ISSN 2789-2786

CAPITULUM

THE INTERNATIONAL COMPOSITAE ALLIANCE NEWSLETTER

TICA
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VOLUME 2(2)- MARCH 2023

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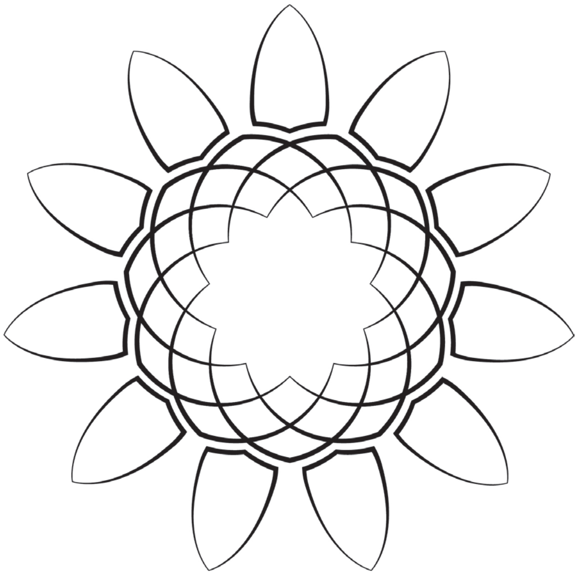

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THE INTERNATIONAL COMPOSITAE ALLIANCE NEWSLETTER
VOLUME 2(2) - MARCH 2023
DOI: http://dx.doi.org/10.53875/capitulum.02.2
VERSION OF RECORD FIRST PUBLISHED ONLINE ON **30 MARCH 2023**

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Cover photo: *Senecio icoglossus* DC. (Senecioneae), Rivera, URUGUAY
Photo by J.M. Bonifacino

Bertil Nordenstam:

the architect behind modern Senecioneae classification

J. Mauricio Bonifacino[1] & Kåre Bremer[2]

[1] Laboratorio de Botánica, Facultad de Agronomía, Av. Garzón 780, Montevideo, CP 12900, URUGUAY.
[2] Stockholm University, Spökslottet, SE-106 91 Stockholm, SWEDEN.

Author for correspondence: J. Mauricio Bonifacino, *mbonifa@gmail.com*

DOI: http://dx.doi.org/10.53875/capitulum.02.2.01

ABSTRACT

Bertil Nordenstam is a Swedish botanist who contributed significantly to the understanding of the Compositae during a career of over 60 years. Nordenstam's botanical work centered on the tribe Senecioneae, a group that he re-circumscribed and modified taxonomically with his many insights into its internal relationships. Nordenstam also participated in major floristic projects, and he collected extensively around the world. He wrote about botanical history with an emphasis on the Linnean disciple Carl Peter Thunberg and he served the community of fellow synantherologists by editing the Compositae Newsletter for 25 years.

Keywords: Compositae, *Euryops*, Japan, Namibia, *Othonna*, South Africa, Sweden, Thunberg.

INTRODUCTION

For all of us interested in Compositae, no matter where we are, the Senecioneae cannot be neglected. It is the largest tribe of all in the Compositae and it is found everywhere (Nordenstam et al., 2009; Pelser et al., 2007). Literally one in ten Compositae is a Senecioneae, and it includes the most species-rich genus of the family, *Senecio* L., which despite much reclassification needs further taxonomic investigation. The tribe is relatively easy to identify, given the uniseriate involucre (Figure 1).

As with almost any large group in the Compositae, the taxonomic recognition of the Senecioneae is found in the classic works of Henri Gabriel Alexandre de Cassini from the early 1800s (Bonifacino et al., 2009). His 20th century successor, who has contributed most to the understanding of the systematics of this important group, is Bertil Nordenstam.

Bertil's contributions to botany extend beyond the realm of synantherology; he has worked with several other plant families and dedicated a considerable amount of time to botanical history and floristic studies. Our objective with this paper is to present some facets from the botanical life of this notable Swedish botanist.

BERTIL'S EARLY LIFE AND EDUCATION

Bertil was born on February 20, 1936, in the small town of Nyköping South of Stockholm in Sweden, as the second of five brothers. His father had medical problems and was hospitalized; Bertil and his brothers were all young boys when his mother was left alone to take care of the family. After the end of World War II, they moved to the city of

Göteborg on the West coast of Sweden, where Bertil continued his education.

> *"My mother was a remarkable woman working hard to keep her five sons alive and happy. We learned to be independent and did well at school until matriculation* [end of high school]. *I enjoyed the summer vacations in various places in Sweden, but usually on the West coast. From the age of ten I spent most of my summers in nature, collecting sea shells, bird´s eggs (not recommended today!) and I enjoyed drying plants. In a couple of years I had assembled a herbarium of 600 Scandinavian plants."*

Bertil was encouraged by his uncle, Sten Nordenstam, who inspired him to pursue a career in the natural sciences. Sten was a forester by profession but also an eminent amateur botanist with a deep knowledge of the Scandinavian flora. He took a special interest in the largely apomictic genera *Hieracium* L. and *Taraxacum* Weber ex F.H.Wigg., each with hundreds of microspecies. Almost every summer as a teenager Bertil would join his uncle on excursions, mainly in the northern mountains of Sweden, Norway, and Finland, but also to the big islands of the Baltic Sea.

After matriculation in 1954 Bertil had already set his mind to become a professional botanist and he decided to study at Lund University in South Sweden. Bertil's M.Sc. from Lund 1958 was based on chemistry, zoology and botany. He obtained some temporary positions as assistant at the Department of Botany at Lund University and was thus able to embark on his career as a botanist.

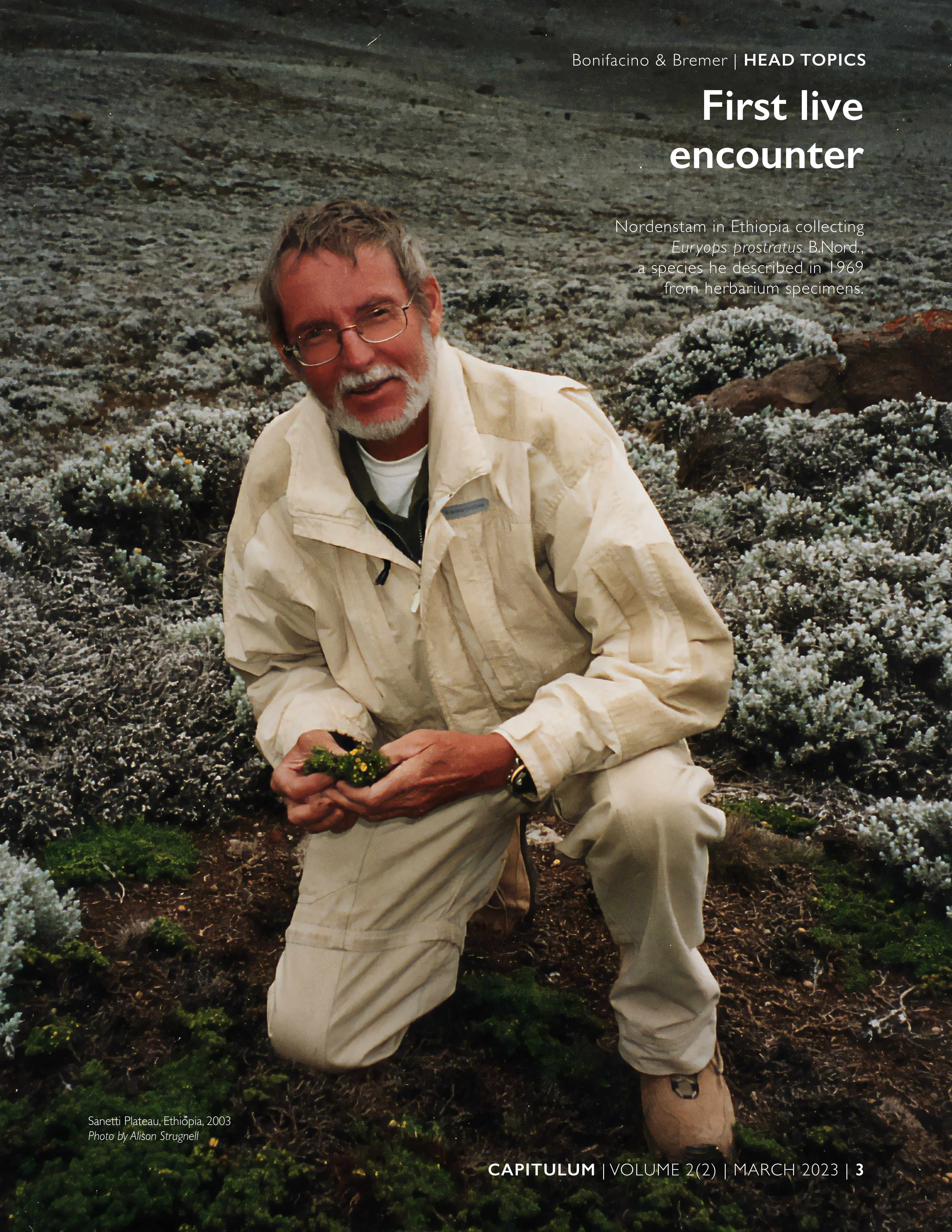
Lund not only offered Bertil a path to become a professional botanist, but also was the setting where he met his future wife Gunilla, in the same university, where she was studying to become a teacher.

> *"Gunilla was an outstanding beauty and a Swedish champion in figure skating, and also much interested in nature, wildlife and adventure. We married in 1966 and were blessed with one daughter Felicia, who is now a Ph.D. and a medical doctor. We travelled together to many countries on all continents but Antarctica, just like the Compositae!"*

Figure 1. *Lamprocephalus montanus* B.Nord., a representative of the Senecioneae from the Cape Province in South Africa together with a red-flowered species of *Erica* L.. Note the uniseriate involucre typical of the Senecioneae, sometimes as in this plant also with a small outer calyculus. *Lamprocepehalus* is one of 50 Compositae genera described by Nordenstam. *Photo by Bertil Nordenstam*

After completing his M.Sc. Bertil started working on his Ph.D., initially focusing on the South African genus *Othonna* L. in the Senecioneae, following a suggestion by the curator at the botanical museum in Lund, Tycho Norlindh. He was a specialist on the tribe Calenduleae and had travelled in southern Africa in the 1930s. Norlindh was the first in a long series of Swedish Compositae taxonomists among them Nordenstam and the co-author of this article, Kåre Bremer.

First live encounter



Nordenstam in Ethiopia collecting *Euryops prostratus* B.Nord., a species he described in 1969 from herbarium specimens.

Sanetti Plateau, Ethiopia, 2003
Photo by Alison Strugnell

When Bertil embarked on his Ph.D. studies Norlindh moved to Stockholm where he was appointed professor and director of the botanical museum at the Swedish Museum of Natural History, and Bertil had to pursue his Ph.D. research essentially on his own. He started to look at *Othonna* in the herbarium and was soon disappointed with the poor quality and the ugly nature of the herbarium specimens. Many *Othonna* species are succulents and they are difficult to press and render dull specimens where a lot of information is missing, hardly sufficient for a successful revision.

> *"I remember my friend Hermann Merxmüller in Munich later telling me he considered Othonna to be the most difficult genus of the Compositae, at least in Africa."*

While looking at the specimens of *Othonna* in the herbarium, Bertil came across the related *Euryops* (Cass.) Cass., a genus of attractive African shrubs with well-preserved specimens. *Euryops* was in obvious need of revision and he decided to tackle this group instead, a decision that proved very convenient.

Bertil told the professor at the Department of Botany, Henning Weimarck, that he wanted to write his Ph.D. thesis on *Euryops* and Weimarck replied something like "Good, come back to me when you are finished." Back in those days Ph.D. studies were more of an enterprise you took on your own rather than an education with teachers and supervisors. Bertil´s Ph.D. work was no exception, and he had to pursue it largely without support or guidance.

After a survey of the major European herbarium collections of *Euryops* (in London, Geneva, Paris among others) it was time to study *Euryops* in its natural environment. Bertil travelled in South Africa extensively between 1962 and 1964, a remarkable collecting endeavour to which we will return below.

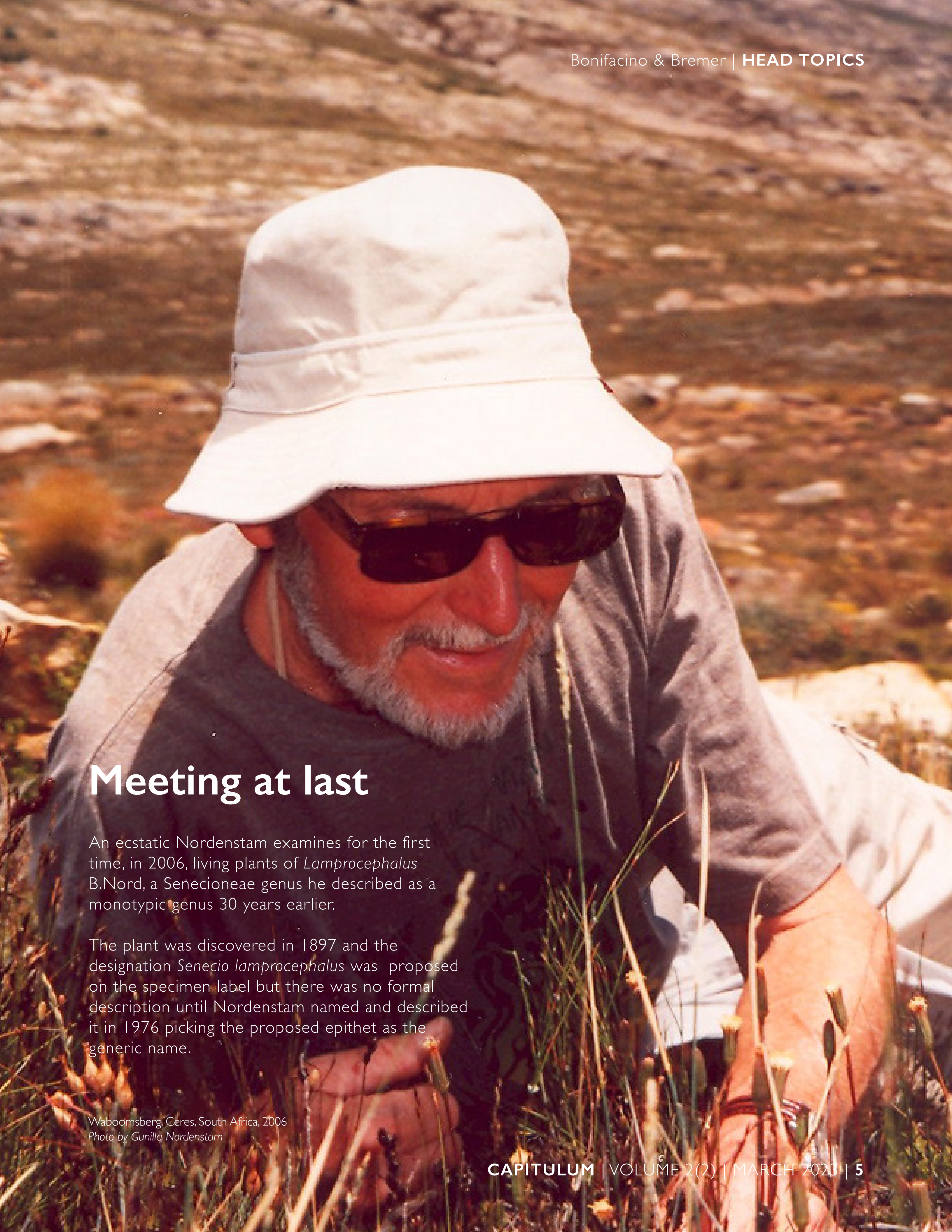
Having returned to Lund from South Africa Bertil worked to complete his revision of *Euryops*, working at the same time between 1966-1968 as a lecturer at the Department of Botany. His taxonomic revision of *Euryops* for which he received his Ph.D. recognized 97 species and was published in the monograph series *Opera Botanica* in 1968 together with a supplement on morphology and cytology.

THE SYNANTHEROLOGIST

Immediately after obtaining his Ph.D. Bertil applied for and was appointed curator at the Swedish Museum of Natural History where Tycho Norlindh was professor and director. Norlindh was soon to retire, and Bertil hoped to succeed him, but after a long application process in 1972 the position went to the more senior Rolf Santesson, a lichenologist from Uppsala. Later in 1980 the professorship was divided in two and the botany department in two sections, for phanerogams and cryptogams, respectively. Bertil then became professor for the phanerogams and Santesson remained as professor for cryptogams. Bertil kept this position until he retired in 2001. During this period, he was periodically commissioned to serve also as deputy museum director, director of research, and director of botany at the museum.

The first symposium entirely devoted to the study of Compositae was held in Reading, England, in July 1975 (Heywood et al., 1977). At this occasion, Bertil assumed his position as the leading specialist on the Senecioneae. The organizers Vernon H. Heywood, Jeffrey B. Harborne and Billie L. Turner assumed that George Bentham´s 19th century tribal classification of the family was essentially correct and that there was a need only for a few transfers of misplaced genera and minor recircumsciptions of the tribes. Consequently, they had asked a selected group of participants to present, at the symposium, an update of Bentham's tribal classification with a list of genera for each tribe.

Bertil was asked by the organizers to do the Senecioneae. The result was the first major redefinition of the tribe since its very creation as he did away with elements introduced by Lessing and perpetuated by De Candolle, i.e., some Anthemideae, Calenduleae and an assorted array of tribes currently part of the Heliantheae alliance, most notably the Helenieae, and partly kept by Bentham as well as further modified by the addition of the Liabeae. Bertil wanted none of that and presented the first narrow definition of the Senecioneae (Nordenstam, 1977). He included not only a revised list of genera with details of number of species, general habit, and distribution, but most notably a discussion on the morphological

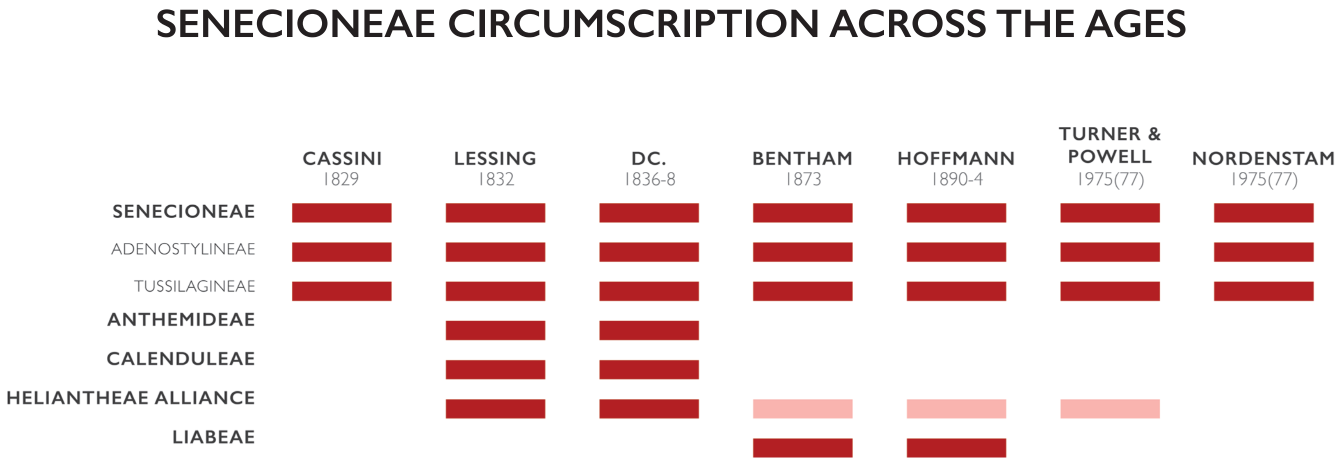


Meeting at last

An ecstatic Nordenstam examines for the first time, in 2006, living plants of *Lamprocephalus* B.Nord, a Senecioneae genus he described as a monotypic genus 30 years earlier.

The plant was discovered in 1897 and the designation *Senecio lamprocephalus* was proposed on the specimen label but there was no formal description until Nordenstam named and described it in 1976 picking the proposed epithet as the generic name.

Waboomsberg, Ceres, South Africa, 2006
Photo by Gunilla Nordenstam



	CASSINI 1829	LESSING 1832	DC. 1836-8	BENTHAM 1873	HOFFMANN 1890-4	TURNER & POWELL 1975(77)	NORDENSTAM 1975(77)
SENECIONEAE	🟥	🟥	🟥	🟥	🟥	🟥	🟥
ADENOSTYLINEAE	🟥	🟥	🟥	🟥	🟥	🟥	🟥
TUSSILAGINEAE	🟥	🟥	🟥	🟥	🟥	🟥	🟥
ANTHEMIDEAE		🟥	🟥				
CALENDULEAE		🟥	🟥				
HELIANTHEAE ALLIANCE		🟥	🟥	▨	▨	▨	
LIABEAE				🟥	🟥		

Figure 2. Circumscription of Senecioneae across the ages. Nordenstam was the person behind the new circumscription which ordered all Senecioneae discovered since the time of Cassini, proposing a narrow definition for the tribe which in a sense was a return to the original concept.

and chemical evidence supporting the new definition. He somewhat reluctantly recognized two subtribes, Blennospermatinae (currently not recognized and including the still troublesome *Abrotanella* (Gaudich.) Cass.) and Senecioninae. Of much importance, inside the latter he outlined the existence of two more or less defined morphological groups, the "cacalioid" assemblage composed by taxa largely characterized by cylindric filaments, continuous stigmatic surfaces, and lack of calyculus; and the "senecioid" assemblage characterized by balusteriform filaments, stigmatic surfaces in two marginal bands, and the presence of a calyculus.

What is interesting from a historical perspective is that at the same meeting some participants argued for another, much broader circumscription of the Senecioneae (Turner & Powell, 1977). This alternative classification conflicted with that of Bertil in the sense that it maintained elements of the Helenieae inside the Senecioneae, most notably *Arnica* L. and related genera. Bertil offered a compelling list of eighteen characters that strongly supported his definition. The proceedings of the Reading meeting were eventually published by Heywood et al. (1977) in "*The Biology and Chemistry of the Compositae*", where Bertil's treatment of a narrowly defined Senecioneae was included. His circumscription of the tribe, with the exclusion of the helenioid elements, was followed by subsequent workers and is now strongly supported by robust phylogenies based on molecular data (Figure 2).

Bertil's review of the Senecioneae for the Reading meeting was soon followed by a milestone in the history of the Senecioneae, his classic Opera Botanica volume from 1978, "Taxonomic studies in the tribe Senecioneae" (Nordenstam, 1978). In this work Bertil continued building on his definition of the tribe by drawing attention to microcharacters, which he considered essential in subtribal and generic taxonomic classification, echoing what Harold E. Robinson and Robert M. King had done for the Eupatorieae (King & Robinson, 1970, 1987). Bertil presented detailed descriptions of the endothecial wall thickenings, the filament shape, the shape of epidermal cell on true ray corollas, and the presence and shape of calcium oxalate crystals, all of significance for clarifying relationships inside the Senecioneae. Furthermore, he included a detailed and lavishly illustrated account on the shapes of style branches. In this publication he also described 22 new genera (Table 1) and proposed over 170 new combinations .

Focusing on the characters that revealed taxonomic affinities and with an understanding of the biogeography of the different groups,

Near Arniston (South Africa), Limestone Fynbos vegetation
Photo by Amida Johns

Felicia nordenstamii

Felicia nordenstamii Grau is described by the German synantherologist Jürke Grau, a specialist in the tribe Astereae. It grows on coastal lime rocks at Cape Agulhas, the southernmost tip of the African continent. The plant is of course named in honour of Nordenstam and it has a special significance for him, since he has a daughter named Felicia. There is also another *Felicia* Cass. species connected with the Nordenstam family, i.e. *Felicia gunillae* B.Nord. which Nordenstam named after his wife Gunilla. *Felicia gunillae* grows near the summit of Brandberg in Namibia and was one of the undescribed species Nordenstam discovered when he successfully climbed the mountain in 1963.

Overhauling the Senecioneae

Through a series of seminal papers, most notably the 1977 presented at the Reading meeting and the *Opera Botanica* from 1978 plus many other subsequent works, Nordenstam redefined the tribe based most notably on morphological grounds that were later nonetheless corroborated with molecular data.

Major morphological characters used were styles as illustrated here, but also the shape of the filament collar and its constitutive cells, the thickenings in the endothecium cells, and the presence of calcium oxalate crystals in achene walls among other microcharacters.

Uniseriate involucre

Key character for identification of Senecioneae.

Senecio crassiflorus DC.,
Photo by Mauricio Bonifacino

STYLE

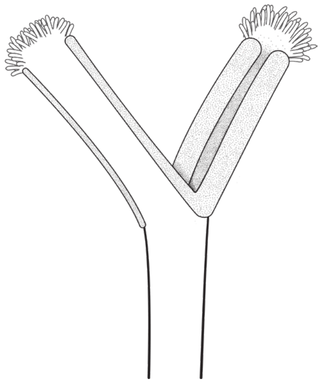
key character in Senecioneae taxonomy

Illustrations redrawn from Nordenstam (1978)

Stigmatic surface in two marginal bands

Style branches truncated with apical tuft of collecting trichomes

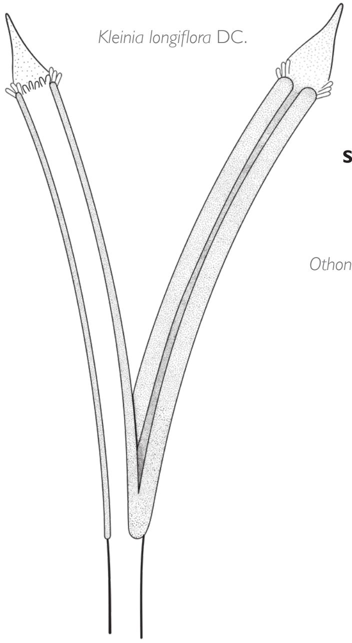
Senecio eligulatus B.Nord.



Stigmatic surface in two marginal bands

Style branches acuminate with ring of collecting trichomes at base of sterile appendage

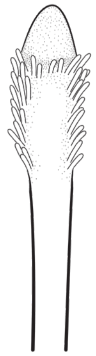
Kleinia longiflora DC.



Undivided style branches

Sterile styles of disk florets

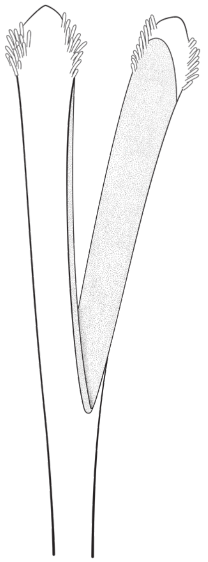
Othonna brandbergensis B.Nord.



Stigmatic surface continuous

The stigmatic surface extends to dorsal surface giving the appearance of marginal bands

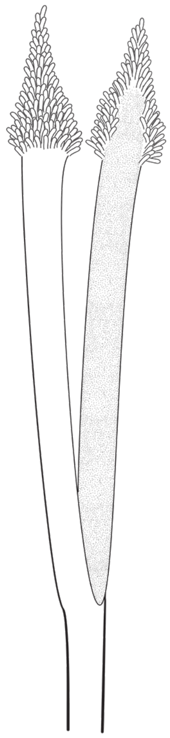
Odontocline tercentenariae (Proctor) B.Nord.



Stigmatic surface continuous

Style branches acuminate covered with collecting trichomes

Jacmaia incana (Sw.) B.Nord.



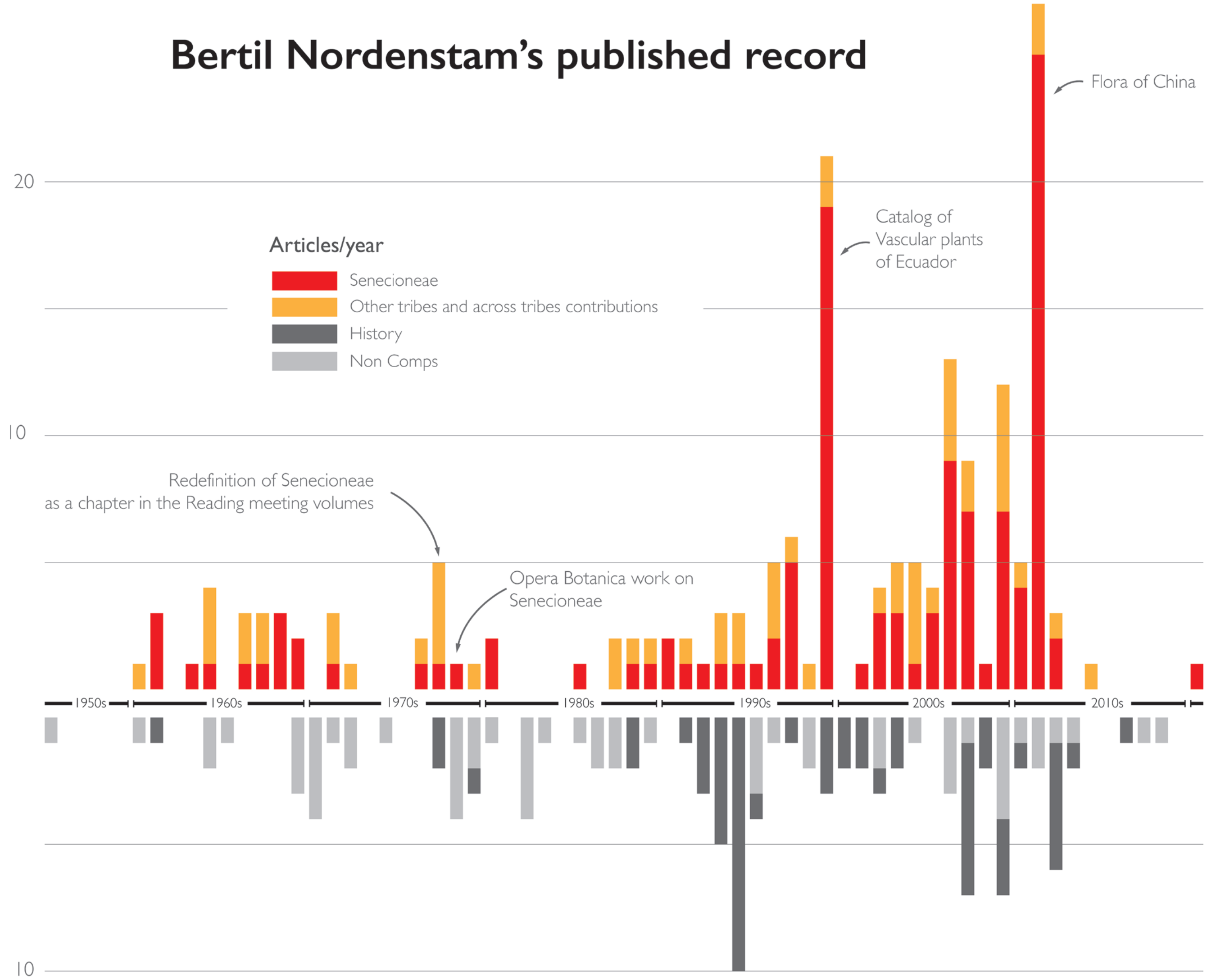


Figure 3. Summary view of Nordenstam's publication record illustrating the dominance of articles about Compositae in general and Senecioneae in particular. Note also the many publications on botanical history.

Bertil continued his work on Senecioneae, and eventually published over 120 scientific articles exclusively dedicated to this tribe. His work on the Compositae, however, has not been limited to the Senecioneae, and he published works in several other tribes, notably in the Calenduleae, Gnaphalieae, and Anthemideae (Figure 3).

> *"I think students should focus on the continued refinement of the circumscription of Senecio, still a very large group, and also in figuring out its geographical origin."*

THE EXPLORER

Bertil has a long track of fieldwork experience, which began together with his uncle Sten Nordenstam. When he came to Lund for his academic studies he joined a senior colleague at the Department of Botany, Hans Runemark, on a collecting trip to Greece in 1960. They rented a fishing vessel and collected nearly 4,000 specimens during three months on many islands in the Aegean sea from Crete to the Northern Sporades. It was during this trip that Bertil became used to intense field work, a characteristic that stayed with him for life.

Namaqualand

Echoing South America's Patagonia, Namaqualand or the land of the Nama Khoe people in the southern end of Africa covers nearly 500000 km^2 and is a synantherologist wonderland. Nordenstam traveled and collected extensively across this territory.

Skilpad camp, Namaqua National Park, South Africa
Photo by Martie De Wijn

In May 1962 Bertil travelled to South Africa mainly to collect *Euryops* for his Ph.D. thesis. He remained there for two years and had the opportunity to visit many remote places, also in Namibia and Lesotho. The trip was made possible by a grant from the National Botanic Garden of South Africa, viz. the Smuts Memorial Fellowship. He was also granted a modest sum (10,000 SEK = approximately 1,000 Euros in today's money) from the Swedish Natural Science Research Council. He purchased a Volvo station wagon to be delivered in Cape Town and assembled a substantial amount of fieldwork equipment and supplies.

In what could be seen as a modern retake of Thunberg's voyage, Bertil's own travel to South Africa was also by sea and made possible by friends in a shipping company that granted him a free voyage from a Norwegian port to Cape Town. The voyage took 32 days including stops at several ports. Since the vessel did not carry passengers, Bertil was listed as a crew member, officially as secretary to the captain, although his only duty consisted of playing bridge with the captain and two other officers each night.

Bertil was well received by the staff at the National Botanic Garden at Kirstenbosch and its Compton Herbarium, where well-known botanists such as Dr. Richard Compton were still active, together with Miss W.F. Barker and Mrs. J. Lewis. After some time in a nearby hotel, he was provided accommodation in a small cottage in Kirstenbosch. This became his base for the following two years, although he was most of the time away in his Volvo collecting plants.

At the time of Bertil's arrival in late austral fall, the weather was cold and rainy in the southwestern Cape, so he spent the first weeks checking specimens in the herbarium and planning his collecting trips. The local botanists suggested many localities where they themselves had done much successful collecting. Most visitors would have followed these suggestions and visited the known localities. Not so Bertil, he noted these localities on his maps and decided to avoid them. He wanted to explore new areas.

After some initial trips in the southwestern fynbos region, Bertil headed north towards Namaqualand. He was fortunate that 1962 was a year with much winter rains that resulted in a prodigious spring flowering. Everywhere the ground was covered in flowers, many of them Compositae. One locality especially worth mentioning is Knersvlakte in the Vanrhynsdorp division. The name alludes to the crackling sound made by the wagon wheels when the first settlers entered the stony and gravelly flats of the area. At Knersvlakte the ground is covered by pebbles and gravel of quartz, an environment filled with endemic plants. Bertil was apparently the first botanist to collect extensively at Knersvlakte, a botanical paradise where he discovered many new species. One day in July 1962, Bertil found three new Compositae and one Iridaceae species which he described later (*Leucoptera subcarnosa* B.Nord., *Othonna hallii* B.Nord., *Pentzia peduncularis* B.Nord., *Babiana lewisiana* B.Nord.). At University of Cape Town there was a specialist on succulent Aizoaceae, Mrs. L. Bolus, and Bertil collected living specimens for her. She described three new species discovered by Bertil at Knersvlakte and named them after him (as well as a fourth species collected by Bertil in Namibia). Knersvlakte is now a nature reserve.

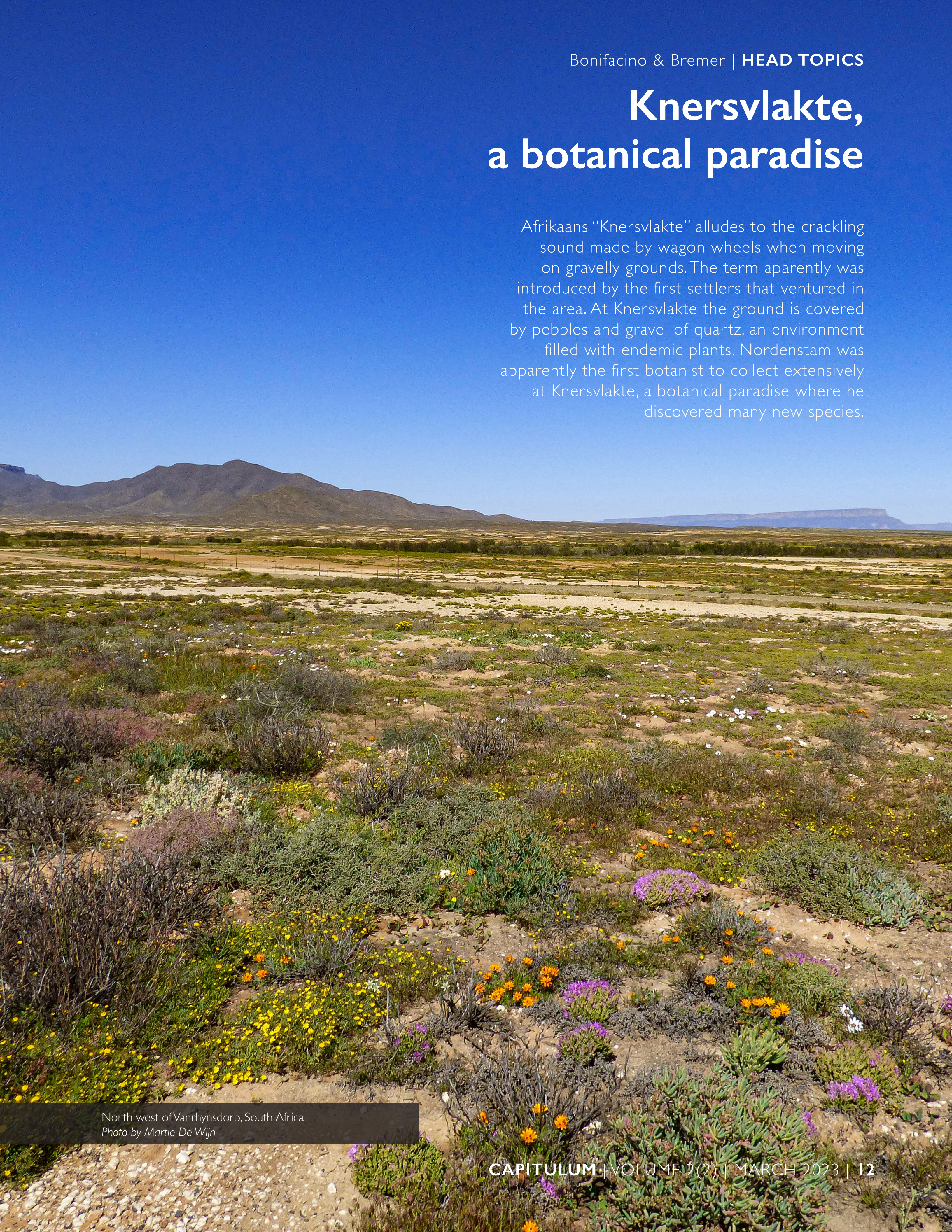
Bertil continued further north through Namaqualand all the way to Richtersveld, the remote northwest corner of South Africa where he also discovered and collected several new species. Among them were four new Compositae species: *Helichrysum jubilatum* Hilliard, *Pteronia anisata* B.Nord., *Pteronia elata* B.Nord., *Oedera nordenstamii* (K.Bremer) Anderb. & K.Bremer.

In 1963 Bertil travelled to Namibia, at that time a protectorate administered by South Africa. He was accompanied by a Swedish globetrotter of the same age, Wilhelm "Ville" Flensburg, who spent his time travelling to remote places. Bertil had met him in Cape Town and Ville cancelled his plans to move on to South America and decided to accompany Bertil on his botanical expeditions. Ville was not interested in plants, but he was a good cook and companion, and he liked the exotic places Bertil planned to visit. In Namibia Bertil´s most remarkable collecting trips were those carried out to the Brandberg massif, its highest mountain.

Brandberg is a massive granite outcrop 2,585 m above sea level, surrounded by the Namib desert (Figure 4). No botanists had visited the uppermost regions. According to local botanists of the time, the mountain probably housed the same plants as the region in

Knersvlakte, a botanical paradise

Afrikaans "Knersvlakte" alludes to the crackling sound made by wagon wheels when moving on gravelly grounds. The term aparently was introduced by the first settlers that ventured in the area. At Knersvlakte the ground is covered by pebbles and gravel of quartz, an environment filled with endemic plants. Nordenstam was apparently the first botanist to collect extensively at Knersvlakte, a botanical paradise where he discovered many new species.



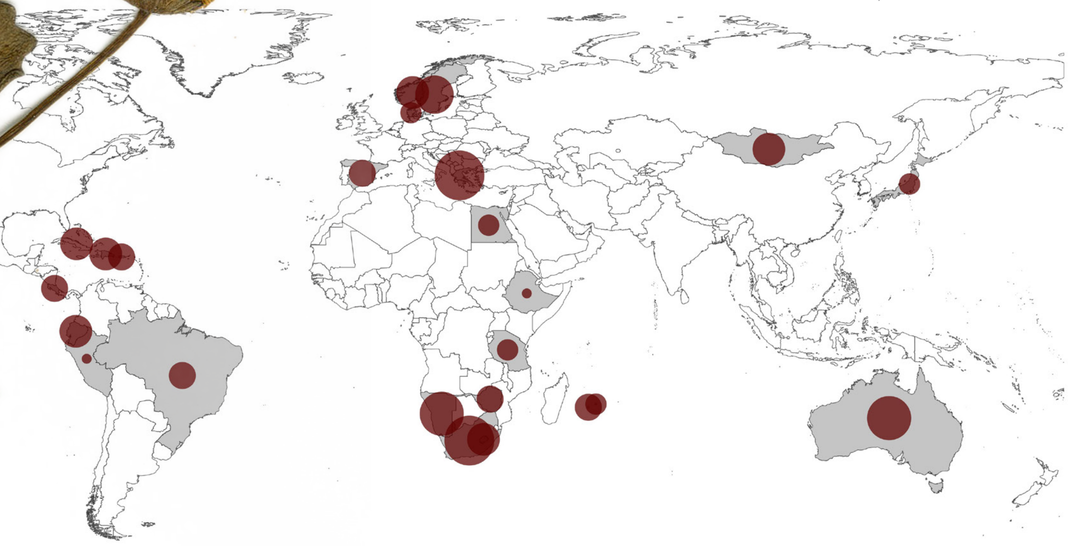
North west of Vanrhynsdorp, South Africa
Photo by Martie De Wijn

A 20th century Linnean disciple

Throughout his whole life Nordenstam was drawn to natural places in pursuit of plants. He collected specimens since his early youth and travelled the world across five continents collecting several thousand specimens, mostly in Greece, Southern Africa, and Australia.

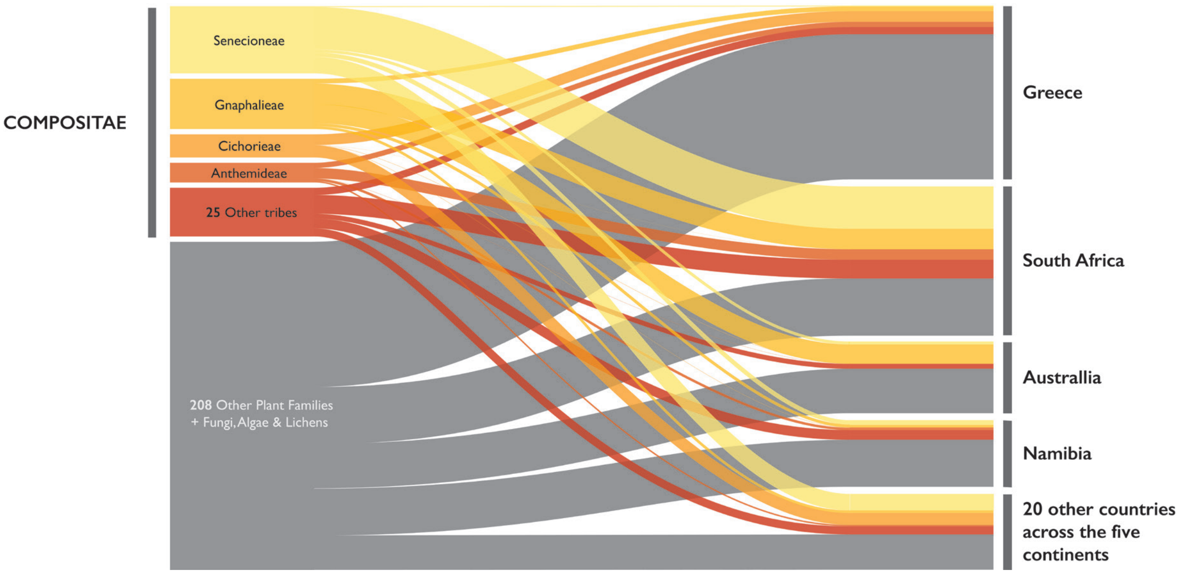
Othonna hederifolia B.Nord.

Fragment of type specimen collected by Nordenstam in South Africa. Scanned by Johannes Lundberg, Swedish Museum of Natural History, reg nr S-G-4416.



Bertil Nordenstam collections in Swedish herbaria

14445 specimens | 209 plant families | 1644 genera | 4744 species



Data obtained from Sweden's Virtual Herbarium available at http://herbarium.emg.umu.se

Records represent specimens collected by Nordenstam as either main or accompanying collector. Duplicates in herbaria outside Sweden are not included and could account for similar numbers of specimens in those herbaria as Nordenstam typically collected duplicates to leave at the country where he collected and to send to other herbaria in the specimen exchange programs at S.

Figure 4. Brandberg is a massive granite outcrop in the Namibian desert, reaching 2,585 m above sea level. When Nordenstam came to Namibia in 1963, at that time a South African protectorate, no botanists had visited the uppermost regions of the mountain. Local botanists assumed that the mountain housed the same plants as the region in general. Nordenstam suspected otherwise and decided to try and explore the upper regions. After five days of strenuous climbing in May 1963 Nordenstam and his companion Ville Flensburg reached the summit where they discovered about 10 species new to science.
Photo by Kåre Bremer.

general. Bertil suspected otherwise and so he set himself to botanize in the area during May-June 1963 and April 1964.

In the beginning of May 1963 Bertil and his companion Ville made a first attempt at exploring Brandberg and ascended along one of the valleys to 1,200 m. They turned back after five days, realizing that they needed more food and equipment to reach the summit. A couple of weeks later, in the end of May, they made a second attempt, with a heavy load of sleeping bags, blankets, field presses and food for about ten days. After five days of strenuous climbing, they reached the summit 31 May 1963.

Again, Bertil was fortunate, 1963 was like 1962 a year with exceptionally good rains resulting in abundant flowering. At the high plateau and on the way to the summit Bertil discovered and collected about 10 new species endemic to Brandberg, among them three Compositae species which he later named *Othonna brandbergensis* B.Nord., *Pentzia tomentosa* B.Nord. and *Felicia gunillae* B.Nord., the last one named after his wife Gunilla.

A true globetrotter

Nordenstam, a Swedish botanist who in pursuit of Compositae has traveled extensively accross the five continents.

Jamaica, 2013
Photo by Gunilla Nordenstam

In April 1964 Bertil and Ville returned to Brandberg. That year there was only little rain, and they were informed by the manager of the nearby tin mine, Mr. J. Botha, that climbing the mountain would not be possible due to lack of water. Instead Mr. Botha offered to fly them in his aeroplane, a Piper Cherokee 180, to a flat but stony strip on the upper plateau. After a dangerous landing on the stony ground, they were left on the mountain for two days until Botha came back to bring them home. A few weeks later Botha crashed when landing on the mountain. He survived and was saved by a rescue expedition.

Bertil's collections from this first journey to southern Africa (1962-1964) have been databased and filed into the S herbarium by Arne Anderberg, Bertil's successor as professor and director of botany at the Swedish Museum of Natural History. Arne Anderberg was impressed by the quality of the material, especially the many fine collections of the often succulent and difficult-to-press *Othonna*.

In 1974 Bertil published a Flora of Brandberg with a checklist of 357 species of vascular plants and an account of his expeditions to the mountain (Nordenstam, 1974; 1982). Bertil´s two years in South Africa comprised many other adventurous botanical expeditions and mountain climbings in the Cape Region, Namibia and Lesotho, but Knersvlakte and Brandberg were perhaps the most memorable places. In May 1964 Bertil flew back to Sweden.

Bertil has also collected extensively in Australia and the West Indies. Most of his collections are stored at the Swedish Museum of Natural History in Stockholm (S) but there are duplicates in many herbaria, especially at Lund university (LD). His fieldwork yielded over 14,000 specimens that have Bertil as collector, encompassing samples gathered in over 20 countries and representing 205 families, almost 40 % of them falling into the Compositae (5624 spp.), and 25 % of these falling into the Senecioneae (1805 spp.).

With this travel experience, having visited over 75 countries Bertil became a fellow of Travellers Club in Stockholm where he served as president for many years, and he was also elected Fellow International in the Explorers Club in New York.

THE HISTORIAN

In addition to his extensive record as plant systematist and taxonomist, Bertil developed a profound interest in the history of botany reflected in more than 50 contributions (Figure 3).

> *"Basic knowledge of the history of science is important and should be included in teaching and research to a greater extent than is currently the case. Students applying molecular techniques should be encouraged to reflect on the history and nomenclature of the taxa involved in their studies. Biology students of today may be ignorant of Linnaeus and his contemporaries, but he is always there because of taxonomic tradition and current rules of nomenclature. In these respects, taxonomy is different from most of modern biology and historical aspects are inevitable in most systematic studies."*

The collections at the Swedish Museum of Natural History (S) began as the natural history collections of the Royal Swedish Academy of Sciences, which was founded in 1739 by Linnaeus himself and five other scholars. As a curator of the herbarium, Bertil saw among all the more recent collections, many 18th century specimens collected by disciples of Linnaeus and also specimens annotated by Linnaeus himself.

When conducting taxonomic revisions involving Linnean names, it is important to know about Linnean disciples and their connections to other 18th and early 19th century botanists. It is not surprising that a Swedish botanist working in Sweden would become interested in some part of the whole universe surrounding Carl Linnaeus, arguably the most famous Swedish botanist of all.

Bertil became interested in botanical history early on, having his first article published on the matter commenting on some Linnean dissertations (Nordenstam, 1961). He has subsequently written books and many articles about Carl Peter Thunberg, Olof Swartz, and other old botanists (Hansen et al., 2012a, 2012b; Nordenstam & Hansen, 2012; Nordenstam, 2012).

Given Bertil's great interest in South African plants, he developed a particular interest in Thunberg, who made extensive collections there ("Father of South

Home is where the heart is

Southern Africa is the region where Nordenstam obtained nearly 25% of his collections, an area rich in Senecioneae, a group that he championed throughout his academic carreer.

Nordenstam collecting Compositae in Lesotho, 2003
Photo by Vicki Funk

Table 1. Compositae genera named by Bertil Nordenstam according to International Plant Names Index with geographic distribution and number of species included. *

Tribe	Genera	Distribution	Species number
Senecioneae	***Acrisione*** B. Nord., Bot. Jahrb. Syst. 107: 582 (1985)	South America	2
	Aequatorium B. Nord., Opera Bot. 44: 59 (1978)	South America	13
	Antillanthus B. Nord., Compositae Newslett. 44: 51 (2006)	Cuba	17
	Capelio B. Nord., Compositae Newslett. 38: 72 (2002)	South Africa	3
	Caputia B.Nord. & Pelser, Compositae Newslett. 50: 59 (2012)	South Africa	5
	Caucasalia B. Nord., Pl. Syst. Evol. 206: 22 (1997)	Asia	4
	Crassothonna B. Nord., Compositae Newslett. 50: 71 (2012)	South Africa	14
	Dauresia B.Nord. & Pelser, Compositae Newslett. 42: 76 (2005)	Namibia	2
	Dendrosenecio (Hauman ex Hedberg) B. Nord., Opera Bot. 44: 40 (1978)	East Africa	12
	Dolichoglottis B. Nord., Opera Bot. 44: 33 (1978)	New Zealand	2
	Elekmania B.Nord., Compositae Newslett. 44: 66 (2006)	Hispaniola	9
	Graphistylis B. Nord., Opera Bot. 44: 56 (1978)	Brazil	9
	Herreranthus B.Nord., Compositae Newslett. 44: 62 (2006)	Cuba	1
	Ignurbia B. Nord.,Willdenowia spec. vol. 31, 1: 464 (2006)	Cuba	1
	Io B.Nord., Compositae Newslett. 40: 47 (2003)	Madagacar	1
	Iranecio B. Nord., in Rech. f. (ed.) Fl. Iran. 164: 53 (1989)	Asia	4
	Jacmaia B. Nord., Opera Bot. 44: 64 (1978)	Jamaica	1
	Lamprocephalus B. Nord., Bot. Notiser 125: 323 (1976)	South Africa	1
	Leonis B.Nord., Compositae Newslett. 44: 55 (2006)	Cuba Hispaniola	1
	Lomanthus B.Nord. & Pelser, Compositae Newslett. 47: 34-36 (2009)	Ecuador Peru Bolivia Argentina	20
	Lordhowea B. Nord., Opera Bot. 44: 38 (1978)	Australia Lord Howe Island	4
	Lundinia B.Nord., Compositae Newslett. 44: 64 (2006)	Cuba, Hispaniola	1
	Nemosenecio (Kitam.) B. Nord., Opera Bot. 44: 45 (1978)	China Japan Taiwan	6
	Nesampelos B.Nord., Compositae Newslett. 44: 58 (2006)	Hispaiola	3
	Odontocline B. Nord., Opera Bot. 44: 23 (1978)	Jamaica	6
	Oldfeltia B.Nord. & Lundin, Compositae Newslett. 38: 66 (2002)	Cuba	1
	Oresbia Cron & B. Nord., Novon 16:216 (2006)	South Africa	1
	Phaneroglossa B. Nord., Opera Bot. 44: 66 (1978)	South Africa	1
	Sinosenecio B. Nord., Opera Bot. 44: 48 (1978)	China to Indochina	44
	Stenops B. Nord., Opera Bot. 44: 73 (1978)	Tanzania Zimbabwe	2
	Urostemon B. Nord., Opera Bot. 44: 31 (1978)	New Zealand	1
	Zemisia B.Nord., Compositae Newslett. 44: 71 (2006)	Central America	2
Anthemideae	***Adenanthellum*** B. Nord., Bot. Notiser 132: 160 (1979)	South Africa	1
	Adenoglossa B. Nord., Bot. Notiser 129: 137 (1976)	South Africa	1
	Cymbopappus B. Nord., Bot. Notiser 129: 150 (1976)	South Africa	3
	Hilliardia B. Nord., Opera Bot. 92: 147 (1987)	South Africa	1
	Leucoptera B. Nord., Bot. Notiser 129: 140 (1976)	South Africa	3
Gnaphalieae	***Anderbergia*** B. Nord., Ann. Wiener Mus. Naturgesch. 98: 407 (1996)	South Africa	6
Astereae	***Roodebergia*** B. Nord., Acta Phytotax. Geobot. 53: 101(2002)	South Africa	1

* Nordenstam described 11 additional genera that have been synonymyzed: SENECIONEAE: ***Canariothamnus*** B.Nord. Compositae Newslett. 44: 24–31 (2006) = ***Bethencourtia*** Choisy in Buch, Phys. Beschr. Canar. Ins.: 148 (1825); ***Iocenes*** B. Nord., Opera Bot. 44: 58 (1978) = ***Senecio*** L., Sp. Pl. 2: 866 (1753); ***Notoniopsis*** B.Nord., Opera Bot. 44: 69 (1978) = ***Kleinia*** Mill., Gard. Dict. abr. ed.: 4 (1754); ***Xyridopsis*** B.Nord., Opera Bot. 44: 75 (1978) = ***Psednotrichia*** Hiern, J. Bot. 36: 289 (1898). ANTHEMIDEAE: ***Adenanthemum*** B.Nord., Bot. Not. 129(2): 157 (1976) = ***Adenanthellum*** B. Nord., Bot. Notiser 132: 160 (1979); ***Scyphopappus*** B.Nord., Bot. Not. 129(2): 147 (1976) = ***Argyranthemum*** Webb, Hist. Nat. Iles Canaries (Phytogr.). 3(2.2, livr. 44). t. 90 (1839). GNAPHALIEAE: ***Comptonanthus*** B.Nord., J. S. African Bot. 30: 54 (1964) = ***Ifloga*** Cass., Bull. Sci. Soc. Philom. Paris 1819: 142 (1819). CALENDULEAE: ***Inuloides*** B.Nord., Compositae Newslett. 44: 44 (2006) = ***Osteospermum*** L., Sp. Pl. 2: 923 (1753); ***Monoculus*** B.Nord., Compositae Newslett. 44: 39 (2006) = ***Osteospermum*** L., id.; ***Nephrotheca*** B.Nord. & Källersjö, Compositae Newslett. 44: 33 (2006) = ***Osteospermum*** L., id.; ***Norlindhia*** B.Nord., Compositae Newslett. 44: 41 (2006) = ***Osteospermum*** L., id. Note that generic classification of Calenduleae is still being discussed and researched. It is a matter of opinion whether ***Osteospermum*** should be widely circumscribed to include most species of the Calenduleae, as it is in the International Plant Names Index, or reclassified into a number of monophyletic genera, as is advocated by Nordenstam.

Figure 5. Japanese Emperor Akihito visited Sweden in connection with the 300th anniversary of Linnaeus' birth. From left Swedish Queen Silvia, Japanese Emperor, Swedish King Carl XVI Gustaf, Japanese Empress Michiko, and Nordenstam showing books about Carl Peter Thunberg. Stockholm, May 2007.
Photo by Swedish Museum of Natural History.

African Botany") and also in Japan ("Japan Linnaeus"). As described above, Bertil spent considerable time in South Africa and visited Japan a total of 24 times, although he was not able to do much collecting there.

In 1976 he was invited to speak about Thunberg at the 200th anniversary of his visit to Japan. On that occasion Bertil was invited to meet Emperor Hirohito, who had a strong interest in biology, botanical history (especially Thunberg's visit to Japan in 1776), and had assembled a substantial herbarium on the premises of the Imperial Palace. Bertil would later also meet with Emperor Akihito (Figure 5) and the present Emperor Naruhito while the latter was Crown Prince.

Bertil´s interest in historical botanists was not restricted to Linnean disciples. He also wrote a book about Erik Leonard Ekman (1883-1931) who spent his life collecting in the Caribbean where he discovered more than 2,000 new species (Nordenstam & Oldfelt, 2007).

THE EDITOR

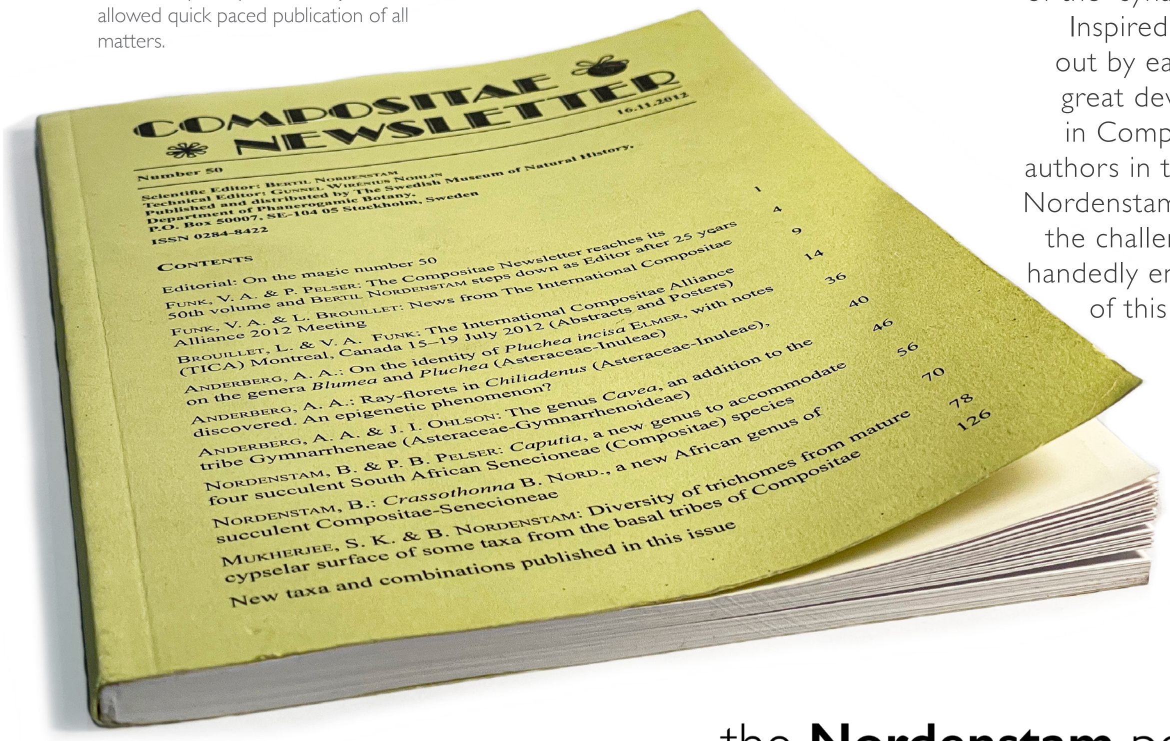
The first periodical exclusively dedicated to the Compositae, the Compositae Newsletter, was founded by Tod F. Stuessy and Robert M. King in 1975, and carried on for some time by Stuessy, Charles Jeffrey and Jette Baagøe. After passing through these editors, it was up to Bertil in 1988 to introduce the classic compact yellow format for which the Newsletter is remembered. Bertil not only introduced a change in format but more importantly he conducted his editorial duties during 25 uninterrupted years, the longest stretch for the journal.

An epoch making publication venue

COMPOSITAE NEWSLETTER

The Compositae Neweslетter offered a communication venue in times with no internet or social media to connect people commonly interested in Compositae. It eventually morphed into a journal that allowed quick paced publication of all matters.

Over 260 articles were published in the COMPOSITAE NEWSLETTER, Nordenstam edited 80% of them, making possible the rapid publication of data from different areas of the synantherological world. Inspired by the work carried out by earlier editors and the great development of studies in Compositae from Swedish authors in the 1980s and 1990s, Nordenstam decided to take on the challenge to almost single-handedly ensure the publication of this journal for 25 years.



COMPOSITAE NEWSLETTER

16.11.2012

Number 50

Scientific Editor: Bertil Nordenstam
Technical Editor: Gunnel Wirénius Nohlin
Published and distributed by The Swedish Museum of Natural History,
Department of Phanerogamic Botany,
P.O. Box 50007, SE-104 05 Stockholm, Sweden
ISSN 0284-8422

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the **Nordenstam** period

25 uninterrupted years of Compositae Newsletter

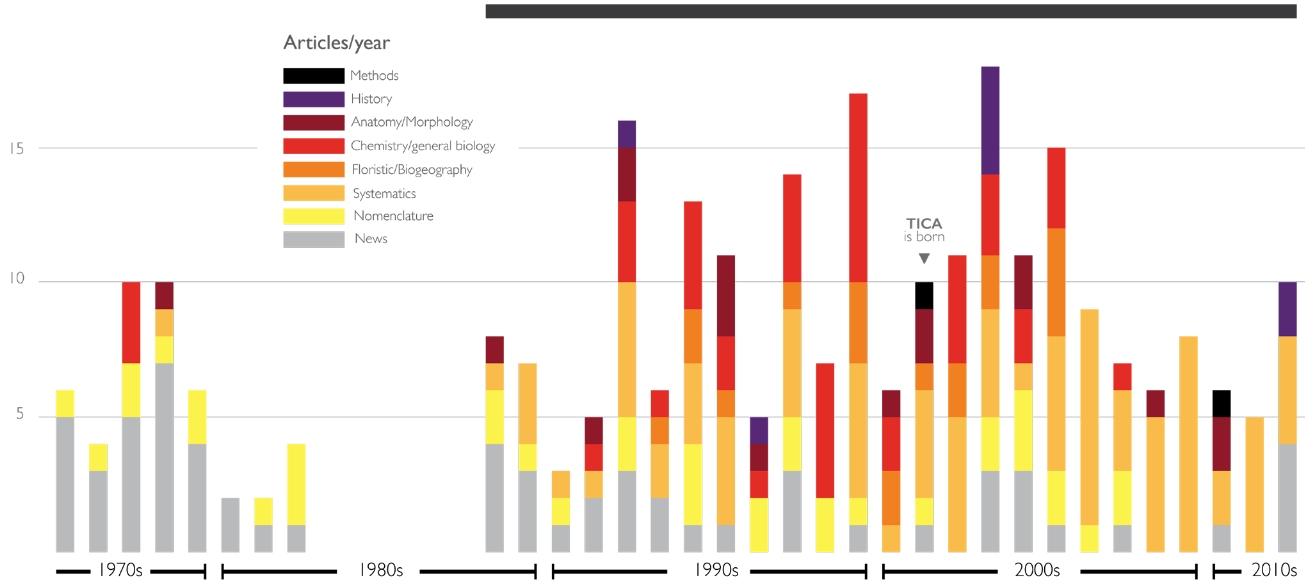


Table 2. Genera and species named after Bertil Nordenstam according to International Plant Names Index. *Hieracium nordenstamii* Rit Visindofj. Islend., Akureyri 37: 82 (1966) from Iceland, was named after Sten Nordenstam, not Bertil.

Family	Tribe	Taxa	Diversity & distribution
COMPOSITAE	Senecioneae	***Bertilia*** Cron, S. African J. Bot. 88: 14 (2013)	1 sp., South Africa
	Senecioneae	***Nordenstamia*** Lundin, Compositae Newslett. 44: 15 (2006).	16 spp., Ecuador, Peru, Bolivia, NW Argentina
	Senecioneae	***Euryops bertilii*** Vlok, S. African J. Bot. 133: 169 (2020)	Little Karroo
	Astereae	***Felicia nordenstamii*** Grau, Mitt. Bot. Staatssamml. München 9: 336 (1973)	Agulhas to Potberg coastal limestone rocks
	Astereae	***Nidorella nordenstamii*** Wild, Bol. Soc. Brot. sér. 2, 43: 230 (1969)	Namibia
	Gnaphalieae	***Oedera nordenstamii*** (K.Bremer) Anderb. & K.Bremer, Ann. Missouri Bot. Gard. 78(4): 1071 (1991); *Relhania nordenstamii* K.Bremer, Opera Bot. 40: 54 (1976)	Richtersveld
	Calenduleae	***Osteospermum nordenstamii*** J.C.Manning & Goldblatt, Bothalia 42(1): 62 (2012)	Namaqualand coastal plain Riethuis to Vredendal
AIZOACEAE		***Antimima nordenstamii*** (L.Bolus) H.E.K.Hartmann, Bothalia 28(1): 77 (1998) = *Ruschia nordenstamii* L.Bolus, J. S. African Bot. 30: 241 (1964).	Van Rhynsdorp
		Drosanthemum nordenstamii L.Bolus, J. S. African Bot. 30: 78 (1964)	Namibia
		Conophytum nordenstamii L.Bolus, J. S. African Bot. 29: 171 (1963) = ***Conophytum wettsteinii*** subsp. fragile (Tischer) S.A.Hammer, Gen. Conophytum 241 (1993)	Van Rhynsdorp
		Oophytum nordenstamii L.Bolus, J. S. African Bot. 28: 291 (1962) = ***Oophytum oviforme*** N.E.Br., Gard. Chron. ser. 3, 79: 48 (1926)	Van Rhynsdorp
ASPARAGACEAE		***Lachenalia nordenstamii*** W.F.Barker, J. S. African Bot. 49(4): 428 (1983)	Namibia

According to Bertil, he was inspired to do so due to the surge of Compositae research carried out in Stockholm. These years at the end of the 20th century stand out as a well-defined Swedish period in the history of study of Compositae.

When Bertil took over as editor of Compositae Newsletter, it was before internet, e-mail, and social media. Compositae Newsletter became a convenient vehicle for general research news in the Compositae, but also for publication of necessary taxonomic and nomenclatural changes and other synantherological matters. Bertil insisted that the journal was to be distributed free of charge to anyone interested and he always encouraged new readers.

CONCLUDING REMARKS

This review has been focused on Bertil's contributions to classification of the Senecioneae and on his remarkable field work carried out in South Africa. Bertil also pursued important work in other plant families, Colchicaceae to take one example, with his fine monographs of the genera *Ornithoglossum* and *Wurmbea*. His collecting trips went not only to Africa, but to other continents as well, notably southwestern Australia, and exotic places like Cuba, Lord Howe Island, and Mongolia. To give a fair review of all his botanical accomplishments necessitates a longer article.

Nordenstamia

Nordenstamia Lundin is an Andean genus of 16 species distributed from Ecuador to northern Argentina. The genus is distinctive in its alternate phyllotaxis, yellow ray corollas and style branches with pointed apical appendages.

Nordenstam has been honored with two genera and five species in Compositae and three species in two other plant families (Aizoaceae and Asparagaceae; Table 2).

Nordenstamia longistyla, Reserva Aguada Blanca, Arequipa, Perú
Photo by Edgar Heim

ACKNOWLEDGMENTS

First and foremost, we thank Bertil Nordenstam for accepting to be the subject of this paper and for his patience to endure several sessions of Q&A. His daughter Felicia Nordenstam supplied contact information. Amida Johns, Martie De Wijn and Edgar Heim allowed us to use their photographs to illustrate this article. Carol Kelloff from the US herbarium put at our disposal the photo collection of the late Vicki Funk and facilitated access to some literature. Arne Anderberg and Johannes Lundberg provided information about Nordenstam's collections at the S herbarium and granted permission to use the image of the *Othonna* type. Torsten Eriksson at University of Bergen helped with early suggestions on matters pertaining to this article and Ken Wurdack from the US herbarium assisted with editorial suggestions on early versions of the manuscript.

LITERATURE CITED

Bonifacino, J.M., Robinson, H, Funk, V.A., Lack, H.W., Wagenitz, G., Feuillet, C. & Hind, N. 2009. A history of research in Compositae: early beginnings to the Reading Meeting (1975). Pp. 3-38, in: Funk, V.A., Susanna, A., Stuessy, T.F. & Bayer, R.J. (eds.), Systematics, evolution, and biogeography of Compositae. Vienna: International Association for Plant Taxonomy.

Hansen, V., Nordenstam, B. & Hansen, L. (eds.). 2012a. The Linnaeus Apostles. Global Science & Adventure. Vol. 8, Encyclopaedia. IK Foundation & Co., London & Whitby, 570 pp.

Hansen, V., Nordenstam, B. & Hansen, L. 2012b. Biographies with maps. Pp. 13—77 in: The Linnaeus Apostles. Global Science & Adventure. Vol. 8, Encyclopaedia. IK Foundation & Co., London & Whitby

Nordenstam, B. 2012. Olof Swartz –A 250 year anniversary. Pp. 2—5 in: Maiti, G & Mukherjee, S. K.(eds.), Multidisciplinary Approaches in Angiosperm Systematics, Kalyani Univ. W. Bengal, India.

Nordenstam, B. & Hansen, V. 2012. Index Volumes One to Seven. Pp. 79—568 in: Hansen, V., Nordenstam, B. & L. Hansen (eds.) 2012. The Linnaeus Apostles. Global Science & Adventure. Vol. 8, Encyclopaedia. IK Foundation & Co., London & Whitby.

Heywood, V.H., Harborne, J.B. & Turner, B.L. (eds.). 1977. The Biology and Chemistry of the Compositae, 2 vols. Academic Press, London.

King, R.M. & Robinson, H. 1970. The New Synantherology. *Taxon* 19(1): 6–11.

King, R.M. & Robinson, H. 1987. The genera of the Eupatorieae (Asteraceae). *Monogr. Syst. Bot. Missouri Bot. Gard.* 22: i–x, 1–581.

Nordenstam, B. 1961. Notes on Some Linnaean Dissertations. *Bot. Notiser* 114(3): 276-280.

Nordenstam, B. 1974. The flora of the Brandberg. *Dinteria* 11: 3-67.

Nordenstam, B. 1977. Senecioneae and Liabeae—systematic review. Pp. 799–830 in: Heywood, V.H., Harborne, J.B. & Turner, B.L. (eds.), The Biology and Chemistry of the Compositae, vol. 2. Academic Press, London.

Nordenstam, B. 1978. Taxonomic studies in the tribe Senecioneae (Compositae). *Opera Bot.* 44: 1–83.

Nordenstam, B. 1982. The Brandberg revisited. *Dinteria* 16: 3-5.

Nordenstam, B., Pelser, P.B., Kadereit, J.W. & Watson, L.E. 2009. Senecioneae. Pp: 503-525 in: Funk, V.A., Susanna, A., Stuessy, T.F. & Bayer, R.J. (eds.), Systematics, evolution, and biogeography of Compositae. Vienna: International Association for Plant Taxonomy.

Nordenstam, B. & Oldfelt, K. 2007. Plantae Ekmanianae. En bok om Erik Leonard Ekman och hans karibiska växter. Atlantis, Stockholm.

Pelser, P.B., Nordenstam, B., Kadereit, J.W. & Watson, L.E. 2007. An ITS phylogeny of tribe Senecioneae (Asteraceae) and a new delimitation of *Senecio* L. *Taxon* 56: 1077–1104.

Turner, B.L. & Powell, A.M. 1977. Helenieae—systematic review. Pp. 699–737 in: Heywood, V.H., Harborne, J.B. & Turner, B.L. (eds.), The Biology and Chemistry of the Compositae, vol. 2. London, Academic Press.

Craspedia diversicolor Breitw. & K.A.Ford. (Gnaphalieae):

Discovery and conservation management of one of New Zealand's rarest and most endangered plants

Ilse Breitwieser

Allan Herbarium, Manaaki Whenua – Landcare Research, P.O. Box 69040, Lincoln 7640, NEW ZEALAND; *breitwieseri@landcareresearch.co.nz*

DOI: http://dx.doi.org/10.53875/capitulum. 02.2.02

ABSTRACT

Craspedia diversicolor (Gnaphalieae), a recently described species from the South Island of New Zealand, is characterised by glomerules (pseudocephalia) having florets with a white corolla and dark red-purple anthers, and rosette leaves being variable from olive-green, grey to dark red, with a very thin, appressed to flocculent, lanate indumentum. The species was once more widespread in the Canterbury Plains but is now restricted to Wakanui Gully in Canterbury on privately owned agricultural land. Only two plants were found recently. After manually cross-pollinating the two plants with a plant we have held in cultivation, we managed to raise 80 seedlings. The majority of those were planted at a reserve where they have meanwhile flowered and produced seedlings. We hope we have saved *Craspedia diversicolor* from the immediate threat of extinction.

Keywords: Asteraceae, Compositae.

INTRODUCTION

Craspedia G.Forst. (Gnaphalieae) is a genus of more than 30 species confined to Australia and New Zealand (e.g. Ford et al., 2007; Castelli et al., 2017). It is characterised by its homogamous capitula crowded together into a dense glomerule (pseudocephalium) borne on an unbranched scape. The species are rosette-forming perennial herbs (except for one Australian species), with the leaves showing considerable variation in form, colour, and indumentum. With the six species in Flora of New Zealand (Allan, 1961) and five species that were described recently as new to science (Breitwieser & Ford, 2022; Breitwieser et al., 2022), 11 species of *Craspedia* are now recognised in New Zealand. Here we relate the story of the discovery and conservation management of one of these new species, *Craspedia diversicolor* Breitw. & K.A.Ford.

DISCOVERY

About 20 years ago we noticed that a herbarium specimen collected by Ruth Mason in 1967 (CHR 167368) in an area south-west of Wakanui Beach (about 100 km south of Christchurch, Canterbury, South Island) and determined by David Drury as *Craspedia lanata* (Hook.f.) Allan differs from this species by having florets with dark red-purple anthers and rosette leaves with a very thin,

Figure 1. *Craspedia diversicolor* Breitw. & K.A.Ford. **A.** Habit. **B.** Glomerule (pseudocephalium). **C.** Side view of capitulum. **D.** Florets: the closed anther tube is dark red-purple but after anthesis it is striped, with only the colour of the ridges being dark red-purple while the areas in between are pale yellow-green. **E.** Close up of androecium showing the closed dark red-purple anther tube. *Photos by: A,B: Rainer W. Vogt; C-E: Ilse Breitwieser.*

The power of a herbarium specimen

A fifty year old herbarium record led us to one of New Zealand's most endangered species. This specimen of *Craspedia diversicolor* Breitw. & K.A.Ford. was collected by another female botanist, Ruth Mason (1913-1990), whose special interest in field botany strengthened her dedication to environmental science and conservation

(see A. D. Thomson, Te Ara biographies https://teara.govt.nz/en/biographies/5m38/mason-ruth)

Nº 167368

BOTANY DIVISION, D.S.I.R.,
CHRISTCHURCH, NEW ZEALAND

Craspedia lanata (Hk.f.) Allan

Loc. ½ mile S.W. of Wakanui Beach, Canterbury
S103/958305

Hab. In grass on shingle ridge

Col. R. Mason 10680 Date: 24-11-1967

Det. Date: 28/3/69

Remarks:

S.I.R. 620

Partial image of *Ruth Mason's 10680* specimen, see whole specimen at:
https://scd.landcareresearch.co.nz/Specimen/CHR%20167368
Photo © Landcare Research 2023

Figure 2. A. Cover of Mr W. Piercy's 1884 Pressed Plant Book. **B.** Mr W. Piercy's specimen of *Craspedia*.
Photo © Landcare Research 2023

appressed to flocculent, lanate indumentum (Figure 1). Ruth Mason reported it as local and common. When we visited the site for the first time in 2001, it was covered by exotic grassland. We counted 30 *Craspedia* plants at two close-by sites. However, when revisiting the site in 2013, we found only eight plants and since 2019 there are only two plants there.

In recent years, we searched New Zealand herbaria for similar looking specimens and their localities. Remembering that about 20 years ago I saw a herbarium specimen from the nineteenth century that was collected in the area of Lincoln, Canterbury, where the Allan Herbarium (CHR) is now housed, I thought it would be interesting to compare it with Ruth Mason's specimen (CHR 167368). However, although all ca. 2000 *Craspedia* specimens at CHR are now databased and imaged, I couldn't find this specimen from the Lincoln area and started to doubt my memory. Our herbarium manager had the idea I should search through old Pressed Plant Books: and there it was, the specimen I had vaguely remembered! A Mr W. Piercy collected plants and pressed them in a book that he presented to his wife A.M. Piercy on 19 October 1884 (Figure 2). One of the specimens in this book was a *Craspedia*, which he had identified as *Craspedia fimbriata* (G.Forst) DC. [=*Craspedia uniflora* G.Forst.] (CHR 653000). I almost couldn't believe it when I studied the specimen: the anthers are still dark red-purple, and the specimen matches Ruth Mason's specimen. Mr Piercy collected the specimen at the Lincoln cemetery. Therefore, we went to the Lincoln cemetery, but since it is nowadays a well maintained, modern cemetery, there is of course no *Craspedia* growing anymore among the graves.

In our search for specimens that are similar to the *Craspedia* from Wakanui Gully, we found only collections from Bankside Reserve in 1969 (CHR 201474), Te Pirita in 1962 (CHR 173458) and the Hinds River in 1965 (CHR 169034), all sites, like Wakanui Gully, about 100 km or less south of Christchurch. We went to these sites, but they are now very weedy, and *Craspedia* has disappeared.

Based on these few earlier collections, we concluded that *Craspedia diversicolor* was once much more widespread in the Canterbury plains. In addition

One of the rarest KIWIS

The solitary terminal glomerule (pseudocephalium) is formed by ca. 60 homogamous, discoid capitula with a total of c. 410 florets. The white corolla is contrasted by an anther tube that is first dark red-purple and later pale yellow-green with dark purple stripes.

Craspedia diversicolor Breitw. & K.A.Ford., Wakanui Gully, south of Christchurch, New Zealand
Photo by Ilse Breitwieser

to the sites where the herbarium specimens were collected, we have meanwhile visited other areas in the Canterbury plains we judged to be potentially good habitats for *C. diversicolor* but could not find any plants. This is not surprising, because the lowland Canterbury Plains have been extensively modified with recent conversions to irrigated dairy farming. Very few remnants of native dryland vegetation remain (e.g. Bowie et al., 2016).

CONSERVATION MANAGEMENT

Craspedia diversicolor is close to extinction. Only two plants of this species are now left in the wild – and their site is on privately owned land and adjacent to a beef feedlot!

The big issue for the conservation management of this species is the degradation of the Canterbury Plains. At its last remaining site at Wakanui Gully, *C. diversicolor*'s habitat changed after grazing of the coastal margin and steep side of the gully ceased when ANZCO Foods' Wakanui Five Star Beef feedlot was established in 1989. This site, which is now on ANZCO Foods' land, is the best remnant of dry, coastal gully shrubland on the Canterbury Plains. A variety of dryland species still just survive. Conservation volunteers have worked hard, supported by ANZCO Foods, to help with conservation management. ANZCO Foods has fenced off an 8 ha area and recently informed us that it will invest a significant amount of funding into amelioration of the land and planting of many rare and threatened plants, including this *Craspedia*. Te Rūnanga o Arowhenua (representative body of the local indigenous people), who have set up a native plant nursery, will grow plants for this re-vegetation project. However, the two plants at Wakanui Gully are not able to produce seed anymore. So, how would we be able to grow plants for the re-vegetation

Figure 3. A. Author hand pollinating one of the two remaining *Craspedia diversicolor* Breitw. & K.A.Ford. plants at their site at Wakanui Gully, south of Christchurch, New Zealand. **B.** Some of the 80 seedlings of *Craspedia diversicolor* at Manaaki Whenua – Landcare Research experimental nursery, Lincoln, New Zealand. *Photos by: A: Rainer W. Vogt; B: Ilse Breitwieser.*

Figure 4. Planting of the *Craspedia diversicolor* Breitw. & K.A.Ford. seedlings. **A.** Some of the seedlings before planting at Harris Reserve, Ashburton, south of Christchurch, New Zealand. **B.** Planting of the seedlings. **C & D.** Seedlings in their bee boxes. *Photos by: A, C-D: Ilse Breitwieser; B: Jane Gosden.*

At the brink of extintion

Only two plants of *Craspedia diversicolor Breitw. & K.A.Ford.* are left. Their last remaining site is at this coastal cliff adjacent to a beef feedlot and the sea is taking each year more and more of the the coast line.

Site of the last two plants of *Craspedia diversicolor* Breitw. & K.A.Ford., Wakanui Gully, south of Christchurch , New Zealand.
Photo by Rainer W. Vogt

project? Since our first visit to Wakanui Gully in 2001 we have grown one of the plants at our experimental nursery at Manaaki Whenua – Landcare Research, Lincoln. Therefore, we hoped that this plant would be genetically a bit more distant to the two remaining plants and maybe cross-pollinating the plants at Wakanui Gully with the pot plant from our nursery might work. In collaboration with conservation volunteers and QEII National Trust, in November 2020 we manually cross-pollinated the two remaining plants at Wakanui Gully with the pot plant from our nursery. We were lucky! In the 2020/2021 season we obtained 18 filled seeds from the two plants at Wakanui Gully as well as 126 filled seeds from our pot plant that we had cross-pollinated with a glomerule from one of the Wakanui Gully wild plants. Our experienced gardener David Purcell managed to raise 80 seedlings (Figure 3). We gave 20 seedlings to the Christchurch Botanic Gardens, kept six for further genetic investigation, and in October 2021 planted the rest at two reserves close to Ashburton (80 km south of Christchurch), hoping that this translocation will lead to new self-sustaining populations. As luck would have it, one of the translocation sites is close to a site where H.H. Allan collected a specimen in 1918 (CHR 10542). I didn't identify this specimen as *C. diversicolor* until after we had planted the seedlings at the reserve. The identification of this specimen gave us therefore a very exciting surprise. The seedlings at the reserves flowered already a month after we planted them and produced numerous offspring. In November / early December 2022, the plants are in full flower and look healthy. We have fenced them in and protected them with bee boxes to shelter them from the dry Canterbury winds and pests like rabbits (Figure 4). We tried cross-pollinating the plants at Wakanui Gully again in 2021, but the plants were in bad condition and produced neither sufficient good pollen for pollination nor seed.

We hope we have saved *Craspedia diversicolor* from the immediate threat of extinction, but because of loss of its habitat in the Canterbury Plains long term survival will probably not be possible without active conservation management.

ACKNOWLEDGEMENTS

I would like to thank Val Clemens and Edith Smith for all their energy and hard work in saving *Craspedia diversicolor* from extinction. I would also like to thank Alice Shanks from QEII Trust and Luke Martin from Christchurch Botanic Gardens as well as my colleagues Kerry Ford, Jane Gosden, Paula Greer, David Purcell, Ines Schönberger, and Rob Smissen. The submitted manuscript benefited from helpful reviews by Andre Messina and an anonymous reviewer.

LITERATURE CITED

Allan, H.H. 1961. Flora of New Zealand. Vol. 1. Wellington: Government Printer.

Bowie, M.H., Black, L., Boyer, S., Dickinson, N.M. & Hodge, S. 2016. Persistence of biodiversity in a dryland remnant within an intensified dairy farm landscape. *N. Z. J. Ecol.* 40:121–130.

Breitwieser, I. & Ford, K.A. 2022. Four new species of *Craspedia* (Compositae/Asteraceae, Gnaphalieae) from the South Island of New Zealand, all characterised by dark red-purple anthers. *New Zealand J. Bot.* DOI: 10.1080/0028825X.2022.2095919

Breitwieser, I., Courtney, S.P. & Ford, K.A. 2022. *Craspedia huriawa* (Compositae/Asteraceae, Gnaphalieae), a new species from Nelson/Tasman, South Island of New Zealand. *New Zealand J. Bot.* DOI: 10.1080/0028825X.2022.2109975

Castelli M, Miller CH, Schmidt-Lebuhn AN. 2017. Polyploidization and genome size evolution in Australian billy buttons (*Craspedia*, Asteraceae: Gnaphalieae). *Int. J. Pl. Sci.* 178:352–361.

Ford, K.A., Ward, J.M., Smissen, R.D., Wagstaff, S.J. & Breitwieser, I. 2007. Phylogeny and biogeography of *Craspedia* (Asteraceae : Gnaphalieae) based on ITS, ETS and *psbA–trn*H sequence data. *Taxon*. 56:1–12.

Haplopappus Cass. (Astereae) *sensu* Hall:
a polyphyletic conundrum revealed by plastid data

Marisa B. Szubryt

University of Oklahoma, Robert Bebb Herbarium, 770 Van Vleet Oval East #208, Norman, Oklahoma 73019, U.S.A.; *marisabszubryt@ou.edu*

DOI: http://dx.doi.org/10.53875/capitulum.02.2.03

ABSTRACT

The genus *Haplopappus* Cass. has undergone drastic taxonomic changes since its inception in 1828 by Cassini. Initially based on a single species from Chile, *H. glutinosus* Cass., it was expanded to over 150 species by Hall and others to encompass cushion-like alpine herbs, caulescent perennials, low-elevation subshrubs, and sizeable shrubs, mostly indigenous to North America. *Haplopappus* means simple or single pappus consisting of scabrous capillary bristles, a feature seized upon by Hall, along with homochromous discoid or radiate capitula usually with yellow corollas, for uniting species in the genus. Various explanations were given to exclude other genera similar in this regard such as *Solidago* L. and *Chrysothamnus* Nutt. Hall's treatment formed the basis for numerous subsequent taxonomic treatments and floras for decades. As cytological and other sorts of data emerged, however, its polyphyly became evident, and many researchers sought to define monophyletic lineages within this artificial group. Subsequently, *Haplopappus* sensu Hall has been disassembled into over thirty genera across several subtribes predominantly within a clade known as "North American Astereae". Previously, limited phylogenetic resolution was achieved in this lineage with nuclear ribosomal data via Sanger Sequencing. In this study, high-throughput sequencing allowed the assembly of whole chloroplast genomes for phylogenetic analyses. The results from this work demonstrate that *Haplopappus* as circumscribed by Hall is deeply polyphyletic.

Keywords: Asteraceae, Compositae, North America, Phylogenetics, Taxonomy.

INTRODUCTION

The cosmopolitan tribe Astereae (Asteraceae) includes over 3,000 species in approximately 200 genera and underwent multiple transitions to the Americas largely from Eurasia and Africa (Nesom & Robinson, 2007; Brouillet et al., 2009). One diverse clade, termed "North American Astereae" (Brouillet et al. 2009) migrated north from Central and South America even though few other Astereae colonized the U.S. and Canada. This lineage subsequently underwent notable diversification and in numerous cases migrated back to South America (Brouillet et al., 2009). The North American Astereae includes many widespread, diverse genera and bears a long, complicated taxonomic history – in large part due to the genus *Haplopappus* Cass.

Haplopappus ("*Aplopappus*" as originally spelled) was defined by Cassini on the basis of a single species (*Haplopappus glutinosus* Cass.) from Chile (Cassini, 1828), as small cushion plants with sticky-glandular foliage and solitary, terminal capitula containing yellow corollas in radiate heads. Later authors significantly expanded the genus describing numerous species, (Gray, 1868, 1873, 1880, 1884; Greene, 1885; Blake, 1922, 1932; Hall, 1928; Anderson, 1980, 1983; Dorn, 1977, 1988) but most notably substantially broadening its morphological circumscription. Hall's (1928) treatment of *Haplopappus* included 16 sections and over 150 predominantly North American species. Other mat or cushion-forming plants, such as *H. pygmaeus* (Torrey & A.Gray) A.Gray (≡*Tonestus pygmaeus* Torrey & A.Gray), were included along species with a wide variety of habits and morphological features.

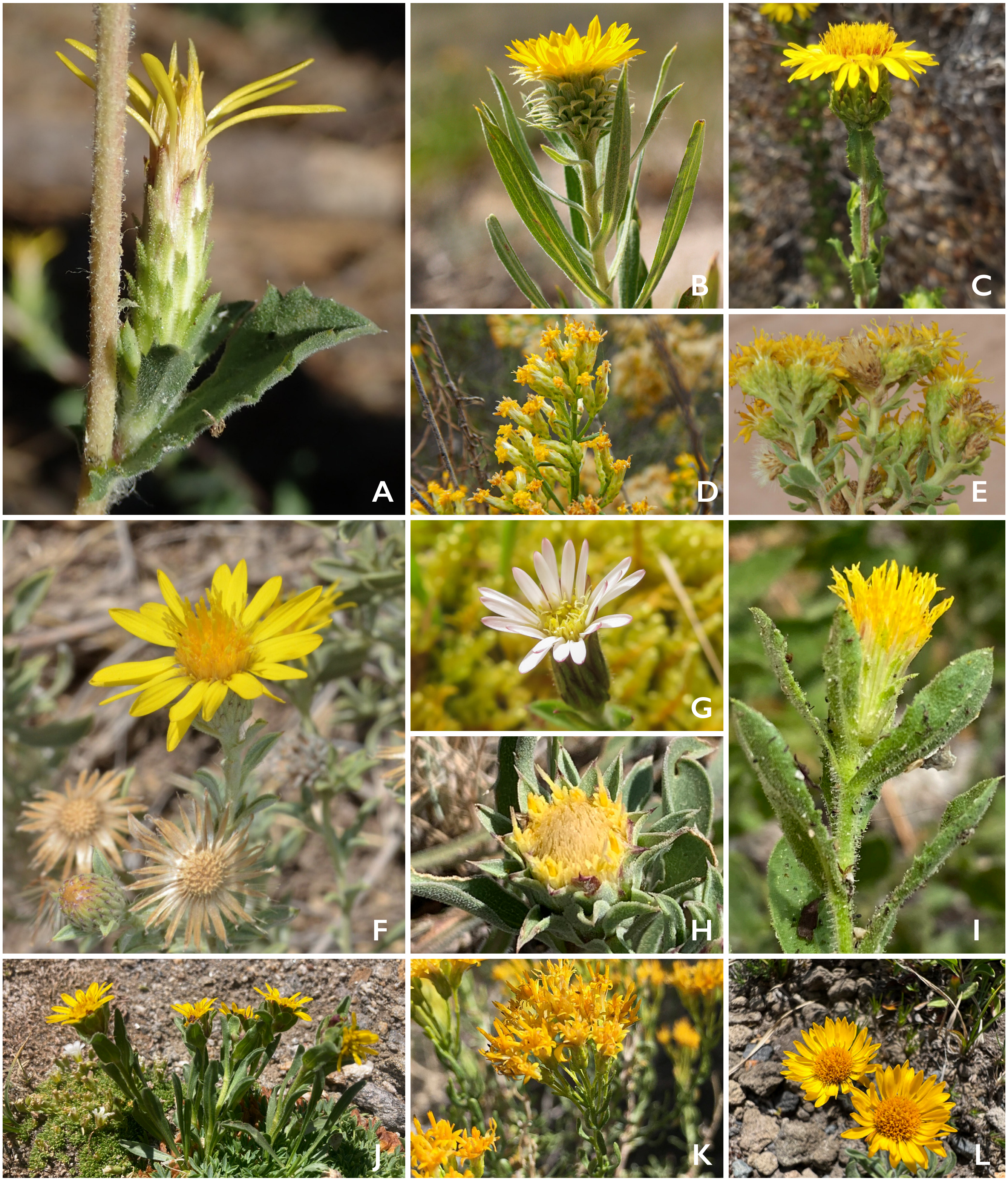
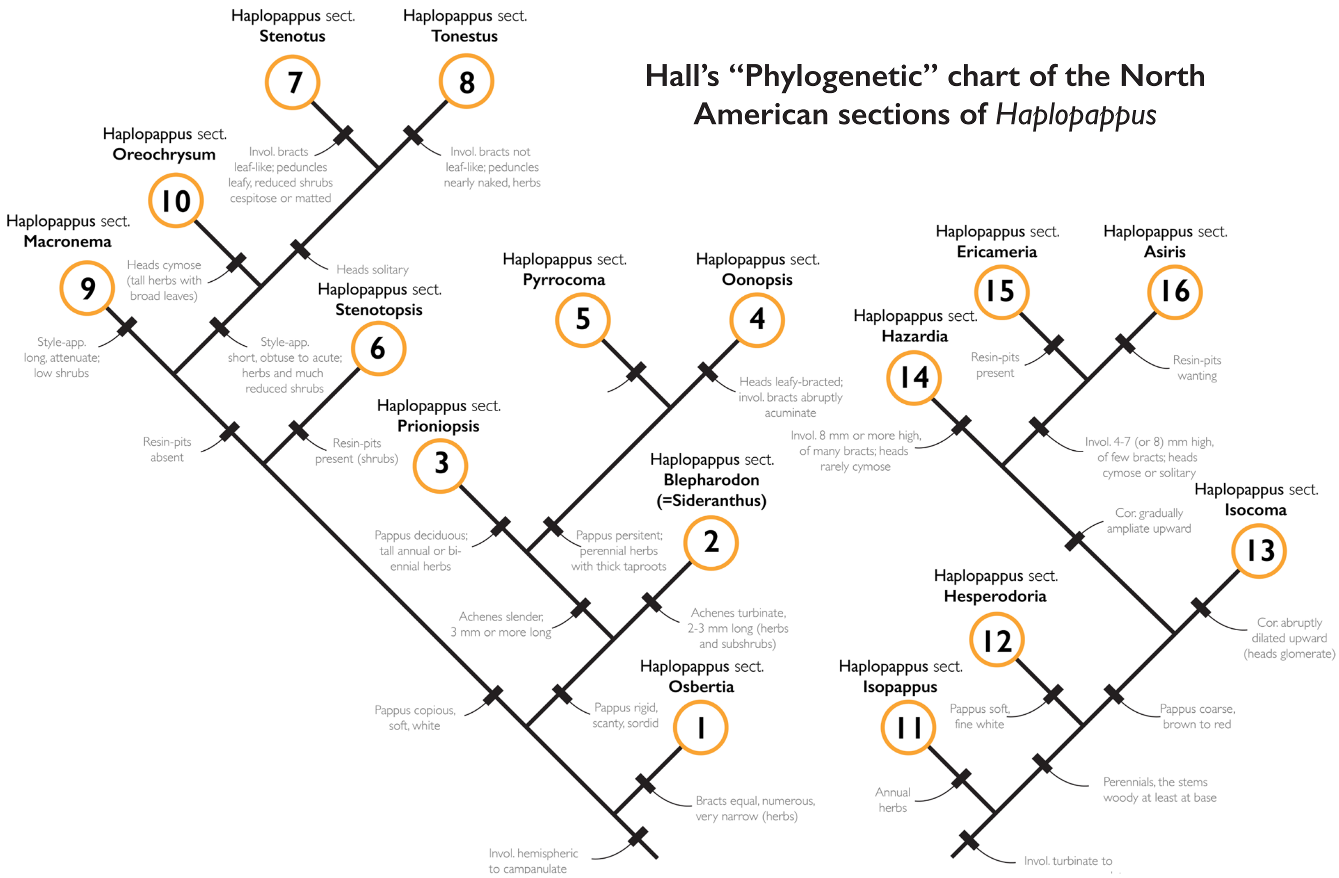


Figure 1. Select genera segregated from *Haplopappus s.l.* **A.** *Adeia whitneyi* (A.Gray) G.L.Nesom. **B.** *Oonopsis puebloensis* S. Kelso, Heckmann, J. Lawton & Maentz. **C.** *Hazardia berberidis* (A.Gray) Greene. **D.** *Xylothamia diffusa* (Benth.) G.L.Nesom. **E.** *Isocoma acradenia* (Greene) Greene. **F.** *Heterotheca canescens* (DC.) Shinners. **G.** *Noticastrum marginatum* (Kunth) Cuatrec. **H.** *Pyrrocoma carthamoides* Hook. **I.** *Triniteurybia aberrans* (A.Nelson) Brouillet, Urbatsch & R.P.Roberts. **J.** *Tonestus pygmaeus* A.Nelson **K.** *Ericameria cooperi* (A. Gray) H.M.Hall. **L.** *Erigeron aureus* Greene. *Photos by: A. Keir Morse (iNaturalist observation: 143617355), B. Richard Bunn (93382668), C. Gwen Fish (133668894), D. Oscar Jimenez (35617164), E. Richard Abbott (133835240), F. Richard Abbott (13612158), G. Omar Javier López Gómez (133778200), H. Matt Reala (143148497), I. Matt Berger (87951215), J. Peter Zika (131061374), K. Jim Tietz (121487540), L. James Thomas (130636095)*

Figure 2. Species of *Haplopappus* s.s. from South America. **A.** *H. macrocephalus* (Poepp. ex Less.) DC. **B.** *H. cf. foliosus* DC. **C.** *H. grindelioides* (Less.) DC. **D.** *H. donianus* (Hook. & Arn.) Sch.Bip. ex Reiche. **E.** *H. velutinus* J.Remy. **F.** *H. taeda* Reiche. **G.** *H. foliosus* DC. **H.** *H. glutinosus* Cass. **I.** *H. chrysanthemifolius* DC. *Photos by: A. Eitel Pinto (iNaturalist observation: 120175330), B. Eitel Pinto (120174775), C. Eitel Pinto (105806884), D. Zona Norte de Quilpué (103767807), E. Nodora Moyano 108700701), F. Orlando Montes (69568777), G. Catalina Chappuzeau (108396872), H. Nicolas Olejnik (1187277), I. Charif Tala (100444307)*



Hall's "Phylogenetic" chart of the North American sections of *Haplopappus*

Figure 3. Hall's interpretation of the relationships among his sections of *Haplopappus* with a dichotomous key separating the supposed clades from his 1928 monograph. Key features of proposed importance included the presence or absence of leafy bracts subtending the capitula and overall capitulescence structure. These features, however, would turn out to be homoplaseous within the American Astereae.

Haplopappus, as conceived by Hall and later authors was morphologically heterogeneous, in habit and plant height, capitulum type, floret number, and pubescence (Figure 1 & Figure 2).

Hall (1928) believed the North and South American species of *Haplopappus* were two discrete clades and greatly increased the number of North American species within the genus. He described and incorporated numerous new taxa, gradually increasing the morphological complexity of the group. Hall created sections defined by similarity and based on various combinations of morphological characters (Figure 3). Before long, the genus existed as a catch-all of sorts that accounted for a substantial portion of mostly species of North American Astereae with yellow corollas bar the "Asters" (including *Eurybia* (Cass.) Cass., *Ionactis* Greene, *Symphyotrichum* Nees), goldenrods (*Chrysoma* Nutt., *Euthamia* (Nutt.) Cass., *Solidago* L.), and snakeweeds (including *Gutierrezia* Lag., *Amphiachyris* (DC.) Nutt.).

Comparative morphological and molecular phylogenetic work (Brouillet et al., 2009; Lane and Hartman, 1996; Suh & Simpson, 1990) resulted in the allocation of over one-hundred North and Central American species of *Haplopappus s.l.* into approximately thirty genera among several subtribes (particularly Chrysopsidinae Nesom, Machaerantherinae Nesom, Pentachaetinae Nesom, and Solidagininae O.Hoffm.; Table 1) as defined by Nesom (2020a) which expanded upon the synopsis presented by Brouillet et al. (2009).

Haplopappus sect. *Blepharodon* DC. was eventually split into several genera (Lane & Hartman 1996), including *Adeia* G.L.Nesom, *Erigeron* L. (*E. aureus* Greene), *Hazardia* Greene, *Rayjacksonia* R.L.Hartm. & M.L.Lane, and *Xanthisma* DC.

Alternatively, genera like *Ericameria* Nutt. in the modern sense include members of several of Hall's

Life in the skies

Tonestus pygmaeus (Torrey & A.Gray) A.Nelson: Morphologically similar to *Nestotus* R.P.Roberts, Urbatsch & Neubig and *Stenotus* Nutt., this alpine or subalpine species was originally described as *Haplopappus pygmaeus* (Torrey & A.Gray) A. Gray. Native to the central and southern Rocky Mountains, this dwarf species is a classic montane “cushion plant:” short stature with deep taproots, densely pubescent foliage, and relatively large flowers/capitula. Dozens of species just within Astereae have converged upon this habitat, including *Heterotheca pumila* (Greene) Semple and *Lorandersonia peirsonii* (D.D.Keck) Urbatsch, R.P.Roberts & Neubig, as it provides protection from frigid and windy conditions throughout short growing seasons.

San Juan mountains in Colorado, USA
Photo by Patrick Alexander

Adapted to the arid

Xanthisma grindelioides (Nutt.) D.R.Morgan & R.L.Hartm., Found throughout much of the low and mid-elevation western U.S., this species exhibits numerous adaptations to drier climates which many other Astereae have converged upon. These subshrubs are coated in dense glands and have lost their ray florets to reduce water loss – similar to many species of *Ericameria* Nutt. and *Isocoma* Nutt. Like many other species in the North American Astereae clade, it has belonged to various genera at different times including *Haplopappus* Cass. and *Machaeranthera* Nees. This species has been previously known as *Ericocarpum grindelioides* Nutt. and *Sideranthus grindelioides* (Nutt.) Britton, but those names would eventually be lumped into *Xanthisma* DC.

Red Canyon of Wyoming, USA
Photo by Patrick Alexander

sections of *Haplopappus*, as *H.* sect. *Asiris* H.M. Hall, *H.* sect. *Ericameria* (Nutt.) A Gray, *H.* sect. *Macronema* (Nutt.) A. Gray, and *H.* sect. *Stenotopis* (Rydb.) H.M.Hall (Roberts, 2002; Urbatsch & Roberts, 2003; Urbatsch et al., 2006).

Additionally, about one-third of the species of *Chrysothamnus* Nutt., a genus largely excluded from *Haplopappus* by Hall (1928), were transferred to *Ericameria* (Nesom & Baird, 1993, 1995; Roberts & Urbatsch, 2003). The sections of *Haplopappus* as defined by Hall were circumscribed according to a combination of several homoplaseous characters, including the loss or reduction of ray florets in several sections (Roberts & Urbatsch, 2003) and shift to annual habit in select members of *Haplopappus* sect. *Blepharodon* DC. (Hartman, 2006) and *H.* sect. *Isopappus* (Torr. & A.Gray) Benth. & Hook.f. (Markos & Strother, 2006; Nesom, 2006). Features such as phyllary, involucre, style, and pappus shape were of principal importance in Hall's (1928) treatment. These morphological features have been interpreted variously to support either lumping or splitting different lineages across numerous genera or sections (Nesom, 1989, 2007, 2018, 2020b; Nesom & Baird, 1993; Nesom et al., 1990), even by the same author with most changes made within the Gutierrezzinae and Solidagininae s.s..

Generic delimitation would not reach a consensus for many groups such as Machaerantherinae (Brouillet & Selliah, 2005; Morgan, 1990, 2003; Morgan et al., 2009; Selliah, 2009; Selliah & Brouillet, 2008) and Solidagininae s.s. (Roberts, 2002; Roberts & Urbatsch, 2003, 2004; Urbatsch et al., 2005) without molecular studies to help identify monophyletic groups.

As speciation within the North American Astereae, many of which were formerly included in *Haplopappus,* the colonization of similar climates by different lineages likely contributed to the rise of many convergences which in turn yielded the rather complex taxonomy of today (Akram et al., 2020; Billing,s 1974; Hughes & Atchison, 2015). Shifts in overall form and habit were likely dictated in large by elevational changes; species approaching or within the alpine zones must grow relatively low to counter the dry air and colder temperatures (Billings, 1974; Billings et al., 1968; Hughes et al., 2015) while those in the lowland deserts faced evolutionary pressure to become either short-lived annuals or (sub)shrubs with deep taproots as drought stress intensified and water availability decreased (Akram et al., 2020; He et al., 2021; Mulroy & Randel, 1977). The colonization and occupation of new niches via speciation occurred repeatedly, making proper classifications difficult at best without the aid of molecular data.

`Through innumerable chromosome counts and molecular phylogenetic data (Brouillet et al., 2009; Morgan, 2003; Morgan et al., 2009; Roberts, 2002; Urbatsch et al., 2003, 2005), it became apparent that *Haplopappus* as originally described constituted numerous independent lineages. Sanger Sequencing helped produce the backbone phylogeny for Astereae that could not be reasonably inferred with morphology alone, and cytological work confirmed the existence of many groups therein often defined by the number of chromosomes present. Gradually, work by several authors (Brown & Keil, 1992; Clark, 1979; Cronquist, 1947; Hartman, 1976; Kartesz, 1994; Kartesz & Gandhi, 1991a, 1991b; Lane, 1993; Mayes, 1976; Nesom, 1991a, 1991b, 1991c; Nesom & Morgan, 1990; Smith, 1981; Turner & Hartman, 1976) established monophyly for the appropriate species into new or existing genera. The last genus to be established out of Hall's definition of *Haplopappus* in North America was *Rayjacksonia* R.L. Hartm. and M.A. Lane of the Machaerantherinae (Lane & Hartman, 1996). With a revised classification of the "North American Astereae" clade (Brouillet et al., 2009), the production of revised keys and an ameliorated understanding of the numerous new clades could begin.

As molecular phylogenetic tools have become far more available and affordable in the past decades, a phylogeny based on whole chloroplast genome data is presented here to highlight the discrepancies between initial treatments of *Haplopappus* and modern taxonomic treatments. Modern molecular data, along with an account of the gradual disarticulation of North American *Haplopappus,* further provides a prime example of how convergent adaptations to various extreme conditions can confound initial treatments. The objective of this paper is to reveal the polyphyletic nature of Hall's *Haplopappus* treatment using whole chloroplast genome sequence data.

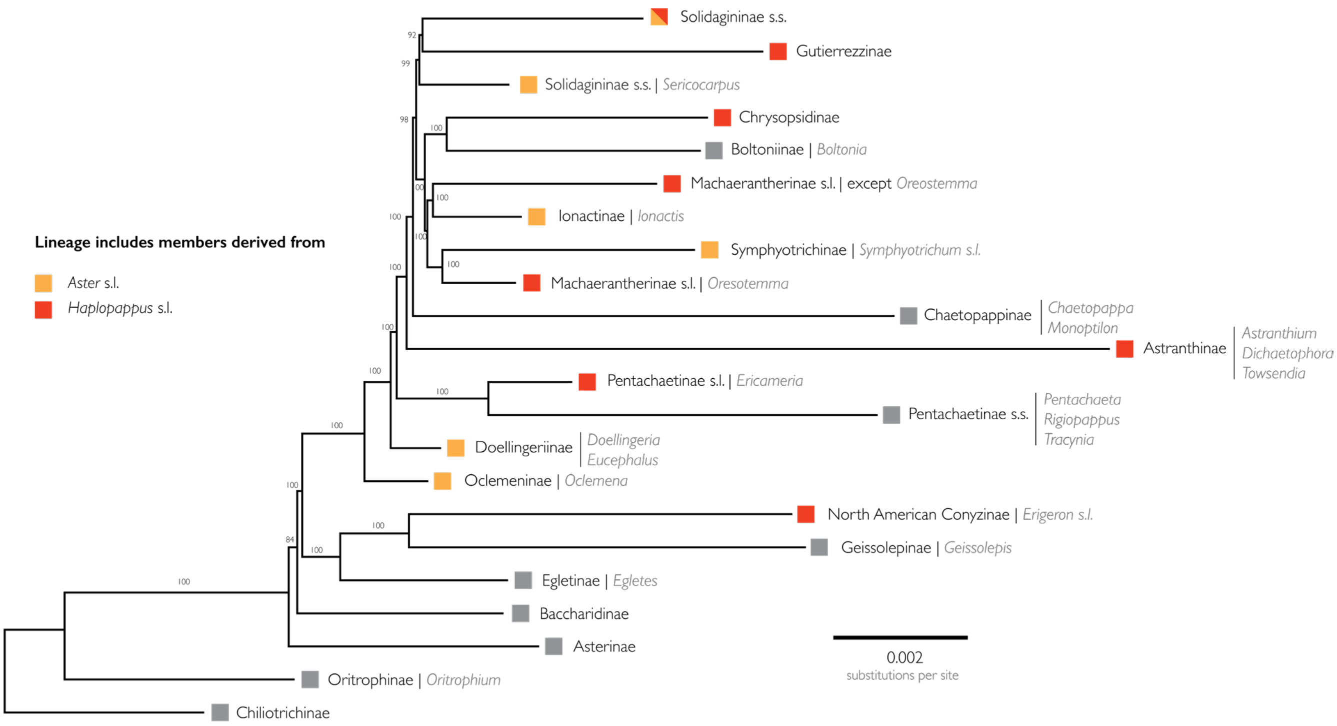


Figure 4. Subtribal relationships within North American Astereae. Lineages in red have members which have been segregated from "*Haplopappus* s.l." while those in orange were segregated from "*Aster* s.l."; lineages with members derived from both are in purple. While both of these previously large genera were once classified as monophyletic, they have since been split into numerous genera spread across various subtribes following the advent of molecular phylogenetic data and additional morphological studies. This topology represents the maximum likelihood tree of the partitioned chloroplast genome dataset generated in IQ-TREE, viewed in FigTree, and edited in Adobe Illustrator.

MATERIALS & METHODS

Taxa were selected to include representatives from each of the subtribes of North American Astereae postulated by Nesom (2020a). Species belonging to *Ericameria, Euthamia,* and species from the Solidagininae *s.s.* and Gutierrezzinae, collectively forming the Solidagininae *s.l.,* were further included as parts of other projects investigating the relationships among and within those lineages. Species of the South American *Haplopappus s.s.,* along with many other genera from Machaerantherinae, were also included to help elucidate the origin of this genus from within the North American Astereae clade identified by Brouillet et al. (2009).

Leaf tissues for phylogenetic studies were gathered either through fresh collections, predominantly by Lowell Urbatsch, and various herbarium specimens. Several herbaria generously permitted the sampling of leaf tissues from specimens, including ACAD, ARIZ, ASC, ASU, AUA, BALT, BRY, COLO, DES, ECS, FLAS, LL, LSU, MICH, MISS, MO, NCU, NLU, NO, NY, OBI, RM, SDS, SIU, STAR, UAL, UCR, UNA, USAM, US, UTC, UWAL, TEX, and TROY (acronyms according to Thiers, 2023); LSU, LL, and TEX warrant particular recognition for providing the majority of samples used here. Genetic or DNA material was extracted from herbarium specimen leaves using a modified CTAB protocol with silica columns (Doyle & Doyle, 1987; Neubig et al., 2014). Samples were then quantified using a QuBit v. 3.0 Fluorometer and evaluated for degradation on an agarose gel. High and medium quality DNA extractions at suitable concentrations were then sent to Rapid Genomics LLC (Gainesville, FL, USA) for library preparation and paired-end

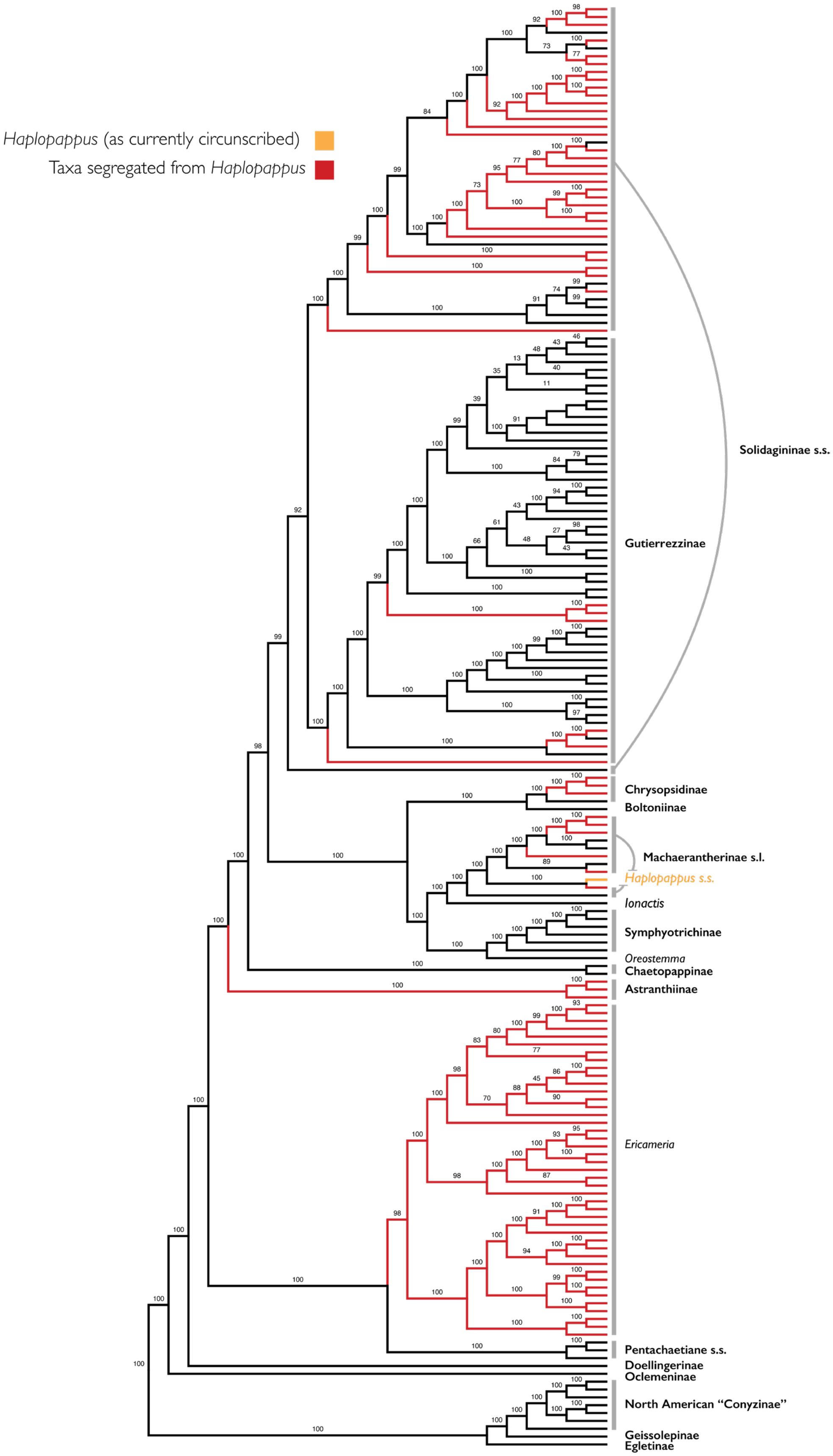


Figure 5. Chloroplast cladogram showing taxa segregated from *Haplopappus* in red with reference to the modern definition of Haplopappus in orange. These data indicate that *Haplopappus*, as Hall defined it, is deeply polyphyletic within the Americas. This partitioned chloroplast cladogram is identical to that to the phylogram in Figure 4 but without any collapsed nodes for various subtribes or genera.

Table 1. Species segregated from *Haplopappus* have been split into the following genera among seven subtribes. Generic circumscription within Solidagininae *s.s.* may change noticeably with additional data.

Genus	Subtribe
Townsendia Hook., Fl. Bor.-Amer. (Hooker) 2(7): 16. t. 119 (1834).	**Astranthinae**
Croptilon Raf., Fl. Tellur. 2: 47 (1837).	**Chrysopsidinae**
Heterotheca Cass., Bull. Sci. Soc. Philom. Paris 1817: 137 (1817)	
Noticastrum DC., Prodr. (DC.) 5: 279 (1836).	
Osbertia Greene, Erythea 3: 14 (1895).	
Pityopsis Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 317 (1841).	
Tomentaurum G.L.Nesom, Phytologia 71: 129 (1991).	
Erigeron L., Species Plantarum. Pl. 2.: 863 (1753).	**Conyzinae**
Gundlachia A.Gray, Proc. Amer. Acad. Arts 16: 100 (1880).	**Gutierrezzinae**
Medranoa Urbatsch & R.P.Roberts, Sida 21(1): 254 (2004).	
Adeia G.L.Nesom, Phytoneuron 39: 1 (2021).	**Machaerantherinae s.l.**
Benitoa D.D.Keck, Leafl. W. Bot. 8: 26 (1957).	
Grindelia Willd., Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 1: 259 (1807).	
Hazardia Greene, Pittonia 1: 28 (1887).	
Isocoma Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 320 (1841).	
Machaeranthera Nees, Gen. Sp. Aster.: 224 (1832).	
Oonopsis (Nutt.) Greene, Pittonia 3: 45 (1898).	
Oreostemma Greene, Pittonia 4: 224 (1899).	
Pyrrocoma Hook., Fl. Bor.-Amer. (Hooker) 1: 306 (1833).	
Rayjacksonia R.L.Hartm. & M.L.Lane, Amer. J. Bot. 83: 368 (1996).	
Xanthisma DC., Prodr. (DC.) 5: 94 (1836).	
Xylorhiza Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 297 (1841).	
Ericameria Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 318 (1841).	**Pentachaetinae s.l.**
Acamptopappus A.Gray, Proc. Amer. Acad. Arts 8: 634 (1873).	**Solidagininae s.s.**
Chrysothamnus Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 323 (1841).	
Columbiadoria G.L.Nesom, Phytologia 71: 249 (1991).	
Lorandersonia Urbatsch, R.P.Roberts & Neubig, Sida 21(3): 1619 (2005).	
Nestotus R.P.Roberts, Urbatsch & Neubig, Sida 21(3): 1650 (2005).	
Oreochrysum Rydb., Bull. Torrey Bot. Club 33: 152 (1906).	
Stenotus Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 334 (1841).	
Toiyabea R.P.Roberts, Urbatsch & Neubig, Sida 21(3): 1652 (2005).	
Tonestus A.Nelson, Bot. Gaz. 37: 262 (1904).	

sequenced on an Illumina MiSeq before processing the data files in Geneious Prime R10.

Sequences were assembled using a mixture of reference and *de novo* assemblies in Geneious to a reference sequence of *Baccharis genistelloides* (Lam.) Pers. (GenBank accession KX063864); the sequences were then aligned on the CIPRES supercomputer cluster (Miller et al., 2015) using MAFFT v. v7.427 (Katoh et al., 2018). Annotations were generated using the 'Annotate from' function in Geneious using *Baccharis genistelloides* (NCBI GenBank accession number: KX063864) at 80% similarity. Truncated annotations were permitted, and annotations which overlapped with the best match by 75% were excluded to avoid annotating the same sequence portion multiple times. The index length was limited to 10 nucleotides, and only 'gene' type sequences were annotated. Sequences were partition based on their type: coding sequence exons and introns, tRNA exons and introns, rRNAs, and intergenic spacers. Each sequence type was evaluated for the optimal substitution model in IQ-TREE v. 1.6.8 using the automatic Model Finder function (Chernomer et al., 2016; Hoang et al., 2018; Nguyen et al., 2015); IQ-TREE further generated maximum likelihood phylogenies for the entire concatenated dataset. The output consensus tree was then viewed in FigTree v. 1.4.4 (Rambaut, 2018) and edited in Adobe Illustrator. The sequences used in this study are available upon request and will be made available through NCBI GenBank in the BioProject SUB12953760 entitled "North American Astereae Genome Skimming project."

RESULTS & DISCUSSION

The chloroplast phylogeny (Figure 4 & Figure 5) obtained from the analysis of a combination of previously unpublished chloroplast genomes and data from NCBI GenBank, confirmed the monophyly of the North American Astereae *sensu* Brouillet et al. (2009) with most relationships being well-supported (>80% bootstrap support). Only two subtribes, Solidagininae *s.s.* and Machaerantherinae *s.l.*, are polyphyletic due to the placement of *Sericocarpus* Nees and *Oresotemma* Greene of the 'Eurybioid grade', respectively (Figure 4). The lineages which contain former *Haplopappus* species did not form a clade but rather indicated that these species had multiple origins, especially for the Machaerantherinae and Solidagininae. Collectively, the species once treated within *Haplopappus* are deeply polyphyletic, having several origins throughout the North American Astereae clade (Fig. 5). These results highlight the strong polyphyletic nature of *Haplopappus* as circumscribed by Hall (1928) whose species have since been segregated into several genera scattered among several subtribes. These trees collectively indicate that previous classifications have been artificial and imply that the characters previously seen as phylogenetically informative among taxa were instead homoplaseous.

The phylogenetic hypothesis presented here can be compared with previously described biogeographic patterns. For example, despite most taxa occurring within the Canada and the U.S., numerous southern migrations have occurred repeatedly. Phylogenetic data (Brouillet et al., 2009) have indicated that multiple dispersal events to Central and South America from North America have occurred within the Chrysopsidinae, Machaerantherinae *s.l.*, Solidagininae *s.l.*, and Conyzinae. *Haplopappus s.s.* of the Machaerantherinae *s.l.* represents the most diverse group whose ancestors migrated south from North America after the group first moved northwards. Other genera (*Erigeron, Eurybia,* and *Solidago*) have migrated even further back to Eurasia or even various Pacific Islands (Brouillet et al., 2009). Further, not all Astereae native to North America fall within the North American clade: *Aster* s.s. and *Baccharis* have dispersed from Eurasia and Central/ South America, respectively, into various parts of North America.

CONCLUSIONS

While great strides have been made to better understand the taxonomy of New World Astereae, there remains much to do. Uncovering the circumscription and biogeographic origin of *Haplopappus* in its modern sense based on molecular phylogenetic data represents considerable progress from treatments published a century ago. Resolving taxonomic issues could not have been done properly without dozens of researchers carefully measuring morphological traits, counting chromosomes, and sequencing genetic material, all to understand how the Astereae have evolved. Efforts to elucidate monophyletic lineages and establish an appropriate taxonomic classification, particularly in Solidagininae *s.s.* and Machaerantherinae *s.l.*, will continue to require thorough work which has been increasingly guided by high-throughput sequence data.

ACKNOWLEDGMENTS

I thank Kurt Neubig and Lowell Urbatsch for providing resources and mentorship towards the production of the chloroplast genomes used in this article. Oscar Vargas, Edgardo Ortiz, and Beryl Simpson generated nearly all of the outgroup chloroplast genomes incorporated here from the South American Astereae lineages which were available via GenBank. I also thank Lowell Urbatsch and an anonymous reviewer for comments and suggestions on the manuscript. Special thanks go to Richard Abbott, Matt Berger, Richard Bunn, Catalina Chappuzeau, Gwen Fish, Omar Javier López Gómez, Orlando Montes, Keir Morse, Nodora Moyano, Nicolas Olejnik, Eitel Pinto, Matt Reala, Charif Tala, James Thomas, Jim Tietz, Peter Zika, and Zona Norte de Quilpué who granted permission to use their photographs from iNaturalist.

LITERATURE CITED

Akram, M., Wang, X., Hu, W., Xiong, J., Zhang, Y., Deng, Y., Ran, J. & Deng, J. 2020. Convergent variations in the leaf traits of desert plants. *Plants* 9: 990.

Anderson, L. 1980. *Haplopappus alpinus* (Asteraceae): A new species from Nevada. *Great Basin Naturalist* 40: 73-77.

Anderson, L. 1983. *Haplopappus crispus* and *H. zionis* (Asteraceae): A new species from Utah. *Great Basin Naturalist* 43: 358-364.

Billings, W. 1974. Adaptations and origins of alpine plants. *Arctic Alpine Res.* 6: 129-142.

Billings, W. & Mooney, H. 1968. The ecology of arctic and alpine plants. *Biol. Rev. Cambridge Philos. Soc.* 43: 481-529.

Blake, S. 1922. New Asteraceae from Utah and Nevada. *Proc. Biol. Soc. Washington* 35: 173-178.

Blake, S. 1932. New Central American Asteraceae collected by H. H. Bartlett. *J. Wash. Acad. Sci.* 22: 382-383.

Brouillet, L., Lowrey, T., Urbatsch, L., Wagstaff, S., Karaman-Castro, V., Sancho, G. & Semple, J. 2009. Phylogeny and evolution of the Astereae. Pp. 449 – 489, in: Funk, V.A., Susanna, A., Stuessy, T.F. & Bayer, R.J. (eds.), Systematics, evolution, and biogeography of Compositae. Vienna. International Association for Plant Taxonomy.

Brouillet, L. & Selliah, S. 2005. *Symphyotrichum pygmaeum*: Transfer of *Eurybia pygmaea* from the eurybioid grade to the subtribe Symphyotrichinae (Asteraceae: Astereae). *Sida 21:* 1633-1635.

Brown, G. & Keil, D. 1992. New combinations in *Pyrrocoma* (Asteraceae: Astereae). *Phytologia* 73: 57-58.

Cassini, A. 1828. *Dictionnaire des Sciences Naturelles* [Second edition] 56: 168-170.

Chernomor, O., Haeseler, A. & Minh, B. 2016. Terrace aware data structure for phylogenomic inference from supermatrices. *Syst. Biol.* 65: 997-1008.

Clark, W. 1979. The taxonomy of *Hazardia* (Compositae: Astereae). *Madroño* 26: 105-127.

Cronquist, A. 1947. Revision of the North American species of *Erigeron*, north of Mexico. *Brittonia* 6: 121-300.

Dorn, R. 1977. *Manual of the vascular plants of Wyoming: Equisetaceae to Grossulariaceae*. Garland Publishing.

Dorn, R 1988. *Vascular plants of Wyoming*. Mountain West Publishing.

Doyle, J. & Doyle, E. 1987. Preservation of plant samples for DNA restriction endonuclease analysis. *Taxon* 36(4): 715–722.

Gray, A. 1868. Characters of new plants of California and elsewhere, principally of those collected by H. N. Bolander in the State Geological Survey. *Proc. Amer. Acad. Arts* 7: 327-401.

Gray, A. 1873. Notes on Compositae and characters of certain genera and species. *Proc. Amer. Acad. Arts* 9: 187-218.

Gray, A. 1880. Contributions to North American botany. *Proc. Amer. Acad. Arts* 16: 78-108.

Gray, A. 1884. *Caprifoliaceae - Compositae. Synoptical Flora of North America* 1(2). Washington. Smithsonian Institution.

Greene, E. 1885. Studies in the Botany of California and parts adjacent II. *Bull. Calif. Acad. Sci.* 1(4A): 179-275.

Hall, H. 1928. *The Genus* Haplopappus: *A Phylogenetic Study in the Compositae.* United States, Carnegie Institution of Washington.

Hartman, R. 2006. *Xanthisma* In: Flora of North America Editorial Committee. Flora of North America North of Mexico [Online]. New York and Oxford. Vol. 20. http://beta.floranorthamerica.org/Xanthisma

He, J., Lyu, R., Luo, Y., Lin, L., Yao, M., Xiao, J., Xie, L., Wen, J., Pei, L., Yan, S., Cheng, J., Li, J. & Li, L. 2021. An updated phylogenetic and biogeographic analysis based on genome skimming data reveals convergent evolution of shrubby habit in *Clematis* in the Pliocene and Pleistocene. *Molec. Phylogen. Evol.* 164: 107259.

Hoang, D., Chernomor, O. Haeseler, A., Minh, B. & Vinh, L. 2018. UFBoot2: Improving the ultrafast bootstrap approximation. *Molec. Biol. Evol.* 35: 518–522.

Hughes, C. & Atchison, G. 2015. The ubiquity of alpine plant radiations: from the Andes to the Hengduan Mountains. *New Phytol.* 207: 275-282.

Kartesz, J. & Gandhi, K. 1991a. A natural intergeneric hybrid in the x = 6 group of the Astereae (Asteraeeae). *Sida* 14: 321-329.

Kartesz, J. & Gandhi, K. 1991b. Nomenclatural notes for the North American flora. VI. *Phytologia* 7 I: 58-65.

Kartesz, J. 1994. *A synonymized checklist of the vascular flora of the United States, Canada, and Greenland*. Timber Press, Portland, OR.

Katoh, K., Rozewicki, J. & Yamada, K. 2018. MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. *Brief. Bioinform.* 20: 1160–1166.

Lane, M. 1993. *Lsocoma*. Pp. 294-295, in: J. C. Hickman (ed.). The Jepson manual: higher plants of California, University of California Press, Berkeley, CA.

Lane, M. & Hartman, R. 1996. Reclassification of North American *Haplopappus* (Compositae: Astereae) completed: *Rayjacksonia* gen. nov. *Amer. J. Bot.* 83: 356-370.

Markos, S. & Strother, J. 2006. *Benitoa* In: Flora of North America Editorial Committee. Flora of North America North of Mexico [Online]. New York and Oxford. Vol. 20. http://beta.floranorthamerica.org/Benitoa

Mayes, R. 1976. *A cytotaxonomic and chemosystematic study of the genus* Pyrrocoma (Asteraceae: Astereae). Ph.D. dissertation. University of Texas. Austin, TX.

Miller, M., Schwartz, T., Pickett, B., He, S., Klem, E., Scheuermann, R., Passarotti, M., Kaufman, S. & Oleary, M. 2015. A RESTful API for access to phylogenetic tools via the CIPRES science gateway. *Evol. Bioinform.* 11: 43–48.

Mulroy, T. & Rundel, P. 1977. Annual plants: adaptations to desert environments. *Biosciences* 27(2): 109-114.

Morgan, D. 1990. *A systematic study of* Machaeranthera *(Asteraceae) and related groups using restriction analysis of chloroplast DNA and a taxonomic revision of* Machaeranthera *section* Psilactis. The University of Texas at Austin.

Morgan. D. 2003. nrDNA external transcribed spacer (ETS) sequence data, reticulate evolution, and the systematics of *Machaeranthera* (Asteraceae). *Syst. Bot.* 28: 179-190.

Morgan, D., Korn, R. & Mugleston, S. 2009. Insights into reticulate evolution in Machaerantherinae (Asteraceae: Astereae): 5S ribosomal RNA spacer variation, estiamting support for incongruence, and constructing reticulate phylogenies. *Amer. J. Bot.* 96: 920-932.

Nesom, G. 1989. A new combination in *Stenotus* (Compositae: Astereae). *Phytologia* 67: 113-114.

Nesom, G. 1991a. Taxonomy of *Isocoma* (Compositae: Astereae). *Phytologia* 70: 69-114.

Nesom, G. 1991b. Transfer of *Heterotheca bartlettii* to *Osbertia* (Asteraceae: Astereae). *Phytologia* 71: 132-135.

Nesom, G. 1991c. Redefinition of *Hesperodoria* (Asteraceae: Astereae) and the segregation of *Columbiadoria*, a new monotypic genus from the western United States. *Phytologia* 71: 244-251.

Nesom, G. 2006. *Croptilon*. In: Flora of North America Editorial Committee. Flora of North America North of Mexico [Online]. New York and Oxford. Vol. 20. http://beta.floranorthamerica.org/Croptilon

Nesom, G. 2007. Notes on the disarticulation of *Xylothamia* (Asteraceae: Astereae). *Journal of the Botanical Research Institute of Texas* 1(1): 145-148.

Nesom, G. 2018. *Aquilula* (Asteraceae: Astereae), a new genus for *Ericameria riskindii. Phytoneuron* 2018-24: 1-11.

Nesom, G. 2020a. Revised subtribal classification of Astereae (Asteraceae). *Phytoneuron* 2020-53: 1–39.

Nesom, G. 2020b. *Toiyabea* (Asteraceae: Astereae) enlarged to include four species. *Phytoneuron* 2020-10: 1-24.

Nesom, G. 2021. Two new North American genera segregated from *Hazardia* (Asteraceae: Astereae). *Phytoneuron* 2021- 39: 1–36.

Nesom, G. & Baird, G. 1993. Completion of *Ericameria* (Asteraceae: Astereae), diminution of *Chrysothamnus. Phytologia* 75: 74-93.

Nesom, G. & Baird, G. 1995. Comments on "The *Chrysothamnus-Ericameria* connection." *Phytologia* 78: 61-65.

Nesom, G. & Morgan, D. 1990. Reinstatement of *Tonestus* (Asteraceae: Astereae). *Phytologia* 68: 174-180.

Nesom, G. & Robinson, H. 2007. Astereae. Pp. 316 – 376. in: J. W. Kadereit & C. Jeffrey (eds), Families and Genera of Vascular Plants vol. 8. Flowering Plants — Eudicots — Asterales, Springer-Verlag, Berlin.

Nesom, G., Suh, Y., Morgan, D. & Simpson, B. 1990. *Xylothamia* (Asteraceae: Astereae), a new genus related to *Euthamia. Sida* 14: 101-116.

Neubig, K., Whitten, W., Abbott, J., Richard Elliott, S., Soltis, D. & Soltis, P. 2014. Variables affecting DNA preservation in archival plant specimens. Pp. 81–136, in: *DNA banking for the 21st century: Proceedings of the US Workshop on DNA Banking*. Missouri Botanical Garden, St. Louis, Missouri, USA: William L. Brown Center.

Nguyen, L., Schmidt, H., Von Haeseler, A. & Minh, B. 2015. IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molec. Biol. Evol.* 32: 268–274.

Rambaut, A. 2018. FigTree v1.4.4. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh. http://tree.bio.ed.ac.uk/software/figtree/

Roberts, R. 2002. *Phylogeny of* Ericameria, Chrysothamnus *and related genera (Asteraceae: Astereae) based on nuclear ribosomal DNA sequence data*. Louisiana State University and Agricultural & Mechanical College.

Roberts, R. & Urbatsch, L. 2003. Molecular phylogeny of *Ericameria* (Asteraceae, Astereae) based on nuclear ribosomal 3' ETS and ITS sequence data. *Taxon* 52: 209-228.

Roberts, R. & Urbatsch, L. 2004. Molecular phylogeny of *Chrysothamnus* and related genera (Asteraceae, Astereae) based on nuclear ribosomal 3' ETS and ITS sequence data. *Syst. Bot.* 29: 199-215.

Selliah, S. 2010. *The molecular phylogeny of the North American genus* Eurybia *(Asteraceae: Astereae) and its close relatives (*Oreostemma, Herrickia, Triniteurybia*).* University of Montreal. Department of Biological Sciences.

Selliah, S. & Brouillet, L. 2008. Molecular phylogeny of the North American eurybioid asters (Asteraceae, Astereae) based on the nuclear ribosomal internal and external transcribed spacers. *Botany* 86(8): 901-915.

Smith, E. 1981. New combinations in *Croptilon* (Compositae: Astereae). *Sida* 9: 59-63.

Suh, Y. & Simpson, B. 1990. Phylogenetic analysis of chloroplast DNA in North American *Gutierrezia* and related genera (Asteraceae: Astereae). *Syst. Bot.* 15: 660-670.

Thiers, B. 2023. *Index Herbariorum*: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/ (last accessed March 2023).

Turner, B. & Hartman, L. 1976. Infraspecific categories of *Machaeranthera pinnatifida* (Compositae). *Wrightia* 5: 308-315.

Urbatsch, L., Roberts, R. & Karaman, V. 2003. Phylogenetic evaluation of *Xylothamia, Gundlachia,* and related genera (Asteraceae, Astereae) based on ETS and ITS nrDNA sequence data. *Amer. J. Bot.* 90: 634-649.

Urbatsch, L., Roberts, R. & Neubig, K. 2005. *Cuniculotinus* and *Lorandersonia*, two new genera of Asteraceae: Astereae and new combinations in *Chrysothamnus*. *Sida 21*: 1615-1632.

Urbatsch, L., Anderson, L., Roberts, R. & Neubig, K. 2006. *Ericameria*. In: Flora of North America Editorial Committee. Flora of North America North of Mexico [Online]. New York and Oxford. Vol. 20. http://beta.floranorthamerica.org/Ericameria

Vargas, O., Edgardo M. & Simpson, B. 2017. Conflicting phylogenomic signals reveal a pattern of reticulate evolution in a recent high-Andean diversification (Asteraceae: Astereae: *Diplostephium*). *New Phytol.* 214: 1736-1750.

APPENDIX

North American Astereae samples, including outgroups from NCBI GenBank, that were used to generate chloroplast genome assemblies. The South American Astereae data were largely taken from Vargas et al. 2017. Multiple specimens used here have not been given formal herbaria accession numbers or digitized yet. GenBank Accession numbers will be deposited in the NCBI GenBank within Bio Project SUB12953760.

Species	Voucher
Acamptopappus shockleyi A.Gray	Lane 3072 (COLO01182724)
Acamptopappus sphaerocephalus A.Gray	Beck s.n. (ASC00063004)
Almutaster pauciflorus (Nutt.) Á.Löve & D.Löve	Sundberg 2568 (Unknown)
Amphiachyris amoena (Shinners) Solbrig	Nesom 7742 (TEX00211062)
Amphipappus fremontii Torr. & A.Gray	Gierisch 4221 (ASC00047356)
Ampelaster carolinianus (Walter) G.L.Nesom	Sundberg 2294 (Unknown)
Aquilula riskindii (B.L.Turner & G.E.Langford) G.L.Nesom	Nesom 7697 (TEX00139365)
Archibaccharis asperifolia S.F.Blake	Olazo 1192 (TEX449024)
Aster alpinus var. vierhapperi (Onno) Cronquist	Weber 18495 (COLO00046375)
Astranthium ciliatum (Raf.) G.L.Nesom	Rosen 3607 (TEX00442205)
Aztecaster matudae (Rzed.) G.L.Nesom	Hinton 29102 (TEX452243)
Baccharis genistelloides (Lam.) Pers.	Vargas 358 (HUSA s.n.)
Baccharis halimifolia L.	Urbatsch 10186 (LSU00133981)
Baccharis tricuneata Pers.	Vargas 356 (HUSA s.n.)
Bigelowia nudata (Michx.) DC.	Abbott 23624 (FLAS227170)
Blakiella bartsiifolia (S.F.Blake) Cuatrec.	Cuatrecasas 28129 (TEX s.n.)
Boltonia asteroides var. recognita (Fernald & Griscom) Cronquist	Swayne 110 (Unknown)
Brintonia discoidea (Elliott) Greene	Urbatsch 11540 (LSU00179297)
Canadanthus modestus (Lindl.) G.L.Nesom	Semple 10290 (LSU00134614)
Chaetopappa ericoides (Torr.) G.L.Nesom	Carr 30166 (MO s.n.)
Chihuahuana purpusii (Brandegee) Urbatsch & R.P.Roberts	Johnson 12105 (LSU s.n.)
Chrysoma pauciflosculosa Greene	Urbatsch 8015 (LSU00061087)
Chrysopsis linearifolia subsp. linearifolia Semple	Abbott 23545 (FLAS227171)
Chrysothamnus depressus Nutt.	Urbatsch 7916 (LSU00179306)
Chrysothamnus eremobius L.C.Anderson	Smith 3745 (UTC00227344)
Chrysothamnus greenei Greene	Urbatsch 7965 (LSU00076515)
Chrysothamnus humilis Greene	Tiehm 9309 (DES00028726)
Chrysothamnus molestus (S.F.Blake) L.C.Anderson	Urbatsch 7963 (LSU s.n.)
Chrysothamnus scopulorum (M.E.Jones) Urbatsch, R.P.Roberts & Neubig	Welsh 24648 (NY2905944)
Chrysothamnus stylosus (Eastw.) Urbatsch, R.P.Roberts & Neubig	Urbatsch 7627 (LSU00063484)
Chrysothamnus vaseyi Greene	Urbatsch 7914 (LSU00179296)
Chrysothamnus viscidiflorus Nutt.	Urbatsch 11062 (LSU00137506)
Chrysothamnus viscidiflorus Nutt.	Urbatsch 11064 (LSU00137508)
Columbiadoria hallii (A.Gray) G.L.Nesom	Urbatsch 7692 (LSU00061150)
Cuniculotinus gramineus (H.M.Hall) Urbatsch, R.P.Roberts & Neubig	Urbatsch 7941 (LSU00177491)
Dichaetophora campestris A.Gray	Lievens 2 (LSU00061061)
Diplostephium barclayanum Cuatrec.	Vargas 477 (QCA s.n.)
Diplostephium callilepis S.F.Blake	Vargas 376 (HUSA s.n.)
Diplostephium crypteriophyllum Cuatrec.	Vargas 467 (QCA s.n.)
Diplostephium ericoides (Lam.) Cabrera	Vargas 489 (QCA s.n.)
Diplostephium foliosissimum S.F.Blake	Sagastegui 16804 (F s.n.)
Diplostephium gnidioides S.F.Blake	Vargas 430 (HUSA s.n.)
Diplostephium gynoxyoides Cuatrec.	Vargas 395 (HUSA s.n.)
Diplostephium hartwegii Hieron.	Vargas 456 (QCA s.n.)
Diplostephium jelskii Hieron.	Cano 14716 (USM s.n.)
Diplostephium lechleri Wedd.	Vargas 381 (HUSA s.n.)
Diplostephium oblanceolatum S.F.Blake	Vargas 465 (QCA s.n.)
Diplostephium pulchrum S.F.Blake	Vargas 404 (HUSA s.n.)
Diplostephium serratifolium Cuatrec.	Sagastegui 16159a (F s.n.)
Doellingeria sericocarpoides Small	Urbatsch 7774 (LSU00032463)
Eastwoodia elegans Brandegee	Urbatsch 12124 (LSU00181276)
Egletes viscosa dissecta Shinners	Roberts 10170 (Unknown)

APPENDIX (CONT.)

Species	Voucher
Ericameria arborescens (A.Gray)Greene	Keil 35389 (OBI s.n.)
Ericameria albida (M.E.Jones ex A.Gray) L.C.Anderson	Urbatsch 7670 (LSU00076170)
Ericameria arizonica R.P.Roberts, Urbatsch & J.Anderson	Crawford 576 (ASC00111045)
Ericameria bloomeri J.F.Macbr.	Urbatsch 7719 (LSU00072800)
Ericameria brachylepis H.M.Hall	Urbatsch 1402 (LSU00209223)
Ericameria brachylepis H.M.Hall	Urbatsch 7090 (LSU00061455)
Ericameria cervina Rydb.	Atwood 13509 (BRYV0250964)
Ericameria cervina Rydb.	Urbatsch 7662 (LSU00179274)
Ericameria compacta (H.M.Hall) G.L.Nesom	Urbatsch 7940 (LSU00076490)
Ericameria cooperi H.M.Hall	Keil 2404 (LSU00061281)
Ericameria cooperi H.M.Hall	Urbatsch 12140 (LSU00181259)
Ericameria cuneata McClatchie	Urbatsch 7092 (LSU00078980)
Ericameria cuneata McClatchie	Urbatsch 7957 (LSU00076491)
Ericameria discoidea (Nutt.) G.L.Nesom	Urbatsch 7654 (LSU00072798)
Ericameria ericoides (Less.) Nutt. ex Jeps.	Keil 10983 (Unknown)
Ericameria fasciculata J.F.Macbr.	Griffin 3963 (Unknown)
Ericameria gilmanii (S.F.Blake) G.L.Nesom	Urbatsch 7948 (LSU00076493)
Ericameria juarezensis (Moran) Urbatsch	Moran 22986 (ASU0017213)
Ericameria laricifolia (A.Gray) Shinners	Urbatsch 1120 (LSU00061374)
Ericameria linearifolia (DC.) Urbatsch & Wussow	Moran 21245 (LSU00179250)
Ericameria martirensis Wiggins	Anderson 4695 (LSU00179260)
Ericameria nana Nutt.	Urbatsch 11073 (LSU00137633)
Ericameria nauseosa (Pursh) G.L.Nesom & G.I.Baird	Urbatsch 10368 (LSU00131738)
Ericameria nauseosa (Pursh) G.L.Nesom & G.I.Baird	Urbatsch 11061 (LSU00137505)
Ericameria nauseosa (Pursh) G.L.Nesom & G.I.Baird	Urbatsch 7722 (LSU00179266)
Ericameria nauseosa var. graveolens (Nutt.) Reveal & Schuyler	Urbatsch 11168 (LSU00137620)
Ericameria obovata (Rydb.) G.L.Nesom	Jones s.n. (NY2076226)
Ericameria obovata (Rydb.) G.L.Nesom	Urbatsch 11079 (LSU00137522)
Ericameria palmeri H.M.Hall	Urbatsch 1105 (LSU00061436)
Ericameria palmeri H.M.Hall	Urbatsch 1106 (LSU00061438)
Ericameria paniculata A.Gray ex Rydb.	Scott 894 (ASC00052925)
Ericameria parishii H.M.Hall	Urbatsch 7082 (LSU00072950)
Ericameria parryi (A.Gray) G.L.Nesom & G.I.Baird	Urbatsch 7931 (LSU00179304)
Ericameria pinifolia H.M.Hall	Urbatsch 7084 (LSU00072951)
Ericameria resinosa Nutt.	Urbatsch 7690 (LSU00076500)
Ericameria sp.	Goorich 28687 (LSU00179347)
Ericameria sp.	Urbatsch 11162 (LSU00137614)
Ericameria suffruticosa (Nutt.) G.L.Nesom	Anderson 4887 (BRYV0251717)
Ericameria teretifolia Jeps.	Urbatsch 7955 (LSU00076501)
Ericameria watsonii (A.Gray) G.L.Nesom	Semple s.n. (LSU00061461)
Ericameria watsonii (A.Gray) G.L.Nesom	Urbatsch 7661 (LSU00179267)
Ericameria winwardii (Dorn & Delmatier) R.P.Roberts & Urbatsch	Windward s.n. (BRYV0048789)
Ericameria zionis (L.C.Anderson) G.L.Nesom,	Urbatsch 7922 (LSU00076504)
Erigeron annuus (L.) Pers.	Unknown (Unknown)
Erigeron bonariensis L.	Unknown (Unknown)
Erigeron breviscapus (Vaniot) Hand.-Mazz.	Unknown (Unknown)
Erigeron breviscapus (Vaniot) Hand.-Mazz.	Unknown (Unknown)
Erigeron canadensis L.	Unknown (Unknown)
Erigeron multiradiatus (Lindl. ex DC.) Benth. & Hook.f.	Unknown (Unknown)
Erigeron vernus (L.) Torr. & A.Gray	Abbott 22381 (Unknown)
Euthamia caroliniana (L.) Greene ex Porter & Britton	Singhurst 15467 (TEX s.n.)
Euthamia caroliniana (L.) Greene ex Porter & Britton	Urbatsch 10780 (LSU00132487)
Euthamia caroliniana (L.) Greene ex Porter & Britton	Urbatsch 11263 (LSU00176929)
Euthamia galetorum Greene	Peck s.n. (ECS029490)
Euthamia galetorum Greene	Smith 7079 (ACAD25860)
Euthamia graminifolia (L.) Nutt.	Szubryt 748 (SIU s.n.)
Euthamia graminifolia (L.) Nutt.	Urbatsch 11019 (LSU00135092)

APPENDIX (CONT.)

Species	Voucher
Euthamia graminifolia (L.) Nutt.	Urbatsch 11220 (LSU00137682)
Euthamia graminifolia (L.) Nutt.	Urbatsch 12167 (LSU s.n.)
Euthamia graminifolia var. tricostata	Brinkman 2529 (US s.n.)
Euthamia gymnospermoides Greene	Reznicek 11027 (MICH1217633)
Euthamia gymnospermoides Greene	Szubryt 52 (SIU s.n.)
Euthamia gymnospermoides Greene	Urbatsch 10809 (LSU00179333)
Euthamia gymnospermoides Greene	Urbatsch 10818 (LSU00134804)
Euthamia gymnospermoides Greene	Urbatsch 12111 (LSU00132485)
Euthamia hirtipes (Fernald) Sieren	Abbott 23380 (FLAS s.n.)
Euthamia hirtipes (Fernald) Sieren	Bell 5291 (NCU00101509)
Euthamia hirtipes (Fernald) Sieren	Szubryt 1 (LSU00179178)
Euthamia leptocephala (Torr. & A.Gray) Greene ex Porter & Britton	Szubrt 630 (LSU00181294)
Euthamia leptocephala (Torr. & A.Gray) Greene ex Porter & Britton	Urbatsch 10790 (LSU00132500)
Euthamia leptocephala (Torr. & A.Gray) Greene ex Porter & Britton	Urbatsch 11212 (LSU00137674)
Euthamia occidentalis Nutt.	Nickrent s.n. (SIU s.n.)
Euthamia occidentalis Nutt.	Urbatsch 7724 (LSU90061862)
Euthamia pulverulenta Greene	Reid 9000 (LSU00139903)
Euthamia scabra Greene	Szubryt 809 (LSU00218467)
Euthamia scabra Greene	Szubryt 98 (SIU s.n.)
Euthamia scabra Greene	Urbatsch 10738 (LSU132431)
Euthamia scabra Greene	Urbatsch 10781 (LSU00132488)
Euthamia scabra Greene	Urbatsch 10784 (LSU00132490)
Euthamia scabra Greene	Urbatsch 10799 (LSU00132516)
Euthamia sp.	Urbatsch 11231 (LSU00176941)
Euthamia sp.	Urbatsch 11236 (LSU00176966)
Euthamia remota Greene	Penskar 1272 (MICH1477521)
Euthamia remota Greene	Urbatsch 11129 (LSU00137581)
Exostigma notobellidiastrum (Griseb.) G.Sancho	Tressens 6388 (TEX s.n.)
Geissolepis suaedifolia B.L.Rob.	Nesom 6634 (ASU0018083)
Grindelia squarrosa (Pursh) Dunal	Szubryt 347 (SIU s.n.)
Gundlachia corymbosa (Urb.) Britton ex Bold.	Keil 16562 (OBI168747)
Gundlachia diffusa (Benth.) Urbatsch & R.P.Roberts	Nash 19640 (LSU00179281)
Gundlachia triantha (S.F.Blake) Urbatsch & R.P.Roberts	Cole 3942 (Unknown)
Gundlachia truncata (G.L.Nesom) Urbatsch & R.P.Roberts	Nesom 5254 (TEX00373677)
Gutierrezia alamanii A.Gray	Bye 8236 (SDS104171)
Gutierrezia californica (DC.) Torr. & A.Gray	Rebman 3037 (SDS139343)
Gutierrezia microcephala (DC.) A.Gray	Murray 1003 (LSU00062063)
Gutierrezia pomariensis (S.L.Welsh) S.L.Welsh	Urbatsch 1337 (LSU00062045)
Gutierrezia ramulosa (Greene) M.A.Lane	Sanders 6408 (SDS124908)
Gutierrezia sarothrae (Pursh) Britton & Rusby	Urbatsch 10386 (LSU00062052)
Gutierrezia texana (DC.) Torr. & A.Gray	Lane 1957 (LSU00062059)
Gymnosperma glutinosum Less.	Urbatsch 3012 (LSU00041279)
Haplopappus macraeanus A.Gray	Gray s.n. (TEX00382772)
Hazardia detonsa Greene	Urbatsch 12150 (LSU s.n.)
Herrickia glauca (Nutt.) Brouillet	Urbatsch 11088 (LSU00137531)
Heterothalamus alienus (Spreng.) Kuntze	Wurdack 20385 (TEX00532276)
Heterotheca subaxillaris (Lam.) Britton & Rusby	Szubryt 770 (LSU00218374)
Hinterhubera ericoides Wedd.	Stergios 20385 (TEX532276)
Ionactis linariifolia (L.) Greene	Abbott 23572 (FLAS233185)
Isocoma acradenia Greene	Tiehm s.n. (Unknown)
Isocoma menziesii (Hook. & Arn.) G.L.Nesom	Urbatsch 12143 (LSU00181263)
Kalimeris altaica Nees ex Fisch., C.A.Mey. & Avé-Lall.	Unknown (Unknown)
Laennecia sophiifolia (Kunth) G.L.Nesom	Reina 2010-805 (TEX s.n.)
Linochilus apiculatus (S.F.Blake) Saldivia & O.M.Vargas	Vargas 332 (ANDES s.n.)
Linochilus colombianus (Cuatrec.) Saldivia & O.M.Vargas	Vargas 299 (ANDES s.n.)
Linochilus floribundus Benth.	Vargas 499 (ANDES s.n.)
Linochilus huertasii (Cuatrec.) Saldivia & O.M.Vargas	Vargas 518 (ANDES s.n.)

APPENDIX (CONT.)

Species	Voucher
Linochilus juajibioyi (Cuatrec.) Saldivia & O.M.Vargas	Vargas 504 (ANDES s.n.)
Linochilus obtusus (S.F.Blake) Saldivia & O.M.Vargas	Dorr 9246 (US s.n.)
Linochilus rhododendroides (Hieron.) Saldivia & O.M.Vargas	Vargas 233 (ANDES s.n.)
Linochilus rupestris (Kunth) Saldivia & O.M.Vargas	Vargas 504 (ANDES s.n.)
Linochilus venezuelensis (Cuatrec.) Saldivia & O.M.Vargas	Norrbom 89V33 (US s.n.)
Llerasia caucana (S.F.Blake) Cuatrec.	Vargas 444 (ANDES s.n.)
Lorandersonia baileyi (Wooton & Standl.) Urbatsch, R.P.Roberts & Neubig	Urbatsch 7970 (LSU00076523)
Lorandersonia linifolia (Greene) Urbatsch, R.P.Roberts & Neubig	Urbatsch 11068 (LSU00137512)
Lorandersonia microcephala (Cronquist) Urbatsch, R.P.Roberts & Neubig	Fletcher 7145 (Unknown)
Lorandersonia microcephala (Cronquist) Urbatsch, R.P.Roberts & Neubig	Lightfoot 22 (Unknown)
Lorandersonia pulchella (A.Gray) Urbatsch, R.P.Roberts & Neubig	Urbatsch 7973 (LSU00179288)
Lorandersonia salicina (S.F.Blake) Urbatsch, R.P.Roberts & Neubig	Urbatsch s.n. (LSU s.n.)
Lorandersonia spathulata (L.C.Anderson) Urbatsch, R.P.Roberts & Neubig	Urbatsch 7983 (LSU00076527)
Machaeranthera tanacetifolia (Kunth) Nees	Szubryt 1000 (LSU00218241)
Monoptilon bellioides H.M.Hall	Hemkamp 2856 (LL s.n.)
Neonesomia palmeri (A.Gray) Urbatsch & R.P.Roberts	Urbatsch 3043 (LSU00179257)
Nestotus macleanii (Brandegee) R.P.Roberts, Urbatsch & Neubig	Culder 24968 (UAL27425)
Nestotus stenophyllus (A.Gray) R.P.Roberts, Urbatsch & Neubig	Atwood 13554 (OSC s.n.)
Noticastrum acuminatum (DC.) Cuatrec.	Tressens 6592 (LSU s.n.)
Oclemena reticulata (Pursh) G.L.Nesom	Abbott 22505 (Unknown)
Oreochrysum parryi Rydb.	Urbatsch 7934 (LSU00179302)
Oreostemma alpigenum (Torr. & A.Gray) Greene	Urbatsch 7704 (LSU00062348)
Oritrophium peruvianum (Lam.) Cuatrec.	Vargas 448 (ANDES s.n.)
Parastrephia quadrangularis (Meyen) Cabrera	Vargas 440 (HUSA s.n.)
Pentachaeta exilis (A.Gray) A.Gray	Taylor 15980 (ARIZ432594)
Petradoria pumila (Nutt.) Greene	Urbatsch 11077 (LSU00137520)
Pityopsis falcata Nutt.	Unknown (Unknown)
Psilactis asteroides A.Gray	Stuessy 980 (TEX00138733)
Rayjacksonia phyllocephala DC.	Szubryt 774 (LSU00218375)
Rigiopappus leptocladus A.Gray	Tiehm 1123 (LSU00062449)
Sericocarpus tortifolius Nees	Urbatsch 11432 (LSU00178890)
Solidago decurrens Lour.	Unknown (Unknown)
Solidago rugosa Mill.	Abbott 23610 (MO100795087)
Solidago sp.	Vanderpool 429 (STAR014693)
Stenotus acaulis (Nutt.) Nutt.	Evert 16458 (RM577351)
Stenotus armerioides Nutt.	Nelson 35157 (LSU00116961)
Stenotus lanuginosus Greene	Evert 8019 (Unknown)
Stenotus pulvinatus (Moran) G.L.Nesom	Rebman 4159 (UCR s.n.)
Symphyotrichum dumosum (L.) G.L.Nesom	Abbott 23667 (FLAS s.n.)
Symphyotrichum subulatum (Michx.) G.L.Nesom	Unknown (Unknown)
Thurovia triflora Rose	Rosen 6165 (TEX00466706)
Toiyabea alpina (L.C.Anderson & Goodrich) R.P.Roberts, Urbatsch & Neubig	Tiehm 14043 (UTC00162139)
Tonestus eximius A.Nelson & J.F.Macbr.	Matson s.n. (LSU00063473)
Tonestus graniticus (Tiehm & L.M.Shultz) G.L.Nesom & D.R.Morgan	Tiehm 15338 (NY1153651)
Tonestus lyallii A.Nelson	Pojar s.n. (LSU00063476)
Tonestus peirsonii (D.D.Keck) G.L.Nesom & D.R.Morgan	Urbatsch 9258 (LSU00179176)
Tonestus pygmaeus A.Nelson	Hartman 69602 (LSU00063479)
Townsendia exscapa (Richardson) Porter	Rosche 75 (Unknown)
Tracyina rostrata S.F.Blake	Orndulb 10106 (UWL274773)
Triniteurybia aberrans (A.Nelson) Brouillet, Urbatsch & R.P.Roberts	Urbatsch 7812 (LSU00179317)
Xanthocephalum benthamianum Hemsl.	Panero 2257A (TEX00029083)
Xanthocephalum centauroides Willd.	Lane 2452d (TEX00139179)
Xanthocephalum sericocarpum A.Gray	Hendricks 482 (Unknown)
Xanthocephalum sphaerocephalum (A.Gray) Shinners	Bollwinkel 68 (Unknown)
Xylovirgata pseudobaccharis (S.F.Blake) Urbatsch & R.P.Roberts	Urbasch 2786 (LSU00179254)

Packed with *Packera* Á. Löve & D. Löve:

Brief history of the "aureoid *Senecio*" subgroup in Senecioneae

Erika R. Moore-Pollard[1] & Jennifer R. Mandel[1]

[1] Department of Biological Sciences, University of Memphis, 3700 Walker Ave, Memphis, TN 38152, U.S.A.

Author for correspondence: Erika R. Moore-Pollard, *moore.erika.r@gmail.com*

DOI: http://dx.doi.org/10.53875/capitulum.02.2.04

ABSTRACT

Senecioneae within Compositae is a very large and complicated tribe. Once considered a tribe composed of many species in the mega-genus *Senecio* and a few smaller genera, it is now delimited to many genera with two-thirds of *Senecio* separated into newly named, smaller genera. These genera typically follow subgroup classifications originally created by taxonomists over a century ago. One of those segregate genera is *Packera*, previously known as the Aureoids or "aureoid *Senecio*" subgroup. *Packera* is a somewhat recently described genus with an estimated 64 species and varieties found exclusively in North America. Members of this group have continuously been grouped together given shared morphological and ecological characteristics. Here, we describe the history of *Packera*'s subgroup classifications as the "aureoid *Senecio*" group over the last century, how this group differs from *Senecio*, and our current understanding of this complicated genus.

Keywords: chromosome counts, classification, hybridization, pollen.

INTRODUCTION

Senecioneae, the largest tribe in Compositae, contains roughly 150 genera and 3,500 species (Mandel et al., 2019). Members of Senecioneae can be found almost everywhere in the world, with centers of diversity in temperate and subtropical arid or montane regions (Funk et al., 2009). The classic view of the tribe has been of a mega-genus *Senecio* L., along with other genera that vary in their level of distinctiveness (Barkley, 1985). Circumscription and delimitation within the tribe have been challenging because of its large size, lack of intergeneric relationship understanding, presence of conflicting morphological characters, and absence of a precise delimitation or circumscription of genus *Senecio* (Pelser et al., 2007).

Senecio is a very large (ca. 1,000 taxa) and complicated genus with a worldwide distribution. Evolutionary relationships within the group are consistently recovered as polyphyletic (i.e., Pelser et al., 2007, 2010; Panero & Funk, 2008; Funk et al., 2009; Fu et al., 2016; Mandel et al., 2019), leading some to suggest that *Senecio* could be further split into additional genera. Initially, species were lumped into the genus for convenience (ca. 3,000 taxa), though taxonomists have tried to break *Senecio* into smaller and more tractable segregate genera, or informal subgroups, for over a century (i.e., Rydberg, 1900; Greenman, 1902; Packer, 1972; Nordenstam, 1977, 1978). For example, North American *Senecio* members were organized into 22 informal subgroups by Jesse M. Greenman in 1901 (Greenman, 1902), one of those subgroups being

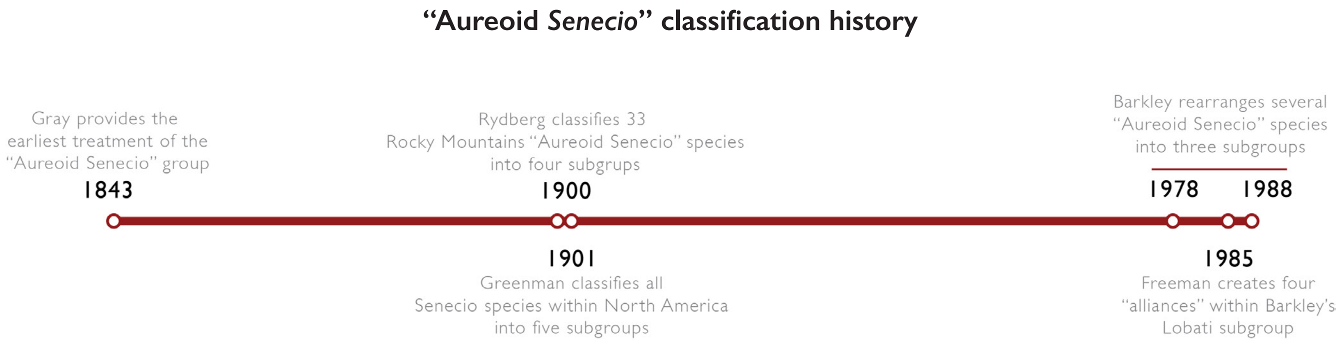


Figure 1. A timeline of "aureoid *Senecio*" subgroups classification over the last two centuries

the "aureoid *Senecios*", later segregated into *Packera* Á. Löve & D. Löve. In this article, we summarize the history of subgroup classification in *Packera* from 1843 to present. Additionally, we discuss our current understandings of this genus and the various ways it differs from *Senecio*.

THE AUREOIDS

Packera was previously included in the genus *Senecio* as the informal group known as the "aureoid *Senecios*" (or Aureoids) first recognized by Asa Gray (Gray & Torrey, 1843; Gray, 1886; Mahoney, 2000). Gray provided the earliest treatments of the group by recognizing that distinct members share most of these characters: perennial herbs arising from creeping rootstocks or a stout caudex; basal leaves well developed, cauline leaves progressively reduced upwards, leaf margins without callose denticles; roots fibrous, thin and branching; and haploid chromosome numbers of 22 or 23 (Barkley, 1988). Asa Gray, along with John Torrey, classified most of the eastern species, later known as the 'Aurei' subgroup by Theodore M. Barkley and Greenman (Greenman, 1918; Barkley, 1968), as varieties of *Senecio aureus* L. (≡*Packera aurea* (L.) Á. Löve & D. Löve; Gray and Torrey, 1843; Gray, 1886), which is also the type species of the group (Löve and Löve, 1975). These taxa consisted of *S. aureus* (with five varieties), *S. tomentosus* Michx. (=*P. dubia* (Spreng.) Trock & Mabb.), *S. canus* Hook. (≡*P. cana* (Hook.) W.A.Weber & Á.Löve), and *S. elliottii* Torr. & A.Gray (=*P. obovata* (Willd.) W.A.Weber & Á.Löve).

Subgroups of these "aureoid *Senecios*" were later proposed by P.A. Rydberg in 1900, who classified 33 of the "aureoid *Senecio*" species into four groups: 'Aureus' (=Aurei [18 species]), 'Tomentosus' (=Tomentosi [9 species]), 'Lobatus' (=Lobati [5 species]), and 'Subnudus' (=Subnudi [1 species]; Figure 1, Table 1; Rydberg, 1900). Within a year of his work, Rydberg discovered that Greenman was also working on classifying *Senecios* in North America into subgroups. Therefore, Greenman and Rydberg reached an agreement that Rydberg would only classify Rocky Mountain *Senecios* and Greenman would classify all *Senecios* within North America (Rydberg, 1900). Greenman recognized the 'Aurei' [51 species], 'Tomentosi' [30 species] and 'Lobati' [14 species] subgroups defined by Rydberg, but added two more sections: 'Bolanderi' [3 species] and 'Sanguisorboidei' [13 species] (Figure 1, Table 1; Trock, 1999).

Later, Barkley followed Greenman and others by recognizing a greater number of species (59 taxa; Rydberg, 1900; Greenman, 1918), better reflecting our current understanding of the Aureoids (Barkley, 1962, 1988). Additionally, Barkley adopted the informal species groups of Rydberg, but followed Greenman in combining the 'Subnudi' with the 'Aurei'. He also combined the 'Bolanderi' and 'Sanguisorboidei' of Greenman with the 'Lobati' and rearranged a number of species within these informal groups; resulting in three subgroups that are currently recognized today: 'Aurei' [27 species], 'Tomentosi' [15 species], and 'Lobati' [18 species] (Figure 1, Table 1; Greenman, 1902; Barkley, 1978, 1988; Freeman, 1985; Trock, 1999). Later, Freeman

The first of many

Packera aurea (L.) Á. Löve & D. Löve, one of the 64 currently recognized species of *Packera* Á. Löve & D. Löve., has a widespread distribution along the east coast of North America. Not only is it the type species of the genus, *P. aurea* is also the "type" for the 'Aurei' subgroup originally defined by Asa Gray in 1843.

Packera aurea (L.) Á. Löve & D. Löve in LaPorte County, Indiana, USA
Photo by Cassi Saari

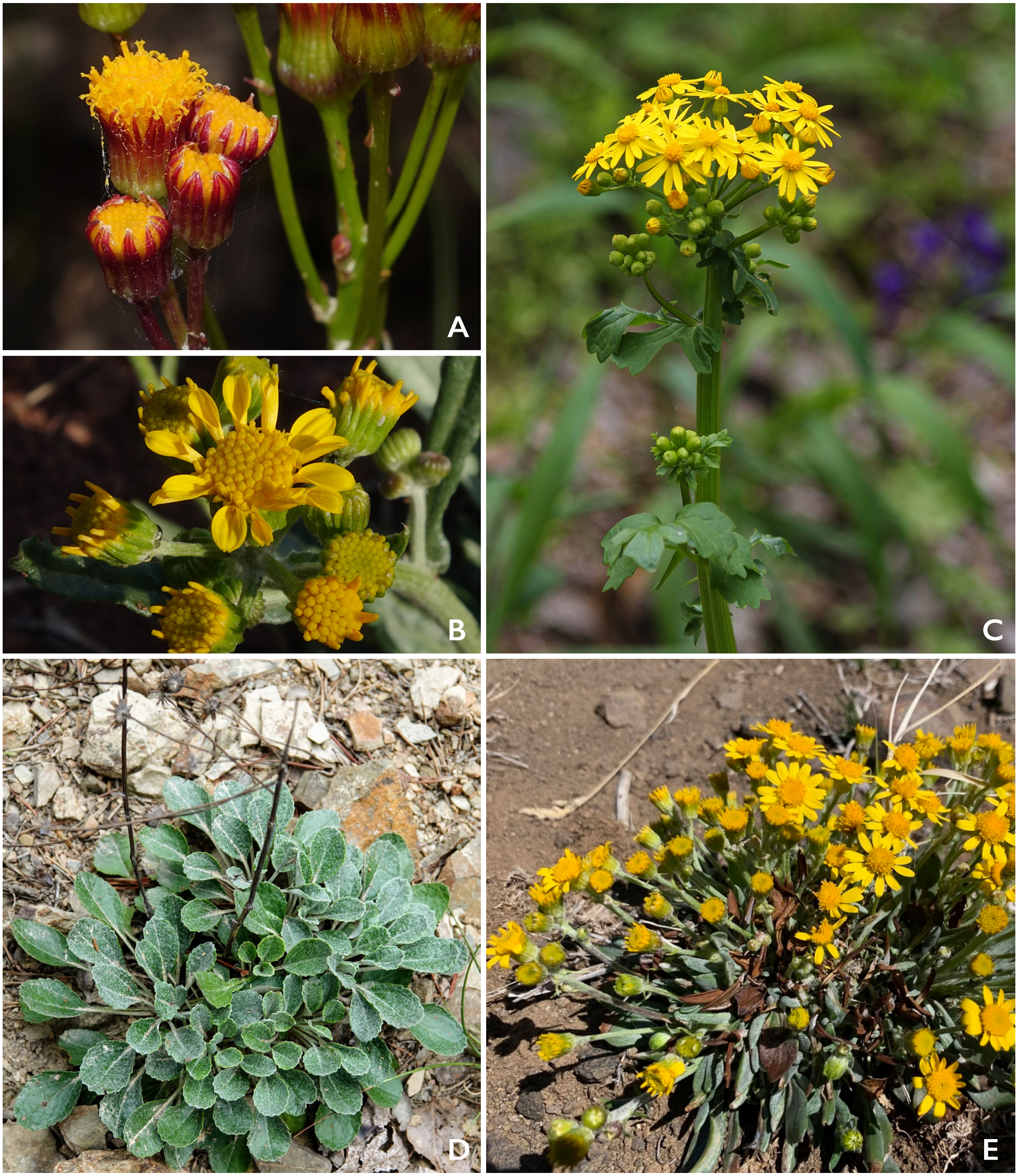


Figure 2. Species of *Packera* in North America. **A.** *P. debilis* (Nutt.) W.A.Weber & Á.Löve. **B.** *P. thurberi* (A.Gray) B.L.Turner **C.** *P. glabella* (Poir.) C.Jeffrey **D.** *P. antennariifolia* (Britton) W.A.Weber & Á.Löve **E.** *P. cana* (Hook.) W.A.Weber & Á.Löve. *Photos: A-B, E, Robert Lagier; C, Cassi Saari; D, Vida Svahnström.*

(1985) investigated members of Barkley's 'Lobati' subgroup within Mexico and created four additional groups (or 'alliances') within 'Lobati' based on morphology, ecological preferences, and distribution: 'Multilobatus', 'Millelobatus', 'Sanguisorbae', and 'Bolanderi'. A full list of the "aureoid *Senecio*" species associated with each subgroup can be found in Supplemental Table 1 on FigShare (https://figshare.com/projects/Packed_with_Packera_Brief_history_of_the_aureoid_Senecio_subgroup_in_Senecioneae/153780).

Originally, many taxonomists treated the various subgroups as formal sections (e.g., Rydberg, 1900; Greenman, 1901); however, it is best to treat them as "groups-of-convenience" since species boundaries are imprecise and are subject to re-interpretation (Barkley, 1988). In addition, phylogenetic studies of *Packera* show that the molecular data does not support the subgroupings or the hypotheses behind the groupings (Bain & Jansen, 1995; Bain & Golden, 2000). For example, Barkley (1988) predicted that the 'Aurei' subgroup would be considered

Table 1. A table summarizing "aureoid *Senecio*" subgroup classifications and their corresponding taxa from 1843 to present. All currently recognized *Packera* species, excluding varieties and hybrid taxa, are listed in the first column. Columns to the right of the species list represent a publication detailing which "aureoid *Senecio*" species were included in specified subgroups given that author and year. Subgroups are colored accordingly; if a species was considered as belonging to more than one subgroup, the block is split diagonally and contain both subgroup colors. No block in a column indicates that the species is not present in the publication. *Packera* taxa not assigned to a subgroup contain no blocks. A complete list of the "aureoid *Senecio*" taxa associated with each subgroup can be found in Supplemental Table 1 on FigShare (https://figshare.com/projects/Packed_with_Packera_Brief_history_of_the_aureoid_Senecio_subgroup_in_Senecioneae/153780).

Senecio subgroup asigned by each author on table

▒ Author did not asign group ⬛ Subnudus 🟦 Bolanderi 🟪 Sanguisorboidei 🟥 Aurei 🟧 Lobati 🟨 Tomentosi

Informal group as currently circumscribed	**Species**	**Gray** 1843	**Rydberg** 1900	**Greenman** 1901	**Barkley** 1978	**Barkley** 1988
Aurei	*Packera anonyma* (Alph.Wood) W.A.Weber & Á.Löve		🟥	🟥	🟥	🟥
	Packera aurea (L.) Á.Löve & D.Löve	▒		🟥	🟥	🟥
	Packera cardamine (Greene) W.A.Weber & Á.Löve			🟥	🟥	🟥
	Packera clevelandii (Greene) W.A.Weber & Á.Löve				🟥	🟥
	Packera crocata (Rydb.) W.A.Weber & Á.Löve		🟥	🟥	🟥	🟥
	Packera cymbalaria (Pursh) W.A.Weber & Á.Löve			🟥	🟥	🟥
	Packera debilis (Nutt.) W.A.Weber & Á.Löve		🟥	🟥	🟥	🟥
	Packera dimorphophylla (Greene) W.A.Weber & Á.Löve			🟥	🟥	🟥
	Packera ganderi (T.M.Barkley & R.M.Beauch.) W.A.Weber & Á.Löve				🟥	🟥
	Packera hartiana (A.Heller) W.A.Weber & Á.Löve			🟥	🟥	🟥
	Packera hintoniorum (B.L.Turner) C.Jeffrey					🟥
	Packera hyperborealis (Greenm.) Á.Löve & D.Löve			🟥	🟥	🟥
	Packera indecora (Greene) Á.Löve & D.Löve		🟥	🟥	🟥	🟥
	Packera layneae (Greene) W.A.Weber & Á.Löve				🟥	🟥
	Packera obovata (Willd.) W.A.Weber & Á.Löve	▒		🟥	🟥	🟥
	Packera pauciflora (Pursh) Á.Löve & D.Löve		🟥	🟥	🟥	🟥
	Packera paupercula (Michx.) Á.Löve & D.Löve		🟥	🟥	🟥	🟥
	Packera plattensis (Nutt.) W.A.Weber & Á.Löve		🟨	🟥	🟥	🟥
	Packera porteri (Greene) C.Jeffrey			🟥	🟥	🟥
	Packera pseudaurea (Rydb.) W.A.Weber & Á.Löve		🟥/🟨	🟥	🟥	🟥
	Packera quebradensis (Greenm.) W.A.Weber & Á.Löve					🟥
	Packera schweinitziana (Nutt.) W.A.Weber & Á.Löve			🟥	🟥	🟥
	Packera streptanthifolia (Greene) W.A.Weber & Á.Löve		🟥	🟥	🟥	🟥
	Packera subnuda (DC.) Trock & T.M.Barkley		⬛	🟥	🟥	🟥
	Packera thurberi (Rydb.) W.A.Weber & Á.Löve		🟥	🟥	🟥	🟥
Lobati	*Packera bolanderi* (A.Gray) W.A.Weber & Á.Löve			🟦	🟧	🟧
	Packera brewerii (Burtt Davy) W.A.Weber & Á.Löve			🟧	🟧	🟧
	Packera coahuilensis (Greenm.) C.Jeffrey			🟪		🟧
	Packera eurycephala (Torr. & A.Gray) W.A.Weber & Á.Löve			🟧	🟧	🟧
	Packera flettii (Wiegand) W.A.Weber & Á.Löve			🟦		🟧
	Packera franciscana (Greene) W.A.Weber & Á.Löve			🟧	🟧	🟧
	Packera glabella (Poir.) C.Jeffrey			🟪	🟧	🟧
	Packera millefolium (Torr. & A.Gray) W.A.Weber & Á.Löve			🟪		🟧
	Packera millelobata (Rydb.) W.A.Weber & Á.Löve		🟧	🟧	🟧	🟧
	Packera montereyana (S.Watson) C.Jeffrey			🟪	🟧	🟧
	Packera multilobata (Torr. & A.Gray) W.A.Weber & Á.Löve		🟧/🟨	🟧		🟧
	Packera quercetorum (Greene) C.Jeffrey			🟨	🟧	🟧
	Packera rosei (Greenm.) W.A.Weber & Á.Löve			🟥	🟧	🟥/🟧
	Packera sanguisorbae (DC.) C.Jeffrey			🟪		🟧
	Packera sanguisorboides (Rydb.) W.A.Weber & Á.Löve		🟧	🟪		🟧
	Packera scalaris var. scalaris (Greene) C.Jeffrey				🟧	🟧
	Packera tampicana (DC.) C.Jeffrey		🟧	🟪		🟧
	Packera zimapanica (Hemsl.) C.C.Freeman & T.M.Barkley			🟪		🟧

Table 1. (cont.) A table summarizing "aureoid *Senecio*" subgroup classifications and their corresponding taxa from 1843 to present.

Senecio subgroup asigned by each author on table

⬛ Author did not asign group 🟥 Aurei 🟧 Lobati 🟨 Tomentosi

Informal group as currently circumscribed	Species	Gray 1843	Rydberg 1900	Greenman 1901	Barkley 1978	Barkley 1988
Tomentosi	*Packera antennariifolia* (Britton) W.A.Weber & Á.Löve			🟨		
	Packera bellidifolia (Kunth) W.A.Weber & Á.Löve					
	Packera bernardina (Greene) W.A.Weber & Á.Löve			🟨		
	Packera cana (Hook.) W.A.Weber & Á.Löve	⬛		🟨		
	Packera candidissima (Greene) W.A.Weber & Á.Löve					
	Packera cynthioides (Greene) W.A.Weber & Á.Löve			🟨		
	Packera dubia (Spreng.) Trock & Mabb.	⬛		🟨	🟨	🟨
	Packera fendleri (A.Gray) W.A.Weber & Á.Löve		🟧🟨	🟨		🟨
	Packera greenei (A.Gray) W.A.Weber & Á.Löve			🟥	🟨	🟨
	Packera hesperia (Greene) W.A.Weber & Á.Löve				🟨	🟨
	Packera ionophylla (Greene) W.A.Weber & Á.Löve			🟧		🟨
	Packera loratifolia (Greenm.) W.A.Weber & Á.Löve				🟨	🟨
	Packera macounii (Greene) W.A.Weber & Á.Löve			🟨	🟨	🟨
	Packera mancosana Yeatts, B.Schneid. & Al Schneid.				🟨	🟨
	Packera moranii (T.M.Barkley) C.Jeffrey				🟨	🟨
	Packera neomexicana (A.Gray) W.A.Weber & Á.Löve		🟨	🟧🟨	🟨	🟨
	Packera umbraculifera (S.Watson) W.A.Weber & Á.Löve			🟨	🟨	🟨
	Packera werneriifolia (A.Gray) W.A.Weber & Á.Löve ex Trock			🟥		
Lugentes	*Packera actinella* (Greene) W.A.Weber & Á.Löve			🟨	🟨	🟨
	Packera toluccana (DC.) W.A.Weber & Á.Löve			🟥		
Not asigned to a group	*Packera castoreus* (S.L.Welsh) Kartesz					🟨
	Packera contermina (Greenm.) J.F.Bain				🟨	🟨
	Packera crawfordii (Britton) A.M.Mahoney & R.R.Kowal					
	Packera heterophylla (Fisch.) E.Wiebe				🟨	🟨
	Packera insulae-regalis R.R.Kowal				🟨	
	Packera malmstenii (S.F.Blake ex Tidestr.) Kartesz					
	Packera musiniensis (S.L.Welsh) Trock					
	Packera ogotorukensis (Packer) Á.Löve & D.Löve					
	Packera serpenticola Boufford, Kartesz, S.H.Shi & R.Zhou					
	Packera spellenbergii (T.M.Barkley) C.Jeffrey					
	Packera texensis O'Kennon & Trock					

the deepest branching lineage/subgroup, and that 'Lobati' and 'Tomentosi' arose from the Aurei during the late Tertiary period; however, Bain & Jansen (1995) or Bain & Golden (2000) have found no support for either hypothesis.

PACKERA

The Aureoids became fully recognized as a new genus by Áskell and Doris Löve in 1976 (Löve & Löve, 1976). Most of the species were not classified as *Packera* until 1981 by William A. Weber and Áskell Löve, largely based on differences in morphology and chromosome numbers (Weber & Löve, 1981; Jeffrey, 1992). Senecioneae specialists initially resisted the idea of separating the Aureoids into a different genus since morphologically, they are not that different from other North American *Senecios* (Barkley, 1988). However, the inclusion of molecular data (Bain & Jansen, 1995; Bain & Golden, 2000; Pelser et al., 2007, 2010; Schilling & Floden, 2015) and the discovery of various morphological characteristics (Barkley, 1988) support its distinctiveness, making the genus more accepted (Trock, 1999). *Packera* differs from *Senecio* with several traits: 1) *Packera* taxa have haploid chromosome numbers [n] of 22 or 23, or polyploids of these numbers, while *Senecio* has n of 20 or 30 (Barkley, 1988; Funk et al., 2009); 2) *Packera* has helianthoid pollen (fully or partially caveate with internal foramina) instead of senecioid pollen (fully or partially caveate without internal foramina), which is the most commonly found type within Senecioneae; and 3) receptacles within *Packera* tend to have extensive fistulosity, while *Senecio* has much less (Funk et al., 2009; Robinson, 2009; Bain & Walker, 1995).

Packera as currently circumscribed has ca. 64 species and varieties (55 species and nine varieties; Trock, 2006; Figure 2), though the number continuously changes with the description of new taxa (e.g., Kowal et al., 2011; Yeatts et al., 2011; Boufford et al., 2014), or from splitting/lumping of already named taxa (e.g., Mohlenbrock, 2004; Mahoney & Kowal, 2008). Most species are endemic to North America, apart from *P. heterophylla* (Fisch.) E.Wiebe in Siberia, with a majority of taxa occurring in the western temperate regions of central to southern North America (Barkley, 1988). *Packera* occurs in multiple ecosystems, with some species abundant and widely distributed, while others are endemic or restricted to specialized or isolated habitats, placing some under conservation concern. *Packera* is taxonomically complex due to the species' ability to easily hybridize and roughly 40% of taxa presenting polyploidy, aneuploidy, and other cytological disturbances (Barkley, 1988; Trock, 2006). This complexity has historically made it difficult to reconstruct evolutionary relationships in this group (Bain & Jansen, 1995; Bain & Golden, 2000), though recent advancements in sequencing technologies (e.g., target-enrichment sequencing) may benefit our current understanding of *Packera* and how it has diversified over time. Given its taxonomic, ecological, and genetic complications, *Packera* is a great system to study complex groups within Compositae.

ACKNOWLEDGEMENTS

We thank Robert Lagier, Cassi Saari, and Vida Svahnström for offering their images.

LITERATURE CITED

Bain, J.F., & Golden, J.L. 2000. A phylogeny of *Packera* (Senecioneae; Asteraceae) based on internal transcribed spacer region sequence data and a broad sampling of outgroups. *Mol. Phylogenet. Evol*. 16: 331–338.

Bain, J.F., & Jansen, R.K. 1995. A phylogenetic analysis of the aureoid *Senecio* (Asteraceae) complex based on ITS sequence data. *Plant Syst. Evol*. 195: 209–219.

Bain, J.F., & Walker, J.F. 1995. A comparison of the pollen wall ultrastructure of aureoid and non-aureoid *Senecio* species (Asteraceae) in North America. *Plant Syst. Evol*. 195: 199–207.

Barkley, T.M. 1962. A Revision of *Senecio aureus* Linn. and Allied Species. *Trans. Kansas Acad. Sci.* 65: 318–364.

Barkley, T.M. 1968. Intergradation of *Senecio* Sections Aurei, Tomentosi and Lobati, through *Senecio mutabilis* Greenm. (Compositae). *Southwest Nat*. 13: 109–115.

Barkley, T.M. 1978. *Senecio*. Pp. 50–139, in: *North American Flora II*.

Barkley, T.M. 1988. Variation among the Aureoid *Senecios* of North America: A geohistorical interpretation. *Bot. Rev*. 54: 82–106.

Boufford, D.E., Kartesz, J.T., Shi, S., & Zhou, R. 2014. *Packera serpenticola* (Asteraceae; Senecioneae), a new species from North Carolina, U.S.A. *Syst. Bot.* 39: 1027–1030.

Freeman, C.C. 1985. *A revision of the aureoid species of* Senecio *(Asteraceae: Senecioneae) in Mexico, with a cytogeographic and phylogenetic interpretation of the aureoid complex*. Kansas State University.

Fu, Z.X., Jiao, B.H., Nie, B., Zhang, G.J., Gao, T.G., Chen, Z.D., Lu, A.M., Kong, H.Z., Wang, X.Q., Wang, Y.Z., Zhou, S.L., Zhang, S.Z., Wang, X.M., Liu, Z.J., Wang, Q.F., Li, J.H., Li, D.Z., Yi, T.S., Hong, M.A., ... & Liu, Q.X. 2016. A comprehensive generic-level phylogeny of the sunflower family: Implications for the systematics of Chinese Asteraceae. *J. Syst. Evol*. 54: 416–437.

Funk, V.A., Susanna, A., Stuessy, T.F., & Bayer, R.J. (Eds.). 2009. Systematics, evolution, and biogeography of Compositae. Vienna: International Association for Plant Taxonomy.

Gray, A. 1886. *Synoptical Flora of North America: The Gamopetalae, Being a Second Edition of Vol I Part II, and Vol II Part I, Collected*. (Vol. 31). Ivison, Blakeman, Taylor.

Gray, A., & Torrey, J. 1843. 163. *Senecio* Linn. Pp. 436–446, in: *A Flora of North America: Containing Abridged Descriptions of All the Known Indigenous and Naturalized Plants Growing North of Mexico, Arranged According to the Natural System.* (Vol. 2).

Greenman, J.M. 1902. Monographie der nord- und centralamerikanischen Arten der Gattung *Senecio*. *Bot. J. Linn. Soc*. 32: 1–33.

Greenman, J.M. 1918. Monograph of the North and Central American Species of the Genus *Senecio* - Part II. *Ann. Missouri Bot. Gard.* 5: 37–109.

Jeffrey, C. 1992. The Tribe Senecioneae (Compositae) in the Mascarene Islands with an Annotated World Check-List of the Genera of the Tribe: Notes on Compositae: VI. *Kew Bull*. 47: 49.

Kowal, R.R., Judziewicz, E.J., & Edwards, J. 2011. *Packera insulae-regalis* (Asteraceae, Senecioneae), a new species endemic to Isle Royale, Michigan, U.S.A. *Brittonia* 63: 343–354.

Löve, Á., & Löve, D. 1976. *Packera* Á. Löve & D. Löve. *Bot. Notiser*. 128: 520–521.

Mahoney, A.M. 2000. *Contributions to the systematics of the* Packera paupercula *complex (Asteraceae: Senecioneae)*. University of Wisconsin-Madison.

Mahoney, A.M. & Kowal, R.R. 2008. Three new varieties of *Packera paupercula* (Asteraceae, Senecioneae) in midwestern and southeastern North America. *Novon:* 18: 220–228.

Mandel, J.R., Dikow, R.B., Siniscalchi, C.M., Thapa, R., Watson, L.E., & Funk, V.A. 2019. A fully resolved backbone phylogeny reveals numerous dispersals and explosive diversifications throughout the history of Asteraceae. *P. Natl. Acad. Sci. USA*. 116: 14083–14088.

Mohlenbrock, R.H. 2004. Validation of new combinations of vascular plants. *Phytoneuron.* 67: 1–3.

Nordenstam, B. 1977. Senecioneae and Liabeae—systematic review. Pp. 799–830 in: Heywood, V.H., Harborne, J.B. & Turner, B.L. (eds.), The Biology and Chemistry of the Compositae, vol. 2. Academic Press, London.

Nordenstam, B. 1978. Taxonomic studies in the tribe Senecioneae (Compositae). *Opera Bot*. 44: 1–83.

Nordenstam, B. 2003. Recent progress in Senecioneae taxonomy. *Compositae Newslett*. 40: 26.

Nordenstam, B. 2007. Tribe Senecioneae. Pp: 208-241, in J.W. Kadereit & C. Jeffrey (Eds.), *Flowering Plants. Eudicots. Asterales*. Vol. 8. Springer, Berlin.

Packer, J.G. 1972. A taxonomic and phytogeographical review of some arctic and alpine *Senecio* species. *Can. J. Bot*. 50: 507–518.

Panero, J.L., & Funk, V.A. 2008. The value of sampling anomalous taxa in phylogenetic studies: Major clades of the Asteraceae revealed. *Mol. Phylogenet. Evol*. 47: 757–782.

Pelser, P.B., Kennedy, A.H., Tepe, E.J., Shidler, J.B., Nordenstam, B., Kadereit, J.W., & Watson, L.E. 2010. Patterns and causes of incongruence between plastid and nuclear Senecioneae (Asteraceae) phylogenies. *Am. J. Bot*. 97: 856–873.

Pelser, P.B., Nordenstam, B., Kadereit, J.W., & Watson, L.E. 2007. An ITS Phylogeny of Tribe Senecioneae (Asteraceae) and a New Delimitation of *Senecio* L. *Taxon*. 56: 1077–1104.

Robinson, H. 2009. An introduction to micro-characters of Compositae. Pp. 89-92, in V. A. Funk, A. Susanna, T. F. Stuessy, & R. J. Bayer (Eds.), Systematics, evolution, and biogeography of Compositae. Vienna: International Association for Plant Taxonomy.

Rydberg, P.A. 1900. Studies on the Rocky Mountain Flora I. *B Torrey Bot. Club*. 27: 169–189.

Schilling, E. & Floden, A. 2015. Barcoding the Asteraceae of Tennessee, Tribe Senecioneae. *Phytoneuron* 19: 1–8.

Trock, D.K. 1999. *A revisionary synthesis of the genus* Packera *(Asteraceae: Senecioneae)*. Kansas State University.

Trock, D.K. 2006. *Packera* Á. Löve & D. Löve. In *Flora of North America Editorial Committee, eds. 1993+* (Vol. 20, pp. 570–602).

Weber, W.A., & Löve, Á. 1981. New combinations in the genus *Packera* (Asteraceae). *Phytologia* 49: 44–50.

Yeatts, L., Schneider, A., & Schneider, B. 2011. *Packera mancosana* (Asteraceae: Senecioneae), a new species and shale barren endemic of Southwestern Colorado. *Phytoneuron* 2011-26: 1–8.

A harried past for a glabrous lettuce:

Resurrection of *Lactuca sanguinea* Bigelow (Cichorieae), the wood lettuce from Nantucket Island, Massachusetts, USA

Steven M. Ballou,[1] Kelly A. Omand,[2] Jennifer Karberg,[2] J. Mauricio Bonifacino[3] & Jennifer R. Mandel[1]

[1] Department of Biological Sciences, University of Memphis, 3700 Walker Ave, Memphis, TN 38152, U.S.A.
[2] Nantucket Conservation Foundation, Science and Stewardship Department, Nantucket MA 02554, U.S.A.
[3] Facultad de Agronomía, Universidad de la República, Av. Garzón 780, Montevideo, URUGUAY

Author for correspondence: Jennifer R. Mandel, *jmandel@memphis.edu*

DOI: http://dx.doi.org/10.53875/capitulum.02.2.05

ABSTRACT

We resurrect from synonymy *Lactuca sanguinea* based on morphological analysis of herbarium specimens and field observations. We report recent populations of *Lactuca sanguinea* occurring in several locations across Nantucket Island in Massachusetts, USA, and provide the first collections in over fifty years within the state. The species consistently has predominantly dark purple-red stems and leaves and crimson corollas, which together with its glabrous nature sets it apart from *Lactuca hirsuta*. We designate a lectotype, present an expanded morphological description and taxonomic history for the species and provide line drawings and images.

Keywords: Asteraceae, collections, Compositae, herbarium, synonym, taxonomy.

INTRODUCTION

In the second edition of *Florula Bostoniensis*, Bigelow (1824) described a new lettuce species, *Lactuca sanguinea* Bigelow (Cichorieae). Following its publication, this taxon has taken a somewhat tortuous journey from a distinct species to being currently synonymized under *L. hirsuta* Muhl. ex Nutt., the tall hairy lettuce (e.g., Strother, 2006; Haines 2011; Weakley 2022).

Recently, while conducting fieldwork on Nantucket Island, Massachusetts, USA, we came across a dark, purple-red, mostly glabrous lettuce mainly in the sandplain grasslands and open heathlands in the southern and western outwash plain areas of the island. These habitats are characterized by sandy soils and little to no shade cover with high salt spray and wind influence. We consider this entity to be Bigelow's *L. sanguinea.* In the summer of 2018, we traveled to Nantucket Island to collect samples for genetic and morphological work and to increase herbarium collections. We found *L. sanguinea* growing in five locations each consisting of over twenty individuals. Additional plants have been found at Head of the Plains and documented with vouchers and with iNaturalist records (2021-2022).

Interestingly, *Lactuca hirsuta* and *Lactuca sanguinea* (treated as *L. hirsuta* var. *sanguinea* [Bigelow] Fernald) are considered rare, endangered, or watch-listed across many parts of their ranges, which occupy the eastern United States and Canada, west to Texas, north to Ontario, south to Georgia, and east to

Prince Edward Island (Lebeda et al. 2019; Strother 2006). Our objectives in this contribution are to resurrect *L. sanguinea* as a distinct entity, to present an account of its taxonomic history, description and illustration.

MATERIALS AND METHODS

We studied herbarium material conserved at CONN, GH, MEM, MT, NHA, NMMA, NY (acronyms according to Thiers, 2023), and analyzed type material and protologues of closely related and morphologically similar species *Lactuca hirsuta* (Nuttall, 1818). Fieldwork was conducted to obtain information on habitat and morphological features usually lost in dried specimens and not present in descriptions, such as plant architecture, involucre shape, and stems, leaves and corolla color.

We photographed plants in their habitat, with details of various morphological parts. The illustrations were prepared based on herbarium material, using a camera lucida attached to a Wild M5 stereoscope, and later edited digitally in Adobe Illustrator and Photoshop. Geographic distribution was obtained from herbarium material and recently collected specimens.

TAXONOMIC HISTORY

According to the preface of the second edition of Florula Bostoniensis (Bigelow, 1824), the first edition mainly contained plant species near the Boston area (Massachusetts), but in the second edition Bigelow indicated he had included, "all such plants I have formerly collected and described in any part of the New-England states." Therein, Bigelow described a new lettuce species, *Lactuca sanguinea,* as having a smooth stem of dark, reddish-purple color, leaves glaucous underneath with the midrib hairy, calyx [involucre] dark purple, and ligulate corollas crimson. He listed the habitat as dry woods, flowering from July to August (Bigelow, 1824, page 287).

Torrey and Gray (1843) synonymized *Lactuca sanguinea* with *L. hirsuta* and treated them as a as a variety of *L. elongata* Muhl. ex Willd. (i.e., *Lactuca elongata var. sanguinea* (Bigelow) Torr. & A.Gray), noting the leaves mostly hirsute-pubescent (as well as the stems) throughout or on the midrib. They described the corollas as yellow-purple, dark-red with a yellowish center, saffron-color, or purple. Interestingly they mention branches and involucres often also purplish.

Nearly a century later, in Noteworthy Plants of Southeastern Virginia, Fernald (1938) gave a detailed and captivating description of *Lactuca hirsuta*, adding information from his own collections made along with Bayard Long, member of the Academy of Natural Sciences of Philadelphia and Herbarium Curator of the Philadelphia Botanical Club, from Southampton and Sussex Counties. Particularly noteworthy in the context of this paper, Fernald (1938) remarked how in typical *Lactuca hirsuta*, the highly pubescent nature of the plant was rare both in nature and collections. However, he and Long collected a specimen with leaves that were "almost velvety to the touch" and exhibited densely villous stems. In seeking to give a more inclusive description of *L. hirsuta*, Fernald examined more than 90 specimens including the type of *L. hirsuta* and also Bigelow's specimen conserved at GH (GH 00009502) and ascribed to *L. sanguinea*. He noted that material from eastern Canada and New England was consistent in having glabrous stems or very rarely sparsely hirsute lower internodes and mostly glabrous leaf surfaces, very rarely pilose. To further investigate variation in pubescence, Fernald assessed *L. hirsuta* and other varietal material from the Academy of Natural Sciences of Philadelphia and noted a continuum of pubescence, ranging from densely hairy as typical of *L. hirsuta* to glabrous as characteristic of *L. sanguinea*. Fernald also noted the capitulescence type of these specimens, describing often in his notes the southern *L. hirsuta* as having to racemiform capitulescences while the Canadian and New England specimens tended to have corymbiform ones. Also notable in Fernald's account, was the footnote on page 479, where he wrote "*Lactuca hirsuta* has yellow flowers" (Fernald, 1938) since the indication of color of any part of the plant in the descriptions of *L. hirsuta* is often lacking (see below).

Based on his studies, Fernald (1938) concluded that the differences between *L. hirsuta* and *L. sanguinea* didn't warrant recognition at the species level and

I went to the woods...

Besides living deliveratedly, Thoreau collected plant specimens, and *Lactuca sanguinea* Bigelow was among them.

At Gray Herbarium of Harvard University, one of the specimens determined as *L. elongata* var. *sanguinea* (Bigelow) Torr. & A. Gray and cited in Flora of North America was likely collected by Henry David Thoreau, but with no data or locality listed. Ray Angelo, Harvard University Herbaria Associate, notes in the Vascular Flora of Concord, Massachusetts (Angelo 2022) that there are four references to *Lactuca* L. in Thoreau's Journal while he was in Concord. Angelo also provides a link to what he considers is a Thoreau's specimen in the herbarium

See specimen here https://www.flickr.com/photos/huh/33316385534/in/album-72157680747810871/

Strafford, New Hampshire
Photo by Kelly Omand

decided to organize the diversity he observed at a lower rank and thus he described two varieties and a form inside *L. hirsuta*: 1) *Lactuca hirsuta* var. *genuina* Fernald. nom. ill. (correct name *Lactuca hirsuta* var. *hirsuta*) with stems densely villous and leaves copiously pilose on both sides, found from Pennsylvania to Virginia and Louisiana, 2) *Lactuca hirsuta* var. *sanguinea* with stems glabrous and lower leaves with midrib villous beneath, from Prince Edward Island and New York, to Virginia, but rare in Texas and Louisiana, and 3) *Lactuca hirsuta* f. *calviofolia* Fernald with leaves and stems glabrous throughout and circumscribed within *Lactuca hirsuta* var. *sanguinea* distributional range.

It is important to note that color of stems, leaves, involucres, and corollas were not included in Fernald's descriptions of the infra taxa he recognized, with the main diagnostic character being the presence or absence of trichomes on the stems and leaves.

TAXONOMIC TREATMENT

Lactuca sanguinea Bigelow, Fl. Bost. Ed 2: 287, 1824 ≡ *Galathenium sanguineum* (Bigelow) Nutt. Trans. Amer. Philos. Soc. Ser. 2, 7: 444, 1841 ≡ *Lactuca elongata* var. *sanguinea* (Bigelow) Torr. & A. Gray, Fl. N. Amer. (Torr & A. Gray) 2: 496, 1843 ≡ *L. hirsuta* var. *sanguinea* (Bigelow) Fernald, Rhodora 40: 481, 1938. **TYPE:** [Boston], *Bigelow s.n. july* (Lectotype here designated: GH 00009502!) Figure 1, Figure 2.

Biennial herbs 45-130 cm tall, stems purple (but often drying to dark brown), basally pubescent, glabrous towards the apex. **Leaves** alternate, sessile, 4 – 20 (-70) × 6-20 cm, pinnatisect, lobes acute, midrib of basal leaves villose, green to purple. Capitulescences paniculiform, capitula 20 to 100 (-850), peduncles short, up to ca. 2 cm long. **Involucres** 14-18 × 4.5 mm, cylindric, phyllaries arranged in 4-5 series, purple; outer phyllaries 2.3-3.4 × 1.5-2.4 mm, triangular to narrowly ovate, herbaceous, inner phyllaries 9.5-13 × 2 mm, oblong to narrowly ovate, membranose, parallelly veined. **Receptacles** alveolate. **Florets** 18 to 26; corollas ligulate, tube ca. 9 mm long, slightly broadened apically, provided with ca. 2 mm long trichomes towards the apex, limb 6-6.2 × 1.5-1.6 mm, oblong, purple to orange-reddish. Anthers ca. 1.9 mm long, apical appendages obtuse. Styles 15-16 mm long, style branches 1.5-1.8 mm long, linear, apex acute. **Achenes** ca. 6.8 mm long, seed part ca. 4 × 2 mm, fusiform, flattened, beak ca. 2.8 mm long, surface black to brown with scales arranged in wavy rows horizontally oriented. **Pappus** ca. 9 mm long, elements capillary bristles tapering towards the end, arranged in a single series.

Nomenclatural note: when describing the new species, Bigelow (1824) did not cite specimens nor a precise location and collector. However, although this information is not given in the protologue, the species was introduced in a larger treatment describing Boston plants. Therefore, the locality could be safely assumed to be Boston or the Boston area as indicated by Bigelow himself in the introduction of his flora, and also collected by him, as he also mentioned in the introduction that he collected plants for the flora in a period of two seasons. Bigelow did mention that the plant was found in "dry woods" in "July, August". At GH there is a specimen (#00009502; Figure 3) that matches the description and was collected by Bigelow himself and has a note in Bigelow's handwriting, identifying it as *Lactuca sanguinea* with a "Jl." written next to "Boston" interpreted as indicating the month of July. Based on all this evidence, the specimen #00009502 at GH could be considered original material and is therefore selected as lectotype, following article 9.3 of the current code (Turland et al. 2018).

Distribution and Ecology: although described by Bigelow from woods, we observed *Lactuca sanguinea* occurring in multiple open, heathland or grassland habitats on the island of Nantucket. This discrepancy in habitat types, however, is common to the flora of Nantucket Island, where plants of woodland openings such as *Cypripedium acaule* Ait, *Anemone quinquefolia* L., and *Epigaea repens* L. are often found in more open habitats, especially low shrublands that offer some late-season shading. Plants in areas excluded from deer browsing were the most robust, e.g., with greater plant height and larger numbers of branches and capitula. Associated plants included *Gaylussacia baccata* (Wangenh.) K. Koch, *Liatris scariosa* (L.) Willd. var. *novae-angliae* (Lunell) Gandhi, S.M.Young & P.Somers, *Cirsium pumilum* Spreng., *Rosa rugosa* Thunb. ex Murray, *Sisyrinchium fuscatum* Bickn., *Baptisia tinctoria* (L.) R.Br., and *Polygala polygama* Walter.

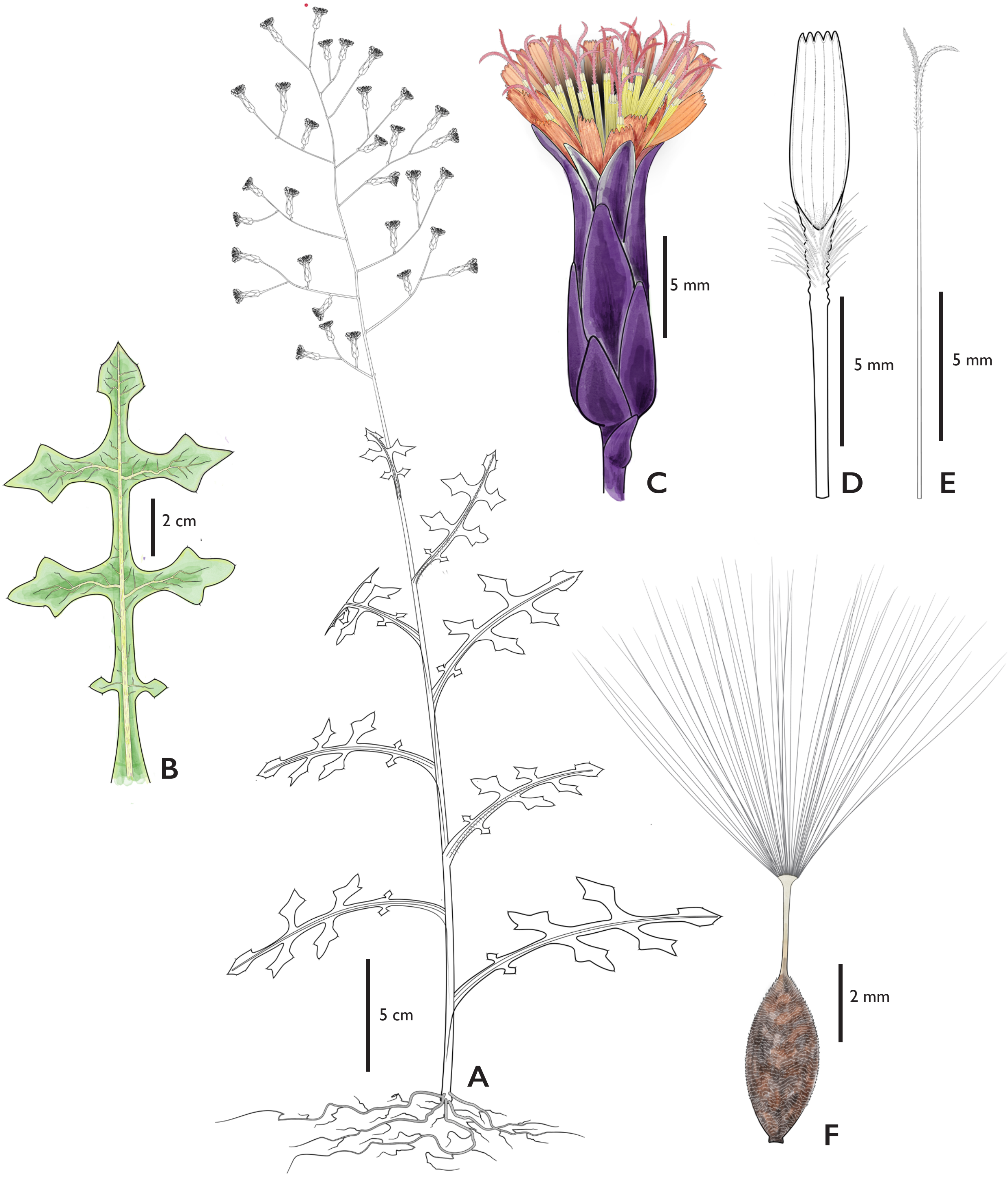


Figure 1. *Lactuca sanguinea* Bigelow. **A.** Habit. **B.** Leaf. **C.** Capitulum. **D.** Corolla. **E.** Style. **F.** Achene with pappus (from *Ballou s.n.* MEM021509).

Figure 2. *Lactuca sanguinea* Bigelow. **A.** Habitat. **B.** Habit. **C.** Leaf. **D.** Capitulum, notice purple involucre and reddish corollas. *Photos by: Kelly Omand.*

Additional specimens examined: CANADA. **Québec.** Pierre-De Saurel, Tracy, près des Grèves, *A. Sabourin & A. Nault 2087*, 28 July 2000 (MT). **USA. Connecticut.** New Heaven County. West Rock Ridge State Park, *E. H. Eames s.n.*, 17 July 1925 (CONN 27927). **Massachusetts.** Essex County. S.l. *W. Oakes s.n.*, 1850 (NY 2201097). Nantucket County. Nantucket, plains N of rail road about 3rd mile, *E. P. Bicknell 9419*, 7 August 1906 (NY); Nantucket, Smooth Hummocks Coastal Preserve, *S. M. Ballou Jr. s.n.*, 15 July 2018 (MEM 21509); id., *P. L. Murin s.n.*, 14 July 2018 (MEM 21508); Nantucket, *J. B. Garner s.n.*, 25 July 1910 (NMMA 524); Head of the Plains, *K. A. Omand s.n.*, 28 July 2017 (NMMA 533). **New Hampshire**. Cheshire County. S.l., *C. F. Batchelder 4700*, 3 August 1918 (NHA). Grafton County. Woodstock, Watershed No. 5, *G. E. Crow & J. A. Crow 8864*, 30 August 1995 (NHA). Hillborough County. Peterborough, *C. F. Batchelder s.n.,* 5 July 1931 (NHA). Strafford County. Strafford, above Power Bridge across Salmon Falls River, *A. R. Hodgdon 6384*, 29 June 1949 (NHA); Strafford, near Newmarket line, near Great Bay, *A. R. Hodgdon 5142*, 25 August 1945 (NHA).

Most modern-day floras and online databases have synonymized *Lactuca sanguinea* with *L. hirsuta*, including Flora of North America (Strother 2006), the Compositae Global Database (CWG 2021), and the World Flora Online (WFO 2022). In fact, Strother (2006) mentioned neither the trichomes on the stems nor color variation, except to say that sometimes the yellow corollas dry bluish. In volume 2 of Steyermark's Flora of Missouri, Yatskievych (1999, page 366) notes *L. hirsuta* stem color ("often purple-streaked or purplish-tinged") and corolla color ("yellow to orangish yellow, sometimes turning blue with age or upon drying"). Yatskievych (1999) remarked that the varieties *Lactuca hirsuta* var. *hirsuta* and *L. h.* var. *sanguinea* did not seem worthy of formal recognition describing the presence of trichomes, or not, respectively, without mention of color for either variety.

An interesting twist to our story is that the specimens we collected, currently conserved at MEM and NMMA lost almost all their red coloration (especially that of the capitulescence) upon drying, though the specimens retained some dark coloration on the lower parts of the stems, almost to brown to black (Figures 3 – 5). If this is typical, we suspect that Bigelow (1824) must have described his *L. sanguinea* from living specimens and that most botanists in the nearly two centuries after him have missed these beautiful dark pigments thereby supporting the various synonym designations.

NANTUCKET HISTORICAL CONTEXT

The island of Nantucket has long been an object of interest botanically, with a number of well-known botanists visiting the island during the late 1800s and early 1900s (neither Bigelow nor Fernald among them, however). The first comprehensive list of Nantucket plant species, *A Catalogue of Plants Growing Without Cultivation in the County of Nantucket, Mass.* was prepared by island botanist Maria L. Owen in 1888 and includes *Lactuca elongata var. sanguinea* listed as a synonym of *Lactuca hirsuta.*

From 1908-1918, New York botanist Eugene P. Bicknell provided a more expansive list of the island flora in a set of twenty volumes published in the Bulletin of the Torrey Botanical Society based on his four visits to the island (1899-1907). Bicknell included *Lactuca hirsuta,* but uncharacteristically did not provide detailed comments about any distinctive characteristics of the plants he encountered on Nantucket, stating only habitat, distribution, and flowering time (Bicknell 1905).

Sorrie and Dunwiddie (1996) included the taxon in *The Vascular Flora of Nantucket, Tuckernuck, and Muskeget* as *Lactuca hirsuta* Muhl. ex Nutt. var. *sanguinea* (Bigelow) Fernald, rather than simply listing it as *Lactuca hirsuta*, indicating that they felt this distinction was important, having observed the plants themselves on island. They noted that the taxon was also present on Tuckernuck and described habitat as coastal heathland and shrubland, including near Sheep Pond, at the western end of island (Head of the Plains) one of the areas where we have been observing this taxon.

Based upon our recent detailed observations of the Nantucket plants included here, and upon reexamination of Bigelow's 1824 description and collection, we assert that the populations occurring on Nantucket Island are distinct enough to deserve recognition at species level and therefore we are hereby resurrecting *Lactuca sanguinea* from its synonymy under *L. hirsuta*. The glabrous nature of the plant added to the distinguishing purple color of stems, leaves and corollas make *Lactuca sanguinea* very distinctive and easily differentiable from *L. hirsuta*.

Figure 3. Lectotype of *Lactuca sanguinea* Bigelow, collected by the Bigelow himself (GH00009502). Image courtesy of the Gray Herbarium, Harvard University.

Finally, regarding the genetics of this interesting group, previous work in *Lactuca* L. has revealed low levels of genetic diversity, e.g., by Jones et al. (2018), though recent work using whole plastomes has revealed some genetic differentiation (Chu et al. 2022). Further studies at the population level, including genomic-level studies employing nuclear loci, across the distribution range of both *Lactuca sanguinea* and *L. hirsuta* may shed light on the relationship of these closely related species.

ACKNOWLEDGEMENTS

We thank Noah Karberg for aiding with collections and Dr. Robert Wernerehl, the State Botanist for Massachusetts, for help with obtaining permits and providing location data for plants. We especially thank Paige Murin for her efforts in collecting and measuring specimens, as well as her input on an earlier version of this manuscript. We thank Harvard University herbaria for granting use of specimen GH00009502 image. We also thank Samantha Drewry for assistance in describing specimens, Kanchi Gandhi for clarifying nomenclatural issues, and Ray Angelo for his insight into Lactuca's references from Thoreau's journals.

LITERATURE CITED

Angelo, R. 2022.Vascular Flora Of Concord, Massachusetts. Published online and accessed at: https://archive.org/details/vascular-flora-of-concord-massachusetts/page/144/mode/2up, April 24, 2022.

Bicknell, E.P. 1915. The Ferns and Flowering Plants of Nantucket – XVI. *Bull. Torrey Bot. Club* 42(10):549-570.

Bigelow, J. 1824. *Florula Bostoniensis*. A collection of plants of Boston and its vicinity, with their generic and specific characters, principal synonyms, descriptions, places of growth, and time of flowering, and occasional remarks. Cummings, Hilliard, & Co., Boston. Accessed at: https://www.biodiversitylibrary.org/item/17931 April 26, 2022.

Chu, R., Xu, X.M., Lu, Z.W., Ma, Y.G., Cheng, H., Zhu, S.X., Bakker, F.T., Schranz, M.E. & Wei, Z. 2022. Plastome-based phylogeny and biogeography of Lactuca L. (Asteraceae) support revised lettuce gene pool categories. Front. Plant Sci. 13:978417. doi: 10.3389/fpls.2022.978417

Compositae Working Group (CWG). 2021. Global Compositae Database. *Lactuca hirsuta* var. *sanguinea* (Bigelow) Fernald. Accessed at: https://www.compositae.org/aphia.php?p=taxdetails&id=1234699 April 26, 2022.

Fernald, M.L. 1938. Noteworthy plants of southeastern Virginia (continued). Rhodora 40: 434-459. Accessed at: https://www.biodiversitylibrary.org/page/605871 April 26, 2022.

Haines, A. 2011. *Flora Novae-Angliae*. New England Wildflower Society. Yale University Press, New Haven, CT, U.S.A.

Jones, K. E., Schilling, E. E., Dias, E. F. & Kilian, N. 2018. Northern hemisphere disjunctions in *Lactuca* (Cichorieae, asteraceae): independent Eurasia to north America migrations and allopolyploidization. *Willdenowia* 48: 259–284. DOI: 10.3372/wi.48.48206.

Lebeda, A., Křístková, E., Doležalová, I., Kitner, M. & Widrlechner, M.P. 2019. Wild *Lactuca* species in North America. In North American Crop Wild Relatives, Vol. 2 (pp. 131-194). Springer, Cham.

Nuttall, T. 1818. The Genera of North American Plants. Philadelphia, USA. Vol. 2. (p. 124).

Owen, M. L. 1888. A Catalogue of Plants Growing Without Cultivation in the County of Nantucket, Massachusetts. Gazette Printing Company, Northampton, Massachusetts, U.S.A.

Sorrie, B.A. & Dunwiddie, P.W. 1996. The Vascular and Non-Vascular Flora of Nantucket, Tuckernuck, and Muskeget Islands. Jointly published by Massachusetts Audubon Society, Massachusetts Natural Heritage and Endangered Species Program, Nantucket Maria Mitchell Association, and The Nature Conservancy, Nantucket, Massachusetts, U.S.A.

Strother, J.L. 2006. 45. *Lactuca*. Pp. 259–263, in: Flora of North American Editorial Committee, eds. Flora of North America north of Mexico, vol. 19. Magnoliophyta: Asteridae, part 6: Asteraceae, part 1. New York, Oxford University Press

Thiers, B. 2023. [continuously updated]. Index Herbariorum: A globaldirectory of public herbaria and associated staff. New York BotanicalGarden's Virtual Herbarium. Accessed at: http://sweetgum.nybg.org/science/ih/

Torrey, J. & Gray, A., 1843. A Flora of North America, vol. 2. Exogenous or Dicotyledonous Plants continued. (Entire volume 1841-1843). New York, Wiley & Putnam. Accessed at: https://www.biodiversitylibrary.org/page/10009784

Turland, N. J., Wiersema, J. H., Barrie, F. R., Greuter, W., Hawksworth, D. L., Herendeen, P. S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T. W., McNeill, J., Monro, A. M., Prado, J., Price, M. J. & Smith, G. F. (eds.). 2018. *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017*. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books. DOI https://doi.org/10.12705/Code.2018

Weakley, A.S. & Southeastern Flora Team. 2022. Flora of the southeastern United States. University of North Carolina Herbarium, North Carolina Botanical Garden. Published online. Accessed at: https://ncbg.unc.edu/research/unc-herbarium/flora-request/ April 24, 2022.

WFO, World Flora Online. 2022. *Lactuca hirsuta* Muhl. ex Nutt. Published on the Internet. Accessed at: http://www.worldfloraonline.org/taxon/wfo-0000005974826 April 24, 2022.

Yatskievych, G. 1999. Steyermark's flora of Missouri, vol. 1 Missouri Department of Conservation in cooperation with the Missouri Botanical Garden Press. St. Louis, MO.

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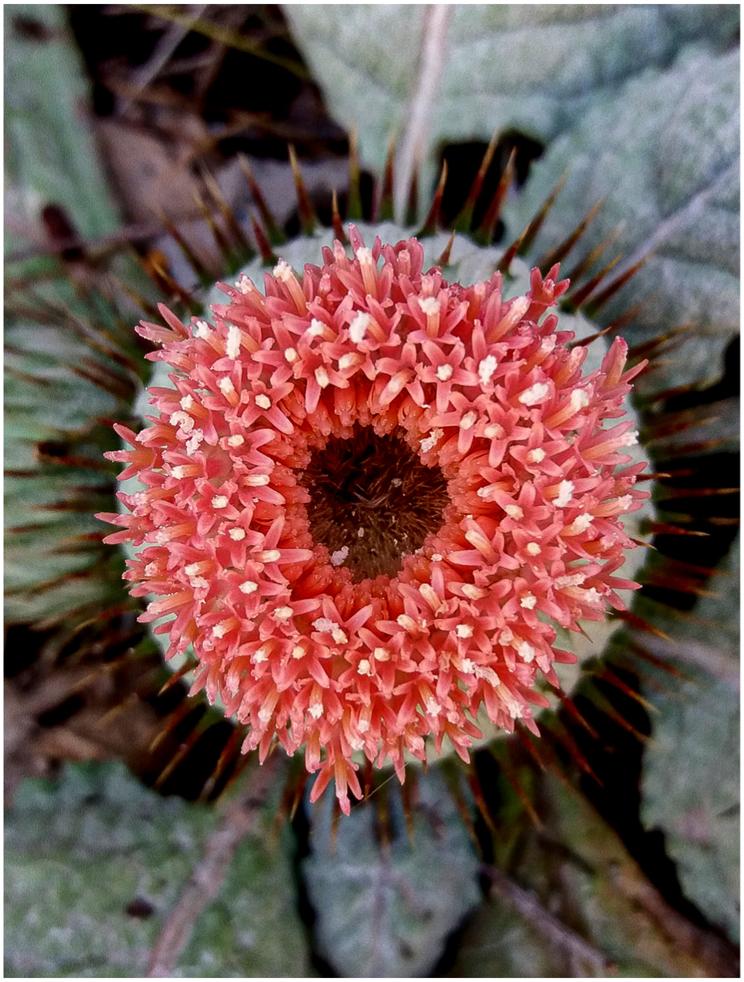

THE EYE OF ZAGROS

Jurinea berardioides (Boiss.) O.Hoffm. (Cardueae) is a beautiful species that grows on the rocks of the Zagros mountain range in southwestern Iran during early spring. Image taken in Shiraz, the capital of southern Fars province.

Ramiar Majidi

TICATIMES

selected Compositae news and updates from
THE INTERNATIONAL COMPOSITAE ALLIANCE

Edited by Jennifer R. Mandel

FEBRUARY 2023

KANCHI GANDHI A PILLAR OF NOMENCLATURAL WISDOM RECEIVES SERVICE RECOGNITION

There are almost 170000 names in the Compositae family. To any of us who has ever been navigating the treacherous waters of nomenclature when deciding the right name for a species, the name of Kanchi Gandhi, the gate keeper at IPNI sounds like a beacon of light signaling safe shore. Kanchi's authoritative and expeditious answers to all questions nomenclatural has gained him broad worldwide recognition.

He has recently received the ***Lifetime Achievment Award*** by the Botanical Survey of India, in appreciation for his outstanding service in the field of Plant Taxonomy and Botanical Nomenclature, making him the second botanist receiving such distinction, paralleling an earlier and similar recognition, the ***Distinguished Service Award*** bestowed upon him by the American Society of Plant Taxonomists in 2010.

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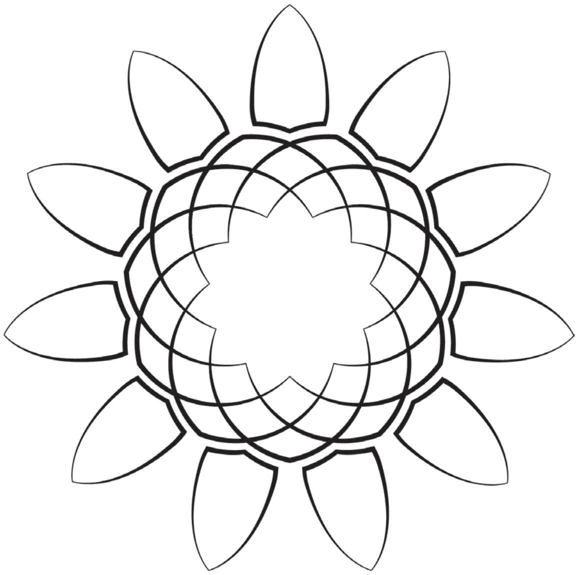

Magno amore in familiam Synantherearum captus
Lessing, 1829

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