra Madre, 1849, *B. Seeman 1982* (lectotype: K [designated by Powell 1974], isolectotypes: K000502193 [photo!], P02140850 [photo!], P02140851 [photo!]).

*Perityle acmella* Harv. & A.Gray, Mem. Amer. Acad. Arts ser. 2, 4: 77, 1849. **TYPE:** Mexico, "California," *Coulter 278* (lectotype: GH00014292 [photo!] [designated by Powell 1974], isolectotypes: K001079924 [photo!], K001079925 [photo!], TCD0090357 [photo!]).

*Perityle microglossa* var. *effusa* A.Gray, Proc. Amer. Acad. Arts 19: 19, 1883. *Perityle effusa* (A.Gray) Rose, Contr. U.S. Natl. Herb. 1(4): 104–105, 1891. **TYPE:** USA, Arizona, Pima Co., Santa Catalina Mtns., 5 June 1882, *C.G. Pringle s.n.* (lectotype: GH00011088 [photo!] [designated by Powell 1974], isolectotypes: US00124636!, UVMVT027702 [photo!]).




**Figure 14.** *Galinsogeopsis microglossa* (Benth.) Lichter-Marck var. *microglossa*, the only self-compatible, weedy annual in the genus; it grows on both decomposed and rocky soils in rural and urban settings **A.** Superior view of compact capitulum with short (1.5–3 mm) ray limbs. **B.** Plant growing out of a 1000 year old pre-colombian structure at Plazuelas, in Guanajuato, Mexico. **C.** Plant as an agricultural weed in a plantation of *Agave angustifolia* Haw. (Asparagaceae) in the town of Tequila, Mexico. *Photos by Isaac Lichter-Marck.*




**Figure 15.** *Galinsogeopsis microglossa* var. *saxosa* (Brandegee) Lichter-Marck is a delicate annual that grows in decomposed substrates in the western Sierra Madre Occidental mountain range. **A.** Lateral view of capitulescence **B.** Superior view of capitulum with white ray floret corollas, showing limbs typically larger than 3.5 mm. *Photos by Isaac Lichter-Marck.*

**4.11 A** **Galinsogeopsis microglossa** var. **saxosa** (Brandegee) Lichter-Marck **comb. nov**. *Perityle saxosa* Brandegee, Zoe 5: 225, 1905. *Perityle microglossa* var. *saxosa* (Brandegee) A.M.Powell, Rhodora 76: 273, 1974. *Galinsogeopsis spilanthoides* var. *saxosa* (Brandegee) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. **TYPE:** Mexico, Sinaloa, vicinity of Culiacán, Cerro Colorado, 5 November 1904, *Brandegee s.n.* (holotype: UC90478!, isotypes: GH00011134 [photo!], RSA0001475!). Figure 15.

*Perityle urticifolia* Rydb., N. Amer. Fl. 34(1): 18, 1914. **TYPE:** Mexico, Nayarit, Tepic, 5 January–6 February 1892, *E. Palmer 1960* (holotype: NY00231078 [photo!], isotype: US00124660!).

***Notes:*** new combinations for varieties of *Galinsogeopsis microglossa* (Benth.) Lichter-Marck are needed, with *G. spilanthoides* Sch.Bip. in heterotypic synonymy because the oldest basionym for this taxon at specific rank *Perityle microglossa* Benth., validly published in 1845, has priority.

**4.12 Galinsogeopsis montana** (A.M.Powell) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. *Perityle montana* (A.M.Powell) B.G.Baldwin, Syst. Bot. 27: 181, 2002. *Corellia montana* A.M.Powell, Brittonia 25: 116, fig. 1, 1973. **TYPE:** Mexico, Chihuahua, in mats on boulders, summit of Sierra Mohinora, 10,000–10,300 ft., 16–17 October 1959, *D.S. Correll & H.S. Gentry 23185* (holotype: LL00374150 [photo!], isotypes: BRIT23475 [photo!], GH00006217 [photo1], , UC1396197!, US00124680!). Figure 16.

***Notes:*** Between the collection of the type by Correll & Gentry (23185) on Sierra Mohinora, Chihuahua state, in 1959 and the present, this extremely rare montane rock daisy has only been reported a handful of times. Powell (1973b) originally placed this species in its own monotypic genus *Corellia* on the basis of the distinctive shape of its stalked glands. In the 1980s, Guy Nesom, Paul Lewis, and Andrew McDonald collected *G. montana* on a series of trips to Turuachi, in the municipality of Guadalupe and Calvo, also in the state of Chihuahua. DNA sequence data from these specimens was amplified for nuclear ribosomal DNA by Baldwin et al. (2002), which resolved its phylogenetic position as nested within *Perityle* sensu lato, leading to a new combination within that genus. More recently, phylogenomic-scale data has provided evidence for its recent divergence from *Galinsogeopsis* species that occur nearby in the Sierra Madre Occidental but that are very different morphologically and grow in very different habitats from the one inhabited by *G. montana*. *Galinsogeopsis montana* is unlike any other rock daisy in that it is found on moist, high elevation mountains, where it forms a dwarf, herbaceous ground cover. In September of 2019, the first photographs of *G. montana* were uploaded to iNaturalist from Sierra Mohinora by two observers, María de Los Ángeles Olvera (@ angie_olvera) and Aarón González Máruqez (@




**Figure 16.** *Galinsogeopsis montana* (A.M.Powell) Lichter-Marck. **A.** Habit and habitat on a mix of shallow volcanic tuff. Bare, exposed outcroppings of volcanic bedrock form a unique habitat in the Sierra Madre Occidental and when they occur, typically host a unique, endemic flora. These photographs suggest for the first time that the unique morphological traits of this species may have arisen as a result of selection driven by this unique microclimate. **B-C.** Close up view of the capitulum showing the four lobed disc corollas. and broad, 3-lobed ray florets corollas. *Photos by María de los Ángeles Olvera (A,C) and Aaron Gonález Márquez (B).*

# Living in the city

There are few niches in cities where wild plants can thrive. Cliff plants might be a rare exception. They establish on old rock walls and cracks in concrete. Most rock daisies are ecological specialists with narrow ranges, but a few species have expanded their territory and make their living in cities. *Galinsogeopsis microglossa* is a widespread, self-compatible annual that establishes in urban zones, and thrives on sidewalks, ditches, and old rock walls. The plants that co-athor Sophia WInitsky is pointing to here were photographed on a break from field work in Tequila, Jalisco, growing out of an old cathedral on the day of the dead.



*Tequila, Jalisco. Photo by Isaac Lichter-Marck*

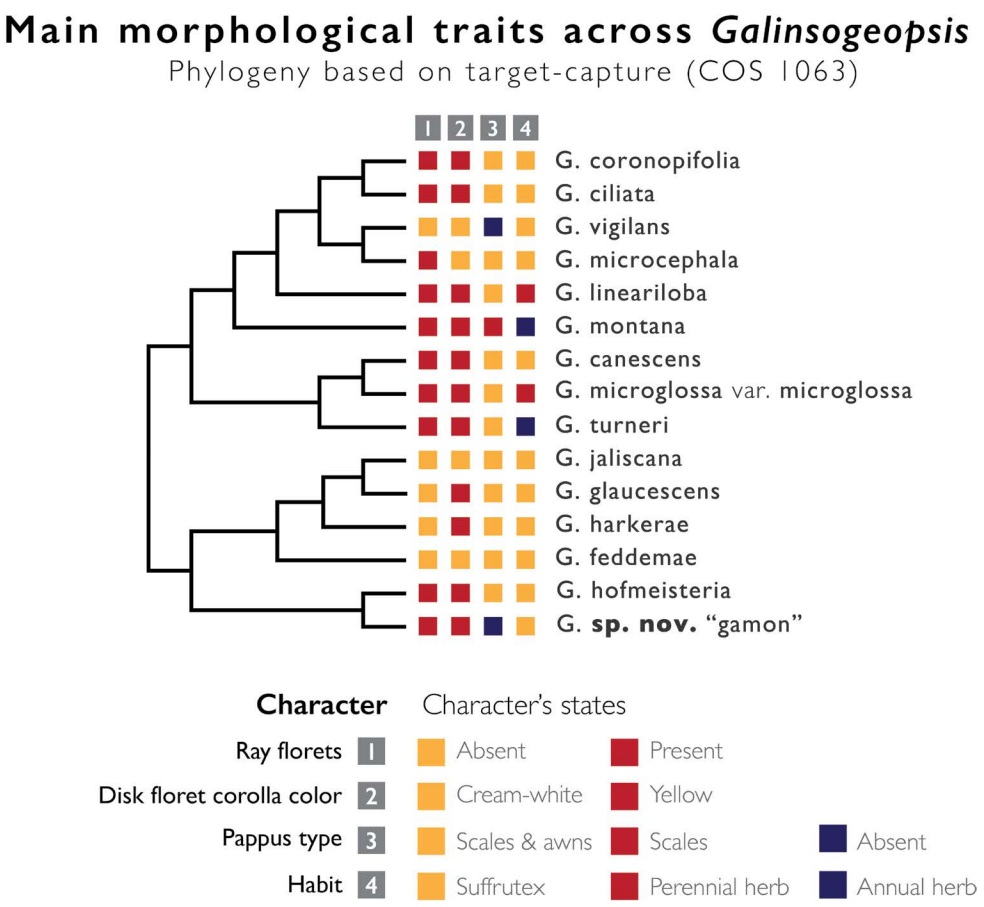



**Figure 17.** Some morphological characters useful in the identification of *Galinsogeopsis* species plotted onto a phylogeny based on Target Capture sequencing (Lichter-Marck & Baldwin 2023).

aaronbalam_tutor). These reveal *G. montana* growing on volcanic mudflow deposits, a distinctive habitat in the Sierra Madre Occidental that has a patchy distribution and often harbors a unique dwarf herb flora. In Yécora, Sonora, floristic surveys of mudflow deposits resulted in the discovery of four species new to western science, and further exploration of these moist, edaphic islands could yield more novelties in the future (Van Devender & Reina-Guerrero, 2016).

**4.13 Galinsogeopsis turneri** (A.M.Powell) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. *Perityle turneri* A.M.Powell, Madroño 21: 456, 1972. **TYPE:** Mexico, Durango, 3.4 mi. east of El Palmito, 2 April 1970, *A.M.Powell 1858* (holotype: TEX00374226 [photo!], isotypes: ASU0017130 [photo!], COLO00397638 [photo!], DES00017701 [photo!], F0050939 [photo!], NY00231077 [photo!], MEXU00398021 [photo!], MO-193722 [photo!], OS0000272 [photo!]).

***Notes:*** *G. turneri* is a rhizomatous perennial found in moist, high elevation temperate forests. It is common along Highway 40 between the cities of Durango and Mazatlán, in Sinaloa, Mexico. The habit and habitat, combined with its delicate creeping stem, and large heads show remarkable convergence with temperate Astereae (e.g. *Erigeron*).

**4.14 Galinsogeopsis vigilans** (Spellenb. & A.M.Powell) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. *Perityle vigilans* Spellenb. & A.M.Powell, Syst. Bot. 15: 252, fig. 1, 1990. **TYPE:** Mexico, Chihuahua, Municipio Maguarichi, on igneous rocks at Maguarichi and to 3 mi. NE along road, just below oak zone, 1700 m, 27°52'30"N, 107°59'30"W, 25 April 1985, *Spellenberg, Soreng, Corral & Todsen 8104* (holotype: NMC096179, isotypes: MEXU00481849 [photo!], NY231079 [photo!], SRSC00001245!, TEX00374228 [photo!], UC1555785!).

***Notes:*** Collections of this species remain limited to the type material collected by R. Spellenberg et al. in the 1980s from the "gate-like" rock formations lining the road to Maguarichi, Chihuahua, Mexico. The Latin name for this taxon means "to stand watch." Sadly, as Maguarichi has grown from a small town in the Copper Canyon country into a bustling city catering to mining exploration, the rock formations along the road have been bulldozed and limited recent exploration of cliffs in the area have not turned up more plants, despite ample suitable habitat (R. Spellenberg, pers. comm.). Recently, a photograph from approximately 40 km to the east near San Rafael, in Bocoyna municipality, Chihuahua, was uploaded to iNaturalist by @eduardovillalobos and shows an individual plant in mostly vegetative condition that resembles *G. vigilans*. This plant differs from previous collections of *G. vigilans* in that it has glabrate, greenish foliage, and does not appear to be densely covered in a grayish layer of fine hairs (Spellenberg & Powell, 1990). It is possible that there is considerable variability in this group that has been difficult to appreciate with only a few, spotty collections. It is also possible that this outlier may represent an additional undescribed taxon of rock daisies for this particularly cliffy and understudied part of the Sierra Madre Occidental.

**5** **Laphamia** A.Gray, Smithsonian Contr. Knowl. 3(5): 99, 1885. **TYPE: Laphamia lindheimeri** A.Gray. Figure 18-40.

*Leptopharynx* Rydb. N. Amer. Fl. 34(1): 21, 1914. **TYPE:** *Leptopharynx parryi* (A.Gray) Rydb.

*Monothrix* Torr., Expl. Surv. Great Salt Lake 389, 1852. **TYPE:** *Monothrix stansburyana* Torr.

*Pappothrix* (A.Gray) Rydb. N. Amer. Fl. 34(1): 26, 1914. **TYPE:** *Pappothrix rupestris* (A.Gray) Rydb.

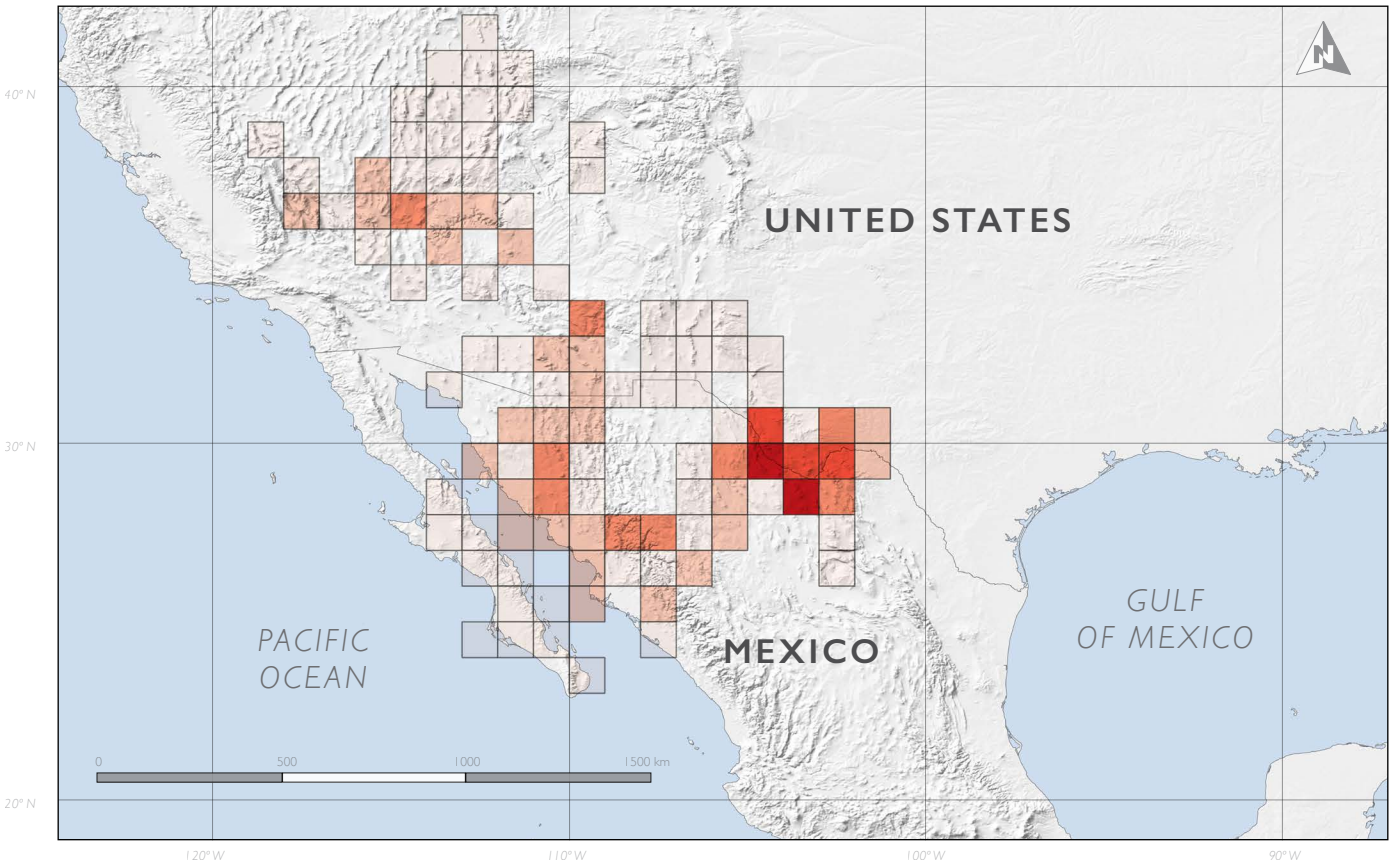



**Figure 18.** Geographic distribution of species diversity in *Laphamia* based on a vetted dataset of digitized herbarium specimen records. Centers of diversity (darker colors) include sky island archipelagos in the northern Chihuahuan, Sonoran, and Great Basin deserts. High species richness is also found in association with bare, rocky outcrops in tropical deciduous forests in northwest Mexico, where the earliest diverging *Laphamia* lineages are found.

# Evolutionary structure of *Laphamia* radiation

Phylogeny based on target-capture (COS 1063) loci

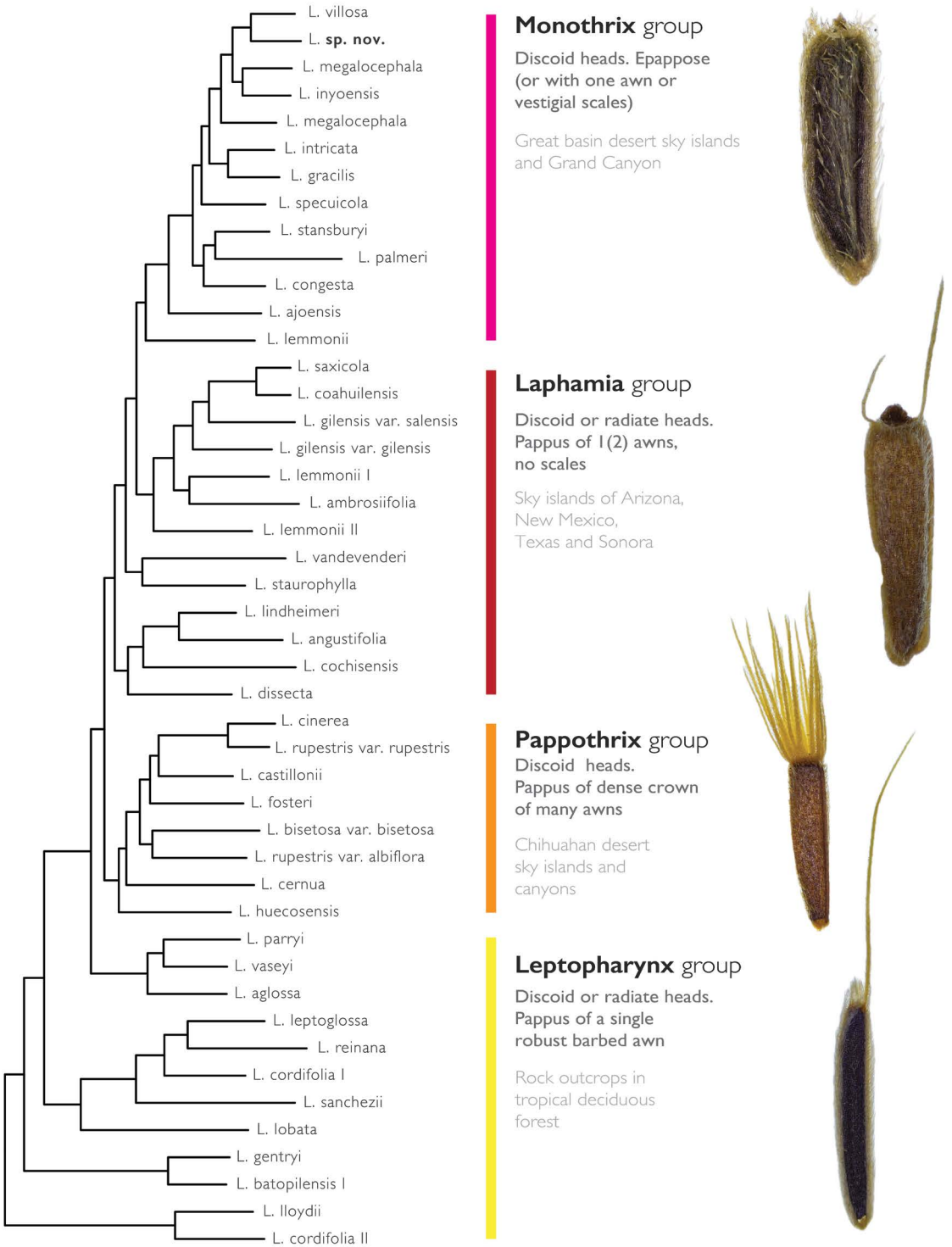



**Figure 19.** Phylogenetic hypothesis of evolutionary relationships among extant taxa in *Laphamia* A.Gray, based on target capture data using the *COS 1061* loci (adapted from Lichter-Marck et al. 2020, Lichter-Marck & Baldwin 2023). Colored lines indicate informal groupings of monophyletic groups that correspond to morphology, geography, and ecology. Photos of fruits were taken using a Leica™ dissecting microscope with focus stacking..

**5.1** **Laphamia aglossa** (A.Gray) Benth. & Hook.f. ex Hemsl., Biol. Cent-Amer., Bot. 2: 210, 1881. *Perityle aglossa* A.Gray, Smithsonian Contr. Knowl. 5(6): 107, 1852. *Leptopharynx aglossa* (A.Gray) Rydb., N. Amer. Fl. 34: 24. 1914. **TYPE:** U.S.A., Texas, Río Grande below Presidio del Norte, August 1852, *C.C. Parry s.n.* (lectotype: GH00011066 [photo!] [designated by Powell 1974], isolectotypes: NY00231052 [photo!], NY00231049 [photo!]).

***Notes:*** The discoid-headed *L. aglossa* grows on bare, rocky outcrops of limestone in the Sierra del Caballo Muerto (Dead Horse Mountains) in western Texas, and in river cut cliffs as far east along the Río Grande as San Rosendo Canyon. Occasionally, *L. aglossa* establishes on talus slopes below cliffs and these individuals may develop into larger sub-shrubs than those that anchor in consolidated rock. Variability in leaf shape, especially in the degree of marginal lobes, appears to follow a cline northward from Boquillas Canyon to the Black Gap Wildlife Management Area, with individuals found further to the north having more irregular leaf margins. Among close relatives, *L. parryi* has radiate heads and is found on decomposed and consolidated volcanic substrates in the Chisos Mountains to the east. *Laphamia vaseyi* has radiate heads and tripartite leaves, is found on decomposed calcareous substrates, and is sympatric with *L. aglossa* at the easternmost edge of its range (e.g. in Ernst Tinaja). These three species of rock daisies provide a compelling example of eco-geographic speciation on the mosaic of mountains and rock types found in the Big Bend region.

**5.2** **Laphamia ajoensis** (Todsen) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. *Perityle ajoensis* Todsen, J. Ariz. Acad. Sci. 9(1): 35, 1974. **TYPE:** U.S.A, Arizona, crevices in a seeping, north-facing volcanic cliff, about 3000 ft., above marker 14, Bull Pasture Trail, Organ Pipe Cactus National Monument, Ajo Mtns., Pima Co., 22 October 1972, *T.K. Todsen 2292* (holotype: NY00231037 [photo!], isotypes: ARIZ0004458 [photo!], ARIZ184596, SRSC00001225!).

***Notes:*** *Laphamia ajoensis* is a rare rock daisy that grows on exposed, consolidated cliffs of rhyolite in the Ajo Mountains in southwestern Arizona. It is a single sky-island endemic and disjunct from other rock daisies in *Laphamia*. Close by, *Galinsogeopsis coronopifolia* has been documented in the Baboquivari Mountains to the east, and *Perityle emoryi* grows as an ephemeral spring annual in neighboring low elevation environments. Phylogenetic data confirm Todsen's (1974) hypothesis that *L. ajoensis* is closely related to rock daisies in the southwest alliance clade (e.g. *L. megalocephala* var. *megalocephala*) in eastern California, Nevada, and Utah than to other rock daisies found in southern Arizona. The Ajo Mountains are part of Organ Pipe National Monument, and to the west of the mountains is a vast roadless expanse where it is possible that more populations of *L. ajoensis* can be found.

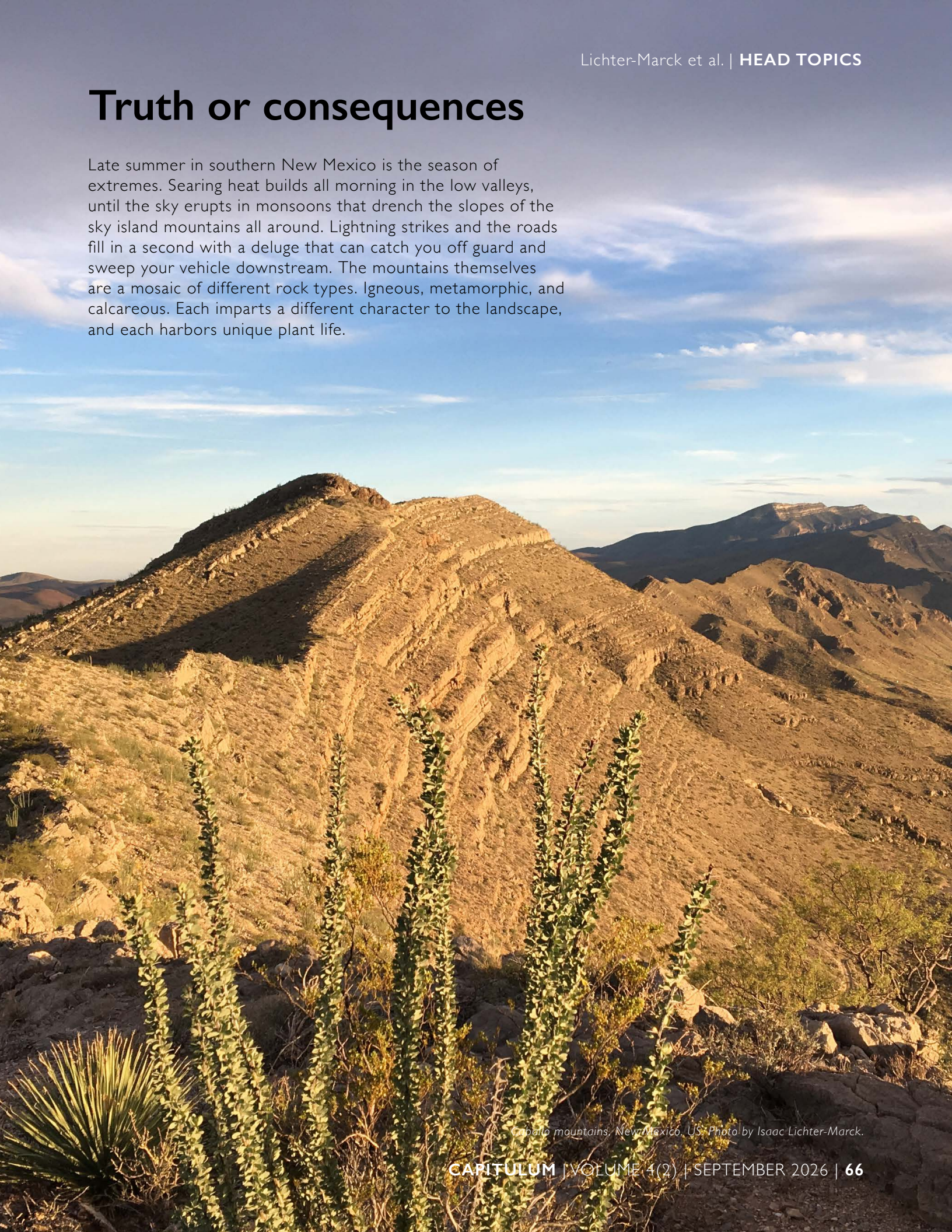
**5.3** **Laphamia ambrosiifolia** (Greene ex A.M.Powell & Yarborough) Lichter-Marck, Syst. Bot. 47(3): 807, 2022. *Perityle ambrosiifolia* Greene ex A.M.Powell & Yarborough, Phytologia 76: 325–327, fig., 1994. **TYPE:** U.S.A., Arizona, Greenlee Co., with *Prosopis*, *Euphorbia*, on face of conglomerate cliff, above San Francisco River bank, S. Clifton, 5 June 1935, *B. Maguire, B.L. Richards Jr. & T Moeller 11787* (holotype: NY00039620 [photo!], isotypes: SRSC00065860 [photo!], SRSC00065861 [photo!], SRSC00065862 [photo!], SRSC00065863 [photo!], SRSC00064221 [photo!], UTC00064687 [photo!], US00432995!).

***Notes:*** *Laphamia ambrosiifolia* is a distinctive narrowly endemic rock daisy that was singled out for description as a new species by E.L. Greene around the turn of the 20th century but never validly published until Powell and Yarborough (1994). Plants grow in cliffs of sandstone and hanging gardens along streams, in association with other hanging garden species such as *Erythranthe guttata*. This species has been highlighted as of conservation concern, because the only populations documented to date occur in Morenci, Greenlee Co., Arizona in the shadow of one of the most active mining operations in the southwest U.S. A photograph posted to iNaturalist (@cbruner:120672373) from the Galiuro Mountains of a rock daisy that slightly resembles *L. ambrosiifolia* may warrant further study as a potential range extension or new taxon because it is morphologically distinctive and geographically isolated from all known populations of *L. ambrosiifolia*.

**5.4** **Laphamia angustifolia** A.Gray, Pl. Wright. 1: 100–101, 1852. **TYPE:** U.S.A., Texas, between Texas and El Paso, 1851, *C. Wright 1194* (lectotype: GH00011068 [photo!] [designated by Powell 1974], isolectotypes: BM000810790 [photo!], GH00011067

# Truth or consequences

Late summer in southern New Mexico is the season of extremes. Searing heat builds all morning in the low valleys, until the sky erupts in monsoons that drench the slopes of the sky island mountains all around. Lightning strikes and the roads fill in a second with a deluge that can catch you off guard and sweep your vehicle downstream. The mountains themselves are a mosaic of different rock types. Igneous, metamorphic, and calcareous. Each imparts a different character to the landscape, and each harbors unique plant life.



*Caballo mountains, New Mexico, US. Photo by Isaac Lichter-Marck.*

[photo!], GH00011069 [photo!], K001079920 [photo!], K001079921 [photo!], NY00180451 [photo!], NY00180453 [photo!], NY00180454 [photo!], PH00016867 [photo!], US00124589!). Figure 20.

*Laphamia angustifolia* var. *laciniata* Torr., Rep. U.S. Mex. Bound. 2(1): 82, 1859. *Laphamia laciniata* (Torr.) Rydb., N. Amer. Fl. 34: 25, 1914. **TYPE:** U.S.A., Texas, crevices of rocks along the Río Grande, October, *Bigelow s.n.* (lectotype: NY00180454 [photo!] [**here designated**], isolectotypes: NY00180453 [photo!], US00124588!).

***Notes:*** *Laphamia angustifolia* grows on bare, rocky outcrops of limestone in the western Edwards Plateau in Texas. Closely related taxa include *L. lindheimeri,* which is found on limestone outcrops as far east as the hill country of Texas, and *L. heucosensis*, a rare rock daisy known only from limestone outcrops around El Paso, Texas and in the mountains above Juarez, Mexico. *Laphamia angustifolia* shows much variability in the degree and number of leaf margin lobes, but it is unclear whether there is an underlying geographic pattern to this morphological variation.

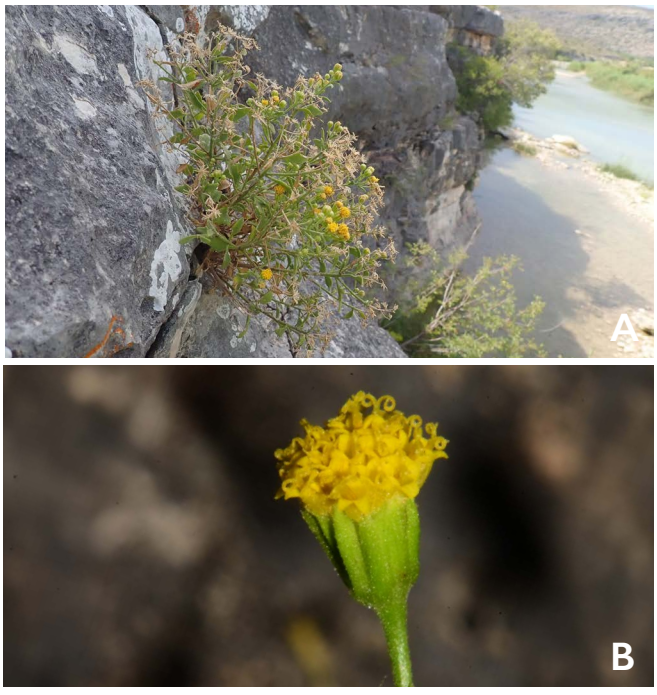



**Figure 20.** *Laphamia angustifolia* A.Gray. **A.** This species is a suffrutescent perennial with a woody caudex that roots into cliffs and caves of Cretaceous limestone on the eroded, western edge of the Edwards Plateau in trans-pecos Texas. **B.** Lateral view of discoid capitulum showing the sparsely glandular, linear, boat-shaped phyllaries and yellow disc floret corollas. *Photos by Isaac Lichter-Marck (A) and Joey Santore (B).*

**5.5 Laphamia batopilensis** (A.M.Powell) Lichter-Marck, Syst. Bot. 47(3): 808, 2022. *Perityle batopilensis* A.M.Powell, Madroño 30: 221–223, fig., 1983. **TYPE:** Mexico, Chihuahua, Municipio Batopilas, N side of Barranca de Batopilas between La Bufa and Quirare, 1590 m, 26 March 1979, *Bye et al. 9276* (holotype: COLO00397604 [photo!], isotypes: AD98614096 [photo!], COLO00397612 [photo!], CM2488 [photo!], GZU000267237 [photo!], MEXU00838932 [photo!], UCR0000086 [photo!]).

***Notes:*** *Laphamia batopilensis* is found on isolated outcroppings of volcanic rocks (mostly rhyolitic tuff) in the transition zone between tropical deciduous scrub and oak forests in the Batopilas (Copper Canyon) region of the Sierra Madre Occidental in Chihuahua, Mexico. To our knowledge, *L. batopilensis* has been collected or photographed only rarely. Photos by R. Spellenberg, C. Alexander, and W. Anderson posted to the CalPhotos webpage reveal the heads bending back and self-sowing the fruits in the cliff. Based on its similarity to *L. gentryi,* Turner (2013) considered these taxa conspecific, but *L. batopilensis* is recognized as distinct here (see comments under *L. gentryi*).

**5.6 Laphamia bisetosa** Torr., Smithsonian Contr. Knowl. 6(6): 106, 1853. *Perityle bisetosa* (Torr.) Shinners, Southw. Naturalist 4: 205, 1959. **TYPE:** U.S.A., Texas, Brewster Co., crevices of rocks in a canyon of the Río Grande below Presidio del Norte, October 1852, *C.C. Parry 579* (lectotype: GH00011071 [photo!] [designated by Powell 1974], isolectotypes: NY00180457 [photo!], NY00180456 [photo!]). Figure 21.

***Notes:*** Thus far, only one variety of *L. bisetosa* has been included in phylogenetic analyses, where it was nested among rock daisies in *Laphamia* found in neighboring habitats that were also included in Powell's (1969) *Perityle* sect. *Pappothrix* based on having a crown of typically 10–20 pappus barbs. *Laphamia bisetosa* usually has 1–2, flattened barbs, but shows similarities with these distinctive rock daisies, including being a caespitose, suffrutescent perennial with white corollas and discoid heads that grows on Cretaceous limestone outcrops. The varieties of *L. bisetosa* are all rare and found in an area with difficult access due to private land and the shifting political landscape of the highly militarized U.S.-Mexico border.

**5.6 A Laphamia bisetosa** var. **appressa** (A.M.Powell) Lichter-Marck, Syst. Bot. 47(3): 808, 2022. *Perityle bisetosa* var. *appressa* A.M.Powell, Sida 3: 178–180, 1967. **TYPE:** U.S.A., Texas, Brewster Co., E face of the limestone caprock of a small mountain peak on the N rim of San Francisco Creek canyon, 5 July 1966, *J. Scudday, S. Sikes & A.M.Powell 626* (lectotype: SRSC00001228 [**here designated**] [photo!], isolectotypes: BRIT23895 [photo!], 00011070 [photo!], SRSC00001227 [photo!], SRSC00001229 [photo!], TEX00374213 [photo!], US00124593!).

**5.6 B Laphamia bisetosa** var. **scalaris** (A.M.Powell) Lichter-Marck, Syst. Bot. 47(3:) 808, 2022. *Perityle bisetosa* var. *scalaris* A.M.Powell, Sida 3: 177–178, 1967. **TYPE:** U.S.A., Texas, Brewster Co. in crevices of lower limestone bluffs, Black Gap Game Preserve, ca. 4 mi S of headquarters, Cave Hill, E side, along Stairstep Mtn., 25 September 1965, *A.M.Powell & T. Watson 1394* (holotype: SRSC00001230!, isotypes: BRIT23896!, TEX00374214 [photo!]).



**Figure 21.** *Laphamia bisetosa* var. *bisetosa* (A.M.Powell) Lichter-Marck is a rare rock daisy found on bare, rocky outcrops of limestone along the Río Grande in western Texas. The individual pictured here was growing as a compact mat, out of a solid calcareous bedrock. Notice the single series of phyllaries and foliage, as well as the discoid capitulum with white disc florets corollas. *Photos by Isaac Lichter-Marck.*

**5.6 C Laphamia bisetosa** var. **spathulata** (A.M.Powell) Lichter-Marck, Syst. Bot. 47(3): 808, 2022. *Perityle bisetosa* var. *spathulata* A.M.Powell, Sida 5: 85, fig. 4, 1973. **TYPE:** Mexico, Coahuila, limestone bluffs in large, dead-end, Boquilla Canyon, Sierra de la Encantada, ca. 92.5 mi NW of Musquiz, 22 May 1968, *A.M.Powell & D. Patterson 1588* (holotype: SRSC00001231!, isotypes: BRIT735555 [photo!], LL00059826 [photo!], LSU00210015 [photo!], TEX00374215 [photo!]).

**5.7 Laphamia carmenensis** (A.M.Powell) Lichter-Marck, Syst. Bot. 47(3): 808, 2022. *Perityle carmenensis* A.M.Powell, Sida 6(4): 311, 1976. **TYPE:** Mexico, Coahuila, Maderas del Carmen, 102° 36' 30" W, 0.5 mi. N of El Dos on trail to El Tres, 2325 m, along stream, on overhanging cliff of igneous rock (rhyolite?) in thin soil, 7 August 1974, *A. Adamcewicz & T. Wendt 525* (holotype: TEX00374216 [photo!], isotype: MEXU00253514 [photo!]).

***Notes:*** *Laphamia carmenensis* remains known only from the type location in the Sierra del Carmen, in Coahuila, Mexico, where it was last collected in 1989. Label data indicates that this species grows on consolidated rhyolitic rock cliffs, including in the shade of overhangs. The presence of ray florets suggests it might represent a close relative of *L. coahuilensis,* which itself is more closely related to rock daisies found in Arizona than species distributed close by in Mexico or Texas. So far, this species has not been included in molecular analyses.

**5.8 Laphamia castillonii** (I.M.Johnst.) Everly, Contr. Dudley. Herb. 3: 378, 1947. *Perityle castillonii* I.M.Johnst., J. Arnold Arbor. 22: 122, 1941. **TYPE:** Mexico, Coahuila, Cañón del Indio Felipe, Sierra Hechiceros, frequent in crevices of cliffs in deep canyon, 18 September 1940, *Johnston & Muller 1359* (lectotype: GH00011101 [photo!] [**here designated**], isolectotypes: F0050935 [photo!], GH00011103 [photo!]).

***Notes:*** This species was last collected in the 1970s and is known from igneous cliffs at only two locations, including the type locality in the Sierra Hechiceros (Johnston & Muller 1359), and an isolated peak to the immediate SE called Picacho de Noche Buena (Chiang, Wendt, & Johnston 9640-B).

**5.9 Laphamia cernua** Greene, Bull. Torrey Bot. Club 25(3): 122, 1898. *Pappothrix cernua* (Greene) Rydb., N. Amer. Fl. 34: 27, 1914. *Perityle cernua* (Greene) Shinners, Southw. Naturalist 4: 20, 1959. **TYPE:** U.S.A., New Mexico, Doña Ana Co., Organ Mts., 6500 ft., 4 September 1897, *E.O. Wooton 476?* (lectotype: NDG00247 [photo!] [designated by Powell 1969], isolectotypes: MO-714504 [photo!], MIN1001582 [photo!], NY00180459 [photo!], US00124596!, US00931224!). Figure 22.

***Notes:*** *Laphamia cernua* has only been documented in the Organ Mountains of southern New Mexico where it grows on difficult to reach, bare, rhyolitic cliffs and overhangs. Recent photographs taken in a natural community context show for the first time that *L. cernua* exhibits "self-sowing" behavior, in which the heads recurve toward the rock face at maturity, releasing fruits back into cracks in the cliff.

**5.10 Laphamia cinerea** A.Gray, Rep. U.S. Mex. Bound. 2(1): 82, 1859. *Pappothrix cinerea* (A.Gray) Rydb., N. Amer. Fl. 34: 27, 1914. *Perityle cinerea* (A.Gray) A.M.Powell, Sida 3: 278, fig. 20, 1968. **TYPE:** U.S.A., Texas, on rocks near Escondido Creek, September, *Bigelow s.n.* (lectotype: GH00011106 [photo!] [designated by Powell 1969], isolectotypes: NY00180458 [photo!], US00124598!).

***Notes:*** Although *L. cinerea* is presumably a common species on limestone outcrops and ledges throughout the Edwards Plateau, access to populations of this plant are severely restricted by private land holdings. The last time this species was collected was in 1977 by Mary Butterwick and Emily Lott. In 2026, Saunders Drucker uploaded the first photos of this species to inaturalist. the first time this plant had been observed in over 49 years. Much of the range of *L. cinerea* is under heavy use for resource extraction of fossil fuels, and exploitation has probably negatively affected the species, but no data on population trends exists.

**5.11 Laphamia coahuilensis** (A.M.Powell) Lichter-Marck, Syst. Bot. 47(3): 808, 2022. *Perityle coahuilensis* A.M.Powell, Sida 5: 10, fig. 9, 1973. **TYPE:** Mexico, Coahuila, deep narrow canyon, ca. 2 km SE of Puertecito, W end of Sierra de la Madera, ca. lat. 27.15° N, 21 September 1941, *I.M.Johnst. 9311* (holotype: GH00011109 [photo!], isotypes: GH00011107 [photo!], LL00374218 [photo!]).




**Figure 22.** *Laphamia cernua* Greene is a rare rock daisy endemic to a single mountain range in southern New Mexico, the organ mountains, where it grows as an extreme edaphic specialist on vertical cliffs of solid rhyolite. **A.** Lateral view of capitulum showing the linear phyllaries and discoid heads with yellow disc floret corollas. Capitula in this species show self-sowing behavior, in which the head bends back toward the cliff upon maturity of the cypselae. **B.** Close up of the cypselae, which have a distinctive pappus characteristic of the *Pappothrix* group within *Laphamia*, that is cylindrical, with callous margins and a dense corona of 15 to 20 antrorsely serrated awns. *Photos by Isaac Lichter-Marck.*

***Notes:*** *Laphamia coahuilensis* occurs in association with bare limestone cliffs in three mountain ranges in Cuatro Cienegas Municipality, Coahuila, Mexico. These include the Sierra del Carmen and Sierra San Marcos, and in the Cañón Ojo de Agua near Las Delicias, off the Federal Highway 30. *Laphamia coahuilensis* is an outlier among rock daisies of the Chihuahuan Desert sky islands for its sub-cruciform leaf shape, radiate heads, fruits lacking conspicuous pappus scales, and a tetraploid chromosome



**Figure 23.** *Laphamia cochisensis* W.E.Niles is endemic to a single sky island, the Chiricahua mountain range in south eastern Arizona, where it is an extreme edaphic endemic growing on vertical cliffs of rhyolite at mid to high elevations. This photograph captures the compact habit and extreme habitat of the plant, as well as its glabrous, deltate leaves with irregular lobes, and discoid capitula with yellow disc floret corollas. *Photo by Isaac Lichter-Marck.*

number. Until recently, phylogenetic relationships of *L. coahuilensis* have remained a head-scratching mystery. To quote Powell (1973a), "this rare and unusual species has commanded special attention regarding systematic studies in sect. *Laphamia*. In the first place, it has not been possible to realize any certain interspecific relationship for *P. coahuilensis*." Molecular phylogenetic data resolved at long last the mystery of *L. coahuilensis* and show that it is more closely related to three geographically distant rock daisies, *Laphamia gilensis* var. *gilensis*, *Laphamia gilensis* var *salensis*, and *Laphamia saxicola*, all endemic to the Superstition Mountains in Arizona. *Laphamia coahuilensis* is morphologically similar to all three of these species. Thus, *L. coahuilensis* constitutes a remarkable case of long-distance dispersal between sky islands 1000 kilometers apart in the Basin and Range province of western North America.

**5.12 Laphamia cochisensis** W.E.Niles, Mem. N.Y. Bot. Gard. 21: 47–49, 1970. *Perityle cochisensis* (W.E.Niles) A.M.Powell, Sida 5: 10, 1973. **TYPE:** U.S.A., Arizona, Cochise Co., north facing cliffs of Echo Canyon, elev. ca. 2000 m, Chiricahua Nat'l Mon., 5 October 1964, *Niles 377* (holotype: ARIZ0004421 [photo!], isotype: TEX00374188 [photo!]). Figure 23.

***Notes:*** *Laphamia cochisensis* is an endemic of the Chiricahua Mountains, a sky island in southeast Arizona, USA, where it grows exclusively on consolidated rock outcrops and cliffs of rhyolite. Populations in the northern Chiricahua Mountains are found within the Chiricahua National Monument and differ in leaf shape and leaf pubescence from populations found at the southern end of the mountain range, amongst the spires of Cave Creek. Northern populations have glabrate leaves that are usually deeply lobed, while plants in the southern portion of the range have appressed-short-villous leaves that are not deeply lobed. An abundance of variation is present overall across both populations, and more study of this rare plant is needed.

**5.13 Laphamia cordifolia** (Rydb.) Lichter-Marck, Syst. Bot. 47(3): 809, 2022. *Leptopharynx cordifolia* Rydb., N. Amer. Fl. 34: 22, 1914. *Perityle cordifolia* (Rydb.) S.F.Blake, Contr. U.S. Natl. Herb. 23: 1602. 1926. **TYPE:** Mexico, Sinaloa, Vicinity of Topolobampo, 23 March 1910, *J.N. Rose, P.C. Standley & P.G. Russell 13294* (holotype: NY00180531 [photo!], isotypes: GH00011110 [photo!], US00124600!). Figure 24.

***Notes:*** *Laphamia cordifolia* is found exclusively on bare rocky outcrops of volcanic bedrock and rhyolitic tuff surrounded by moist, tropical deciduous forests in the foothills of the Sierra Madre Occidental in Sonora and Sinaloa. The capitula exhibit self-sowing behavior, in which the heads bend back upon maturity and effectively plant their fruits into the cliff face below the broad, cordate leaves. The samples included to date in molecular phylogenies do not support the monophyly of this taxon, with scattered populations that have been documented between Ciudad Obregón, in Sonora, and Culiacán, in Sinaloa, forming one group, and the populations documented along the road to Yécora (*Reina 98-256*, *Reina 2001-159*) forming another. More detailed morphological study may reveal that the populations from along Highway 16 constitute a new taxon as these are phylogenetically distinct, geographically disjunct, and found at a higher elevation.




**Figure 24.** *Laphamia cordifolia* (Rydb.) Lichter-Marck. **A.** Habit and habitat: This rock daisy grows exclusively on bare, rocky outcrops of volcanic substrates surrounded by a matrix of tropical deciduous forest in northwestern Mexico. **B.** Superior view of an individual showing the large capitula with yellow corollas, ray corollas with long-linear (10–15mm) limbs, as well as the broad, green, cordate leaves with a dense glandular indumentum. *Photos by Isaac Lichter-Marck.*

**5.14 Laphamia dissecta** Torr., Smithsonian Contr. Knowl. 5(6): 81, 1853. *Perityle dissecta* (Torr.) A.Gray, Syn. Fl. N. Amer. 1(2): 320–321, 1884. *Leptopharynx dissecta* (Torr.) Rydb., N. Amer. Fl. 34(1): 24, 1914. **TYPE:** U.S.A., Texas, Presidio Co., Presidio Del Norte, August 1852, *J.M. Bigelow 77* (lectotype: NY [designated by Powell 1974], isolectotypes: GH00011116 [photo!], US!).

***Notes:*** *Laphamia dissecta* is found exclusively on bare outcrops of limestone on isolated sky islands across a large geographic range in western Texas and may constitute a species complex. *Laphamia dissecta* is associated with calcareous cliffs, such as those found along the Río Grande near Santa Elena Canyon in Big Bend National Park, however populations have also been found on flat karst outcroppings in the Chinati Mountains in western Texas. The population at Santa Elena Canyon was observed in the 1970's and not observed again for 50 years until its recent re-discovery by C. Frasch. The phylogenetic position of *L. dissecta* is unclear. Limited sampling so far has resolved *L. dissecta* in three equally supported positions, as the sister clade to those taxa found in Big Bend NP (*L. vaseyi, L. parryi,* and *L. aglossa*), those of the Edwards Plateau further east (e.g. *L. angustifolia, L. lindheimeri, L. cinerea*), and the rock daisies found in sky islands of New Mexico and Arizona (e.g. *L. staurophylla* and *L. lemmonii*). More dense population and genomic sampling may be needed to help solve the equivocal placement of this taxon.

**5.15 Laphamia fosteri** (A.M.Powell) Lichter-Marck, Syst. Bot. 47(3): 809, 2022. *Perityle fosteri* A.M.Powell, Madroño 30: 217–219, fig., 1983. **TYPE:** U.S.A., Texas, Culberson Co., Apache Mts., Panther Canyon, limestone boulders and bluffs, 3 July 1978, *A.M.Powell 3365* (holotype: SRSC00001233 [photo!], isotypes: NY231040 [photo!], MO101406562 [photo!], TEX00374220 [photo!]).

***Notes:*** Four decades after it was described, *L. fosteri* is still known only from the type location in Panther Canyon, in the Apache Mountains of western Texas. The plant was named by A. M. Powell for a prominent rancher who had owned the property where the plant was found. Ironically, efforts to relocate the plant have been unsuccessful because of strict private property rules. Phylogenetic data obtained from leaf tissue on specimens is supportive of *L. fosteri* as a distinctive taxon closely related to rock daisies found in neighboring sky islands in western Texas.

**5.16 Laphamia gentryi** (A.M.Powell) Lichter-Marck, Syst. Bot. 47(3): 809 (2022). *Perityle gentryi* A.M.Powell, Sida 5: 10, 1973. **TYPE:** Mexico, Sonora, Saguaribo, Río Mayo, transition pine country, 5500 ft., 2 November 1935, *H.S. Gentry 2109* (holotype: GH00011117 [photo!], isotypes: ARIZ0004463 [photo!], ARIZ0005301 [photo!], MEXU01220284 [photo!], PH00021280 [photo!], TEX00060074 [photo!], UC576839!, US00124611!). Figure 25.

*Perityle alamosana* B.L.Turner, Phytologia 74: 265, 1993. **TYPE:** Mexico, Sonora, Rancho San Pedro and upper entrance of the cañón, *P.S. Martin, C. Lindquist, S. Meyer s.n.* (holotype: TEX00374212 [photo!], isotype: ARIZ297838 [photo!]).




**Figure 25.** *Laphamia gentryi* (A.M.Powell) Lichter-Marck. **A.** Habit and habitat: This rare rock daisy grows as a suffrutescent perennial subshrub on bare, rocky outcrops and at the entrance to bat caves in tropical deciduous forests and mid-elevation oak forests in northwestern Mexico. Individuals shown here are hanging from rock. **B.** Close up of radiate capitulum showing yellow corollas. *Laphamia gentryi* is one of the rock daisies that show a unique "self-sowing" behavior in which the heads bend back upon maturity, self seeding in the cliff face. *Photos by Isaac Lichter-Marck (A) and Alejandro Sigala Chávez.*

***Notes:*** *Laphamia gentryi* is found on isolated outcroppings of volcanic rocks in tropical deciduous and mid-elevation oak forests on the western slopes of the Sierra Madre Occidental in Sonora, Mexico. *Laphamia batopilensis* was considered conspecific with *L. gentryi* by Turner (2013) but is retained here as a distinct taxon. Ray florets are present in *L. gentryi* and absent *in L. batopilensis*, and *L. batopilensis* is found on eastern slopes of the Sierra Madre Occidental while all known populations of *L. gentryi* thus far known occur on western slopes. Photos taken by R. Villa at Rancho Santa Bárbara in Álamos, show that *L. gentryi* self-sows its seeds by bending of the peduncle back upon maturity. These taxa are resolved as sister taxa in phylogenies.

**5.17 Laphamia gilensis** M.E.Jones, Zoe 2: 15, 1891. *Leptopharynx gilensis* (M.E.Jones) Rydb., N. Amer. Fl. 34(1): 24, 1914. *Perityle gilensis* (M.E.Jones) J.F.Macbr., Contr. Gray Herb. 56: 39, 1918. **TYPE:** U.S.A., Arizona, growing among rocks at Putnam's ranch, near the Gila River, 23 May 1890, *M.E.Jones s.n.* (lectotype: POM[RSA0001349] [photo!] [designated by Powell 1973a], isolectotypes: UC90442!, US00124612!). Figure 26.

*Laphamia arizonica* Eastw., Proc Calif. Acad. Sci. ser. 4, 20: 159, 1931. **TYPE:** U.S.A., Arizona, Maricopa Co., Fish Creek, Apache Trail, 18 May 1919, *A. Eastwood 8753* (holotype: CAS00123290!, isotype: US00124590!).

*Laphamia dura* A.Nelson, Amer. J. Bot. 23: 266, 1936. **TYPE:** U.S.A., Arizona, Maricopa Co., Salt River Valley, near Canyon Lake, 3 May 1925, *A.Nelson 10323* (lectotype: RM138006 [designated by Powell 1974]).

***Notes:*** *Laphamia gilensis* var. *gilensis, L. gilensis* var. *salensis* and *L. saxicola* are distinctive evolutionary lineages of rock daisies all found within the geologically complex Superstition Mountains in central Arizona. All three taxa are found exclusively on bare outcrops of volcanic bedrock and cliffs, which are common in the Superstition range. A fourth taxon, *L. coahuilensis* is phylogenetically nested within the Superstition Mountains clade and represents an example of long-distance dispersal across a huge expanse of desert to sky island habitats in Coahuila, Mexico. Populations of *L. gilensis* var. *gilensis* found around Oak Flat, Arizona are in danger of habitat loss due to mining expansion.



**Figure 26.** *Laphamia gilensis* var. *gilensis* M.E.Jones. Lateral view of the radiate capitulum shows the linear phyllaries, as well as the yellow ray and disc corollas. This is a rock daisy species restricted a single mountain range, the Superstition Mountains in Arizona, where it occurs at low elevations on bare, rocky outcrops and cliffs. *Photo by Isaac Lichter-Marck.*

**5.17 A** **Laphamia gilensis** var. **salensis** (A.M.Powell) Lichter-Marck, Syst. Bot. 47(3): 809, 2022. *Perityle gilensis* var. *salensis* A.M.Powell, Sida 5(2): 104–106, 1973. **TYPE:** U.S.A., Arizona, Gila Co., Salt River canyon between Globe and Show Low, 18 August 1869, *S. Sikes 428* (holotype: SRSU00001235 [photo!], isotype: TEX00374221 [photo!]).

*Laphamia gilensis* subsp. *longiloba* W.E.Niles, Mem. New York Bot. Gard. 21(1): 51, fig. 30, 1970. *Perityle gilensis* var. *longiloba* (W.E.Niles) A.M.Powell & Yarb. Phytologia 82: 328, 1997. **TYPE:** U.S.A., Arizona, Gila Co., lowermost, north-facing cliffs of Salt River canyon, near crossing of Highway 60, ca. 915 m, 13 October 1964, *W.E.Niles 453* (holotype: ARIZ0004422!).

***Notes:*** This variety is still only known from the type locality at the crossing of Highway 60 over the Salt River in the Superstition Mountains of Arizona. Future work via raft may uncover additional populations downstream.

**5.18** **Laphamia gracilis** M.E.Jones, Proc. Calif. Acad. Sci. ser. 2, 5: 703–704, 1895. *Perityle gracilis* (M.E.Jones) Rydb., N. Amer. Fl. 34(1): 19, 1914. **TYPE:** U.S.A., Arizona, below Nagle's Ranch, edge of Buckskin Mtns., crevices of limestone rocks, 7000 ft, in very dry places. 15 September 1894. *M.E.Jones 6050c* (lectotype: POM[RSA0001350]! [designated by Powell 1974], isolectotype: US00124613!).

*Laphamia fastigiata* Brandegee, Bot. Gaz. 27: 450, 1899. *Monothrix fastigiata* (Brandegee) Rydb., N. Amer. Fl. 34(1): 21, 1914. *Perityle fastigiata* (Brandegee) Shinners, Southw. Naturalist 4: 204, 1959. **TYPE:** U.S.A. Nevada, Sheep Mtns., 4–5000 ft, May-October 1898, *C.A. Purpus 6142* (lectotype: UC90434! [designated by Powell 1974], isolectotypes: E00417410 [photo!], M0030096 [photo!], US00931225!, US00124609!).

***Notes:*** *Laphamia gracilis* is a species complex that includes morphologically diverse populations of rock daisies found in sky islands across a huge area of Great Basin Desert from Clark County, Nevada in the east, to Great Basin National Park in the west, and the Kaibab Plateau of northern Arizona to the south. Although the type of *L. gracilis* was apparently collected in the Buckskin Mountains of Arizona by Marcus Jones, the type location has not been recollected, and the species had not been documented again in Arizona until recently, when a disjunct population was found in Diablo Canyon and posted to iNaturalist by J. Santore in 2019. At least three distinct morphological forms fall under *L. gracilis* and these are supported as distinct lineages in molecular analyses. The common apomorphy of three-lobed (more or less) or sub-cruciform leaves with an attenuate leaf base is present in all of these, but the leaves of plants found in eastern Nevada (e.g. in Condor Canyon) are broader and more glandular hairy than populations in western Nevada. These plants also differ in odor and phyllary shape. The more western populations that conform to the descriptions in the Intermountain Flora and Flora of North America may be assignable to the name *L. fastigiata,* which was described from a type specimen collected in the Sheep Mountains, Nevada. The obstacle in recognizing these as separate from *L. gracilis* is confusion surrounding Marcus Jones' type collection from the Buckskin Mountains in Arizona, which

resembles neither of the morphological forms mentioned above. Phylogenetic analyses support a close relationship between the population found in Diablo Canyon and the rock daisies that occur in the Superstition Mountains in Arizona, suggesting it may represent an undescribed taxon, pending further study.

**5.19 Laphamia grandifolia** (Brandegee) Everly, Contr. Dudley Herb. 3: 379, 1947. *Perityle grandifolia* Brandegee, Zoe 5: 224–225, 1905. *Leptopharynx grandifolia* (Brandegee) Rydb., N. Amer. Fl. 34: 23. 1914. **TYPE:** Mexico, Sinaloa, Cerro Colorado, vicinity of Culiacán, 5 November 1904, *T.S. Brandegee s.n.* (lectotype: UC90479! [designated by Powell 1973a], isolectotypes: GH00011118 [Photo!], US00124614!). Figure 27.

***Notes:*** Following its description by T.S. Brandegee in 1904, *L. grandifolia* was "lost" and not documented again for 116 years. In 2020, as part of Fernando Pio Leon's floristic work in Sinaloa, this species was rediscovered near the type locality and photos were uploaded to iNaturalist, where they selected as the "observation of the day." Photos reveal that the plant grows on bare outcrops of volcanic bedrock surrounded by tropical deciduous forests. The heads are borne on long peduncles that are arranged in a paniculiform array, and the capitula appear to bend back towards the rock, "self-sowing" upon maturity. An additional population has been posted to iNaturalist by @mar_y_sierra_silvestre (obs. 264893492) in Palmarito de San Javier, Sinaloa that extends the known range by about 40 km.

**5.20 Laphamia huecoensis** (A.M.Powell) Lichter-Marck, Syst. Bot. 47(3): 809, 2022. *Perityle huecoensis* A.M.Powell, Madroño 30: 219–221, fig., 1983. **TYPE:** U.S.A., Texas, El Paso Co., North Hueco Mts., Hueco Tanks area, Navar Ranch, ca. 31°54'N, 106°07'W, 24 September 1977, *McCarten & Van Devender 2508* (holotype: SRSC00001236!, isotypes: BRIT329199!, NY00231042 [photo!]).

***Notes:*** Recent attempts to access the type location of *L. huecosensis* have so far been unsuccessful due to private land restrictions. A second population uncovered by R. Spellenberg in the Sierra Juarez in 1993 is the only other known location for this species. Phylogenetic data supports its close relationship to *L. cernua* in the neighboring, yet geochemically distinct, Organ Mountains, in New Mexico.




**Figure 27.** *Laphamia grandifolia* (Brandegee) Everly. **A.** Superior view of the radiate capitulum showing the yellow corollas. **B.** Lateral view of the capitulum revealing the linear, pilose phyllaries. **C.** A single individual found growing on a bare rocky outcrop with signs of calcareous caliche; this unique species has the largest leaves (5–7cm long) of any rock daisy. *Photos by @mar_y_sierra_silvestre (A), J. Fernando Pío León (B), and Efraín Payán Cázarez @licepayan (C) on iNaturalist.*

**5.21 Laphamia intricata** Brandegee, Bot. Gaz. 27: 450, 1899. *Monothrix intricata* (Brandegee) Rydb., N. Amer. Fl. 34(1): 20, 1914. *Laphamia megacephala* subsp. *intricata* (Brandegee) D.D.Keck, Aliso 4: 101, 1958. *Perityle intricata* (Brandegee) Shinners, Southw. Naturalist 4: 204, 1959. *Perityle megalocephala* var. *intricata* (Brandegee) A.M.Powell, Sida 5: 94, 1973. **TYPE:** U.S.A., Nevada, Sheep Mountain, on rocks, May–October, 1898. *C.A. Purpus 6134* (lectotype: [designated by Powell 1973a], UC90437!, isolectotypes: CAS00123292!, PH00016865 [photo!], US01101414!). Figure 27.

***Notes:*** *Laphamia intricata* grows on bare outcrops of calcareous bedrock in desert sky islands in the Great Basin and Mojave deserts. Phylogenetic data support the recognition of *L. intricata* at species rank, rather than as a subspecific variety of *L. megalocephala,* as has been suggested in the past. It is the sister lineage to *L. gracilis* and distinguished by its heads arranged in tight corymbiform arrays.



**Figure 28.** *Laphamia intricata* Brandegee is a suffrutescent perennial rock daisy that roots into bare, rocky outcrops of limestone and cliffs in sky islands of the Great Basin desert. The discoid capitula are sparsely short-hairy, have yellow corollas, and are typically aggregated into loose corymbiform arrays. *Photo by Isaac Lichter-Marck.*



**Figure 29.** *Laphamia inyoensis* Ferris is a rock daisy endemic to the southern Inyo mountains in California, where it is threatened by the encroachment of resource extraction (gold mining). Superior view of discoid capitulum shows the yellow, four-lobed disc corollas with exserted style-branches. *Photo by Isaac Lichter-Marck.*

**5.22 Laphamia inyoensis** Ferris, Contr. Dudley Herb. 5(4): 104–106, f. 2, 1958. *Perityle inyoensis* (Ferris) A.M.Powell, Sida 3(4): 278, 1968. **TYPE:** U.S.A., California, Inyo Co., Cerro Gordo peak, 8200ft. 7 July 1942. *A. Alexander & L. Kellogg 3056a* (holotype: DS[CAS00123294]!, isotypes: CAS00123293!, GH00011078 [photo!], LL00374222 [photo!], NY00180468 [photo!], RSA0001351!, US00124622!). Figure 29.

***Notes:*** In ten years, our knowledge of *L. inyoensis* has grown tremendously, in part because its narrow range is the center of controversy. It is the site of a proposed gold mining exploration project, the so-called Mojave Project by the Canadian gold corporation K2. In 2016 when the project was in its initial planning phases, *L. inyoensis* was known only from a couple of collections near the type locality on Cerro Gordo, in the southern Inyo Mountains. In 2018 and 2019, additional occurrences of *L. inyoensis* were documented further south and throughout the area proposed for mining. Most of these new occurrences were documented by Maria Jesus, Duncan Bell, Naomi Fraga and other botanists from California Botanical Garden as part of Jesus' masters thesis on the Conglomerate Mesa flora (Jesus, 2021). Katy Allerton and I also documented populations throughout Conglomerate Mesa and just north of Cerro Gordo as part of general collecting for phylogenetic studies of Perityleae. In addition to her excellent flora, Maria Jesus also completed

a detailed conservation plan for *L. inyoensis,* which formed the basis for her petition to list *L. inyoensis* as a state endangered species. After reviewing detailed ecological, evolutionary, and occurrence data, California CDFW approved this petition, effectively protecting the mesa from proposed mining activities until the project could undergo a detailed review and approval process, which is ongoing.

**5.23 Laphamia lemmonii** A.Gray, Proc. Amer. Acad. Arts 16: 101, 1880. *Leptopharynx lemmonii* (A.Gray) Rydb., N. Amer. Fl. 34(1): 24, 1914. *Perityle lemmonii* (A.Gray) J.F.Macbr., Contr. Gray Herb. 56: 39, 1918. **TYPE:** U.S.A., Arizona, Pima Co., near Camp Lowell, Tucson, 1880. *Lemmon s.n.* (lectotype: [designated by Powell 1973a] GH00011079 [photo!]; isolectotypes: MO100507844, NDG61179 [photo!]). Figure 29.

*Laphamia lemmonii* var. *pedata* A.Gray, Proc. Amer. Acad. Arts 16: 101, 1880. **TYPE:** U.S.A., Arizona, Pima Co., Santa Catalina Mountains, near Camp Lowell, Tucson, *Lemmon s.n.* (lectotype: [designated by Powell 1973a], GH00011079 [photo!]).

***Notes:*** *Laphamia lemmonii* grows on bare rocky outcrops of various lithologies (substrate types). This taxon is a widespread complex found on isolated sky islands throughout southeast Arizona and southwest New Mexico. Morphological variation in leaf shape and vestiture appears to track geography and ecology in terms of elevation and rock substrate type. Limited phylogenetic data have thus far shown that the populations referred to as *L. lemmonii* do not form a monophyletic group, and a detailed morphometric and genetic study is underway.




**Figure 30.** *Laphamia lemmonii* A.Gray represents a rock daisy species complex that occurs on isolated sky island mountain ranges throughout southeastern Arizona and southern New Mexico, where it shows variability in leaf moprphology and ecology across its range. Molecular phylogenetic data suggests the complex does not form a monophyletic group, and therefore needs further attention. **A.** Habit and habitat on a granite cliff face in the Graham mountain range, Arizona. **B.** Habit and habitat on igneous rock outcrops in the Rincon mountain range. **C.** Lateral view of the discoid capitulum with yellow disc corollas. The phyllaries found in this population differ from the typically dense pubescence found in most populations of *L. lemmonii. Photo by Isaac Lichter-Marck.*

**5.24 Laphamia lindheimeri** A.Gray, Smithsonian Contr. Knowl. 3(5): 101, 1852. *Perityle lindheimeri* (A.Gray) Shinners, Southw. Naturalist 4: 205, 1959. **TYPE:** U.S.A., Texas, Comal Co., perpendicular rocks on the banks of the Guadalupe River, Comanche Spring, near New Braunfels, May 1850, *Lindheimer 937* (lectotype: GH00011084 [photo!] [designated by Powell 1973a], isolectotypes: BR0000005491209 [photo!], F0050513F [photo!], GH00011085 [photo!], MEXU01220318 [photo!], NY00180469 [photo!], NY00180470 [photo!], PH00016863 [photo!], PH00016864 [photo!], US00124626!).

*Laphamia rotundata* Rydb. N. Amer. Fl. 34: 25, 1914. *Perityle rotundata* (Rydb.) Shinners, Southw. Naturalist 4: 205, 1959. **TYPE:** U.S.A., Texas, San Esteban, 3 September 1852, *Bigelow s.n.* (holotype: NY00180472 [photo!]; isotypes: DS [photo!], GH, NY, UC!, US!).

**5.24 A Laphamia lindheimeri** A.Gray var. **halimifolia** (A.Gray) Lichter-Marck, Syst. Bot. 47(3): 809, 2022. *Laphamia halimifolia* A.Gray, Pl. Wright. 1: 100, 1852. *Perityle halimifolia* (A.Gray) Shinners, Southw. Naturalist 4: 205, 1959. *Perityle lindheimeri* var. *halimifolia* (A.Gray) A.M.Powell, Sida 3: 278, 1968. **TYPE:** U.S.A., Texas, Val Verde Co., crevices of rocks, on the summit of hills, near the San Pedro River, July 1849, *C. Wright 301* (lectotype: GH00263133 [photo!][designated by Powell 1973a], isolectotypes: BM000810787 [photo!], BM000810788 [photo!], CAS0012329!, GH00263134 [photo!], GH00263135 [photo!], GH00011081 [photo!], GH00011082 [photo!], GH00011083 [photo!], K001079919 [photo!], NY00180465 [photo!], PH00016866 [photo!], US00124617!, WIS0256922 [photo!]).

***Notes:*** *Laphamia lindheimeri* grows on bare outcrops of calcareous rock in the Edwards Plateau and is one of the most extensively documented species of *Laphamia*, although no detailed studies of its ecology or population structure have yet been carried out. This species was the first described for *Laphamia* by A.Gray in 1852 and is therefore the type species for this genus.

**5.25 Laphamia leptoglossa** (Harv. & A.Gray ex A.Gray) Lichter-Marck, Syst. Bot. 47(3): 810, 2022. *Perityle leptoglossa* Harv. & A.Gray ex A.Gray, Mem. Amer. Acad. Arts ser. 2, 4(1): 77, 1849. *Leptopharynx leptoglossa* (Harv. & A.Gray ex A.Gray) Rydb., N. Amer. Fl. 34: 22, 1914. **TYPE:** Mexico, Sonora, vicinity of Hermosillo, 1829–1830, *Coulter 277* (lectotype: GH00011080 [photo!] [designated by Powell 1973a], isolectotypes: K001079928 [photo!], K000502187 [photo!], RSA0037659!, TCD0090360 [photo!], RSA0037660!, US00131458!). Figure 31.

***Notes:*** *Laphamia leptoglossa* occurs on bare outcrops of volcanic substrates throughout the sky islands and lowlands of northern Sonora. Wide geographic range and morphological variability, especially in leaf shape and indument, raise the possibility that *L. leptoglossa* is a species complex. Phylogenetic data thus far support the monophyly of *L. leptoglossa* with respect to two closely related rock daisies, *L. sanchezii* and *L. reinana*. *Laphamia reinana* often occurs sympatrically with *L. leptoglossa* but tends to be associated with granitic outcrops and lacks ray florets. *Laphamia sanchezii* is a succulent (not woody) perennial and differs from *L. leptoglossa* and *L. reinana* in having broader leaves that are glandular hairy, not canescent. All three species self-sow.



**Figure 31.** *Laphamia leptoglossa* (Harv. & A.Gray ex A.Gray) Lichter-Marck is a relatively wide ranging rock daisy that grows as a suffrutescent perennial on rocky cliffs and outcrops through out northern Sonora, Mexico. The individual illustrated here was found on an urban hill within the city limits of Hermosillo (Sonora). The radiate heads have yellow corollas, and they bend back upon maturity to self-sow the cypselae in the cliff face. *Photo by Isaac Lichter-Marck.*

**5.26 Laphamia lloydii** (B.L.Rob. & Fernald) Lichter-Marck, Syst. Bot. 47(3): 810, 2022. *Perityle lloydii* B.L.Rob. & Fernald, Proc. Amer. Acad. Arts 30: 118, 1894. *Leptopharynx lloydii* (B.L.Rob. & Fernald) Rydb., N. Amer. Fl. 34: 22, 1914. **TYPE:** Mexico, Sonora, Badehuaci, 2 December 1890, *C.E. Lloyd 400* (lectotype: GH00011127 [photo!] [designated by Powell 1973a], isolectotypes: K000502186 [photo!], F0050937 [photo!], NY00231068 [photo!], PH00021284 [photo!], UC90480!, US00124629!, US00124630!).

***Notes:*** *L. lloydii* occurs on bare outcrops of rock of an unknown substrate type in lowland tropical thornscrub in Sonora, Mexico. This species was "lost" for over a hundred years after its description, but was rediscovered by Ana Lilia Reina, Tom Vandevender, and M.J. Galaz during field work on a ranch property along Arroyo Bacadehuachi. The locality on the type "Badéhuachi" does not exist in Sonora and was likely a misspelling. Phylogenetic data supports the relationship of *L. lloydii* to other rock daisies found in Sonora, which are one of the least understood groups of rock daisies.



**Figure 32.** *Laphamia lobata* (Rydb.) Lichter-Marck is a common rock daisy on rocky substrates and decomposed soils at the base of cliffs in the Sierra de la Giganta of Baja California Sur, Mexico. The capitula are radiate and have yellow corollas, and the heads reflex upon maturity as seen here, presumably to self sow their cypselae back into the rock face. *Photo by Isaac Lichter-Marck.*

**5.27 Laphamia lobata** (Rydb.) Lichter-Marck, Syst. Bot. 47(3): 810, 2022. *Leptopharynx lobata* Rydb., N. Amer. Fl. 34: 23, 1914. *Perityle lobata* (Rydb.) I.M.Johnst., Proc. Calif. Acad. Sci. ser. 4, 12: 1205, 1924. **TYPE:** Mexico, Baja California, Commondu, 19 February 1889, *T.S. Brandegee* s.n. (holotype: GH00011128 [photo!], isotypes: UC90481!, US00124631!). Figure 32.

***Notes:*** *Laphamia lobata* occurs on bare rocky outcrops of volcanic substrates and decomposed soils usually in open habitats in the tropical Cape Region and Sierra Giganta of Baja California Sur. It is the only *Laphamia* that occurs in Baja California, although *Perityle aurea*, which has not yet been included in phylogenetic analyses, may turn out to be a close relative. *Laphamia lobata* is closely related to *Laphamia* species found in Sonora and represents a case of recent dispersal over the Gulf of California. Like its Sonoran relatives, *L. lobata* self-sows its seeds in the rock by bending back of the peduncle upon maturity.

**5.28 Laphamia megalocephala** S.Watson, Amer. Naturalist 7: 301, 1873. *Monothrix megalocephala* (S.Watson) Rydb., N. Amer. Fl. 34(1): 20, 1914. *Perityle megalocephala* (S.Watson) J.F.Macbr., Contr. Gray Herb. 56: 39. 1918. **TYPE:** U.S.A., Nevada, 1872, *Wheeler s.n.* (lectotype: US00124634 [photo!] [designated by Powell 1973a], isolectotypes: GH00011129 [photo!], LE00017999 [photo!], PH00016862 [photo!], YU064510 [photo!]). Figure 33A-B.

**5.28 A Laphamia megalocephala** var. **oligophylla** (A.M.Powell) Lichter-Marck, Syst. Bot. 47(3): 810, 2022. *Perityle megalocephala* var. *oligophylla* A.M.Powell. Sida 5: 91, 1973. **TYPE:** U.S.A., California, Inyo Co., Lost Burro Gap, Cottonwood Mtns., Death Valley Nat'l Monument., 17 September 1957, *R.S. Ferris & W.R. Ernst 13162* (holotype: DS[CAS0006614]!, isotypes: CAS0006615!, DAV32954 [photo!], RSA0001474 !, NY00231043 [photo!], TEX00374223 [photo!]). Figure 33C.

***Notes:*** *Laphamia megalocephala* is one of the most widespread rock daisies in the Great Basin region, and phylogenetic data show it to be a non-monophyletic species complex; however, its reduced morphology and growth in a difficult to access landscape have so far limited the data available to accurately delimit taxa.

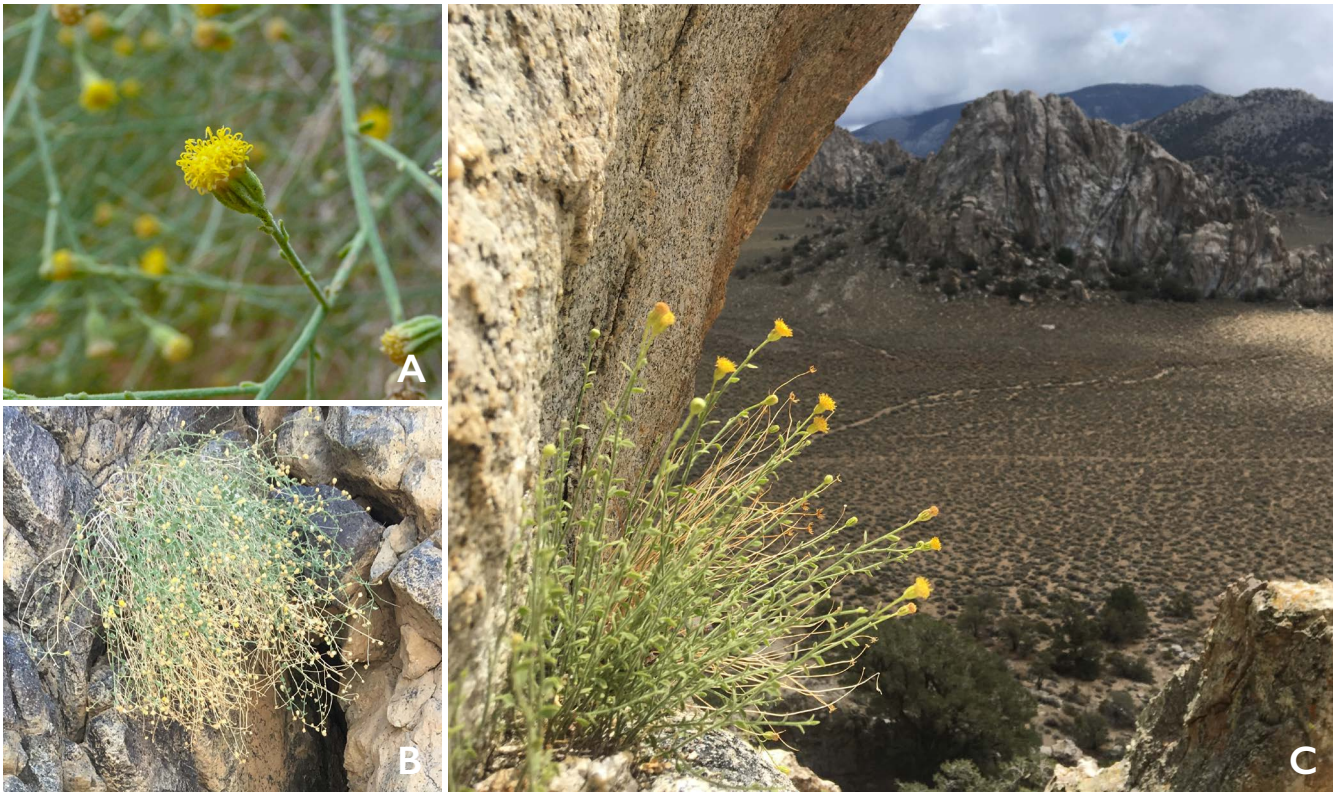



**Figure 33.** The two varieties of *Laphamia megalocephala* S.Watson grow as cliff dwelling perennials in sky island mountain ranges surrounded by Great basin Desert in western Nevada and eastern California. **A.** Lateral view of the discoid capitulum of *Laphamia megalocephala* var. *megalocephala* showing the yellow corollas with exserted style branches. **B.** *Laphamia megalocephala* var. *megalocephala* growing out of a cliff of limestone in the White mountains, California. **C.** *Laphamia megalocephala* var. *oligophylla* growing on granite outcroppings on Papoose flat, a secret destination for hardcore climbers in the Inyo mountains, California. *Photos by Isaac Lichter-Marck.*

*Laphamia megalocephala* var. *megalocephala* occurs in the White Mountains and in the foothills of desert mountains in western Nevada. *Laphamia megalocephala* var. *oligophylla* occurs in the Inyo Mountains and on isolated sky islands throughout the Death Valley region. Most populations occur on bare outcrops of rocks of various substrates; however, in parts of the White Mountains, individuals of *L. megalocephala* var. *megalocephala* have successfully established on talus slopes, where they tend to grow into some of the largest rock daisies (> 2 m) found anywhere. In the southern Inyo Mountains, near Talc city on the Darwin Plateau, are putatively hybrid populations that show intermediate morphology between *L. megalocephala* var. *oligophylla* and *L. inyoensis.*

**5.29 Laphamia palmeri** A.Gray, Proc. Amer. Acad. Arts 13: 372–373, 1878. *Monothrix palmeri* (A.Gray) Rydb., N. Amer. Fl. 34(1): 21, 1914. **TYPE:** U.S.A., Arizona, at Beaverdam, in crevice of rock canyons, 1877, *E. Palmer 199* (lectotype: GH00009570 [photo!] [designated by Powell 1973a], isolectotypes: AC00319466 [photo!], K001079915 [photo!], K001079916 [photo!], ISC0000126 [photo!], MO714497 [photo!], NY00180474 [photo!], NY00180475 [photo!], NY00180476 [photo!], NY00180477 [photo!], NY00180473 [photo!], NDG61181 [photo!], PH00016861 [photo!], RSA0001353!, US00124640!, US00124641!). Figure 34.

> *Laphamia palmeri* var. *tenella* M.E.Jones, Proc. Calif. Acad. Sci. ser. 2, 5: 703, 1895. *Perityle tenella* (M.E.Jones) J.F.Macbr., Contr. Gray Herb. n.s. 56: 39, 1918. **TYPE:** U.S.A., Utah, Springdale, in crevices of sandstone rocks, 4000 ft, 16 May 1894, *M.E.Jones 5249aa* (lectotype: POM [RSA0001353] [designated by Powell 1973a], isolectotype: US00124641!).

***Notes:*** *Laphamia palmeri,* which includes what has recently been referred to as *Perityle tenella,* grows on bare outcrops of limestone and sandstone. At least some of the populations growing on sandstone are associated with calcareous deposits of caliche created by water filtering though the sandstone.

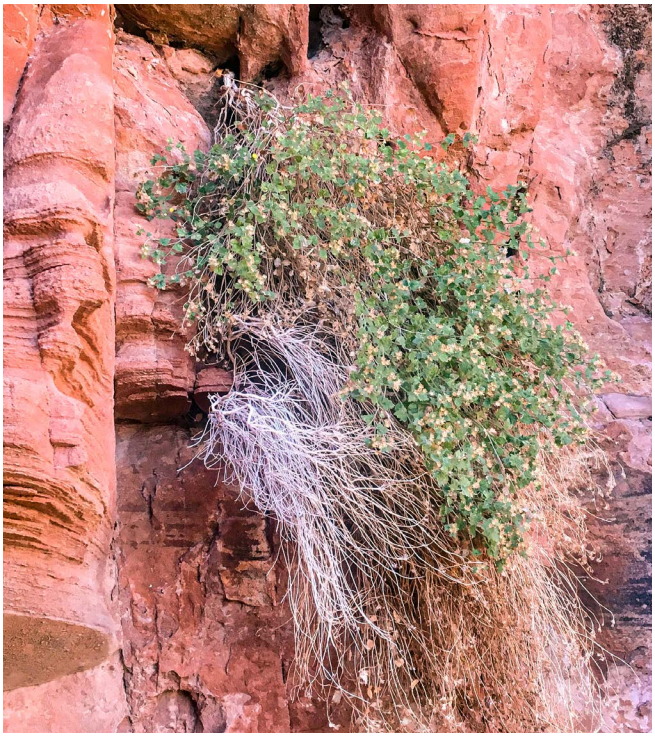


**Figure 34.** *Laphamia palmeri* A.Gray is a cliff dwelling species found in sandstone and limestone canyons of the colorado plateau in Utah and Nevada. Image shows individual growing out of a dry waterfall sculpted from Navajo sandstone on the eroded edge of an ancient reef. *Photo by Isaac Lichter-Marck.*

**5.30 Laphamia parryi** (A.Gray) Benth. & Hook.f. ex Hemsl., Biol. Cent-Amer., Bot. 2: 210, 1881. *Perityle parryi* A.Gray, Smithsonian Contr. Knowl. 2: 106, 1853. *Perityle parryi* A.Gray, Smithsonian Contr. Knowl. 2: 106, 1853. **TYPE:** U.S.A., Texas, Canyon of the Río Grande, August 1852, *C.C. Parry 521* (lectotype: POM [RSA0001353] [designated by Powell 1973a], isolectotype: US00124641!).

*Leptopharynx trisecta* Rydb. N. Amer. Fl. 34: 23. 1914. *Perityle trisecta* (Rydb.) J.F.Macbr., Contr. Gray Herb. 56: 39, 1918. **TYPE:** Mexico, Chihuahua, dry cliffs, rocky hills near Chihuahua, 20 March 1885, *C.G. Pringle 183* (holotype: NY00180532 [photo!], isotypes: BR0000005490516 [photo!], CAS0003162!, K000502188 [photo!], NY00180533 [photo!], WIS0256928 [photo!], US00124659!).

***Notes:*** *Laphamia parryi* is one of the only rock daises that grows both in decomposed soils as well as consolidated, solid rock. Discoid populations are known to occur at the eastern edge of its range, and recent observations by C. Frasch also show that some small-rayed intermediates occur in the vicinity. Phylogenetic data supports *L. parryi* as closely related to *L. vaseyi* and *L. aglossa*. Populations in Chihuahua show elements of both *L. parryi* and *L. vaseyi,* and with more study might be worthy of recognition using as basionym the existing name *Leptopharynx trisecta* Rydb., which was based on a type specimen from Chihuahua.

**5.31 Laphamia quinqueflora** Steyerm., Ann. Missouri Bot. Gard. 19: 392–393, 1932. *Pappothrix quinqueflora* (Steyerm.) Everly, Contr. Dudley Herb. 3: 379, 1947. *Perityle quinqueflora* (Steyerm.) Shinners, Southw. Naturalist 4: 205, 1959. **TYPE:** U.S.A., New Mexico, Culberson Co., niches in exposed limestone cliffs, lower McKittrick Canyon, Guadalupe Mts., alt. 1900 m., 20 July 1931, *Moore & Steyermark 3547* (holotype: GH00061913 [photo!], isotypes: CAS00123295!, MICH1107496 [photo!], MIN1001583 [photo!], MO714305 photo!], NY00180471 [photo!], PH00016860 [photo!], US00931226!, US00124644!). Figure 35.



**Figure 35.** *Laphamia quinqueflora* Steyerm. is a narrowly endemic rock daisy that grows in solid rock faces of cliffs and canyons in the Guadalupe and Brokeoff mountains. The common name of this species, the five flowered rock daisy, refers to the capitula having only 5(8) florets; capitula are discoid and florets have yellow corollas. *Photo by Isaac Lichter-Marck.*

**5.32 Laphamia reinana** (B.L.Turner) Lichter-Marck, Syst. Bot. 47(3): 810, 2022. *Perityle reinana* B.L.Turner, Phytologia 88(1): 94–96, 2006. **TYPE:** Mexico, Sonora, Municipio de Ures, Cañada de Mazatán, oak woodland on granite, 1383 m, *T.R. Van Devender, Reina-G, Sanchez-E., Ferguson, Anderson & Johnson 2004-476* (holotype: TEX00208166 [photo!], isotypes: ARIZ0004464!, MEXU01240489 [photo!]).

***Notes:*** *Laphamia reinana* is a discoid species of rock daisy that mostly grows on bare outcrops of granite. Until recently, *L. reinana* was known only from the Sierra Mazatan, a sky island outside of Hermosillo, Sonora. In 2019, a new population was uncovered during a Madrean Discovery expedition to the Sierra los Locos, about 100 km to the north. The new population was in a similar habitat as the type locality, mostly on granite boulders along a steep arroyo in mid-elevation, sky island oak forest. A couple of populations found lower on the Sierra los Locos were growing out of volcanic substrates and occurred in the same area as populations of *L. leptoglossa*. A third population of this rare species was uncovered in April of 2023, again during a Madrean Discovery expedition, in a deep narrow canyon just north of Huépari, Sonora. Overall, *L. reinana* and *L. leptoglossa* are very similar and the range of *L. leptoglossa* encompasses the isolated populations discovered thus far of *L. reinana.* This raises the question of whether *L. reinana* should be recognized as a species or merely as a variety or populational variant of *L. leptoglossa*. However, phylogenomic data sequenced from multiple populations of *L. leptoglossa* and *L. reinana* do not support lumping these taxa together: the disjunct populations of *L. reinana* were supported as more closely related to each other than to *L. leptoglossa* populations found in their immediate vicinity.

**5.33 Laphamia rupestris** A.Gray, Smithsonian Contr. Knowl. 3(5): 100, 1852. *Pappothrix rupestris* (A.Gray) Rydb., Fl. N. Amer. 34: 26, 1914. *Perityle rupestris* (A.Gray) Shinners, Southw. Naturalist 4: 205, 1959. **TYPE:** U.S.A., Texas, Jeff Davis Co., crevices of rocks, on mountains, in the pass of the Limpia, August 1849, *C. Wright 300* (lectotype: GH00011090 [photo!] [**here designated**], isolectotypes: BM000810786 [photo!], GH00011091 [photo!], GH00011092 [photo!], K001079912 [photo!], NY00180478 [photo!], PH00016859 [photo!], US00124648!, WIS0256923 [photo!]). Figure 36A-B.

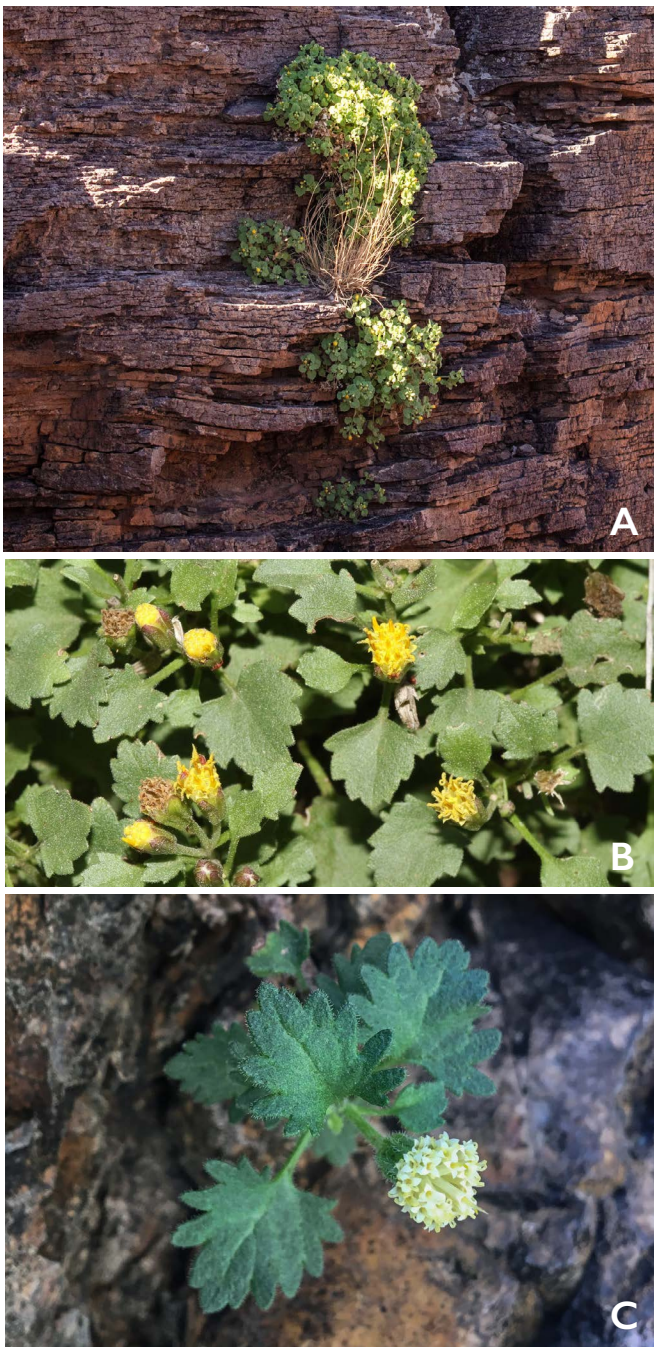



**Figure 36.** *Laphamia rupestris* A.Gray is a heterogeneous species complex with two varieties found on cliffs in sky islands of the chihuahuan desert in western Texas. **A.** *Laphamia rupestris* var. *rupestris* occurs on igneous and calcareous rock substrates and is a complex polyploid species. **B.** Habit of *L. rupestris* var. *rupestris; notice* discoid heads and florets with yellow corollas; leaves are entire, deltoid with serrate margins. **C.** *Laphamia rupestris* var. *albiflora* (A.M. Powell) Lichter-Marck shown here growing from a tiny crack in igneous rocks along the window trail in the Chisos mountains, Big Bend national Park. The superior view of the capitulum shows the white disc corollas. Molecular data do not support the monophyly of this species complex, thus further work is needed. *Photos by Steven Wang (A), James Bailey (B), and Isaac Lichter-Marck (C).*

**5.33 A Laphamia rupestris** var. **albiflora** (A.M.Powell) Lichter-Marck, Syst. Bot. 47(3): 810, 2022. *Perityle rupestris* var. *albiflora* A.M.Powell, Sida 3: 180, 1967. **TYPE:** U.S.A., Texas, Brewster Co., in crevices of igneous bluffs, ca. 3 mi. W of Alpine in Tronto Pass, 3 June 1965, *A.M.Powell & S. Sikes 1320* (holotype: SRSC, isotypes: BRIT23897 [photo!], MO714535 [photo!], OS0000271 [photo!], TEX00374224 [photo!], US00124649!). Figure 36C.

***Notes:*** Both varieties of *Laphamia rupestris* grow on bare outcrops of volcanic, limestone, and novaculite rocks in western Texas. These taxa show complex patterns of polyploidy, with documented tetraploids, hexaploids, and octoploids (Powell 1969). Phylogenetic data do not support the monophyly of *L. rupestris* with respect to the two recognized varieties, but molecular phylogenetic analyses can be misleading when whole genome duplications are present.



**Figure 37.** *Laphamia sanchezii* Lichter-Marck is an herbaceous perennial rock daisy with radiate heads that bend back at maturity to self sow. This is one of only a few species that grows both on solid rock faces and decomposed substrates. It occurs in an arid part of western Sonora, Mexico that borders the Gulf of California and overlaps with the territory of the Comcaac indigenous peoples, who have called the plant "*hee cotopl*", which translates to "*the one who clings.*" *Photo by Anna Laura Botello.*

**5.34 Laphamia sanchezii** Lichter-Marck, Syst. Bot. 47(3): 810, 2022. *Perityle palmeri* S.Watson, Proc. Amer. Acad. 24: 57, 1889. *Leptopharynx palmeri* (S.Watson) Rydb., N. Amer. Fl. 34: 23. 1914. **TYPE:** Mexico, Sonora, Guaymas, October 1887, *E. Palmer 308* (lectotype: GH00011135 [photo!] [designated by Powell 1974], isolectotypes: C10007750 [photo!], K000502287 [photo!], MEXU01220311 [photo!], NDG61172 [photo!], NY00231072 [photo!], PH00021285 [photo!], UC90483!, US00124639!, US00124638!, US00124637!, YU002285 [photo!]). Figure 37.

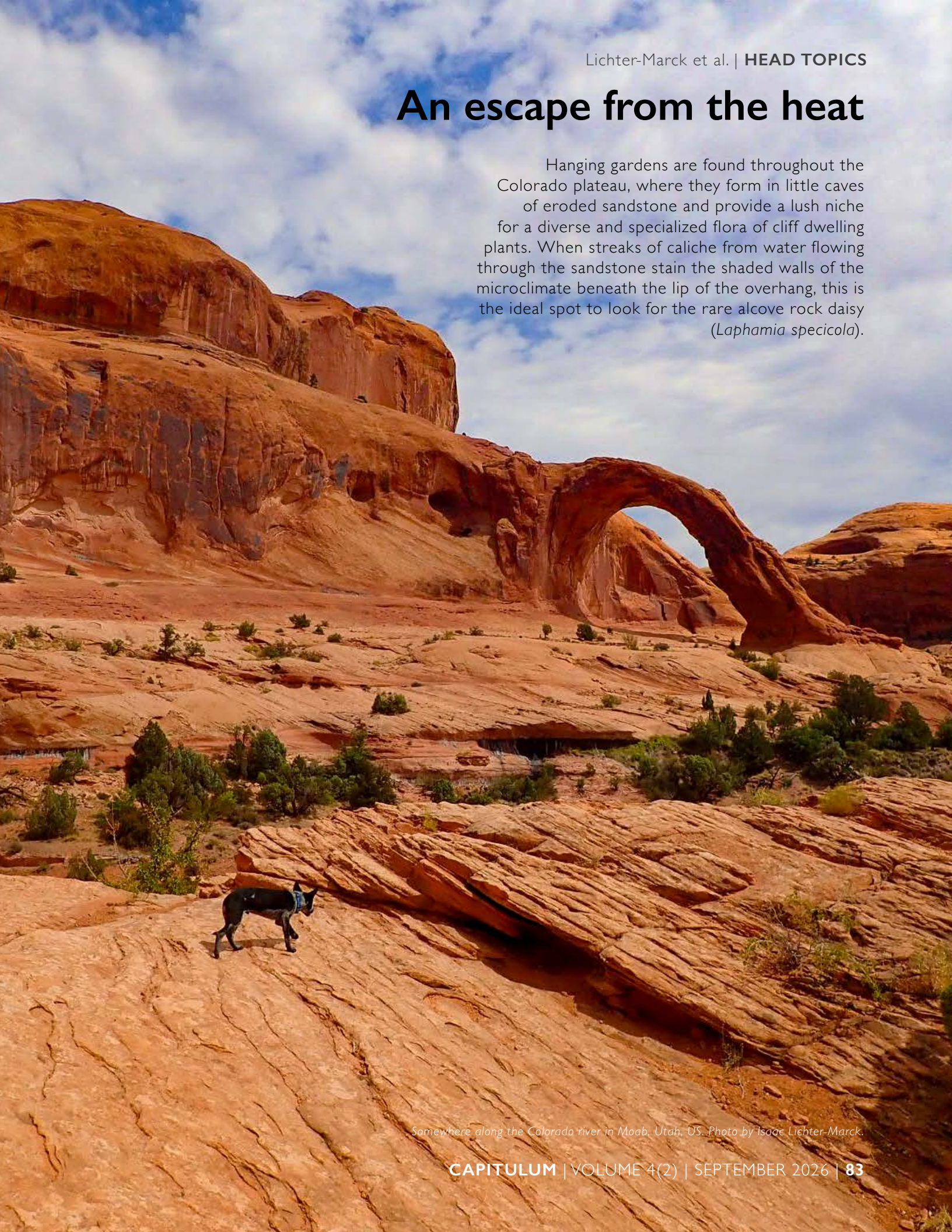
***Notes:*** *Laphamia sanchezii* grows on bare rocky outcrops and decomposed talus of volcanic substrates in western Sonora and the Comca'aq (Seri) nation. *Laphamia sanchezii* is a new name that needed to be chosen when making a new combination for *Perityle palmeri* in *Laphamia*, because *Laphamia palmeri* A.Gray was already taken (see *Laphamia palmeri* above). Populations in west-central Sonora, near Desemboque, differ in leaf shape, which may be a plastic response to the drier more exposed habitats present there. According to Chloe Novak, one of the names for rock daisies in the Comca'aq language Cmiique iitom (pronounced Kween-keh ee-tom) is *Hee Cotopl*, which translates roughly to "the one who clings."

**5.35 Laphamia saxicola** Eastw., Proc. Calif. Acad. Sci. ser. 4, 20: 159–160, 1931. *Perityle saxicola* (Eastw.) Shinners, Southw. Naturalist 4: 205, 1959. **TYPE:** U.S.A., Arizona, Maricopa Co., near the Roosevelt Dam on the road to Fish Creek, Apache Trail, 22 May 1929, *A. Eastwood 17401* (holotype: CAS00123296!, isotypes: CAS00123297 US00124652 [photo!], GH00011093 US00124652 [photo!], K001079917 [photo!], LL00374190 NY00180481 US00124652 [photo!], RSA0001354!, US00124652 [photo!], WIS0256924 [photo!]).

**5.36 Laphamia specicola** (S.L.Welsh & Neese) Lichter-Marck, Syst. Bot. 47(3): 810, 2022. *Perityle specicola* S.L. Welsh & Neese, Great Basin Naturalist 43: 373, 1983. **TYPE:** U.S.A., Utah, T25S, R21E, S24, 2 mi. due NNE of Moab, Grandstaff Canyon, 1220 m, Navajo sandstone, hanging garden community. 6 October 1977, *S.L. Welsh 16365* (holotype: BRY0001333, isotypes: NY00231045 [photo!], SRSC00064232, WTS0015798). Figure 38.

# An escape from the heat

Hanging gardens are found throughout the Colorado plateau, where they form in little caves of eroded sandstone and provide a lush niche for a diverse and specialized flora of cliff dwelling plants. When streaks of caliche from water flowing through the sandstone stain the shaded walls of the microclimate beneath the lip of the overhang, this is the ideal spot to look for the rare alcove rock daisy (*Laphamia specicola*).



*Somewhere along the Colorado river in Moab, Utah, US. Photo by Isaac Lichter-Marck.*



**Figure 38.** *Laphamia specicola* Welsh & Neese, the alcove or hanging-garden rock daisy, seen here on steep sandstone cliffs in Arches National Park in Moab, Utah, is a pendent subshrubby rock daisy with discoid heads and yellow disc corollas. This species occurs in communities known as hanging gardens, found throughout the Colorado plateau, that form in vertical or overhanging walls of eroded sandstone and provide a lush niche for a diverse and specialized flora of cliff dwelling plants. *Photo by Isaac Lichter-Marck.*

***Notes:*** *Laphamia specicola* grows on bare vertical exposures along river-cut canyons, where it often forms parts of hanging gardens, in southeastern Utah and the Navajo nation. It was recently documented for the first time in Canyonland National Park by an observer on INaturalist (@Blazeclaw 217838875). According to Arnold Clifford, Dine botanist and curator of the Carrizo Mountain Herbarium, these alcove rock daisies have ceremonial importance for the practice of manipulating the wind.

**5.37** **Laphamia stansburyi** A.Gray, Smithsonian Contr. Knowl. 3(art. 5): 101, 1852 [as "stansburii"]. *Monothrix stansburyana* Torr., In Stan. Utah Exped. 389, t. 390, 1852, **nom.illeg.** *Monothrix stansburyi* (A.Gray) Rydb. N. Amer. Fl. 34(1): 21, 1914. *Perityle stansburyi* (A.Gray) J.F. Macbr,, Contr. Gray Herb. 56: 39, 1918. **TYPE:** U.S.A., Utah, Tooele Co., crevices of limestone rocks, Stansbury's Island, 26 June 1850, *Stansbury s.n.* (lectotype: NY00180482 [photo!] [designated by Powell 1973a], isotype: GH00263142 [photo!]).

***Notes:*** *Laphamia stansburyi* is a widespread rock daisy that grows on bare, rocky outcrops, mostly of limestone, throughout northwest Utah.

**5.38** **Laphamia staurophylla** Barneby, Leafl. W. Bot. 8: 168, fig., 1957. *Perityle staurophylla* (Barneby) Shinners, Southw. Naturalist 4: 205. 1959. **TYPE:** U.S.A., New Mexico, Otero Co., limestone bluffs in La Luz Canyon below High Rolls, western slope of Sacramento Mts., 2 September 1956, *R.C. Barneby 12889* (holotype: CAS00123298!, isotypes: GH00011095 [photo!], K001079922 [photo!], NY00180483 [photo!], RSA0001356!, UNM00122 [photo!], US00124656!).

**5.38 A** **Laphamia staurophylla** Barneby var. **homoflora** (Todsen) Z. S. Rodgers & Spellenb. Novon 31(1): 155, 2023. *Perityle staurophylla* Barneby var. *homoflora* Todsen, Madroño 30: 116, 1983. **TYPE:** U.S.A., New Mexico, Sierra Co., San Andres Mtns., Rhodes canyon, 17 km of Rhodes canyon range center in S13 R03E T13S, locally common on limestone bluffs, 1650 m, 7 August 1971, *R. W. Spellenberg & T. K. Todsen 2637* (holotype: NY [currently lost], isotype: NMC036973 [photo!], SRSC).

***Notes:*** *Laphamia staurophylla* is a fascinating rock daisy found on several of the north-south oriented mountain ranges in southern New Mexico, where its typical growth is directly out of consolidated limestone or rhyolite subtrates. The rare, discoid *L. staurophylla* var. *homoflora* is found within the closed portion of the White Sands Missile Range. Rodgers and Spellenberg (2023) put together a strong justification for its recognition and status as a rare plant. The holotype of *L. staurophylla* var. *homoflora* at NY is apparently lost, but an isotype is retained at NMSU. This taxon is ripe for a focused study of eco-geographic speciation as it occurs on a variety of isolated habitats and lithologies.

**5.39** **Laphamia toumeyi** B.L.Rob. & Greenm., Amer. J. Sci. ser. 3, 50: 176, August 1895. *Monothrix toumeyi* (B.L.Rob. & Greenm.) Rydb., N. Amer. Fl. 34(1): 21, 1914. *Perityle toumeyi* (B.L.Rob. & Greenm.) J.F.Macbr., Contr. Gray Herb. 56: 39, 1918. **TYPE:** U.S.A., Arizona, in the Grand Canyon, 12 July 1892, *J.W. Toumey 645l* (lectotype: US00124657!, [designated by Powell 1973a], isolectotypes: DS [CAS00123299]!, GH00009569 [photo!])

*Laphamia congesta* M.E.Jones, Proc. Calif. Acad. Sci. ser. 2, 5: 703, November 1895. *Monothrix congesta* (M.E.Jones) Rydb., N. Amer. Fl. 34(1): 21, 1914. *Perityle congesta* (M.E.Jones)

Shinners, Southw. Naturalist 4: 204, 1959. **TYPE:** U.S.A., Arizona, in clefts of rocks in mesa below the Buckskin Mountains, 7000 ft, 21 September 1894, *M.E.Jones 6063* (lectotype: POM [RSA0001347] [photo!][designated by Powell 1973a], isolectotypes: BM000810789 [photo!], MO714505 [photo!], NY00180460 [photo!], RSA0001348 [photo!], RM0001206 [photo!], US00124599 [photo!])

***Notes:*** *Laphamia toumeyi* is recognized here as the correct name for plants treated under *Perityle congesta* (M.E.Jones) Shinners, Southw. Naturalist and *Laphamia congesta* M.E.Jones. A typesetting error in Lichter-Marck and Baldwin (2022) put *Laphamia toumeyi* into heterotypic synonymy with *L. cochisensis*. instead of *L. congesta,* where it belongs. Both leaf characteristics (entire, ovate, and lacking lobes) and location ("Grand Canyon") of the type of *L. toumeyi* conform with *L. congesta* better than with *L. cochisensis,* which is an endemic taxon of the Chiricahua Mountain range in southeastern Arizona. In addition, a closer review of type material of *L. toumeyi* has called attention to the fact that original publication of the name was in the same year as Marcus Jones' *L. congesta* (1895), with *L. toumeyi* published in August and *L. congesta* published in November. *Laphamia toumeyi* is conspecific with *L. congesta* and is the older name, therefore it has priority and is reinstated here as the first validly published basionym for this taxon.

**5.40 Laphamia vandevenderi** (B.L.Turner) Lichter-Marck, Syst. Bot. 47(3): 810, 2022. *Perityle vandevenderi* B.L.Turner, Phytologia 66: 504, 1989. **TYPE:** Mexico, Sonora, Palm Canyon, 17 mi SE of Magdalena on road to Cucurpe, "Sierra Baviso," 6 September 1976, *N.F. McCarten 2315* (holotype: ARIZ0004465 [photo!], isotypes: ARIZ0004466 [photo!], TEX00374227 [photo!]). Figure 39.

***Notes:*** Until recently, this rare rock daisy was known only from the type location in Magdalena Palm Canyon in the Sierra Baviso of Sonora, Mexico, where it has not been revisited in nearly 50 years. While clearly a *Laphamia*, *L. vandevenderi* stands out from the rest of the genus with its densely lanate foliage. Individual plants grow in minute cracks and crevices of solid rock and eventually develop a conspicuous gnarled, woody base that makes them appear ancient.In 2018, an additional occurrence of *L. vandevenderi* was discovered by Sky Jacobs during a Madrean Discovery expedition,



**Figure 39.** *Laphamia vandevenderi* (B.L.Turner) Lichter-Marck is a unique rock daisy whose leaves, stems and involucre are densely covered in tomentose trichomes. This species is rare, and until recently was known only from the type location in Magdalena palm canyon in northern Sonora. In recent years photographs, and new collections documenting a much broader range have greatly increased the natural history information available about this mysterious rock daisy species. *Photo by Joey Santore.*

on a cliff face in the neighboring Sierra Cucurpe. Molecular data sequenced from leaf material collected from this population showed that *L. vandevenderi* is nested within the core radiation of arid-adapted *Laphamia* and supports a provocative biogeographic link to the desert sky islands of the southwest U.S. as *L. vandevenderi* is more closely related to rock daisies found in the sky islands of southeastern Arizona and southern New Mexico, than it is to rock daisies found in nearby sky islands in Sonora, Mexico. In 2019, ILM revisited the type locality and found only a small population of approximately 10 bedraggled plants persisting on rhyolite rock outcrops about ¼ mile upstream a side arroyo that intersects the mouth of the Magdelena Palm Canyon. During a recent Madrean Discovery Expedition (MDE) in September 2023, the largest population of *L. vandevenderi* yet, consisting of approximately 100 individuals, was discovered in the Sierra Alacran, just south of the city of Cananea. As in the previous cases, plants at this site were found exclusively growing on cliffs and outcrops of extrusive igneous rock and were attached to solid, consolidated cliff faces by virtue of a hefty, wooden root base, sometimes forming a "trunk" and giving them the appearance of miniature old growth rock daisy trees. This new discovery extends the range of this species northward by over 100 km. More populations of *L. vandevenderi* might occur in the

heterogeneous landscape between these two localities, especially on rocky mountain slopes or canyons that have exposed igneous bedrock.

**5.41 Laphamia vaseyi** (J.M.Coult.) Lichter-Marck, Syst. Bot. 47(3): 811, 2022. *Perityle vaseyi* J.M.Coult., Contr. U.S. Natl. Herb. 1: 42, 1890. **TYPE:** U.S.A., Texas, Brewster Co., Chisos Mts. 1889, *G.C. Nealley 245* (lectotype: US00124661 [photo!] [designated by Powell 1973a]).

***Notes:*** *Laphamia vaseyi* is an herbaceous perennial rock daisy that occurs on decomposed calcareous soils and talus in western Texas, where it is sympatric with two similar and closely related rock daisies, *L. parryi* and *L. aglossa*. Abundant variation in leaf morphology is present in the populations recognized as *L. vaseyi*. In Chihuahua there are populations that appear to show overlapping variation with *L. vaseyi* and *L. parryi* yet are mostly suffrutescent perennials, and these may need to be recognized with a new combination using an older name proposed by Rydberg, *Leptopharynx trisecta*. See notes under *L. parryi* for more details.

**5.42 Laphamia villosa** S.F.Blake, Proc. Soc. Biol. Washington 45: 142, 1932. *Perityle villosa* (S.F.Blake) Shinners. Southw. Naturalist 4: 205, 1959. **TYPE:** U.S.A., California, Inyo Co., Middle Fork Hanaupah Canyon, Panamint Mtns., 2090 m, 22 September 1931. *F.V. Coville & A.F. Gilman 108* (lectotype: US00124662 [photo!] [designated by Powell 1973a], isolectotype: US00931227 [photo!]). Figure 40.

***Notes:*** *Laphamia villosa* is a mysterious and understudied rock daisy found on vertical limestone cliffs in the Panamint Range in Death Valley National Park, mostly within the jagged contours of Hanaupah Canyon, which descends roughly 3350 vertical meters from Telescope Peak to Badwater Basin in less than 8 km. *Laphamia villosa* is also apparently found in the Grapevine Mountains in Nevada, across the expansive Death Valley, but is only known from one collection on Mt. Palmer (*Kurzius 1588*) collected in 1980. Collections of this species made by Mary Dedecker in the Cottonwood Mountains about 80 km to the north have been alternatively determined as *L. inyoensis* and, in fact, constitute an unrecognized new species of rock daisy in the process of being described. These populations are on Tin Mountain, a calcareous caprock sky island that is only accessible by a near-vertical hiking route that climbs ~2600 meters from low desert to the summit. The original collections by Dedecker were made via helicopter.



**Figure 40.** *Laphamia villosa* S.F.Blake is a rare species of rock daisy endemic to the Panamint mountains and neighboring sky islands in Death Valley National Park in California, where it is a cliff dwelling subshrub found on limestone slopes of steep canyons. The foliage of the individual shown here is covered in glandular trichomes and the discoid heads are borne singly, with yellow disc corollas that fade to red. *Photo by Isaac Lichter-Marck.*

**5.43 Laphamia vitreomontana** (Warnock) Lichter-Marck, Syst. Bot. 47(3): 811, 2022. *Perityle vitreomontana* Warnock, Southw. Naturalist 12(4): 475–476, 1967. **TYPE:** U.S.A., Texas, Brewster Co., limestone bluffs, W slopes of Old Blue, Glass Mtns., ca. 4500 ft., 22 September 1963, *B.H. Warnock & A.M.Powell 19111* (holotype: SRSC00001239 [photo!], isotypes: BRIT23898 [photo!], GH00011096 [photo!], NY00231046 [photo!], TEX00374229 [photo!]).

***Notes:*** *Laphamia vitreomontana* has not been recently collected or photographed and is still known only from the type locality in the Glass Mountains in Trans-Pecos Texas, where it apparently grows abundantly on limestone cliffs. Phylogenetic results support Powell's hypothesis that *L. vitreomontana* is closely related to *L. rupestris* var. *albiflora*. Despite

resemblance in leaf morphology to *L. bisetosa, L. vitreomontana* possesses abundant pappus elements, which is a trait seen in *L. rupestris* var. *alibflora* and a few other rock daisies from Trans-Pecos Texas and southern New Mexico.

**5.44 Laphamia warnockii** (A.M.Powell) Lichter-Marck, Syst. Bot. 47(3): 811, 2022. *Perityle warnockii* A.M.Powell, Sida 3: 177, 1966. **TYPE:** U.S.A., Texas, Val Verde Co., NW part of county, in crevices and small pockets of solid Cretaceous limestone exposures, ca. 40–50 mi. NE of Dryden, ca. 1 mi E of Pecos River, 11 October 1964, *A.M.Powell 1311* (holotype: SRSC00001241 [photo!], isotypes: NY00231047 [photo!], SRSC00001240 [photo!], TEX00374230 [photo!]).

***Notes:*** *Laphamia warnockii* has only been collected a handful of times since its original discovery and description by A.M Powell in the 1960s and no photographs of this species are available. It is a small rock daisy, reaching a maximum of 6 cm, and a suffrutescent perennial that grows on Cretaceous caprock (limestone) in the Edwards Plateau of Trans-Pecos Texas. *Laphamia warnockii* was collected in 1995 by Burford L. Westlund ("Cactus Bur") in Val Verde Co. on Rancho de los tres Ninos, and again in 1999 by Grady Webster and Westlund, in the same location.

**6 Nesothamnus** (A.Gray) Rydb. N. Amer. Fl. 34(1):12 (1914). **TYPE: Nesothamnus incanus** (A.Gray) Rydb. Figure 41 & Figure 42; see map on page 88.

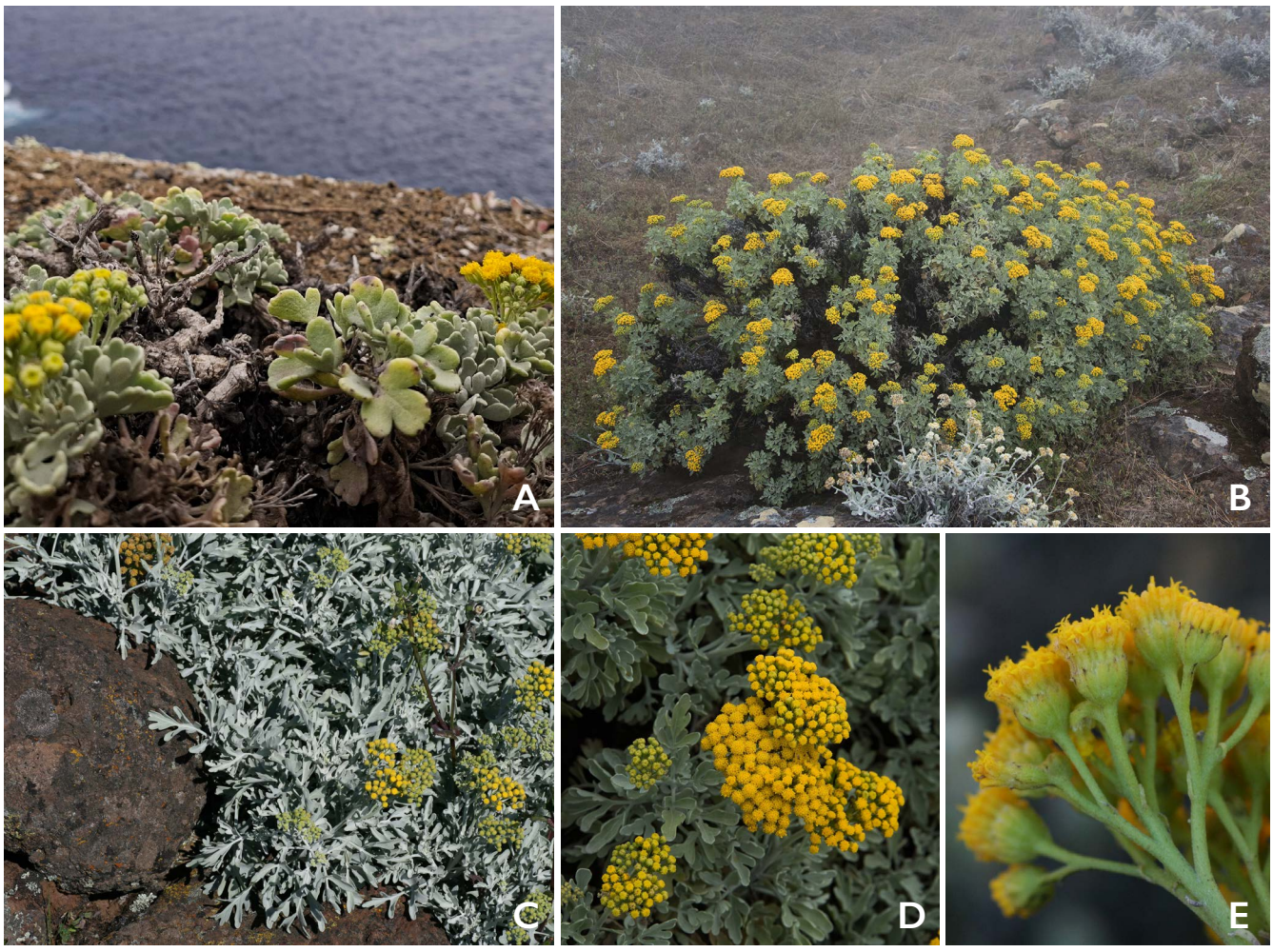
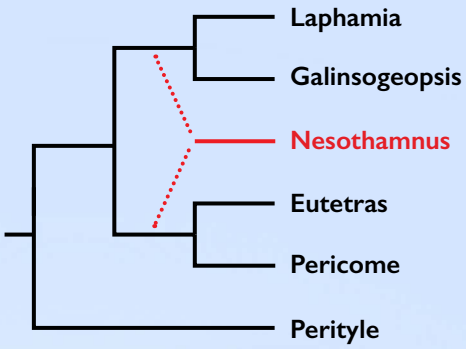



**Figure 41.** *Nesothamnus incanus* (A.Gray) Rydb., Guadelupe island endemic shrub. **A-B.** Habit: sprawling individual, robust and woody with a convoluted multi stemmed trunk. **C.** This unique rock daisy has large, highly dissected leaves that are covered in a densely matted layer of canescent trichomes. **D.** Superior view of dense corymbiform capitulescence. **E.** Lateral view of the discoid capitula. *Photos by Norma Castillo (A) and Jon Rebman (B-E).*

# *Nesothamnus*: island evolution in action:

*Nesothamnus incanus*, the rock daisy endemic to Guadalupe Island—250 km off Baja California and ringed by great white sharks—is an anomaly within tribe Perityleae, morphologically closer to island Compositae from other tribes than to its mainland relatives. The puzzle may lie in its genome: hexaploid, triple the typical diploid chromosome count, apparently formed through allopolyploid fusion of distantly related lineages that met via independent long-distance dispersal to the island. Current research targets the timing of this fusion to explain the plant's rapid adaptation to island conditions.









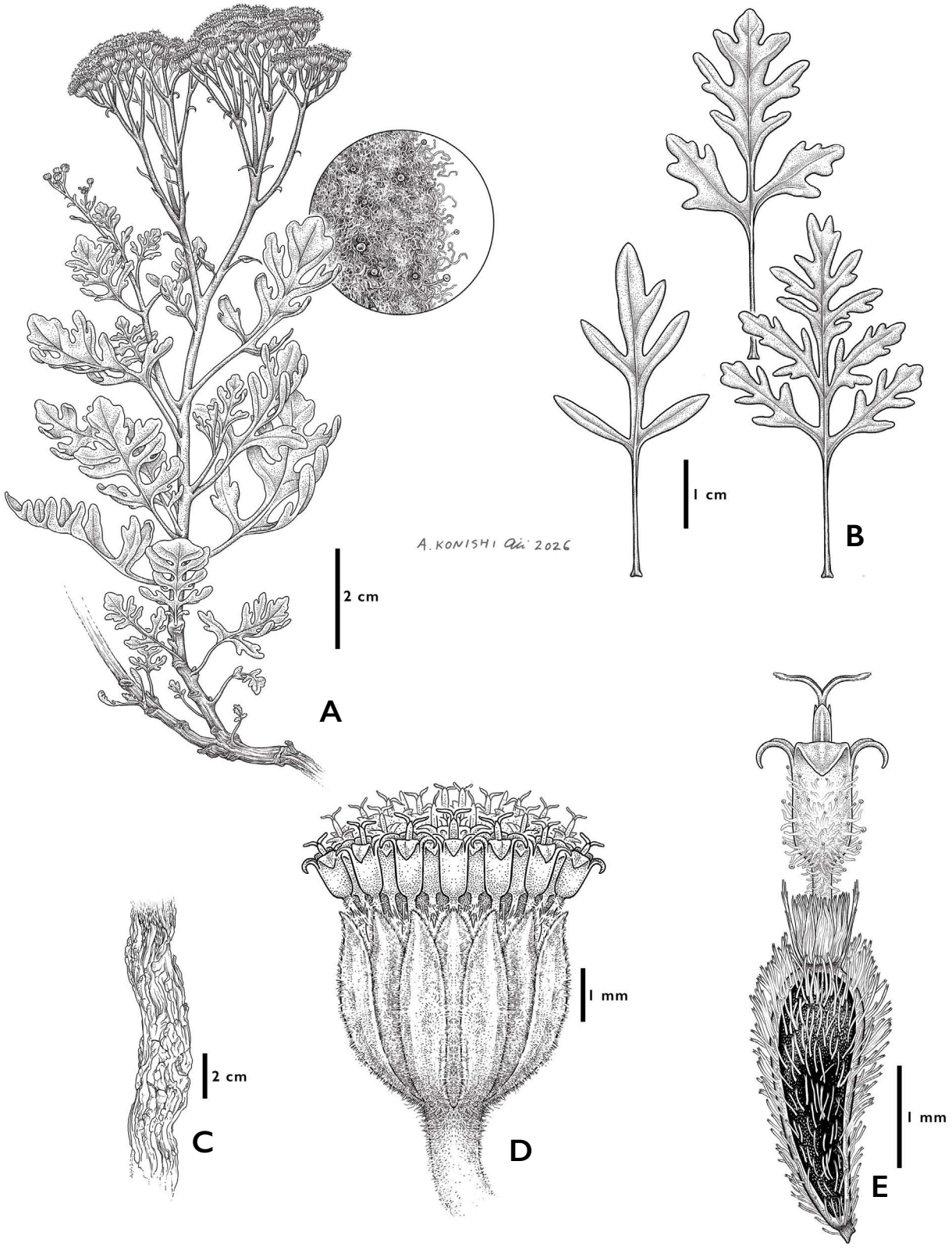



**Figure 42.** *Nesothamnus incanus* (A.Gray) Rydb. **A.** Habit, with indumentum in detail. **B.** Leaf. **C.** Detail of woody branch. **D.** Capitulum. **E.** Floret. Illustrations by Amanda Konishi from specimens in the CAS herbarium (A: CAS 382510, B: CAS 38212, C: CAS 382512, D: CAS 382505, and E: CAS 382506).

**6.1** **Nesothamnus incanus** (A.Gray) Rydb., N. Amer. Fl. *Perityle incana* A.Gray, Proc. Amer. Acad. Arts 11: 78, 1876. **TYPE:** Mexico, Baja California, Guadalupe Island, *E. Palmer 43* (lectotype: GH00011124 [photo!] [designated by Powell 1974], isolectotypes: CM2489 [photo!], F13929 [photo!], K000502198 [photo!], MO5116267 [photo!], NY00231060 [photo!], NY,00231059 [photo!] PH0021281 [photo!], US00124619 [photo!], YU002283 [photo!]).

***Notes:*** The genus *Nesothamnus* Rydb. was reinstated in 2022 following phylogenetic results supporting the island-endemic species *N. incanus* as an outlier in the higher-level classification of the rock daises. *Nesothamnus incanus* is one of the most morphologically distinctive rock daisies, with densely silver-tomentose foliage, shrubby habit, and heads clustered into a dense capitulescence. It is entirely endemic to Guadalupe Island, a volcanic island 240 km off the coast of Baja California. *Nesothamnus incanus* is of allopolyploid hybrid origin and may represent a paleopolyploid that was once more widespread before going extinct on the mainland and persisting on the island, or an insular neoendemic that was produced when distantly related rock daisies met and hybridized following transoceanic dispersal to Guadalupe Island. Genetic data and new bioinformatic approaches for teasing apart the evolutionary histories of hybrids are a promising avenue for weighing the evidence for these two scenarios.

**7** **Pericome** A.Gray, Smithsonian Contr. Knowl. 5(6): 82. 1853. **TYPE: Pericome caudata** A.Gray. Figure 43-45.

**7.1** **Pericome caudata** A.Gray, Smithsonian Contr. Knowl. 5(6): 82, 1853. **TYPE:** U.S.A., New Mexico, Among rocks, mountainsides, at the copper mines, Santa Rita del Cobre, October 1851, *C. Wright 1195* (lectotype: GH00263234 [photo!] [designated by Powell 1973c], isolectotypes: GH00011062 [photo!], NY00231035 [photo!], PH00021259 [photo!], US00124664!). Figure 43.

*Pericome glandulosa* Goodman, Rhodora 39: 209 (t. 459, fig. 1), 1937. *Pericome caudata* var. *glandulosa* (Goodman) H.D.Harr., Man. Pl. Colorado 589, 641, 1954. **TYPE:** U.S.A., Oklahoma, Cimarron Co., 3 miles E of Kenton, 27 August 1934, *G.J. Goodman 2291* (holotype: GH00011064 [photo!], isotypes: CAS0006617 [photo!], ISC-v-0000141 [photo!], MO1118435 [photo!], RM0001303 [photo!], US00124665 [photo!]).




**Figure 43.** *Pericome caudata* A.Gray is a widespread species found in scattered sky island environments in the southwest U.S. and extreme northern Mexico. **A.** Habit: multistemmed shrub that thrives on talus slopes and along riparian corridors. **B.** Lateral view of the discoid capitulum showing the yellow corollas, which appear to spill out of the involucre. **C.** Involucre with single series of coalescent (laterally fused) phyllaries. **D.** Detail of androecium, notice four anthers and conspicuous connectival appendix. *Photos by Isaac Lichter-Marck.*




**Figure 44.** This herbarium specimen of *Pericome macrocephala* B.L. Rob. collected by Molly Harker in an urban habitat island in Guadalajara represents the first known collection (and first photographs) of this rare species since its original collection by Edward Palmer in 1906. The plant is a shrub that resembles the more common sister species *P. caudata,* but heads are larger, ovoid-shaped, fruits have broad winged margins, and the foliage is covered in a dense mate of silvery trichomes.

# In search of lost rock daisies

*Two days earlier Pablo Carrillo Reyes and I were in the IBUG herbarium staring at one of the only specimens of* Pericome macrocephala *ever collected. It was Molly Harker, a local legend, who had found it ten years earlier on an urban hillside on the outskirts of Guadalajara. Spontaneously, a group of graduate student including myself assembled to visit the Cerro del Colli and hopefully find the first individual of this plant that had not been seen in over 100 years. Our trek took us through a lush forest of oaks, figs, plumerias, and ceiba trees where we found orchids,* Pinguicula, *and* Verbesina sphaerocephala. *When we arrived at Molly Harker's point, we found only houses and disturbed vegetation. To this day the lost* Pericome macrocephala *remains to be found.*

Isaac Lichter-Marck,October 2019

*Cerro del Colli, Guadalajara, Jalisco, Mexico. Photo by Isaac Lichter-Marck*

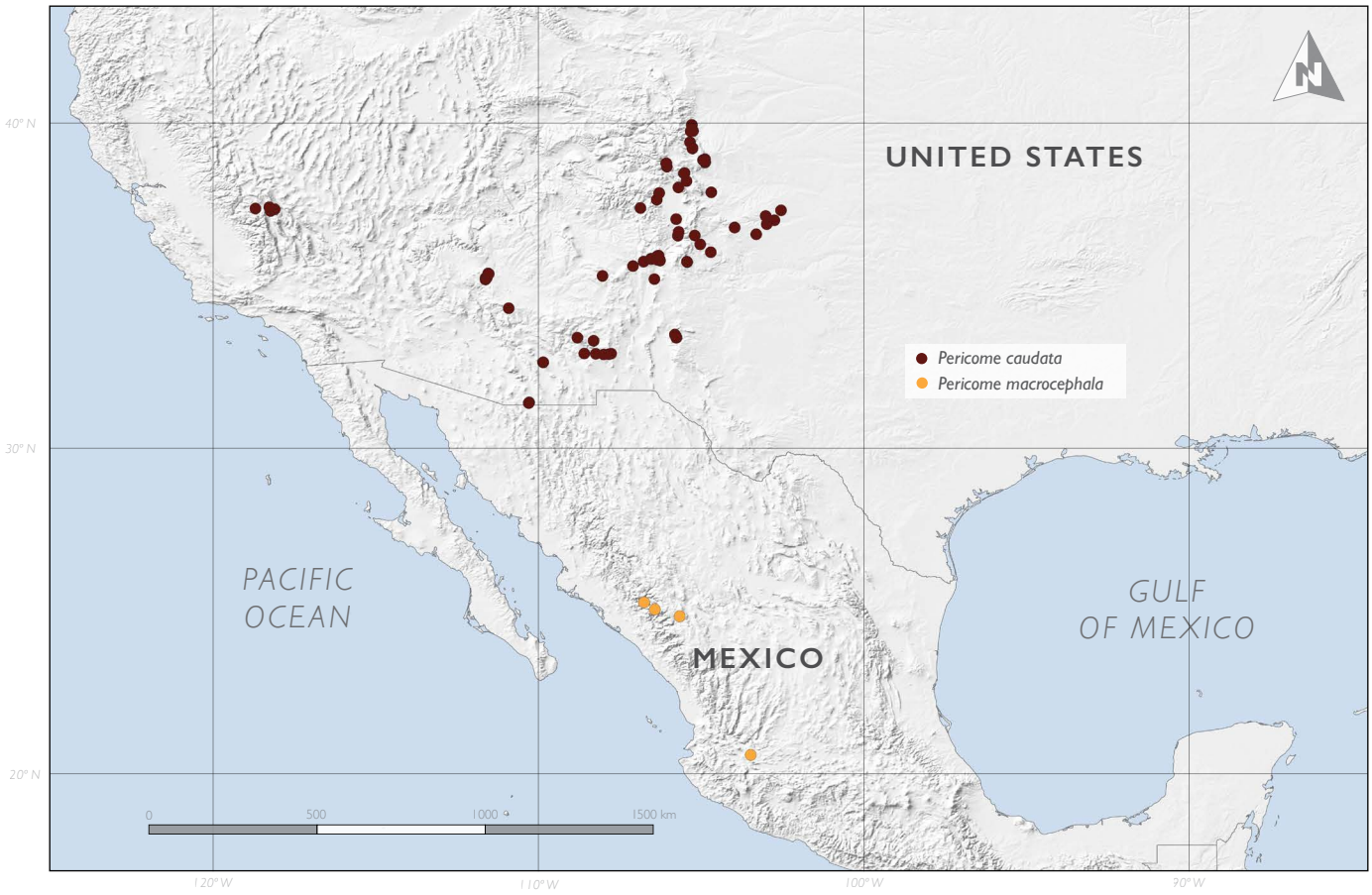



**Figure 45.** Geographic distribution map of *Pericome* occurrences based on digitized herbarium records. Both species show a disjunction in their distribution, although this may be due to how infrequently the species is collected. The collection of *Pericome macrocephala* by Molly Harker extends the range of this species south by over 600 km, but it is likely that populations occur within that gap that have yet to be documented.

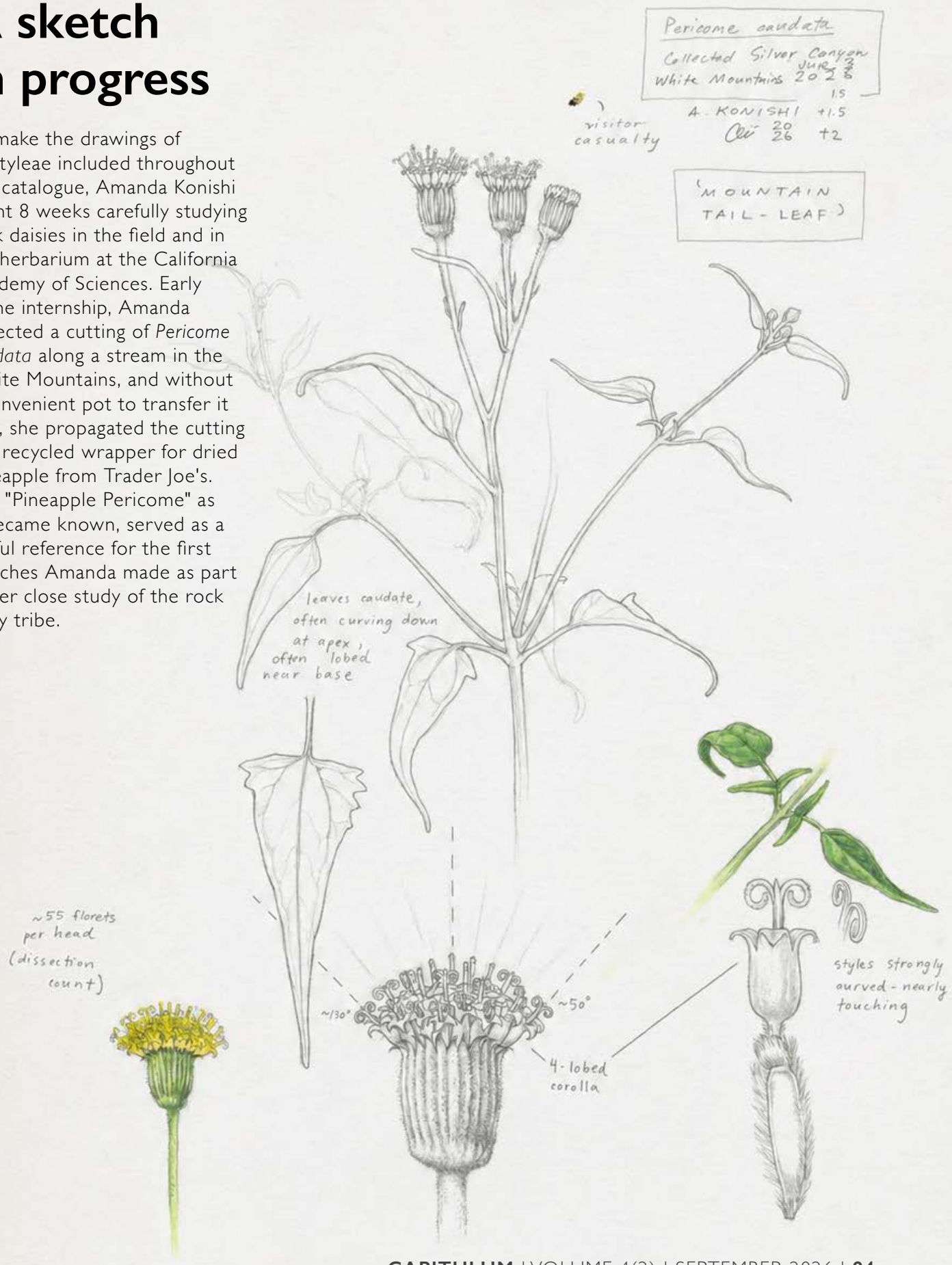
***Notes:*** *Pericome caudata* is a widespread shrub found in mid-elevation, mesic micro-habitats across western North America (Powell, 1973c). Specimens of *P. caudata* collected by Ana-Lilia Reina *et al.* around Yécora (e.g., *Reina 2000-782*) are indistinguishable from *P. caudata* specimens collected in the far eastern or western parts of the species range, and convincingly extend the range of this species to the Sierra Madre Occidental, where it may be sympatric, or come close to, *Pericome macrocephala*.

**7.2** **Pericome macrocephala** B.L.Rob., Proc. Amer. Acad. Arts 43: 42, 1907. **TYPE:** Mexico, Durango, near San Ramon, 21 April – 18 May 1906, *E. Palmer 69* (lectotype: GH00011065 [photo!] [designated by Powell 1973c], isolectotypes: CM2487 [photo!], F212870 [photo!], K000502331 [photo!], NY00231036 [photo!], UC148553 [photo!], US00124666!).

***Notes:*** After Palmer's type collection in 1906, *P. macrocephala* was not documented again for over 100 years. In 2009, Molly Harker rediscovered and collected (*Harker 3959*) this 2 m tall, locally abundant shrub on the Cerro del Colli, a small hill on the outskirts of Guadalajara, in Jalisco. The rediscovery of *P. macrocephala* by Harker extends the range of this species tremendously, by over 500 km and provides convincing evidence of its distinctiveness from *P. caudata*. In 2019, I visited the Cerro del Colli with Dr. Juvenal Aragon-Parada, but unfortunately we did not locate *P. macrocephala* in the cerro, and instead found the specific location mentioned by Harker "adelante la colonia 'Colinas de la Primavera'" developed into an urban housing development.

# A sketch in progress

To make the drawings of Perityleae included throughout this catalogue, Amanda Konishi spent 8 weeks carefully studying rock daisies in the field and in the herbarium at the California Academy of Sciences. Early in the internship, Amanda collected a cutting of *Pericome caudata* along a stream in the White Mountains, and without a convenient pot to transfer it into, she propagated the cutting in a recycled wrapper for dried pineapple from Trader Joe's. The "Pineapple Pericome" as it became known, served as a useful reference for the first sketches Amanda made as part of her close study of the rock daisy tribe.



**8** **Perityle** Benth. Bot. Voy. Sulphur [Bentham] 23, 1844. **TYPE: Perityle californica** Benth. Figure 46-47; see map on page 96.

*Amauria* Benth. Bot. Voy. Sulphur [Bentham], 31, 1844. **TYPE:** *Amauria rotundifolia* Benth.

*Closia* J.Rémy. Fl. Chil. [Gay] 4(1): 119, t. 46, f. 2, 1849. **TYPE:** *Closia cotula* J.Rémy.

*Lycapsus* Phil. Phil., Bot. Zeitung (Berlin) 28: 499, t. 8, 1870. **TYPE:** *Lycapsus tenuifolius* Phil.

**8.1** **Perityle aurea** Rose, Contr. U.S. Natl. Herb. 1: 84. 1890. **TYPE:** Mexico, Baja California, Santa Rosalia, 24 February – 3 March 1889, *E. Palmer 185a* (lectotype: US00124592! [designated by Powell 1974], isolectotypes: CAS0003920!, K000502199[photo!], GH00011097[photo!], NY00231050 [photo!], UC90499!).

***Notes:*** *Perityle aurea* is a rare, annual rock daisy endemic to gypsum substrates on the Baja California Peninsula. This species remains an evolutionary outlier within the rock daisy tribe that has been retained provisionally in the genus *Perityle* pending detailed study. Meiotic chromosome numbers reported by Powell for this species (*n*=17) as well as morphological traits such as yellow ray florets and heads bending back at maturity are similar to traits of *Laphamia,* including the sympatric *L. lobata.* On the other hand, *P. aurea* has an annual life history and fruits with pappus squammellae (scales) and a single pappus awn that terminates in a retrorse barb that matches the "grappling hook" also found in nearby *Perityle,* such as *P. robusta.* As noted by Powell (1974), there are two distinct growth forms of this species, one more succulent, robust, and glabrous, the other ephemeral, lower-statured, and puberulent. There is a possibility that *P. aurea* represents a homoploid hybrid species formed in situ on the Baja California Peninsula persisting in part due to a hybrid advantage associated with the extreme rock substrate of gypsum.

**8.2** **Perityle brandegeeana** Rose, Bot. Gaz. 15: 114, pl. 13, 1890. *Amauria brandegeeana* (Rose) Rydb., N. Amer. Fl. 34(1): 30, 1914. **TYPE:** Mexico, Baja California, Lagoon Head, 6-15 March 1889, *E. Palmer 800* (lectotype: US00124594! [designated by Powell 1974], isolectotypes: BKL00000174 [photo!], CAS0003922!, GH00011099 [photo!], NY00231051 [photo!]).

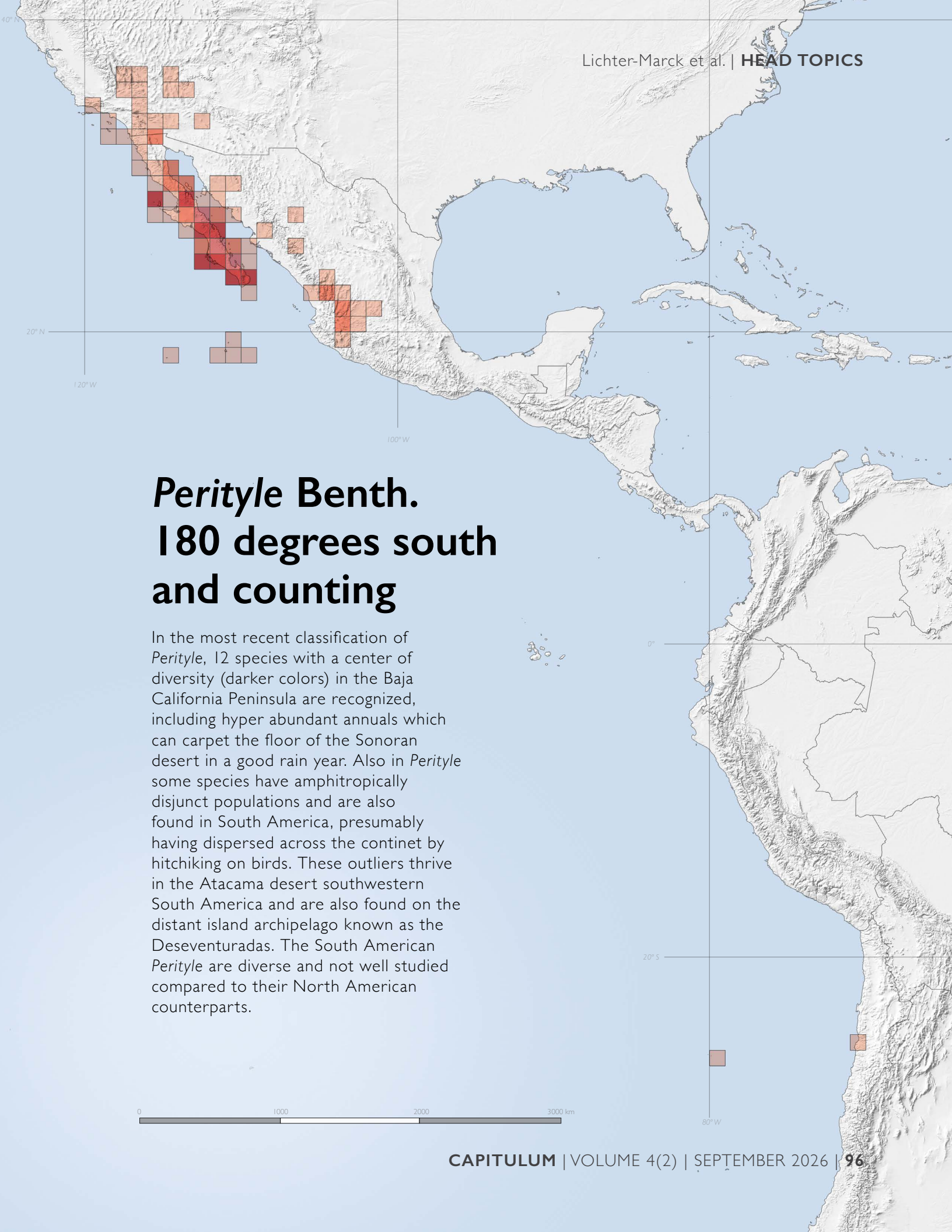
***Notes:*** In a good year on the Baja California Peninsula, *Perityle brandegeeana* is one of the most abundant annuals in low deserts from the Magdalena Plateau to the Vizcaino Peninsula. In poor rain years, however, it is scant and difficult to find. The combination of white rays and yellow disks, pungent glandular foliage, and herbaceous life history is typical of many of the *Perityle* on the peninsula. Until recently, *P. brandegeeana, P. carterae,* and *P. rotundifolia* were recognized in a different genus *Amauria,* endemic to the Baja California Peninsula, which had been a subject of fierce contention among rock daisy taxonomists for nearly a century. Townshend Brandegee was the first to submerge *Amauria* into *Perityle*, writing "the long doubtful genus *Amauria* disappears from our flora at last!" The genus was reinstated by Rydberg and has stood the test of time until now by virtue of the unique fruit characters that set these three species apart from other *Perityle*. The fruit is tetramerous with two wide sides and two narrow sides, giving it a rectangular shape in cross section. In *P. brandegeeana* the faces of the fruit are adorned with short, stubby cylindrical glands, which are found in no other *Perityle.*

**8.3** **Perityle californica** Benth., Bot. Voy. Sulphur [Bentham] 23, t. 15, 1844. **TYPE:** Mexico, Baja California Sur, Magdalena Bay, 1837, *R.B. Hinds s.n.* (lectotype: K000502285 [photo!] [designated by Powell 1974]).

*Perityle plumigera* Harv. & A.Gray ex A.Gray, Mem. Amer. Acad. Arts ser 2, 4(1): 77, 1849. **TYPE:** Mexico, Sonora, California, *T. Coulter 279* (lectotype: GH [designated by Powell 1974], isolectotypes: TCD0090361 [photo!], UC, US00124643).

*Perityle deltoidea* S.Watson, Proc. Amer. Acad., 24: 57, 1889. **TYPE:** Mexico, Baja California, Los Angeles Bay, 1887, *E. Palmer 568* (lectotype: GH00257541 [photo!] [designated by Powell 1974], isolectotypes: C10007749[photo!], NDG61159[photo!], NY00124605 [photo!], PH00021278[photo!], UC90503!, US00124605!, YU002282[photo!]).

***Notes:*** *Perityle californica* is the type species for the genus *Perityle* and is a ubiquitous annual in low desert environments in a good rain year in Baja California Sur and Sonora, Mexico, where it grows on decomposed soils, talus, and occasionally consolidated rocky outcrops. Phylogenetic data supports the monophyly




# *Perityle* Benth. 180 degrees south and counting

In the most recent classification of *Perityle*, 12 species with a center of diversity (darker colors) in the Baja California Peninsula are recognized, including hyper abundant annuals which can carpet the floor of the Sonoran desert in a good rain year. Also in *Perityle* some species have amphitropically disjunct populations and are also found in South America, presumably having dispersed across the continet by hitchiking on birds. These outliers thrive in the Atacama desert southwestern South America and are also found on the distant island archipelago known as the Deseventuradas. The South American *Perityle* are diverse and not well studied compared to their North American counterparts.

of this widespread species complex, which is unique among rock daisies for possessing chromosome number variation in a descending dysploid series (*n* = 13, 12, 11, 10; Powell 1974). In the Cape RegionCape Region, *P. californica* shows a parapatric distribution with *P. marginata* and *P. cuneata*, two close relatives that have been recognized as conspecific in the past but which are elevated as species in this work. *P. californica* is difficult to distinguish from each of these species based on inflorescence or vegetative characters but possesses a distinctive pappus of scales and a single awn with spreading barbs on the distal end.

**8.4** **Perityle carterae** (A.M.Powell) Lichter-Marck, Syst. Bot. 47(3): 811, 2022. *Amauria carterae* A.M.Powell, Madroño 21: 457, 1972. **TYPE:** Mexico, Baja California Sur, Sierra de la Giganta, Cerro Mechudo, 600 m alt., ca lat. 25° 55'N, long. 110° 45''W, 21 February 1970, *A. Carter 5439* (holotype: UC1367544!, isotypes: MEXU00158031 [photo!], TEX00000368 [photo!], US01049790 [photo!]).

***Notes:*** *Perityle carterae* is known only from areas surrounding the type locality on Cerro Mechudo, deep in the jagged backcountry of the Sierra la Giganta in Baja California Sur, Mexico. *Perityle carterae* is also the only woody suffrutescent perennial *Perityle* on the peninsula and grows on consolidated, volcanic rocks and cliffs. It was first collected by and named after Annetta Carter, a botanist based at the University Herbarium at U.C. Berkeley, who spent decades exploring and studying the flora of the rugged Sierra la Giganta, often on her own. Carter's herbarium specimens are a work of art and include exquisitely detailed (and sometimes whimsical) habitat information. Jose Luis León de la Luz, who worked closely with Carter for many years, has carried on studies of the Sierra, recollecting *P. carterae* on Cerro Mechudo in 2004 and making many other important discoveries, such as *Ambrosia humi* Leon de la Luz & Rebman. Following a rugged hike bushwacking through tropical thornscrub, I was able to observe and photograph *P. carterae* at Mesa las Tinajas, a prominent ridge near the type locality in 2018.

**8.5** **Perityle crassifolia** Brandegee, Proc. Calif. Acad. Sci. ser. 2, 3: 147, 1891. **TYPE:** Mexico, Baja California Sur, San Jose del Cabo, 6 October 1891, *T.S. Brandegee s.n.* (lectotype: UC90493! [designated by Powell 1974], isolectotypes: GH0001112[photo!], US00124603!).

***Notes:*** *Perityle crassifolia* var. *crassifolia* is a robust succulent perennial or annual that grows on coastal sand dunes, rocky sites, and saline decomposed soils in the Cape Region of Baja California Sur, Mexico where it is threatened by coastal development. Questions have been raised about the efficacy of the arachnoid-villous leaf pubescence to distinguish this variety from *P.* var. *robusta*, which is a hypervariable taxon. Leaves of *P.* var. *crassifolia* are generally highly dissected and crisped, giving a crumpled appearance, and the heads of *P. crassifolia* var. *crassifolia* become swollen around their equator upon maturity.

**8.5 A** **Perityle crassifolia** var. **robusta** (Rydb.) Everly, Contr. Dudley Herb. 3: 382, 1947. *Perityle robusta* Rydb. N. Amer. Fl. 34(1): 16. 1914. **TYPE:** Mexico, Baja California Sur, Cerralvo island, 19 April 1911, *J.N. Rose 16880* (lectotype: NY00231075 [photo!] [designated by Powell 1974], isolectotypes: UC415560!, US00124645[photo!]).

*Perityle incompta* Brandegee, Univ. Calif. Publ. Bot. 6: 503. 1919. **TYPE:** Mexico, Baja California Sur, Los Dolores, *W.E. Bryant s.n.* (lectotype: UC90513! [designated by Powell 1974].

*Perityle macromeres* S.F.Blake, Proc. Biol. Soc. Washington 37: 59. 1924. **TYPE:** Mexico, Baja California Sur, La Paz, *E.W. Nelson & E.A. Goldman 7483* (lectotype: US00124632! [designated by Powell 1974]).

***Notes:*** *Perityle crassifolia* var. *robusta* is a widespread herbaceous annual or perennial that grows in a wide variety of substrates and habitats in Baja California Sur, Mexico. It is a variable taxon that spans the range from individuals resembling *P. crassifolia* var. *crassifolia,* a silvery-pubescent and glandular coastal form, and *P. emoryi,* which is generally distributed further north and has greenish, glandular foliage, and smaller heads. Both varieties of *P. crassifolia* form a natural group with *P. socorrosensis,* which is endemic to the Revillagigedo archipelago, a group of four volcanic islands approximately 500 km south of the southern Baja California Peninsula.

**8.6** **Perityle cuneata** Brandegee, Zoe 1: 54, 1890. **TYPE:** Mexico, Baja California Sur, Sierra de la Laguna, near Todos Santos, 26 January 1890, *T.S. Brandegee s.n.* (lectotype: UC90467! [designated by Powell 1974], isolectotype: US00124604!).

***Notes:*** *Perityle cuneata* is found in the Sierra la Laguna of Baja California Sur, where it grows in decomposed soils and occasionally rock outcrops in tropical thorn scrub and oak forest habitats. The heads and leaves of *P. cuneata* tend to be larger than in *P. marginata* and the fruits differ from them in being cuneate, rather than obovate.

**8.7** **Perityle emoryi** Torr., Notes Milit. Reconn. [Emory] 142, 1848. **TYPE:** U.S.A., California, mountains east of San Diego, 29 November 1846, *W.H. Emory s.n.* (lectotype: NY00231039[photo!] [designated by Powell 1974]). Figure 46.

*Perityle nuda* Torr. ex A.Gray, Pacific Railr. Rep. 4(5, no. 4) [Whipple]. 100, 1857. *Perityle californica* var. *nuda* (Torr. ex A.Gray ) A.Gray, Syn. Fl. N. Amer. 1(2): 321. 1884. *Perityle emoryi* var. *nuda* (Torr. ex A.Gray ) A.Gray, Bot. California [W.H. Brewer] 1: 397, 1876. **TYPE:** U.S.A., California, Williams Fork, 7 February 1853–1854, *J.N. Bigelow s.n.* (lectotype: NY00231048[photo!] [designated by Powell 1974], isolectotype: GH00106295[photo!]).

*Closia cotula* J.Rémy, Fl. Chil. [Gay] 4(1): 120. 1849. **TYPE:** Chile, Copaipo, *C. Gay s.n.* (lectotype: P04337380[photo!] [**designated here**], isolectoptype: NY00167578[photo!]).

*Closia chilensis* Regel & Korn., Index Seminum [St. Petersburg (Petropolitanus)] 39, 1857. **TYPE:** Chile, Paposo, *R.A. Phillipi s.n.* (type: unknown )

*Closia pusilla* Phil., Fl. Atacam. 31, 1860. **TYPE:** Chile, Pan de Azucar, no date, *R.A. Phillipi s.n.,* (type: unknown).

*Closia discoidea* Phil., Fl. Atacam. 31, 1860. *Perityle discoidea* (Phil.) I.M.Johnst. Contr. Gray Herb. 85: 128, 1929. **TYPE:** location unknown (type: unknown).

*Closia anthemoides* Phil., Fl. Atacam. 31, 1860. **TYPE:** Chile, *R.A. Philippi s.n.* (lectotype: SGO000005249! [**designated here**], isolectotypes: B, F[photo!]).

*Closia elata* Phil., Fl. Atacam. 31, 1860. *Closia cotula var. elata* (Phil.) Reiche, Anales Univ. Chile 112: 159, 1903. *Perityle emoryi var. elata* (Phil.) I.M.Johnst. Contr. Gray Herb. 85: 128, 1929. **TYPE:** Chile, no date, *A.R. Philippi s.n.* (lectotype: SGO000005255! [**designated here**]).

*Perityle fitchii* var. *palmeri* A.Gray, Syn. Fl. N. Amer. 1(2): 321, 1884. *Perityle grayi* Rose, Bot. Gaz. 15: 114, 1890. **TYPE:** Mexico, Baja California, Guadalupe Island, *E. Palmer 44* (lectotype: GH00011120 [photo!] [designated by Powell 1974], isolectotypes: US, NY).

*Perityle rothrockii* Rose, Bot. Gaz. 15: 114, 1890. **TYPE:** U.S.A., Nevada, *G.M. Wheeler s.n.*(lectotype: US00124647! [designated by Powell 1974]).

*Perityle greenei* Rose, Bot. Gaz. 15: 114, 1890. **TYPE:** U.S.A., California, Santa Cruz Island, Jul–Aug 1886, *E.L. Greene s.n.* (lectotype: NDG61165 [designated by Powell 1974], isolectotypes: GH00011122[photo!], NY00231041, UC, US00124615[photo!]).

*Perityle emoryi* var. *orcuttii* Rose, Bot. Gaz. 15: 114, 1890. **TYPE:** Mexico, Baja California, Sierra Juarez, Cantillas Canyon, *C. R. Orcutt 1102* (lectotype: US01101238! [designated by Powell 1974], isolectotype: GH00011077[photo!]).

*Closia brachypetala* Phil., Anales Univ. Chile, 87: 711, 1894. **TYPE:** Chile, no date, *R.A. Philippi s.n.* (lectotype: SGO065342! [**designated here**]).

*Closia digitata* Phil., Anales Univ. Chile 87: 711, 1894. **TYPE:** Chile, no date, collector unknown (lectotype: SGO000005253! [**designated here**]).

*Closia elata* var. *nana* Phil., Anales Univ. Chile 87: 711, 1894. **TYPE:** Chile, no date, collector unknown (type: unknown).

*Closia foliosa* Phil., Anales Univ. Chile 87: 711, 1894. **TYPE:** Chile, no date, *R.A. Philippi s.n.* (lectotype: SGO000005257! [**designated here**]).

*Closia viridis* Phil., Anales Univ. Chile 87: 711, 1894. **TYPE:** Chile, no date, *R.A. Philippi s.n.* (syntypes: B, F[photo!], SGO).

*Closia villosa* Phil., Anales Univ. Chile 87: 711, 1894. **TYPE:** Chile, Cordilleras east of Copaipo, no date, R.A. *Phillipi s.n.* (type: unknown).

***Notes:*** *Perityle emoryi* is the most widespread species complex in tribe Perityleae and is found throughout low desert environments in northern Mexico and the southwest U.S. as well as the Atacama Desert in northern Chile and southwestern Peru. *Perityle emoryi* grows in a wide variety of habitats including decomposed soils, seeps, and rocky outcrops. It ranges from a minute ephemeral




**Figure 46.** *Perityle emoryi* Torr. is a self compatible annual that grows in both decomposed and rocky substrates. it is one of the most widespread species of rock daisies, occurring both in North and South America. **A.** Habit; this individual germinated and it is thriving despite it being an extremely dry year in the Atacama desert. **B.** Lateral view of the compact, urceolate involucre, and the densely glandular and non-glandular trichomes on the phyllaries. **C.** Superior view of the radiate capitulum showing white ray corollas and yellow disc floret corollas. **D.** Close up of two-sided carbonized cypselae with callous, ciliate margins. *Photos by Isaac Lichter-Marck.*

annual to a robust herbaceous perennial, especially where it is found growing on maritime islands or in perennially moist places. Phylogenetic data show *P. emoryi* to have a complex evolutionary history as an allopolyploid hybrid species. South American populations long referred to this species do not form a monophyletic group with populations of *P. emoryi* from North America and are more closely related to *P. crassifolia*. The South American populations therefore constitute at least one, and possibly several, unrecognized taxa. In the past, the hypervariable populations of *P. emoryi* found in the Atacama Desert had been classified in a separate genus *Closia* with fourteen species. In addition to clarifying the nomenclatural complexity of *Closia,* recent field and herbarium work in Chile has aimed at resolving the appropriate number of taxa to reinstate for Chilean *Perityle*. The Desventuradas Islands endemic rock daisy *Perityle tenuifolius* is phylogenetically nested within samples from the Atacama Desert, suggesting that Chilean *Perityle* are the result of both intercontinental and trans-oceanic long distance dispersal events.

**8.8** **Perityle marginata** Rydb., N. Amer. Fl. 34(1): 14, 1914. *Perityle cuneata* var. *marginata* (Rydb.) I.M.Johnst., Proc. Calif. Acad. Sci. ser. 4, 12: 1204, 1924. **TYPE:** Mexico, Baja California Sur, San Jose del Cabo, 25 March 1911, *J.N. Rose 16349* (lectotype: NY00231069[photo!] [designated by Powell 1974], isolectotypes: UC415558!, US00124633!). Figure 47.

***Notes:*** Phylogenetic, biogeographic, morphological, and cytological data all support recognition of *P. cuneata* and *P. marginata* as distinct entities at the species rank. *Perityle marginata* is a widespread




**Figure 47.** *Perityle marginata* Rydb. is an herbaceous annual that grows in decomposed substrates at low elevations of the cape region of Baja California Sur. **A.** Habit; an individual showing the weedy habit, growing in decomposed granite at the edges of a road. **B.** Lateral view of capitulum. **C.** Superior view of radiate capitulum showing the yellow corollas. **D.** Involucre phyllaries of this species and many close relatives reflex at maturity, exposing the cypselae, which have two-sided with ciliate margins and a crown of scales and awns. *Photos by Isaac Lichter-Marck.*

annual that grows in decomposed soils at low elevations in the Cape Region of Baja California Sur, Mexico, occurring in arid thornscrub and coastal environments, and has 12 chromosomes. *Perityle cuneata* occurs at mid to high elevations in the Sierra de la Laguna and has 16 chromosomes. Populations of these plants included in phylogenetic analyses form a grade, with *P. californica* sister to *P. cuneata* sensu stricto, and *P. marginata* shows a parapatric (non-overlapping but neighboring) distribution with both *P. californica* and *P. cuneata*.

**8.9** **Perityle rosei** Greenm., Proc. Amer. Acad. Arts 40: 45, 1904. **TYPE:** Mexico, Jalisco, Bolaños, 15-17 September 1897, *J.N. Rose 2947* (lectotype: US00124646! [designated by powell 1974], isolectotypes: GH00011136[photo!], K000502191[photo!], NY00231076).

*Perityle trichodonta* S.F.Blake, Soc. Biol. Washington 37: 60, 1924. **TYPE:** Mexico, Jalisco, Sierra Madre west of Bolaños, 15–17 September 1897, *J.N Rose 2978* (Lectotype: US00124658!, [designated by Powell 1974], isolectotypes: GH00011139[photo!], K000502189[photo!]).

***Notes:*** *Perityle rosei* and *P. trichodonta* are recognized as one species here, as suggested by Powell (1974). Both were described based on type specimens collected in the village of Bolaños, Jalisco, in the southern Sierra Madre Occidental, and the nearly identical type locality and similarity between the two taxa has made them difficult to distinguish in collections made elsewhere, where the two names have been used interchangeably. Phylogenetic data suggests that *P. rosei* in the new, expanded sense, along with an anomalous population of rock daisy collected in the Sierra la Primavera by Pablo Carrillo Reyes and ILM, may constitute a cryptic undescribed genus more closely

related to *Eutetras* than to *Perityle* or *Galinsogeopsis*. *Perityle rosei* is similar to species of *Galinsogeopsis* found nearby, such as *G. harkerae, G. feddemae*, and *G. glaucescens*, but also shares habitat characteristics and an abutting distribution with members of *Eutetras*. Although fruits of *P. rosei* are typically two-sided, occasionally on herbarium specimens fruits have been observed that are tetramerous (square in cross section), a trait typical of *Eutetras*. These plants need to be studied in more detail.

**8.10 Perityle rotundifolia** (Benth.) Brandegee, Zoe 4: 210, 1893. *Amauria rotundifolia* Benth., Bot. Voy. Sulphur [Bentham], 31, 1844. **TYPE:** Mexico, Baja California, San Quintin, 1841, *R.B Hinds s.n.* (lectotype: K000502240[photo!] [designated by Powell 1972]).

*Perityle fitchii* Torr. ex. A.Gray Pacif. Railr. Rep. 4 (5 no. 4) [Whipple]. 100, 1857. **TYPE:** Mexico, Baja California, *Rev. A. Fitch s.n.* (lectotype: NY [designated by Powell 1972], isolectotype: US00124610[photo!]).

*Laphamia peninsularis* Greene, Bull. Calif. Acad. Sci. 1(1): 8, 1884. **TYPE:** Mexico, Baja California, Scammon's Lagoon, *collector unknown* (lectotype: US00124642! [designated by Powell 1972], isolectotype: GH).

***Notes:*** *Perityle rotundifolia* is a widespread annual or herbaceous perennial rock daisy that is common in a good rain year in Baja California Sur. At the southern end of its range it can be an abundant ephemeral annual, and in the north it is typically a more robust perennial. This taxon is one of the species that until recently has been classified in a separate genus, *Amauria*. The fruits are of the *Amauria* type. They are tetramerous, with two of the sides notably wider than the others. The fruit is epappose and lacks the cylindrical glands present on the cypsela surface in *P. brandegeeana.*

**8.11 Perityle socorrosensis** Rose, Bot. Gaz. 15: 118 pl. 13, 1890. **TYPE:** Mexico, Colima, Revillagigedo archipelago, Socorro Island, March 1889, *G.H. Townshend s.n.* (lectotype: US00124654! [designated by Powell 1974], isolectotypes: GH, K, NY).

***Notes:*** *Perityle socorrosensis* is endemic to the Revillagigedo archipelago approximately 500 km south of the Baja California Peninsula. This species has been photographed and collected recently by Jon Rebman and Sula Vanderplank, showing the variability within and between islands. Further sampling might support recognizing these entities as distinct taxa. An interesting evolutionary question concerns the progressive loss of pappus elements, which correlated with dispersal limitation, on the more distant islands. Phylogenetic data thus far have shown that all island populations are closely related to populations of *P. crassifolia* found the Baja California Peninsula, and that these in turn are sister to populations from the Atacama Desert, suggesting a possible link to trans-oceanic dispersal to coastal northern Chile.

**8.12 Perityle tenuifolius** (Phil.) Lichter-Marck, Syst. Bot. 47(3): 811, 2022. *Lycapsus tenuifolius* Phil., Bot. Zeitung (Berlin) 28: 499, t. 8, 1870. *Alomia tenuifolia* (Phil.) Benth. & Hook.f. ex Reiche, Flora de Chile 3(59): 255–330, 1901. **TYPE:** Chile, Islas Desventuradas, rocas al sur de San Ambrosio, 1869, *Simpson s.n.* (syntypes: GH00009901 [photo!], K, SGO, US!).

***Notes:*** *Perityle tenuifolius* is so distinct from other rock daisies that it has been classified as a separate, monotypic genus, *Lycapsus*, and at times has been placed in its own subtribe, Lycapsinae. Phylogenetic data robustly supports this species as nested within the genus *Perityle,* suggesting that its unique traits evolved as adaptations to its insular environment. This same pattern of insular endemics to the Desventuradas Islands being found to be nested within a more widespread genus has also been found for *Sanctambrosio* (Caryophyllaceae), in contrast to *Thamnoseris* (Compositae), which is the sister lineage to the diverse Juan Fernandez endemic genus *Dendroseris* (Kool and Thulin 2017; Cho et al. 2024). Recent field work on the island of San Felix and San Ambrosio by Lukas Mekis has revealed new aspects of the ecology of this species that may have accelerated its morphological evolution. It is a derived woody perennial that forms large clumps on sea cliffs, where it is regularly used as nesting and roosting shelter for seabirds. The leaves are deeply divided and succulent, and presumably aide in drought tolerance or fog capture. Four-lobed florets match this species to tribe Perityleae; however, the heads appear more open because they possess paleae throughout the receptable, a trait not seen in any other rock daisy. Some questions remain regarding the reproductive mode of *P. tenuifolius.* It is unclear if the disk florets are

# Somewhere over the rainbow

Rock daisies grow in scattered locations across thousands of kilometers of mostly road-less, arid terrain. As you explore further and further into the desert, the stakes at play get higher and higher. Eventually you get to a point when you become walking a fine line. It's the line between possibly finding the discovery of a lifetime, or possibly getting into a situation that could end it. The landscape is harsh, unforgiving, desolate. The brief periods of good weather that produce flowers are short, far and in between. Help, if you need it, is often far away. But when all the stars align, and the rains arrive on time and produce outstanding blooms, you can experience the most amazing phenomena.



*Somewhere in Baja California Norte, Mexico. Photo by Isaac Lichter-Marck*

monoclinouos or functionally staminate and sterile, as they do not appear to produce fruit despite possessing a gynoecium.

## UNCERTAIN NAMES:

*Chlamysperma polygama* Triana, Ann. Sci. Nat. Bot., ser. 4 9: 40, 1858. **TYPE:** Colombia, Cundinamarca, Anapoima, *Triana J.J. 1525* (lectotype: COL000004839[photo!] [**here designated**]).

***Notes:*** *Chlamysperma polygama* was collected as part of J Triana's expedition in Colombia 1851-1857. It is a sparse specimen with few leaves and minute heads. From the photograph of the type specimen available online it is difficult to confirm the identity with certainty but the determination of Santiago Diaz of *Galeana pratensis* is probably in error given that *G. pratensis* is only known to occur in Mexico.

*Villanova pinnatifida* Lag., Gen. Sp. Pl. [Lagasca] 31, 1816. **TYPE:** Argentina, Falkland (Malvinas) Islands, *collector unknown* (type: unknown).

***Notes:*** *Villanova pinnatifida* is described in *Genera et Species Plantarum* as being from the Falkland Islands. No mention of the species could be found in contemporary floristic work from the islands and we assume it refers to a different accepted name of a taxon of another genus; however, the type still needs to be located and investigated before any definitive assignment is given.

## EXCLUDED NAMES:

*Amauria dissecta* A.Gray, Mem. Amer. Acad. Arts n.s., 4: 104, 1849. ≡ **Hymenothrix dissecta** (A.Gray) B.G.Baldwin, Taxon 65(5): 1074, 2016 (tribe Bahieae).

*Villanova bipinnatifida* Ortega, Nov. Rar. Pl. Descr. Dec. 47, 1797. = **Parthenium hysterophorus** L., Sp. Pl. 2: 988, 1753 (tribe Heliantheae).

*Villanova biternata* (A.Gray) Wooten & Standl., Contr. U.S. Natl. Herb. 19: 725, 1915. ≡ **Hymenothrix biternata** (A.Gray) B.G.Baldwin, Taxon 65(5): 1074, 2016 (tribe Bahieae)

*Villanova chrysanthemoides* A.Gray, Smithosnian Contr. Knowl. 5(6): 96, 1853. = **Hymenothrix biternata** (A.Gray) B.G.Baldwin, Taxon 65(5): 1074, 2016 (tribe Bahieae).

*Villanova dissecta* (A.Gray) Rydb., Bull. Torrey Bot. Club 37: 333, 1910. ≡ **Hymenothrix dissecta** (A.Gray) B.G.Baldwin, Taxon 65(5): 1074, 2016 (tribe Bahieae).

## DISCUSSION

### Taxonomic overview

The 90 currently recognized minimum-rank taxa in tribe Perityleae include dramatic examples of plant insular diversification and disparity that continue to beguile those of us who study them. The common name "rock daisy" for the North and South American representatives of the tribe Perityleae was most likely inspired by the species that grow on consolidated barren rock outcrops and vertical to overhanging cliffs. This tendency is most common in the genera *Laphamia* and *Galinsogeopsis*, which are two clades that have speciated extensively onto far-flung, and often geologically distinct, canyons, and sky islands. The recent eco-geographic evolution of these highly specialized cliff-dwelling rock daisies occurred in parallel with the radiation of the genus *Perityle,* which occurs widely across the Americas and is distributed over a wide range of habitats and soils in tropical forests, hyper-arid deserts, and high alpine tundra.

Most rock daisies are rare plants found in difficult-to-access habitats scattered across thousands of miles of roadless terrain, and our knowledge of the basic biology and natural history of taxa in this group has in many cases been assembled from few collections and observations. The goal of this collaborative work was to spark the process of gathering those scattered bits of knowledge into one location as a first step on the path to building a comprehensive understanding of Perityleae. Besides stimulating monographic work, our hope is that the list of accepted names and synonyms for specific and infraspecific taxa in Perityleae compiled for the first time here also serves as a resource for herbarium curators, field biologists, and dedicated naturalists. The detailed notes on recent discoveries and taxonomic puzzles are meant to inspire collaborative

# Risk it for a biscuit

The bare, rocky outcrops on which many Perityleae are found, are hotspots for unique plant diversity, but botanists have to risk their lives to study these rare species. Many botanists have met their end while collecting on cliffs. In 1932, the botanist Ralph Hoffman famously fell to his death while collecting a rare *Dudleya* Britton & Rose (Crassulaceae) species on a steep cliff in the California channel islands. Legend has it that they found his body still clutching the succulent in hand, and after colleagues pressed the plant and studied it in detail, it was named in his honor.

*Mesa de Caballos, Jalisco, Mexico. Photo by Isaac Lichter-Marck*

efforts to scour collections, organize expeditions to collect new specimens and take photos, and make carefully documented observations in the field to learn whatever we can about these rare, specialized, and sometimes endangered plants.

## Contributions to our understanding of rock daisies

To our knowledge, the nomenclator and checklist presented here accounts for all taxonomic names that have been validly published and applied to the tribe Perityleae. In total, 273 names are accounted for, including 90 accepted minimum rank taxa, 125 homotypic synonyms, 53 heterotypic synonyms, and 5 names that apply to taxa in other tribes of Compositae. Type specimen details are given for the vast majority of the 143 designated basionyms in Perityleae; however, types have not yet been located for some names, especially those in the strictly South American genus *Closia*, which is now recognized as being included in *Perityle*. Some types are lost; for example, Rodgers and Spellenberg (2023) were unable to locate the holotype of *Laphamia staurophylla* var. *homoflora*, which was supposedly deposited in the Steere Herbarium at the New York Botanical Garden.

The vast majority of validly published names applicable to Perityleae were published before 1958, when the International Code of Nomenclature first required that new species descriptions designate an explicit holotype. Most, though not all, of these pre-1958 names instead had multiple specimens, or an entire gathering, designated as types. Powell's monographic work on Perityleae (1969, 1973a, 1974) listed type information for each taxon, specifying a single herbarium as holding the holotype — thereby inadvertently lectotypifying the majority of names in the tribe. Here, we follow articles 9.11, 9.17, 9.19 and recommendation 9C of the Madrid Code (Turland et al. 2025). Where Powell's lectotypification was incomplete, or unclear because more than one specimen was held in the herbarium he indicated, we have completed the process with a second step lectotypification.

The 90 accepted minimum-rank taxa of Perityleae were grouped into three subtribes by Panero (2007). The monotypic subtribe Lycapsinae however, is nested within Peritylinae. Here, and going forward, we therefore recognize only two subtribes, Galeaninae and Peritylinae. In total, the tribe Perityleae includes 8 currently recognized genera with the following number of minimum rank taxa: *Eutetras* (2), *Galeana* (1), *Galinsogeopsis* (15), *Laphamia* (52), *Nesothamnus* (1), *Pericome* (2), *Perityle* (13), and *Villanova* (4). Future work needs to carefully consider the generic placement of two taxa, *Perityle aurea* and *Perityle rosei*. *Perityle aurea* is a rare species found on gypsum outcrops in Baja California Sur, Mexico where it is threatened by mining exploitation. This species has not yet been included in molecular phylogenies and shows similarities with two genera, *Perityle* and *Laphamia*. *Perityle rosei,* which is here treated broadly to include *Perityle trichodonta*, was included in molecular studies and found to be more closely related to long recognized species in the genus *Eutetras* than to any of the taxa in *Perityle*, suggesting it may constitute a cryptic ninth genus of rock daisies.

In the aftermath of recent taxonomic rearrangements and in the process of compiling this nomenclator, several minor but significant nomenclatural changes needed to be made. Since the main goal of this nomenclator was to account for all previously published scientific names applied to tribe Perityleae and not to create new ones, we refrained from making novel combinations and describing new species here. Instead, the changes presented here are cases where the synonymy has been previously published. To summarize taxonomic novelties presented here, we elevated two infraspecific taxa to species level (*Perityle cuneata* and *Perityle marginata*), we placed five names in synonymy (*Galinsogeopsis stevensii* [synonym of *Galinsogeopsis canescens*], *G. pennellii* [synonym of *G. hofmeisteria*], *G. scopulorum* and *G. pseudociliata* [both synonyms of *G. coronopifolia*], and *Perityle trichodonta* [synonym of *P. rosei*], and we reinstated basionyms with nomenclatural priority in three cases, involving two new combinations and four names (*Galinsogeopsis microglossa* var. *migroglossa*, *G. microglossa* var. *saxosa*, *Laphamia toumeyi,* and *Villanova anemonifolia*). New names and new combinations will no doubt need to be published in the near future to account for the full diversity in tribe Perityleae. One benefit moving forward is that this nomenclator clarifies all previously proposed names, reducing confusion about when and where new names are needed, and helping to avoid duplicated effort.



# Adaptation on the sharp edge

Sheer cliffs are among the world's most iconic landmarks but our knowledge of the enigmatic plants that live in them is as fragmented as a chossy rock face. Plants of many distantly related families live on cliffs, some extravagant and others cryptic. Wherever they are coming from, these plants converge on similar traits, specialized root structures, drought tolerant leaves, reductions in dispersability, and so on. A remarkable case of convergence between rock daisies and rock nettles (*Eucnide aurea* (A.Gray) H.J.Thomps. & W.R.Ernst in the Loasaceae shown here) occurs on cliffs in Baja California. The leaves are sometimes so similar that they are difficult to distinguish in the absence of blooms. The flowers couldn't be more distinct, but one of the most remarkable things occurs as the fruits mature. Both species have independently evolved self-sowing behaviors, in which the heads bend back towards the cliff upon maturity, dispersing seeds back into the nooks and crannies.

*Sierra de la Giganta, Baja California Sur, Mexico. Photo by Isaac Lichter-Marck*

## The lost rock daisies and recent discoveries from the field

The annotated taxonomic checklist presented here is accompanied by general notes about ecology and distribution, and where relevant, highlights of recent fieldwork that has expanded our natural history knowledge of rock daisies. We uncovered ten cases in which rock daisies that had been "lost" for decades, or in some cases over a century, were recently "rediscovered" through the efforts of dedicated field botanists. Most of these rediscoveries have been in the difficult-to-access and understudied Sierra Madre Occidental in northwest Mexico or in adjacent thornscrub habitats in Sonora, Mexico. These include *Galinsogeopsis canescens*, *G. feddemae*, *G. lineariloba*, *G. montana*, *Laphamia grandifolia*, *L. lloydii, L. vandevenderi,* and *Pericome macrocephala*. Most of these rediscoveries have occurred when field botanists revisited notable collecting localities of early collectors such as Edward Palmer from which the type specimens of numerous taxa were originally described. In most cases, individual plants at these locations have been relatively well conserved but not studied in detail in decades. In contrast, new populations of *Galinsogeopsis lineariloba* and *Pericome macrocephala,* two taxa that were previously known only from century-old collections, have been rediscovered hundreds of kilometers away from the type locality, drastically expanding the range for these understudied taxa.

First photographs of rock daisies have surfaced for dozens of species and have been critical for clarifying the ecology of rare species, including their preferences for bare, rocky habitats and particular rock substrate types (lithologies). Based on publicly available data and the information compiled here, first photographs have surfaced for 16 taxa. These include *Galinsogeopsis canescens, G. feddemae, G. lineariloba, G. montana, G. vigilans, Laphamia bisetosa* var. *bisetosa, L. bisetosa* var. *scalaris, L. dissecta, L. gentryi, L. gilensis* var. *salensis, L. grandifolia, L. vandevenderi, L. villosa, Perityle carterae, P. socorrosensis*, and *Villanova robusta* (Fig. 3). Photographs of rare rock daisies have most often surfaced along with new collections made by professional field botanists, thanks in part to the greater ease and availability of digital photography. In other cases, photographs submitted to iNaturalist by dedicated observers have turned out to be significant rock daisy discoveries. For example, from Sierra Mohinora, an isolated peak in the Sierra Madre Occidental, two iNaturalist users, Maria de Los Angeles Olvera (@angie_olvera) and Aaron Balam (@aaronbalam_tutor), uploaded the first photographs to our knowledge of the rare, enigmatic *Galinsogeopsis montana*, which is so distinct from other rock daisies that it was once recognized within its own monotypic genus, *Correllia.* These photographs revealed for the first time that *G. montana* represents one of a specialized and highly endemic assemblage of plant species in the Sierra Madre Occidental that grow on mud-flow deposits in mesic forests, a unique edaphic environment that presumably drove the recent evolution of this species' unique morphological features.

Despite the extensive efforts by botanists of all backgrounds to document rock daises, we found that there are still at least ten rock daisy taxa that remain "lost," meaning that we lack information about their contemporary status and whereabouts. For these taxa, we often have been able to study herbarium collections made decades in the past to assess their validity as distinct taxa of rock daises but have not been able assess the current state of these taxa in terms of their persistence, demographics, or ecology. The lost rock daisies include *Laphamia bisetosa* var. *appressa, Laphamia bisetosa* var. *spathulata*, *L. carmenensis, L. castillonii, L. cinerea, L. fosteri, L. huecosensis, L. vitreomontana, L. warnockii*, and *Villanova titicacaensis*. Apart from *V. titicacaensis*, which occurs in Peru and Bolivia, all the lost rock daises are narrowly distributed taxa on private land in western Texas. Texas is a majority privately-owned state, with 93% of the territory in the hands of ranchers and other private interests, and access for field biologists has been severely restricted in this biodiverse region for decades.

New observations of rock daisies that in the past were known from few collections has clarified many aspects of the biology of rare species, but in many cases it has also revealed taxonomic complexities that will need closer study before they are resolved. A priority focus for ongoing research on rock daisies is to resolve taxonomic puzzles in the following species complexes: *Galinsogeopsis feddemae, G. hofmeisteria, Laphamia ambrosiifolia, L. cordifolia, L. gracilis, L. lemmonii, L. megalocephala , L. parryi, L. villosa*, *Perityle emoryi,* and *P. rosei*. For instance, ongoing research in the Atacama Desert in Chile on amphitropically disjunct populations of *Perityle*

# On the origins of cliff species

How did so many species of plants that grow on vertical cliffs evolve? This has been a topic of debate among botanists for decades. The most common families tend to be the ones that are good at living in other stressful environments like deserts, Composites, succulents, xeric ferns, spiny, drought-tolerant shrubs, etc. This makes sense, since cliff environments really are a lot like micro-deserts. Yet deserts are young biomes on a geological time scale, whereas rocky outcrops have been a perennial feature of the earth's landscape through time. This raises the possibility that cliffs might be a special type of stressful environment for plants: the original place where the ancient ancestors of stress tolerant plant lineages evolved.



*Igneous cliffs in the Gila Mountains, New Mexico. Photo by Sophia Winitsky.*

*emoryi* will greatly benefit from the accounting of synonyms for South American *Perityle* compiled here. In the past, populations of *Perityle* found in Chile were recognized in a separate genus *Closia* with more than a dozen distinct species. Currently all this previously recognized species diversity is lumped into one extremely widespread species complex, *Perityle emoryi,* found both in North and South America. Sampling in the field and herbarium in 2024 is aimed at circumscribing distinct species of the South American *Perityle* into readily diagnosable taxonomic units and testing these using molecular data.

The rock daisy tribe is only moderately diverse by the standards of other tribes of Compositae, yet it is a group where description of new species has continued without reaching an apparent plateau. This is due in part to the difficult-to-study terrain in which rock daisies grow, and the insular nature of these habitats, which makes these plants prone to diversify locally into many narrow endemics that can be difficult to find. Anomalous populations of rock daisies that may meet the criteria for new species once they can be studied in detail are common. Field botanists and naturalists are encouraged to document rock daisies wherever they are found, especially those encountered while exploring difficult to reach vertical rock habitats in arid or subtropical terrain. All are welcome to join the collaborative effort to learn as much as we can about these eccentric plants and their fascinating natural history.

## NOMENCLATOR

Accepted names are in **bold**.
Homotypic synonyms marked with ≡
Heterotypic synonyms marked with =

*Alomia tenuifolia* (Phil.) Benth. & Hook.f. ex Reiche
≡ **Perityle tenuifolius** (Phil.) Lichter-Marck
*Amauria* Benth. = **Perityle** Benth.
*Amauria brandegeeana* (Rose) Rydb.
≡ **Perityle brandegeeana** Rose
*Amauria carterae* A.M.Powell
≡ **Perityle carterae** (A.M.Powell) Lichter-Marck
*Amauria dissecta* A.Gray,
≡ **Hymenothrix dissecta** (A.Gray) B.G.Baldwin (tribe Bahieae)
*Amauria rotundifolia* Benth.
≡ **Perityle rotundifolia** (Benth.) Brandegee
*Chlamysperma* Less. = **Galeana** La Llave
*Chlamysperma arenarioides* Hook. & Arn.
= **Galeana pratensis** (Kunth) Rydb.
*Chlamysperma polygama* Triana **insertae sedis**
*Chlamysperma pratense* (Kunth) Less.
≡ **Galeana pratensis** (Kunth) Rydb.
*Closia* J.Rémy = **Perityle** Benth.
*Closia anthemoides* Phil. = **Perityle emoryi** Torr.
*Closia cotula* J.Rémy = **Perityle emoryi** Torr.
*Closia brachypetala* Phil. = **Perityle emoryi** Torr.
*Closia chilensis* Regel & Körn. = **Perityle emoryi** Torr.
*Closia digitata* Phil. = **Perityle emoryi** Torr.
*Closia elata* Phil. = **Perityle emoryi** Torr.
*Closia elata* var. *nana* Phil. = **Perityle emoryi** Torr.
*Closia foliosa* Phil. = **Perityle emoryi** Torr.
*Closia viridis* Phil. = **Perityle emoryi** Torr.
*Closia villosa* Phil. = **Perityle emoryi** Torr.
*Corellia* A.M.Powell = **Galinsogeopsis** Sch.Bip.
*Corellia montana* A.M.Powell
≡ **Galinsogeopsis montana** (A.M.Powell) Lichter-Marck
**Eutetras** A.Gray
**Eutetras palmeri** A.Gray
**Eutetras pringlei** Greenm.
**Galeana** La Llave
*Galeana hastata* La Llave
= **Galeana pratensis** (Kunth) Rydb.
**Galeana pratensis** (Kunth) Rydb.
**Galinsogeopsis** Sch.Bip.
**Galinsogeopsis canescens** (Everly) Lichter-Marck
**Galinsogeopsis ciliata** (L.H.Dewey) Lichter-Marck
**Galinsogeopsis coronopifolia** (A.Gray) Lichter-Marck
**Galinsogeopsis feddemae** (McVaugh) Lichter-Marck
**Galinsogeopsis glaucescens** (B.L.Turner) Lichter-Marck
**Galinsogeopsis harkerae** (P.Carrillo) Lichter-Marck
**Galinsogeopsis hofmeisteria** (Rydb.) Lichter-Marck
**Galinsogeopsis jaliscana** (A.Gray) Lichter-Marck
**Galinsogeopsis lineariloba** (Rydb.) Lichter-Marck
**Galinsogeopsis montana** (A.M.Powell) Lichter-Marck
**Galinsogeopsis microcephala** (A.Gray) Lichter-Marck
**Galinsogeopsis microglossa** (Benth.) Lichter-Marck
**Galinsogeopsis microglossa** var. **saxosa** (Brandegee) Lichter-Marck
*Galinsogeopsis pennellii* (B.L.Turner) Lichter-Marck
= **Galinsogeopsis hofmeisteria** (Rydb.) Lichter-Marck
*Galinsogeopsis pseudociliata* (A.M.Powell & Yarborough) Lichter-Marck = **Galinsogeopsis coronopifolia** (A.Gray) Lichter-Marck

*Galinsogeopsis scopulorum* (M.E.Jones) Lichter-Marck
= **Galinsogeopsis coronopifolia** (A.Gray) Lichter-Marck
*Galinsogeopsis spilanthoides* var. *saxosa* (Brandegee) Lichter-Marck ≡ **Galinsogeopsis microglossa** var. **saxosa** (Brandegee) Lichter-Marck

*Galinsogeopsis spilanthoides* Sch.Bip. in B.Seemann var. *spilanthoides* = **Galinsogeopsis microglossa** (Benth.) Lichter-Marck var. **microglossa**
*Galinsogeopsis stevensii* (B.L.Turner) Lichter-Marck
= **Galinsogeopsis canescens** (Everly) Lichter-Marck
**Galinsogeopsis turneri** (A.M.Powell) Lichter-Marck
**Galinsogeopsis vigilans** (Spellenb. & A.M.Powell) Lichter-Marck
**Laphamia** A.Gray
**Laphamia aglossa** (A.Gray) Benth. & Hook.f. ex Hemsl.
**Laphamia ajoensis** (Todsen) Lichter-Marck
**Laphamia ambrosiifolia** (Greene ex A.M.Powell & Yarborough) Lichter-Marck
**Laphamia angustifolia** A.Gray
*Laphamia angustifolia* var. *laciniata* Torr.
= **Laphamia angustifoli**a A.Gray
*Laphamia arizonica* Eastw.
= **Laphamia gilensis** M.E.Jones var. **gilensis**
**Laphamia batopilensis** (A.M.Powell) Lichter-Marck
**Laphamia bisetosa** var. **appressa** (A.M.Powell) Lichter-Marck
**Laphamia bisetosa** Torr. var. **bisetosa**
**Laphamia bisetosa** var. **scalaris** (A.M.Powell) Lichter-Marck
**Laphamia bisetosa** var. **spathulata** (A.M.Powell) Lichter-Marck
**Laphamia carmenensis** (A.M.Powell) Lichter-Marck
**Laphamia castillonii** (I.M.Johnst.) Everly
**Laphamia cernua** Greene
*Laphamia ciliata* L.H.Dewey
≡ **Galinsogeopsis ciliata** (L.H.Dewey) Lichter-Marck
**Laphamia cinerea** A.Gray
**Laphamia coahuilensis** (A.M.Powell) Lichter-Marck
**Laphamia cochisensis** W.E.Niles
*Laphamia congesta* M.E.Jones
= **Laphamia toumeyi** B.L.Rob. & Greenm.
**Laphamia cordifolia** (Rydb.) Lichter-Marck
**Laphamia dissecta** Torr.
*Laphamia dura* A.Nelson
= **Laphamia gilensis** M.E.Jones var. **gilensis**
*Laphamia fastigiata* Brandegee
= **Laphamia gracilis** M.E.Jones
**Laphamia fosteri** (A.M.Powell) Lichter-Marck
**Laphamia gentryi** (A.M.Powell) Lichter-Marck
*Laphamia gilensis* subsp. *longiloba* W.E.Niles
= **Laphamia gilensis** var. **salensis** (A.M.Powell) Lichter-Marck
**Laphamia gilensis** M.E.Jones var. **gilensis**
**Laphamia gilensis** var. **salensis** (A.M.Powell) Lichter-Marck
**Laphamia gracilis** M.E.Jones
**Laphamia grandifolia** (Brandegee) Everly
*Laphamia halimifolia A.Gray*
≡ **Laphamia lindheimeri** *var.* **halimifolia** (A.Gray) Lichter-Marck
**Laphamia huecoensis** (A.M.Powell) Lichter-Marck
**Laphamia intricata** Brandegee
**Laphamia inyoensis** Ferris
*Laphamia laciniata* (Torr.) Rydb. = **Laphamia angustifolia** A.Gray
**Laphamia lemmonii** A.Gray
*Laphamia lemmonii* var. *pedata* A.Gray = **Laphamia lemmonii** A.Gray
**Laphamia leptoglossa** (Harv. & A.Gray ex A.Gray) Lichter-Marck
**Laphamia lindheimeri** A.Gray
**Laphamia lindheimeri** var. **halimifolia** (A.Gray) Lichter-Marck
**Laphamia lloydii** (B.L.Rob. & Fernald) Lichter-Marck
**Laphamia lobata** (Rydb.) Lichter-Marck
*Laphamia megalocephala subsp. intricata (Brandegee) D.D.Keck*
≡ **Laphamia intricata** *Brandegee*
**Laphamia megalocephala** S.Watson var. **megalocephala**
**Laphamia megalocephala** var. **oligophylla** (A.M.Powell) Lichter-Marck
**Laphamia palmeri** A.Gray
*Laphamia palmeri* var. *tenella* M.E.Jones
= **Laphamia palmeri** A.Gray
**Laphamia parryi** (A.Gray) Benth. & Hook.f. ex Hemsl.
*Laphamia peninsularis* Greene
= **Perityle rotundifolia** (Benth.) Brandegee
**Laphamia quinqueflora** Steyerm.
**Laphamia reinana** (B.L.Turner) Lichter-Marck
*Laphamia rotundata* Rydb.
= **Laphamia lindheimeri** A.Gray var. **lindheimeri**
**Laphamia rupestris** A.Gray var. **rupestris**
**Laphamia sanchezii** Lichter-Marck
**Laphamia saxicola** Eastw.
*Laphamia scopulorum* M.E.Jones
= **Galinsogeopsis coronopifolia** (A.Gray) Lichter-Marck
**Laphamia specicola** (S.L.Welsh & Neese) Lichter-Marck
**Laphamia stansburyi** A.Gray
**Laphamia staurophylla** Barneby
**Laphamia toumeyi** B.L.Rob. & Greenm.
**Laphamia vandevenderi** (B.L.Turner) Lichter-Marck

**Laphamia vaseyi** (J.M.Coult.) Lichter-Marck
**Laphamia villosa** S.F.Blake
**Laphamia vitreomontana** (Warnock) Lichter-Marck
**Laphamia warnockii** (A.M.Powell) Lichter-Marck
*Leptopharynx* Rydb. = **Laphamia** A.Gray
*Leptopharynx aglossa* (A.Gray) Rydb.
≡ **Laphamia aglossa** (A.Gray) Benth. & Hook.f. ex Hemsl.
*Leptopharynx cordifolia* Rydb.
≡ **Laphamia cordifolia** (Rydb.) Lichter-Marck
*Leptopharynx dissecta* (Torr.) Rydb.
≡ **Laphamia dissecta** Torr.
*Leptopharynx gilensis* (M.E.Jones) Rydb.
= **Laphamia gilensis** M.E.Jones var. **gilensis**
*Leptopharynx grandifolia* (Brandegee) Rydb.
≡ **Laphamia grandifolia** (Brandegee) Everly
*Leptopharynx lemmonii* (A.Gray) Rydb.
≡ **Laphamia lemmonii** A.Gray
*Leptopharynx leptoglossa* (Harv. & A.Gray ex. A.Gray) Rydb.
≡ **Laphamia leptoglossa** (Harv. & A.Gray ex A.Gray) Lichter-Marck
*Leptopharynx lloydii* (B.L.Rob. & Fernald) Rydb.
≡ **Laphamia lloydii** (B.L.Rob. & Fernald) Lichter-Marck
*Leptopharynx lobata* Rydb.
≡ **Laphamia lobata** (Rydb.) Lichter-Marck
*Leptopharynx palmeri* (S.Watson) Rydb.
≡ **Laphamia sanchezii** Lichter-Marck
*Leptopharynx trisecta* Rydb.
= **Laphamia parryi** (A.Gray) Benth. & Hook.f. ex Hemsl.
*Lycapsus* Phil. = **Peritule** Benth.
*Lycapsus tenuifolius* Phil.
≡ **Peritule tenuifolius** (Phil.) Lichter-Marck
*Melampodium achilleoides* (Less.) Hemsl.
= **Villanova anemonifolia** (Kunth) Less.
*Melampodium minutiflorum* M.E.Jones
= **Galeana pratensis** (Kunth) Rydb.
*Monothrix* Torr. = **Laphamia** A.Gray
*Monothrix congesta* (M.E.Jones) Rydb.
= **Laphamia toumeyi** B.L.Rob. & Greenm.
*Monothrix fastigiata* (Brandegee) Rydb
= **Laphamia gracilis** M.E.Jones
*Monothrix intricata* (Brandegee) Rydb.
≡ **Laphamia intricata** Brandegee
*Monothrix megalocephala* (S.Watson) Rydb.
≡ **Laphamia megalocephala** S.Watson var. **megalocephala**
*Monothrix palmeri* (A.Gray) Rydb.
≡ **Laphamia palmeri** A.Gray
*Monothrix stansburyi* (A.Gray) Rydb.
≡ **Laphamia stansburyi** A.Gray
*Monothrix toumeyi* (B.L.Rob. & Greenm.) Rydb.
≡ **Laphamia toumeyi** B.L.Rob. & Greenm.
**Nesothamnus** (A.Gray) Rydb.
**Nesothamnus incanus** (A.Gray) Rydb.
*Pappothrix* (A.Gray) Rydb. = **Laphamia** A.Gray
*Pappothrix cernua* (Greene) Rydb.
≡ **Laphamia cernua** Greene
*Pappothrix cinerea* (A.Gray) Rydb.
≡ **Laphamia cinerea** A.Gray
*Pappothrix quinqueflora* (Steyerm.) Everly
≡ **Laphamia quinqueflora** Steyerm.
*Pappothrix rupestris* (A.Gray) Rydb.
≡ **Laphamia rupestris** A.Gray var. **rupestris**
**Pericome** A.Gray
**Pericome caudata** A.Gray
*Pericome glandulosa* Goodman = **Pericome caudata** A.Gray
**Pericome macrocephala** B.L.Rob.
*Pericome spilanthoides* (Sch.Bip.) Benth. & Hook.f. ex. Hemsl.
= **Galinsogeopsis microglossa** (Benth.) Lichter-Marck var. **microglossa**
**Peritule** Benth.
*Peritule* sect. *Laphamia* = **Laphamia** A.Gray
*Peritule* sect. *Pappothrix* = **Laphamia** A.Gray
*Peritule acmella* Harv. & A.Gray
= **Galinsogeopsis microglossa** (Benth.) Lichter-Marck var. **microglossa**
*Peritule aglossa* A.Gray
≡ **Laphamia aglossa** (A.Gray) Benth. & Hook.f. ex Hemsl.
**Peritule aurea** Rose
*Peritule ajoensis* Todsen
≡ **Laphamia ajoensis** (Todsen) Lichter-Marck
*Peritule alamosana* B.L.Turner
= **Laphamia gentryi** (A.M.Powell) Lichter-Marck
*Peritule ambrosiifolia* Greene ex A.M.Powell & Yarborough
≡ **Laphamia ambrosiifolia** (Greene ex A.M.Powell & Yarborough) Lichter-Marck
*Peritule angustifolia* (A.Gray) Shinners
≡ **Laphamia angustifolia** A.Gray
*Peritule batopilensis* A.M.Powell
≡ **Laphamia batopilensis** (A.M.Powell) Lichter-Marck
*Peritule bisetosa* var. *appressa* A.M.Powell
≡ **Laphamia bisetosa** var. **appressa** (A.M.Powell) Lichter-Marck
*Peritule bisetosa* var. *bisetosa* (Torr.) Shinners
≡ **Laphamia bisetosa** Torr. var. **bisetosa**
*Peritule bisetosa* var. *scalaris* A.M.Powell
≡ **Laphamia bisetosa** var. **scalaris** (A.M.Powell) Lichter-Marck

*Perityle bisetosa* var. *spathulata* A.M.Powell
≡ **Laphamia bisetosa** var. **spathulata** (A.M.Powell) Lichter-Marck
**Perityle brandegeeana** Rose
*Perityle californica* var. *nuda* (Torr. ex A.Gray ) A.Gray
= **Perityle emoryi** Torr.
*Perityle canescens* Everly
≡ **Galinsogeopsis canescens** (Everly) Lichter-Marck
*Perityle carmenensis* A.M.Powell
≡ **Laphamia carmenensis** (A.M.Powell) Lichter-Marck
**Perityle carterae** (A.M.Powell) Lichter-Marck
*Perityle cernua* (Greene) Shinners
≡ **Laphamia cernua** Greene
*Perityle ciliata* (L.H.Dewey) Rydb.
≡ **Galinsogeopsis ciliata** (L.H.Dewey) Lichter-Marck
*Perityle cinerea* (A.Gray) A.M.Powell
≡ **Laphamia cinerea** A.Gray
*Perityle coahuilensis* A.M.Powell
≡ **Laphamia coahuilensis** (A.M.Powell) Lichter-Marck
*Perityle cochisensis* (W.E.Niles) A.M.Powell
≡ **Laphamia cochisensis** W.E.Niles
*Perityle congesta* (M.E.Jones) Shinners
= **Laphamia toumeyi** B.L.Rob. & Greenm.
*Perityle cordifolia* (Rydb.) S.F.Blake
≡ **Laphamia cordifolia** (Rydb.) Lichter-Marck
*Perityle coronopifolia* A.Gray
≡ **Galinsogeopsis coronopifolia** (A.Gray) Lichter-Marck
**Perityle crassifolia** var. **robusta** (Rydb.) Everly
**Perityle cuneata** Brandegee
*Perityle cuneata* var. *marginata* (Rydb.) I.M.Johnst.
≡ **Perityle marginata** Rydb.
*Perityle deltoidea* S.Watson
= **Perityle californica** Benth.
*Perityle dissecta* (Torr.) A.Gray
≡ **Laphamia dissecta** Torr.
*Perityle effusa* (A.Gray) Rose
= **Galinsogeopsis microglossa** (Benth.) Lichter-Marck var. **microglossa**
**Perityle emoryi** Torr.
*Perityle emoryi* var. *elata* (Phil.) I.M.Johnst.
= **Perityle emoryi** Torr.
*Perityle emoryi* var. *nuda* (Torr. ex A.Gray ) A.Gray
= **Perityle emoryi** Torr.
*Perityle emoryi* var. *orcuttii* Rose
= **Perityle emoryi** Torr.
*Perityle fastigiata* (Brandegee) Shinners
= **Laphamia gracilis** M.E.Jones
*Perityle feddemae* McVaugh
≡ **Galinsogeopsis feddemae** (McVaugh) Lichter-Marck
*Perityle fitchii* Torr. ex. A.Gray
= **Perityle rotundifolia** (Benth.) Brandegee
*Perityle fitchii* var. *palmeri* A.Gray
= **Perityle emoryi** Torr.
*Perityle fosteri* A.M.Powell
≡ **Laphamia fosteri** (A.M.Powell) Lichter-Marck
*Perityle gentryi* A.M.Powell
≡ **Laphamia gentryi** (A.M.Powell) Lichter-Marck
*Perityle gilensis* (M.E.Jones) J.F.Macbr.
≡ **Laphamia gilensis** M.E.Jones var. **gilensis**
*Perityle gilensis* var. *salensis* A.M.Powell
≡ **Laphamia gilensis** var. **salensis** (A.M.Powell) Lichter-Marck
*Perityle glaucescens* B.L.Turner
≡ **Galinsogeopsis glaucescens** (B.L.Turner) Lichter-Marck
*Perityle gracilis* (M.E.Jones) Rydb.
≡ **Laphamia gracilis** M.E.Jones
*Perityle grandifolia* Brandegee
≡ **Laphamia grandifolia** (Brandegee) Everly
*Perityle greenei* Rose
= **Perityle emoryi** Torr.
*Perityle halimifolia* (A.Gray) Shinners
= **Laphamia lindheimeri** A.Gray var. **lindheimeri**
*Perityle harkerae* P.Carrillo
≡ **Galinsogeopsis harkerae** (P.Carrillo) Lichter-Marck
*Perityle hofmeisteria* Rydb.
≡ **Galinsogeopsis hofmeisteria** (Rydb.) Lichter-Marck
*Perityle huecoensis* A.M.Powell
≡ **Laphamia huecoensis** (A.M.Powell) Lichter-Marck
*Perityle incana* A.Gray
≡ **Nesothamus incanus** (A.Gray) Rydb
*Perityle incompta* Brandegee
= **Perityle crassifolia** var. **robusta** (Rydb.) Everly
*Perityle intricata* (Brandegee) Shinners
≡ **Laphamia intricata** Brandegee
*Perityle inyoensis* (Ferris) A.M.Powell
≡ **Laphamia inyoensis** Ferris
*Perityle jaliscana* A.Gray
≡ **Galinsogeopsis jaliscana** (A.Gray) Lichter-Marck
*Perityle lemmonii* (A.Gray) J.F.Macbr.
≡ **Laphamia lemmonii** A.Gray
*Perityle leptoglossa* Harv. & A.Gray ex A.Gray
≡ **Laphamia leptoglossa** (Harv. & A.Gray ex A.Gray) Lichter-Marck
*Perityle lindheimeri* (A.Gray) Shinners
≡ **Laphamia lindheimeri** A.Gray var. **lindheimeri**
*Perityle lindheimeri* var. *halimifolia* (A.Gray) A.M.Powell
= **Laphamia lindheimeri** A.Gray var. **lindheimeri**
*Perityle lloydii* B.L.Rob. & Fernald
≡ **Laphamia lloydii** (B.L.Rob. & Fernald) Lichter-Marck

*Perityle lobata* (Rydb.) I.M.Johnst.
≡ **Laphamia lobata** (Rydb.) Lichter-Marck
**Perityle marginata** Rydb.
*Perityle megalocephala* (S.Watson) J.F.Macbr. var. *megalocephala*
≡ **Laphamia megalocephala** S.Watson var. **megalocephala**
*Perityle megalocephala* var. *oligophylla* A.M.Powell
≡ **Laphamia megalocephala** var. **oligophylla** (A.M.Powell) Lichter-Marck
*Perityle microcephala* A.Gray
≡ **Galinsogeopsis microcephala** (A.Gray) Lichter-Marck
*Perityle microglossa* Benth.
≡ **Galinsogeopsis microglossa** (Benth.) Lichter-Marck var. **microglossa**
*Perityle microglossa* var. *effusa* A.Gray
= **Galinsogeopsis microglossa** (Benth.) Lichter-Marck var. **microglossa**
*Perityle microglossa* var. *saxosa* (Brandegee) A.M.Powell
= **Galinsogeopsis microglossa** var. **microglossa** (Benth.) Lichter-Marck
*Perityle montana* (A.M.Powell) B.G.Baldwin
≡ **Galinsogeopsis montana** (A.M.Powell) Lichter-Marck
*Perityle nuda* Torr. ex A.Gray
= **Perityle emoryi** Torr.
*Perityle parryi* A.Gray
≡ **Laphamia parryi** (A.Gray) Benth. & Hook.f. ex Hemsl.
*Perityle palmeri* S.Watson
≡ **Laphamia sanchezii** Lichter-Marck
*Perityle pennellii* B.L.Turner
= **Galinsogeopsis hofmeisteria** (Rydb.) Lichter-Marck
*Perityle plumigera* Harv. & Gary ex. A.Gray
= **Perityle californica** Benth.
*Perityle pseudociliata* A.M.Powell & Yarborough
= **Galinsogeopsis coronopifolia** (A.Gray) Lichter-Marck
*Perityle quinqueflora* (Steyerm.) Shinners
≡ **Laphamia quinqueflora** Steyerm.
*Perityle reinana* B.L.Turner
≡ **Laphamia reinana** (B.L.Turner) Lichter-Marck
**Perityle rosei** Greenm.
*Perityle robusta* Rydb.
≡ **Perityle crassifolia** var. **robusta** (Rydb.) Everly
*Perityle rothrockii* Rose= **Perityle emoryi** Torr.
*Perityle rotundata* (Rydb.) Shinners
= **Laphamia lindheimeri** A.Gray var. **lindheimeri**
**Perityle rotundifolia** (Benth.) Brandegee
*Perityle rupestris* (A.Gray) Shinners
≡ **Laphamia rupestris** A.Gray
*Perityle rupestris* var. *albiflora* A.M.Powell
≡ **Laphamia rupestris** var. **albiflora** (A.M.Powell) Lichter-Marck
*Perityle saxicola* (Eastw.) Shinners
≡ **Laphamia saxicola** Eastw.
*Perityle saxosa* Brandegee
≡ **Galinsogeopsis microglossa** var. **saxosa** (Brandegee) Lichter-Marck
*Perityle scopulorum* (M.E.Jones) A.M.Powell & B.L.Turner
= **Galinsogeopsis coronopifolia** (A.Gray) Lichter-Marck
**Perityle socorrosensis** Rose
*Perityle specicola* S.L.Welsh & Neese
≡ **Laphamia specicola** (S.L.Welsh & Neese) Lichter-Marck
*Perityle spilanthoides* (Sch.Bip.) Rydb.
= **Galinsogeopsis microglossa** var. **microglossa** (Benth.) Lichter-Marck
*Perityle stansburyi* (A.Gray) J.F.Macbr.
≡ **Laphamia stansburyi** A.Gray
*Perityle staurophylla* (Barneby) Shinners
≡ **Laphamia staurophylla** Barneby
*Perityle stevensii* B.L.Turner
= **Galinsogeopsis canescens** (Everly) Lichter-Marck
*Perityle tenella* (M.E.Jones) J.F.Macbr.
= **Laphamia palmeri** A.Gray
**Perityle tenuifolius** (Phil.) Lichter-Marck
*Perityle toumeyi* (B.L.Rob. & Greenm.) J.F.Macbr.
≡ **Laphamia toumeyi** B.L.Rob. & Greenm.
*Perityle trichodonta* S.F.Blake
= **Perityle rosei** Greenm.
*Perityle trisecta* (Rydb.) J.F.Macbr.
= **Laphamia parryi** (A.Gray) Benth. & Hook.f. ex Hemsl.
*Perityle turneri* A.M.Powell
≡ **Galinsogeopsis turneri** (A.M.Powell) Lichter-Marck
*Perityle urticifolia* Rydb.
= **Galinsogeopsis microglossa** var. **saxosa** (Brandegee) Lichter-Marck
*Perityle vandevenderi* B.L.Turner
≡ **Laphamia vandevenderi** (B.L.Turner) Lichter-Marck
*Perityle vaseyi* J.M.Coult.
≡ **Laphamia vaseyi** (J.M.Coult.) Lichter-Marck
*Perityle vigilans* Spellenb. & A.M.Powell
≡ **Galinsogeopsis vigilans** (Spellenb. & A.M.Powell) Lichter-Marck
*Perityle villosa* (S.F.Blake) Shinners
≡ **Laphamia villosa** S.F.Blake
*Perityle vitreomontana* Warnock
≡ **Laphamia vitreomontana** (Warnock) Lichter-Marck
*Perityle warnockii* A.M.Powell
≡ **Laphamia warnockii** (A.M.Powell) Lichter-Marck
*Unxia achilleoides* Less.
= **Villanova anemonifolia** (Kunth) Less.

*Unxia alternifolia* (Lag.) Spreng.
= **Villanova oppositifolia** Lag.
*Unxia anemonifolia* Kunth
≡ **Villanova anemonifolia** (Kunth) Less.
*Unxia pratensis* Kunth
≡ **Galeana pratensis** (Kunth) Rydb.
*Vasquezia* Phil. = **Villanova** Lag.
*Vasquezia anemonifolia* (Kunth) S.F.Blake
≡ **Villanova anemonifolia** (Kunth) Less.
*Vasquezia oppositifolia* (Lag.) S.F.Blake
≡ **Villanova oppositifolia** Lag.
*Vasquezia titicacensis* (Meyen & Walp.) S.F.Blake ex Herrera
≡ **Villanova titicacensis** (Meyen & Walp.) Walp.
**Villanova** Lag.
*Villanova achilleoides* (Less.) Less
= **Villanova anemonifolia** (Kunth) Less.
*Villanova alternifolia* Lag.
= **Villanova oppositifolia** Lag.
**Villanova anemonifolia** (Kunth) Less.
*Villanova bipinnatifida* Ortega
=**Parthenium hysterophorus** L.
(tribe Heliantheae).
*Villanova biternata* (A.Gray) Wooten & Standl
≡ **Hymenothrix biternata** (A.Gray) B.G.Baldwin
(tribe Bahieae)
*Villanova chrysanthemoides* A.Gray
= **Hymenothrix biternata** (A.Gray) B.G.Baldwin
(tribe Bahieae).
*Villanova dissecta* (A.Gray) Rydb.
≡ **Hymenothrix dissecta** (A.Gray) B.G.Baldwin
(tribe Bahieae).
**Villanova oppositifolia** Lag.
*Villanova perpusilla* Phil.
= **Villanova oppositifolia** Lag.
*Villanova pinnatifida* Lag. **insertae sedis**
*Villanova pratensis* (Kunth) Benth. & Hook.f.
≡ **Galeana pratensis** (Kunth) Rydb.
**Villanova robusta** Phil.
**Villanova titicacaensis** (Meyen & Walp.) Walp.
*Wedelia titicacensis* Meyen & Walp.
≡ **Villanova titicacensis** (Meyen & Walp.) Walp.

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# STYLE

Where art and science converge



**HEADWORM**

*Criscia stricta* (Spreng.) Katinas (Nassauvieae) is a perennial herb from the Río de la Plata Grasslands getting ready for color explosion in N Tacuarembó, Uruguay

*J. Mauricio Bonifacino*



**MIDSUMMER IN THE WARNERS**

*Erigeron glacialis* (Nutt.) A.Nelson (Asteareae) emerges from crevices between basaltic rocks in the alpine headwaters of the Sacramento River, one of California's largest watersheds.Warner Mountains, California, USA

*Ben Sims*



**MAGELLAN's NASSAUVIA**

Secondary heads are common in the Nassauvieae, and they are well exemplified by this specimen of *Nassauvia magellanica* J.F.Gmel., in which numerous few-flowered heads are densely packed together into what appears to be a single head.
Foothills of Mount Fitz Roy (Chaltén) in Santa Cruz province, Argentina
*J. Mauricio Bonifacino*



**SOMETHING IS MISSING**
A pollenless apomictic dandelion from *Taraxacum* sect. *Borea* Sahlin ex A.J.Richards. Despite not needing pollen for their reproduction, lack of pollen production is rare among apomictic dandelions. Dunes of Schiermonnikoog island, The Netherlands.
*Yannick Woudstra*

# TICATIMES

selected Compositae news and updates from
THE INTERNATIONAL COMPOSITAE ALLIANCE

*Edited by Jennifer R. Mandel*

## 12-15 January 2026

### DIGITAL FRONTIERS 2026: TRANSFORMING RESEARCH AND TRAINING IN SYNANTHEROLOGY

Many members of the synantherology community came together this year online and in-person for the Digital Frontiers 2026: Transforming research and training in synantherology held, 12-15 January 2026, at The Botanical Research Institute of Texas (BRIT), Fort Worth, Texas, USA. Thank you to local organizers Oyetola Oyebanji, Andotiana Andriamanohera, and Morgan Gostel for a wonderful meeting. The event hosted 81 registrants, including 24 in-person and 57 virtual participants, from senior, mid-career, and early-career researchers, and graduate students. We heard talks from Alicia Rojas-Leal, Brendan J. Lepschi, Carolina M. Siniscalchi, Carolina Siniscalchi, Christoph Oberprieler, Daniel Martín Martínez-Quezada, Daniel S. Jones, Fabio Andrés Ávila, Isaac Lichter-Marck, Jaydeep J. Sharma, Jennifer Ackerfield, Jennifer R. Mandel, J. Mauricio Bonifacino, John M. Burke, José Luis Villaseñor, Michelle Rafter, Patricia Rivera, Ricardo Reyes-Chilpa, Saúl Manzano, Stephanie H. Chen, Teresa Terrazas, and Yannick Woudstra. A Report of the event will be published soon in Taxon.




*In person and virtual participants gather for a photo op during workshop*

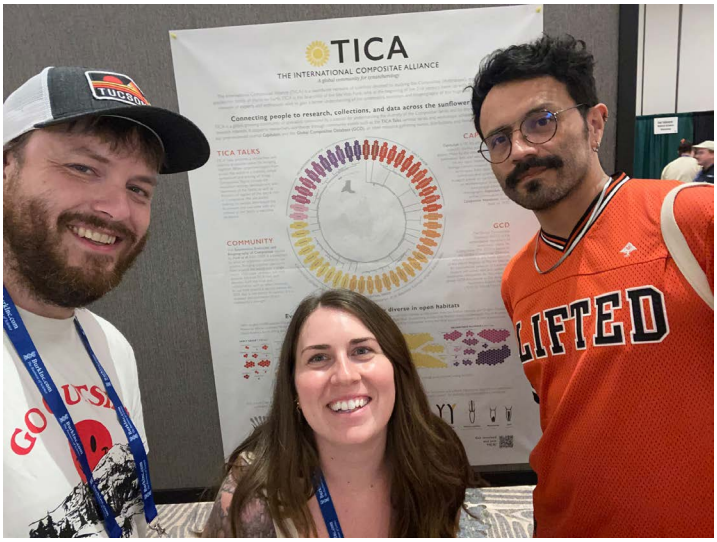
## August 2026

### TICA Tucson, Arizona Botany Conference 2026

At the 2026 Botany meeting in Tucson, Arizona, TICA hosted a "Lettuce Lunch" on August 4, bringing together Compositae researchers in-person and online. The gathering provided an opportunity for members to share updates on key community initiatives, including the TICA website hosted by GBIF, the CAPITULUM journal's forthcoming new OJS site, and the Global Compositae Database.




*In person and virtual participants gather for a photo op during Lettuce Lunch*

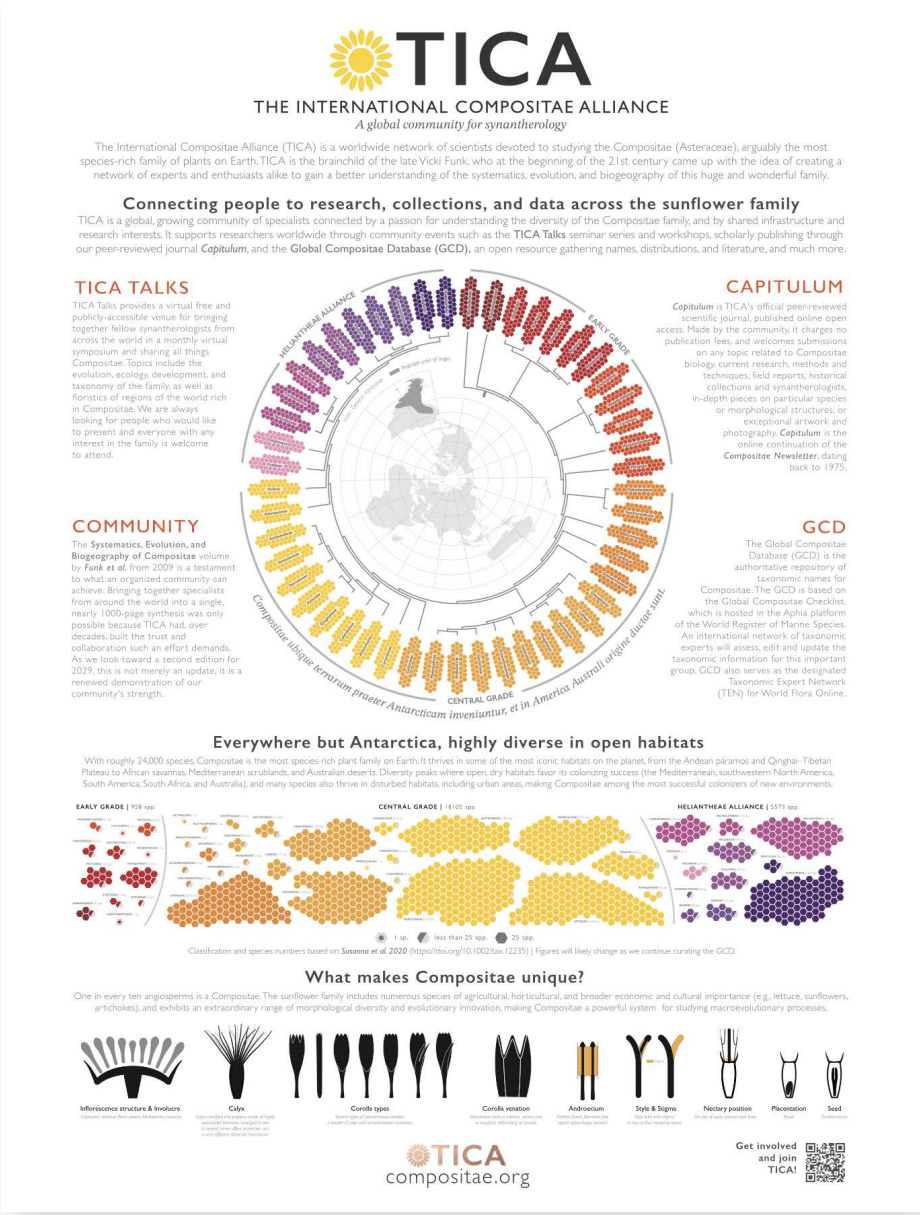



*From left to right: Yannick Woudstra, Erika Moore-Pollard and Fabio A. Avila at Botany 2026, posing next to TICA poster (see next page)*

## August 2026

### TICA POSTER at Tucson, Arizona Botany Conference 2026

The poster introduced TICA to the wider botanical community. TICA grew out of the collaborative community that the family has attracted worldwide, and today it sustains a set of freely available resources: the Global Compositae Database, the journal Capitulum, the monthly webinar series TICA Talks, and other online tools. The poster traced the alliance's history and goals, and set out how researchers, students and enthusiasts alike can take part in the study of arguably the most diverse plant family on Earth.




**DOWNLOAD POSTER HERE**

Google drive link

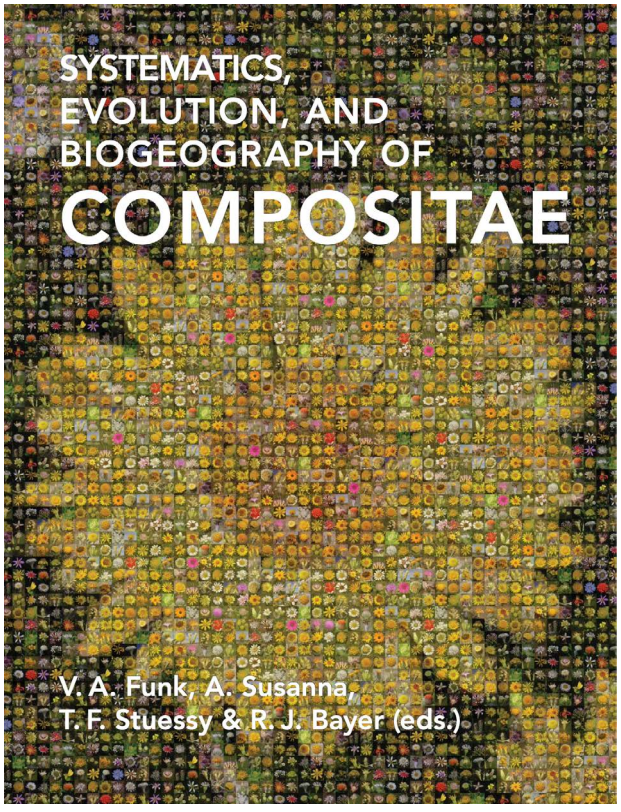
## September 2026

### 2nd EDITION OF THE COMPOSITAE BOOK

The 'big Compositae book' will be updated with a second edition, 20 years after the publication of the first. The editorial committee is now inviting formal chapter proposals from prospective authors. The book is planned for publication in 2029, to be released at the International Botanical Congress in Cape Town, South Africa.

When *Systematics, Evolution and Biogeography of Compositae* by Funk et al. was published in 2009, it offered a synthesis that the field had long required: a comprehensive, phylogenetically grounded treatment of the entire family, informed by molecular data that was transforming our understanding of relationships in the family at every level. The impact of this volume was recognized through several awards, including the Smithsonian Secretary's Award for Excellence in Collaboration in 2009 and having received the Stebbins Medal in 2010. That synthesis has served its purpose well — as a reference, teaching tool, and platform for the research that followed.

Twenty years is a long time in any field of biology, and in Compositae systematics it has been a particularly eventful two decades. The pace of molecular investigation has accelerated and genomic approaches have deepened our understanding of the biology of this remarkable group of plants. The aim of this second edition is to update this synthesis incorporating phylogenetic, taxonomic, and other advances throughout the intervening years; to reflect the current state of the field with the same breadth and rigor as its predecessor; and to provide once again a coherent and comprehensive account of the family that can serve both the specialist and the student.




*Cover of Compositae book first edition*

**September 2026**

Call for papers

# Urban Compositae

## CAPITULUM SPECIAL ISSUE

Few plant families are as much at home in cities as the Compositae. As the most diverse plant family and one of the most ecologically dominant, it includes many successful urban colonisers: dandelions (*Taraxacum* F.H.Wigg.) crack pavements, mugworts (*Artemisia* L.) hug walls, horseweeds colonise vacant lots, and ragweed pollen fills the summer air. Heat islands, trampling, mowing and fragmented habitats put city plants under heavy pressure, and many composites, as ruderals, thrive under exactly these conditions. Cities are also laboratories of rapid evolution: on Marseille's pavements, *Crepis sancta* (L.) Bornm. has shifted towards fewer dispersing seeds within a few generations.

This special issue is looking for stories from cities around the world, from Buenos Aires to Beijing and from Nairobi to Stockholm, on how Compositae colonise, survive, thrive and diversify in urban life. We welcome work on any member of the family in any region, provided the focus is urban, whether on ecology, evolution, systematics, invasions, pollinators, horticultural escapes, allergenic species or citizen-science records. Contributions from cities whose floras remain little documented are especially welcome. Submissions are invited in all sections of the journal:

**Head Topics & Brevia:** research articles on urban Compositae, including floristics.
**Pipet & Press:** methods and techniques for studying urban Compositae.
**The Involucre:** the stories of the botanists behind the study of urban Compositae
**The Handlens:** a close look at an urban Compositae, or at a structure that aids its survival or adaptation in cities.
**The Cabinet:** the stories behind historical or recent herbarium collections of urban Compositae.
**From the Field:** reports from urban fieldwork on rare and exciting or common but intriguing Compositae
**Style:** artistic photography, botanical illustrations or creative infographics that celebrate urban Compositae.

**Submission deadline**: June 2027
**Guest editor**: Yannick Woudstra



*Tripleurospermum inodorum (L.) Sch.Bip. . Finding cracks in the pavement in Stockholm, Sweden. Photo by Yannick Woudstra*

## September 2026

### KÅRE BREMER CONFERRED AS JUBILEE DOCTOR

On 25 September 2026, Kåre Bremer was conferred as *jubeldoktor* (jubilee doctor) at Stockholm University's Inauguration and Conferment Ceremony in Stockholm City Hall. Swedish universities bestow the title on those who received their doctorates fifty years earlier, a custom first documented at Uppsala University in 1804 that symbolically links newly conferred doctors with earlier generations of scholars.

Doctoral conferment in Sweden is an elaborate ceremony with roots in medieval European universities, drawing on both ecclesiastical ritual and guild tradition. Each candidate is individually admitted to the doctoral rank and receives symbolic insignia: traditionally a hat or laurel wreath, a ring, and a diploma. Jubilee doctors receive a new laurel wreath and diploma, but no ring. Processions, Latin formulas, music and fanfares complete the ceremony, although participation is now voluntary and practices vary among institutions.

Bremer received his doctorate in 1976 with a thesis on *Relhania* L'Hér. and *Rosenia* Thunb. in the Gnaphalieae (currently placed in *Oedera* L.). As President of Stockholm University from 2004 to 2013, he hosted the very ceremonies at which he has now been honoured. A more detailed account of his life and career appears in the portrait published on this issue.

Asked about his memories of the 1976 ceremony, he recalled nearly arriving late, after a mishap with his wife Birgitta's dress obliged them to make an unplanned stop on the way to City Hall. He reached the Blue Hall with only a minute to spare. Fifty years on, his reaction to becoming a jubilee doctor was simply: "*Already?*"

*Based on Stockholm University interview made by Per Larsson and a booklet edited by Anne Heikkinen Sandberg on the Swedish Universities ceremonies and traditions.*



*Photo by Johan Lundberg. August 25th, 2026*

## September 2026

### Compositae symposium at the XIII Colombian Botanical Congress

The Compositae will take centre stage at the XIII Congreso Colombiano de Botánica in Medellín, with the symposium Avances Recientes en la Investigación de Compositae (Asteraceae) ("Recent Advances in Compositae Research"), on Wednesday 7 October 2026 at 8:00 a.m. in the Salón Cerro Quitasol at Plaza Mayor Medellín. The family is among the most diverse in Colombia, from sunflowers and daisies to the iconic frailejones of the páramos, and the symposium will present recent work on new tools for building phylogenetic hypotheses, progress in the classification of tribes and genera across the Americas, and contributions to regional and national checklists. The congress is organised by the Jardín Botánico de Medellín, the Universidad Católica de Oriente, the Universidad de Antioquia and the Asociación Colombiana de Botánica, with the Alcaldía de Medellín as strategic ally. Anyone attending the congress is warmly invited to join.

+ info



# TICA talks

THE INTERNATIONAL COMPOSITAE ALLIANCE

*Edited by Jennifer R.* ***Mandel*** *&* *Colin* ***Hoag***

2026 has been an especially fruitful year for synantherologists eager to learn about the latest developments in the field. This is because the 2026 TICA Talks Committee put together an extraordinary lineup of speakers from across the globe and across disciplines—and who work across Compositae's major groups. Many thanks to the efforts of this year's committee, comprised of Fabio Andrés Ávila, Carme Blanco Gavaldà, Colin Hoag, Abby Moore, and Erika Moore-Pollard. Many thanks also to the speakers who have so far presented, as well as those whose presentations are yet to come.

For those unfamiliar with TICA Talks, these meetings are held virtually on the second Monday of each month. 2-3 speakers give presentations of between 15-30 minutes, followed by questions and comments. Most presentations are recorded and posted on our YouTube channel at the following link: https://www.youtube.com/@theinternationalcompositae2637/featured. This year, the Committee grouped speakers into themed panels, including "Floristics and Taxonomy," "Systematics and Biogeography," "Developmental Biology," "Ecology and Anatomy," and "The Herbarium."

We kicked off the year with two presentations. The first was by Liliana Katinas (Universidad Nacional de La Plata, Argentina), who described the tremendous diversity in Compositae trichome morphology and her efforts to create a unified classification that researchers can use. Mauricio Bonifacino (Universidad de la República, Uruguay) then presented an account of the Flora Uruguaya Online (https://florauruguaya.org), an innovative and beautifully designed online flora for Compositae-rich Uruguay that he and collaborators have developed, which one attendee described as the "gold standard" for such online resources. The following month featured two presentations on biogeography and systematics in mountain environments. Glynis Goodman-Cron (University of the Witwatersrand, South Africa) described the influence of topography on diversification of the large genus *Helichrysum* Mill. (Gnaphalieae Cass. ex Lecoq & Juill.) in Southern Africa. Oscar Vargas (California State Polytechnic University, Humboldt, USA) described the use of phylogenetics to unravel diversity patterns in two genera from Astereae Cass.: *Diplostephium* Kunth. and *Linochilus* Benth.

In April, we returned to *Helichrysum* and to South Africa with a talk by Zaynab Shaik (Stellenbosch University, South Africa), who described evolutionary shifts between hermaphroditism and gynomonoecy in that group. Second, the developmental biologist Regine Claßen-Bockhoff (Johannes Gutenberg-Universität Mainz, Germany) spoke about the evolution of syncephalia in Compositae. Three talks in our May meeting returned us to Gnaphalieae and Astereae, with Oscar Castillo Agudo (Instituto de Productos Naturales y Agrobiología (IPNA-CSIC) & Universidad de La Laguna, Spain) describing research on Hyb-Seq insights into the paper daisies, and with Nicolás Ramírez (Universidad Nacional de Colombia, Colombia) presenting findings from a taxonomic revision of *Achyrocline* (Less.) DC. Additionally, Juan Manuel Gorospe Ballesteros, Universidad de Almería, Spain) outlined an integrative approach to the taxonomy of *Oritrophium* (Kunth) Cuatrec. (Astereae) in the tropical high Andes.

Our June meeting was focused on ecology and evolution, with a presentation by Julia Freeman (University of Illinois at Urbana-Champaign, USA) on the role of thrips as pollinators for the endemic species *Hymenoxys texana* (J.M.Coult. & Rose) Cockerell (Helenieae Lindl.), a presentation by Miranda Sinnott-Armstrong, Duke University, USA) on defense traits in the thistles (Cardueae Cass.), and another by Thaabiet Parker (The Compton Herbarium, South African National Biodiversity Institute, South Africa) on the persistence of clinal morphotypes in the species complex *Dimorphotheca* Vaill. ex Moench (Calenduleae Cass.). July brought us a talk on the phylogenomics and biogeography of Zinniinae Benth. & Hook.f. (Heliantheae Cass.) by Sam Skibicki (California Department of Food

and Agriculture, USA), a presentation by Marisa Szubryt (University of Oklahoma, USA) on ways to resolve paralogs and phylogenetic discordances in *Heterotheca* Cass. (Astereae), and a presentation by Geoffrey Finch (University of Arizona, USA) on the effects of aridity and UV-B radiation on chromosome numbers in some species of Machaerantherinae G.L.Nesom (Astereae).

In August, Ary Mailhos (Universidad de la República, Uruguay) provided an overview of pappus diversity across the Compositae, and Joseph Kleinkopf (Cornell University, USA) outlined the evolution of the alpine fleabanes (*Erigeron* L. Astereae) in North America. September's meeting highlighted the importance and history of herbaria. Krishna Shenoy (Fort Worth Botanic Garden, USA) presented on Sherwin Carlquist's botanical photographs, while Chiara Montagnani (University of Milano-Bicocca, Italy) outlined research on *Ambrosia* L. (Heliantheae) using herbarium specimens to understand their invasion history in Italy.

In the final months of 2026, we have still more talks to come. October will feature work by Victoria Valtierra (Universidad de la República, Uruguay) on the systematics and evolution of *Baccharis* L. Caulopterae s.s. (Astereae), and two talks on the taxonomy of South American comps. José Aguilar-Cano (Jardín Botánico de Bogotá, Colombia) will be speaking about efforts to document the diverse Compositae flora of Bogotá, and Italo Revilla (Herbario HSP, Instituto Científico Michael Owen Dillon, Perú) will present a synopsis of the genus *Jungia* L.f. (Nassauvineae Cass.) in Peru. Finally, November and December will feature talks focused on New World comps. Arturo Castro Castro (Instituto Politécnico Nacional, Mexico) will present on the floristics and taxonomy of Coreopsideae Lindl. in Mexico, while Isaac Lichter-Marck (California Academy of Sciences, USA) will outline an effort to build collaboration among researchers called the Heliantheae Alliance Alliance (HAA). In addition to a presentation by Marianna Grossi (Universidad Nacional de La Plata, Argentina) focused on Eupatorieae Cass., Andrés Ávila (New York Botanical Garden, USA) will present work on the wood anatomy of *Critoniopsis* Sch.Bip. (Vernonieae Cass.), and Colin Hoag (Smith College, USA) will discuss ongoing work on the geography and natural history of *Hecastocleis shockleyi* A. Gray (Hecastocleideae Panero & V.A.Funk).

If you are interested in giving a TICA Talk, contact Dr. Colin Hoag: *choag@smith.edu*.




**TICA TALKERS.**
**A.** Liliana Katinas; **B.** Mauricio Bonifacino; **C.** Glynis Goodman-Cron; **D.** Oscar Vargas; **F.** Regine Claßen-Bockhoff; **E.** Zaynab Shaik; **G.** Oscar Castillo Agudo; **I.** Juan Manuel Gorospe Ballesteros; **H.** Nicolás Ramírez; **J.** Julia Freeman; **L.** Thaabiet Parker; **K.** Miranda Sinnott-Armstrong; **O.** Geoffrey Finch; **M.** Sam Skibicki; **N.** Marisa Szubryt; **P.** Ary Mailhos; **Q.** Joseph Kleinkopf; **R.** Krishna Shenoy; **S.** Chiara Montagnani.

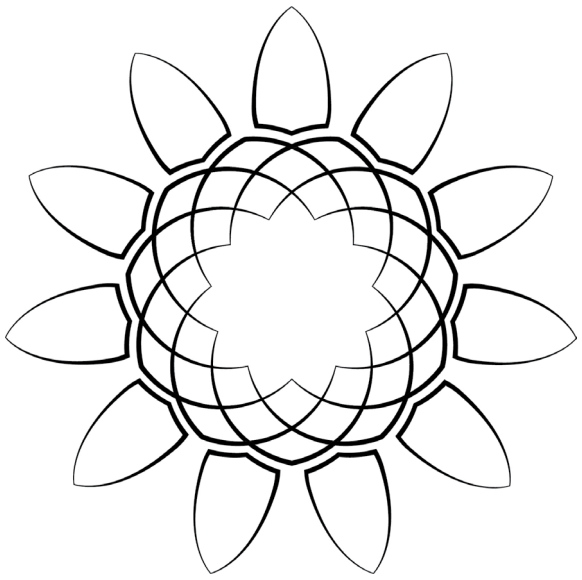
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*Magno amore in familiam Synantherearum captus*
Lessing, 1829

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