

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

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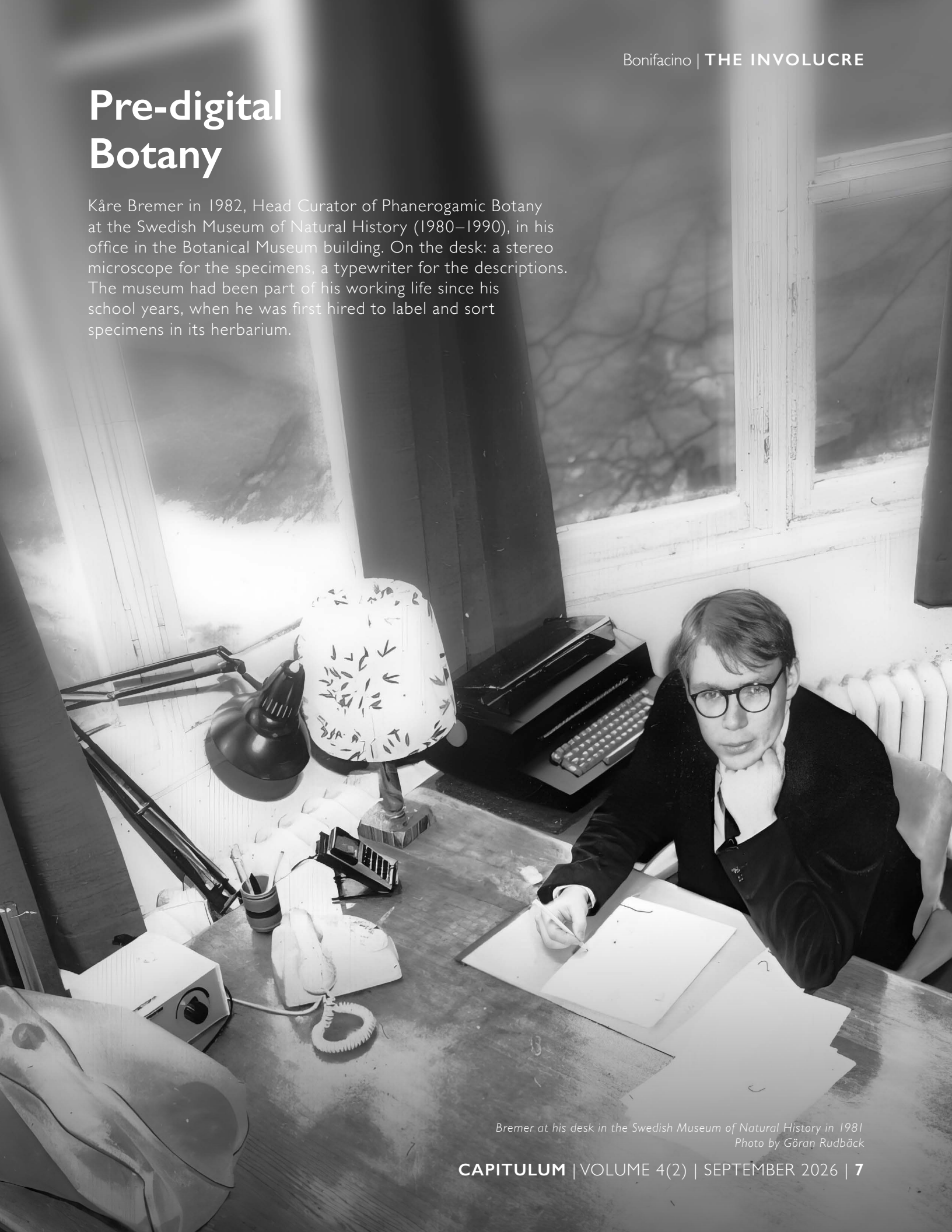
Kåre Bremer at the National Botanic Gardens at Kirstenbosch, Cape Town, 1972 —checking specimens after drying during his six-month collecting expedition through South Africa and Namibia.



*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 Klackenborg 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.



Oedera 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.

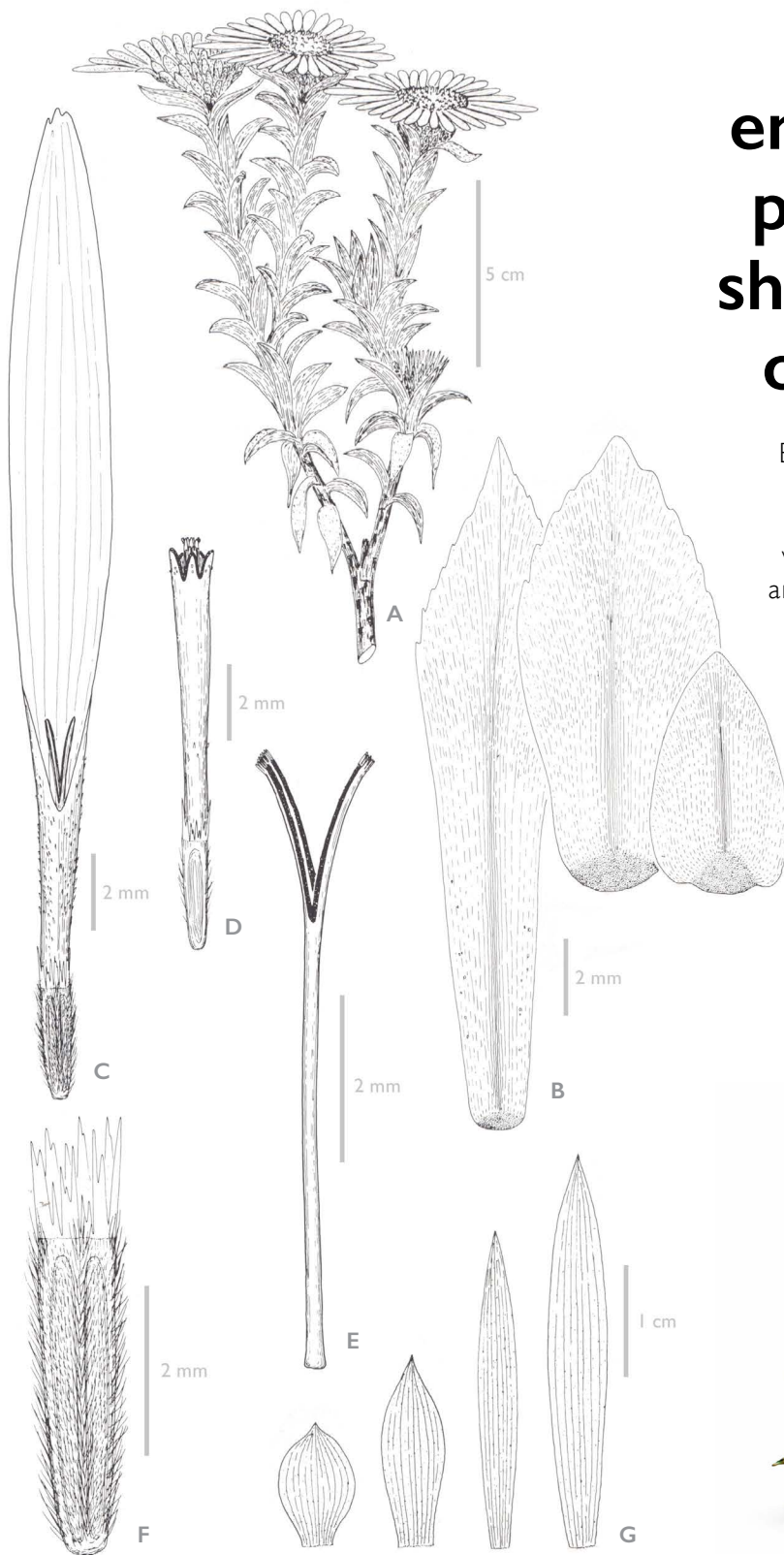


Photo of *Oedera speciosa* taken by Bremer in 1972

▲ ***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. *Scorzoneroideis 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 *Microlooma* 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 Ilitis'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 it 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

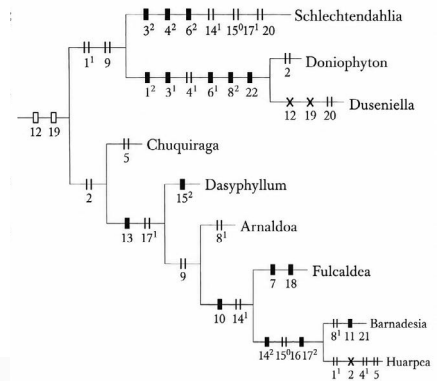
THE COMPOSITAE

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

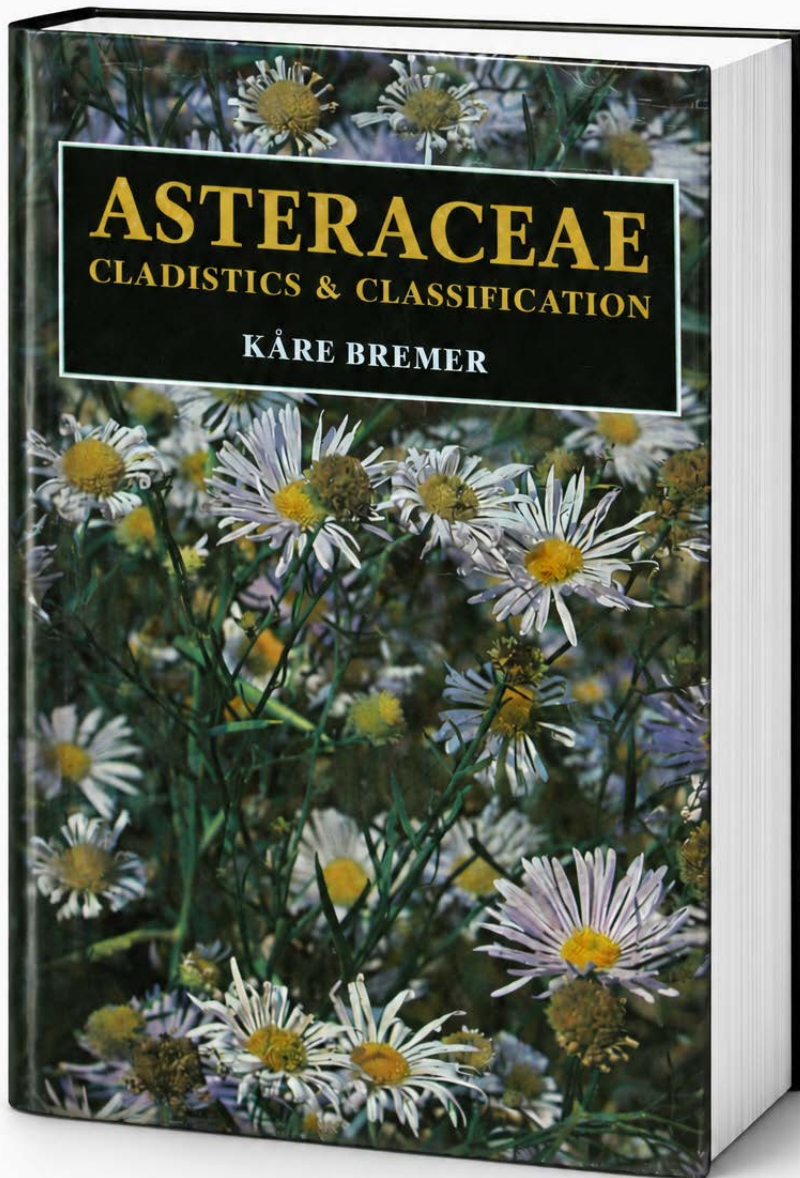
Seven years in the making, with five collaborators, this 766-page monograph treats all 1,535 genera of the Compositae, across the three subfamilies and 17 tribes recognized in 1994. It was the first encyclopedic synthesis of the family in nearly a century, and the first to apply a cladistic framework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

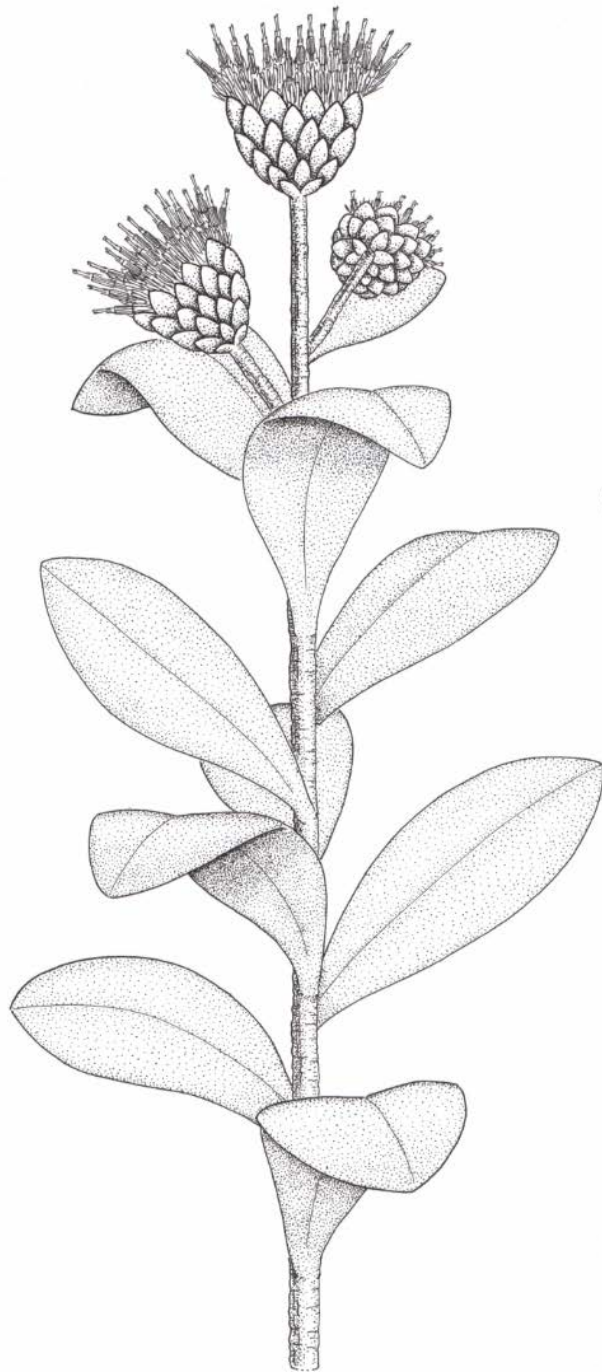
Their monograph on the Anthemideae appeared in 1993 (Bremer & Humphries, 1993): a generic-level treatment of all 108 genera of the tribe. Each genus receives a diagnostic description, general distribution, taxonomic commentary, and a list of its constituent species, while cladistic analyses of generic 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.

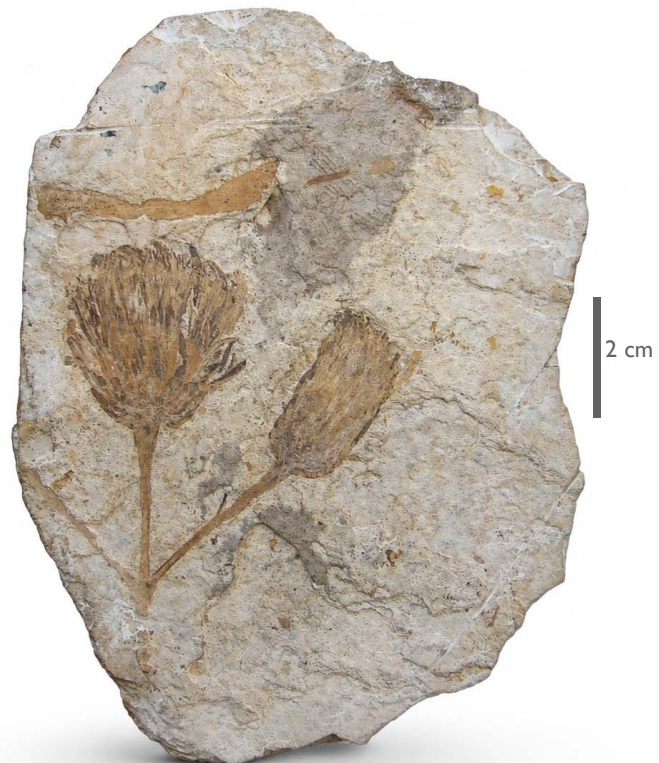


Image of fossil courtesy of Asociación Paleontológica Bariloche

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.

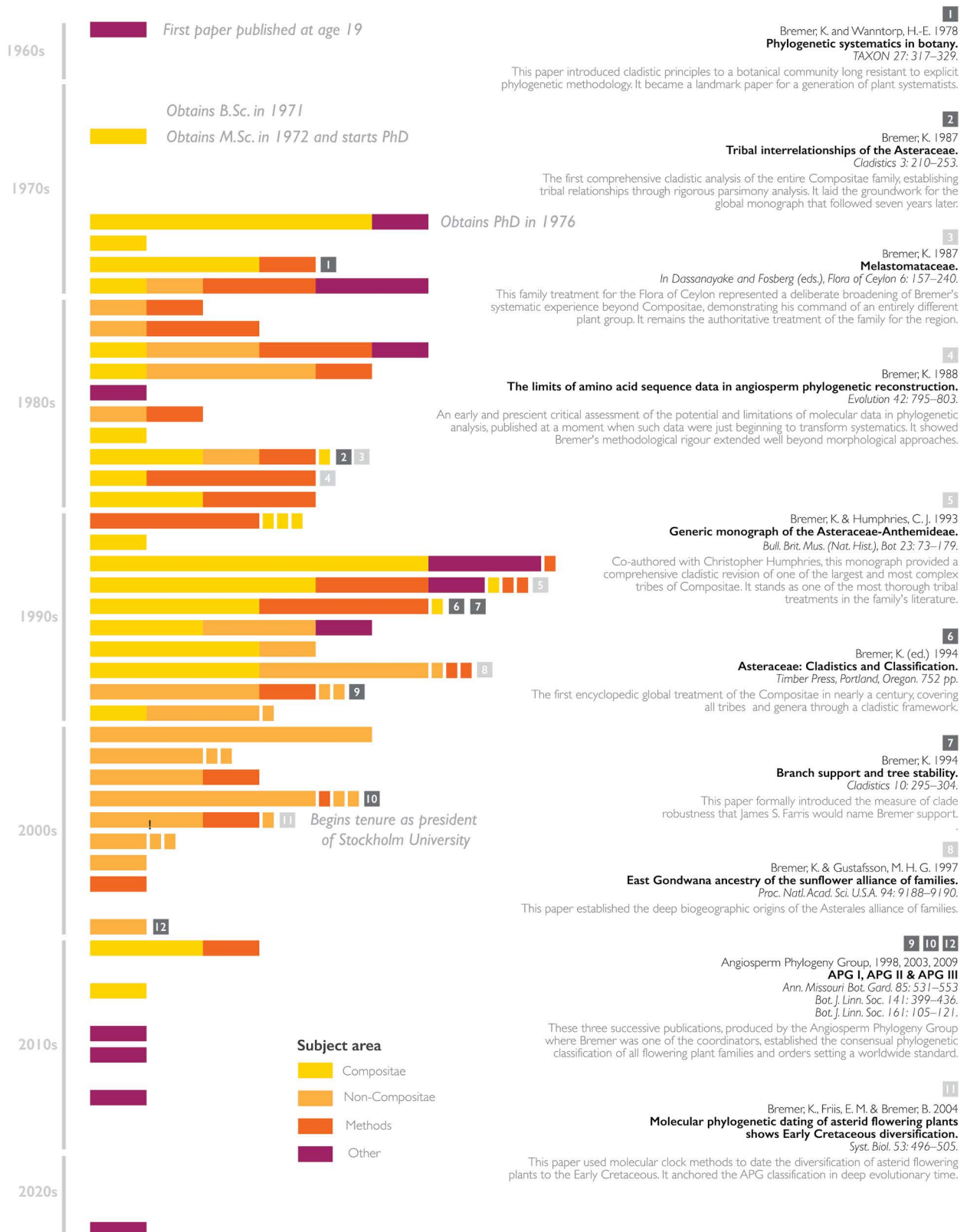
The cladogram that emerged from the analysis — a working hypothesis of tribal interrelationships based on 27 terminal taxa and run through Swofford's *PAUP* package — was the first explicit, reproducible phylogenetic reconstruction of the entire family. Its conclusions were in several respects as destabilizing 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

— I publication — I abstract at meeting



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.

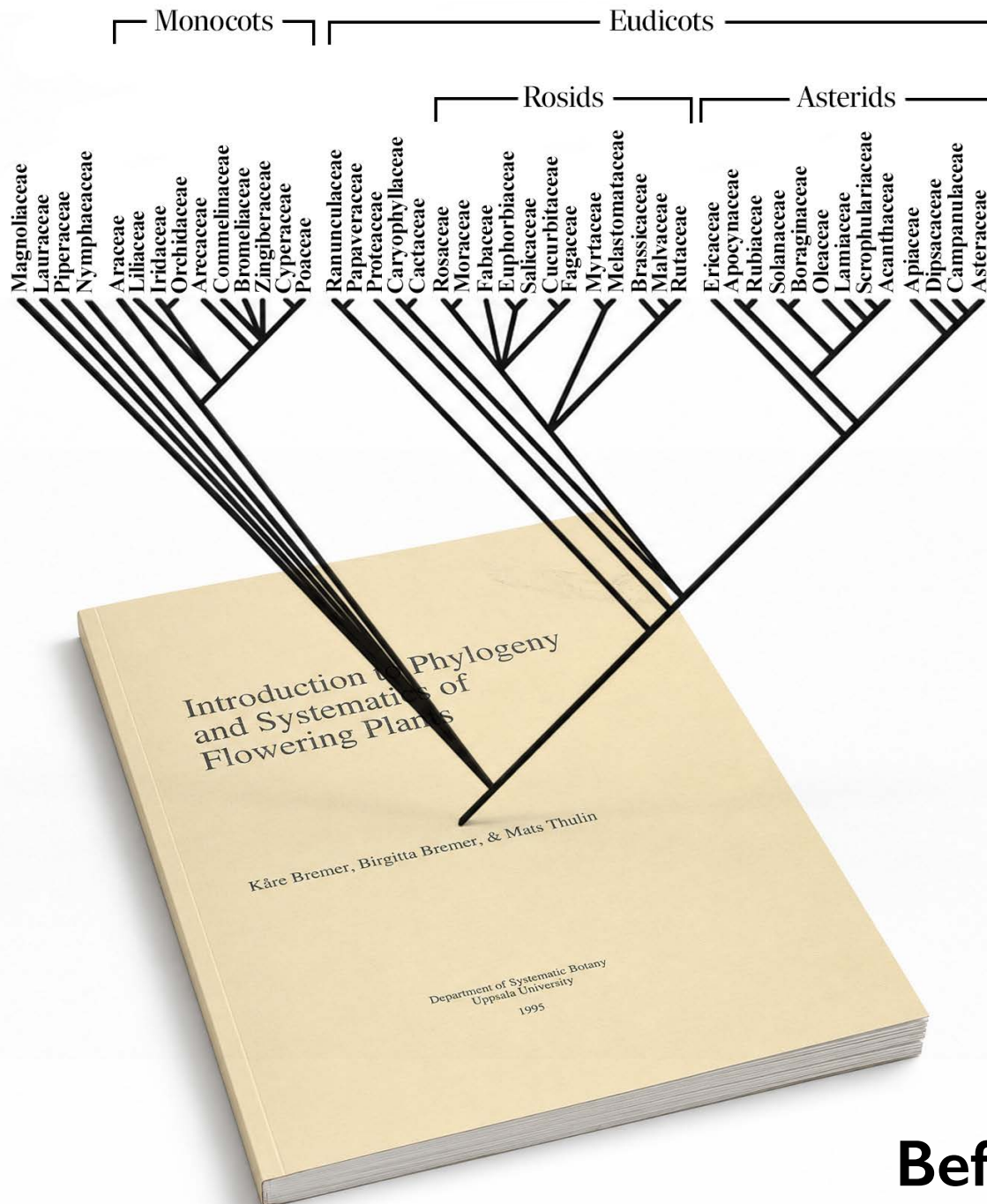
In the years following Yokohama, the rapidly improving *rbcL* phylogeny made the older morphology-based classifications increasingly difficult to teach, and provisional reclassifications began to appear at several institutions. In Uppsala, Bremer, Birgitta Bremer, and their colleague Mats Thulin produced 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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