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# COMPOSITAE



# NEWSLETTER

Number 50

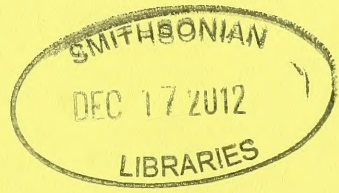
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Scientific Editor: BERTIL NORDENSTAM

Technical Editor: GUNNEL WIRÉNUS NOHLIN

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## Editorial

### On the magic number 50

In nuclear physics the number 50 is one of seven so-called magic numbers, and they are involved with nuclear isotope stability. In the plant world there is no such thing as magic numbers connected with stability, although the frequent occurrences of somewhat magic Fibonacci numbers are noted in the Compositae, e.g., in number of phyllaries, ray-florets, disc-florets etc. Sunflowers and artichokes are well known examples. These numbers are part of the Fibonacci series 0, 1, 1, 2, 3, 5, 8, 13, 21, 34, 55 etc., and there is no room for 50 there. Also, although strived for, stability is not as obvious in taxonomy as maybe in nuclear physics.

#### Compositae Newsletter No. 50

To me, at this moment, the number 50 nevertheless has some magic. This is the final issue of the Compositae Newsletter, at least under my editorship, and it bears the number 50.

#### 50 years of research on Compositae

My own research on the family has been ongoing for >50 years. In 1962 I went to South Africa for a two-year period of field and herbarium work, as the first non-South African Smuts Memorial Fellow. Although I have visited more than 75 countries in all continents (except Antarctica), Southern Africa remained my main hunting grounds for plants, with another half-year stay in 1974 and several shorter later visits – in all about three years.

#### 50 new Compositae genera

By magic coincidence I have now published 50 names of new genera of Compositae. Some have gone into synonymy, e.g. due to refined knowledge on phylogeny especially through molecular studies, but most of them are still valid and in current use. Here is the list of the genera in alphabetical order.

1. *Acrisione* B. NORD. – Bot. Jahrb. Syst. 107(1–4): 582 (1985)
2. *Adenanthellum* B. NORD. – Bot. Not. 132(2): 160 (1979)
3. *Adenanthemum* B. NORD. – Bot. Not. 129(2): 157 (1976)
4. *Adenoglossa* B. NORD. – Bot. Not. 129(2): 137 (1976)



5. *Aequatorium* B. NORD. – Opera Bot. 44: 59 (1978)
6. *Anderbergia* B. NORD. – Ann. Naturhist. Mus. Wien 98B(Suppl.): 407 (1996)
7. *Antillanthus* B. NORD. – Compositae Newslett. 44: 51 (2006)
8. *Canariothamnus* B. NORD. – Compositae Newslett. 44: 26 (2006)
9. *Capelio* B. NORD. – Compositae Newslett. 38: 72 (2002)
10. *Caputia* B. NORD. & PELSNER – Compositae Newslett. 50: (2012)
11. *Caucasalia* B. NORD. – Pl. Syst. Evol. 206(1-4): 22. (1997)
12. *Comptonanthus* B. NORD. – J. S. African Bot. 30: 54 (1964)
13. *Crassothonna* B. NORD. – Compositae Newslett. 50: (2012)
14. *Cymbopappus* B. NORD. – Bot. Not. 129(2): 150 (1976)
15. *Dauresia* B. NORD. & PELSNER – Compositae Newslett. 42: 76 (2005)
16. *Dendrosenecio* (HAUMAN ex. HEDBERG) B. NORD. – Opera Bot. 44: 40 (1978)
17. *Dolichoglottis* B. NORD. – Opera Bot. 44: 33 (1978)
18. *Elekmania* B. NORD. – Compositae Newslett. 44: 66 (2006)
19. *Graphistylis* B. NORD. – Opera Bot. 44: 56 (1978)
20. *Herreranthus* B. NORD. – Compositae Newslett. 44: 62 (2006)
21. *Hilliardia* B. NORD. – Opera Bot. 92: 147 (1987)
22. *Ignurbia* B. NORD. – Willdenowia 36(1): 464 (2006)
23. *Inuloides* B. NORD. – Compositae Newslett. 44: 44 (2006)
24. *Io* B. NORD. – Compositae Newslett. 40: 47 (2003)
25. *Iocenes* B. NORD. – Opera Bot. 44: 58 (1978)
26. *Iranecio* B. NORD. – Fl. Iranica [Rechinger] 164: 53 (1989)
27. *Jacmaia* B. NORD. – Opera Bot. 44: 64 (1978)
28. *Lamprocephalus* B. NORD. – Bot. Not. 128(3): 323 (1976)
29. *Leonis* B. NORD. – Compositae Newslett. 44: 55 (2006)
30. *Leucoptera* B. NORD. – Bot. Not. 129(2): 140 (1976)
31. *Lomanthus* B. NORD. & PELSNER – Compositae Newslett. 47: 34 (2009)
32. *Lordhowea* B. NORD. – Opera Bot. 44: 38 (1978)



33. *Lundinia* B. NORD. – Compositae Newslett. 44: 64 (2006)
34. *Monoculus* B. NORD. – Compositae Newslett. 44: 39 (2006)
35. *Nemosenecio* (KITAM.) B. NORD. – Opera Bot. 44: 45 (1978)
36. *Nephrotheca* B. NORD. & KÄLLERSJÖ – Compositae Newslett. 44: 33 (2006)
37. *Nesampelos* B. NORD. – Compositae Newslett. 45: 37 (2007)
38. *Norlindhia* B. NORD. – Compositae Newslett. 44: 41 (2006)
39. *Notoniopsis* B. NORD. – Opera Bot. 44: 69 (1978)
40. *Odontocline* B. NORD. – Opera Bot. 44: 23 (1978)
41. *Oldfeltia* B. NORD. & LUNDIN – Compositae Newslett. 38: 66 (2002)
42. *Oresbia* CRON & B. NORD. – Novon 16(2): 216 (2006)
43. *Phaneroglossa* B. NORD. – Opera Bot. 44: 66 (1978)
44. *Roodebergia* B. NORD. – Acta Phytotax. Geobot. 53(2): 101 (2002)
45. *Scyphopappus* B. NORD. – Bot. Not. 129(2): 147 (1976)
46. *Sinosenecio* B. NORD. – Opera Bot. 44: 48 (1978)
47. *Stenops* B. NORD. – Opera Bot. 44: 73 (1978)
48. *Urostemon* B. NORD. – Opera Bot. 44: 31 (1978)
49. *Xyridopsis* B. NORD. – Opera Bot. 44: 75 (1978)
50. *Zemisia* B. NORD. – Compositae Newslett. 44: 72 (2006)

About 20 of the genera are South African, and 16 are New World genera including the West Indies. Most of the new genera belong in the tribe Senecioneae, but some are members of other tribes such as the Calenduleae, Astereae, Anthemideae and Gnaphalieae. This is not the end, rather the end of a beginning. A few more genera of Senecioneae will have to be described, and the future of Compositae Newsletter is under discussion (see elsewhere in this issue).

I wish to thank everybody involved in the Compositae Newsletter for support and contributions over the years – authors as well as subscribers and technical support first of all from Mrs. GUNNEL WIRÉNIUS NOHLIN and also from other staff in the Swedish Museum of Natural History.

BERTIL NORDENSTAM

# The *Compositae Newsletter* reaches its 50<sup>th</sup> volume and BERTIL NORDENSTAM steps down as Editor after 25 years

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Professor BERTIL NORDENSTAM (S) has been the editor of the *Compositae Newsletter* (*Comp. Newsl.*) for 25 years and he recently announced that he is stepping down after number 50 (this issue).

The *Compositae Newsletter* began in 1975 and throughout its entire history it has always been free of charge. The scientific editing has been a "labor of love" by our colleagues and the technical editing, printing, and distribution has been supported by an institution or a donation. The first issue was a short announcement and the editors were TOD STUESSY (Ohio State University) and ROBERT M. KING. It was organized by STUESSY and printed and mailed by the Smithsonian Institution. By the second issue STUESSY was the only editor and it was distributed by Ohio State University. STUESSY continued as editor until number 5 was published in 1980. For numbers 6 – 12 (1977 – 1982) it moved to Kew and CHARLES JEFFREY served as Editor. Numbers 4 – 12 received financial support from Mr. SVEN KOELTZ and numbers 9 – 12 were jointly sponsored by the Bentham-Moxon Trust at Kew. One issue, Number 13, was edited by JETTE BAAGØE, University of Copenhagen, and printed by the University of Stockholm out of the office of the *Nordic Journal of Botany*. For more information on the early history of the *Compositae Newsletter* see NORDENSTAM (1988). The first 13 numbers began as a true newsletter with information on recent publications, requests for samples, and announcements. Over the years it gradually added articles of general use such as lists of types, verification of names, and lists of literature pertaining to the *Compositae*.

For six years no numbers of the *Compositae Newsletter* were published. Then, like a Phoenix rising from the ashes, Professor BERTIL NORDENSTAM (S) brought it back to life in a new and improved form. It still included announcements and lists



of types but it also began to publish journal articles and comprehensive works. Some examples include JANSEN et al.'s chloroplast DNA paper (1988), BREMER's discussion on corolla types (1988), HIND & JEFFREY's work on the Compositae of HBK (2001), HERRERA & VENTOSA's Cuban Asteraceae (2005), the Asteraceae of Chacoan Plain (FREIRE et al. 2005), and the molecular work on *Dipterocome* (ANDERBERG et al. 2007). It now has a well developed following and people regularly submit articles of interest. Other changes include its association with The International Compositae Alliance (TICA) and its move into the digital age: all issues are available free of charge through the *Biodiversity Heritage Library* web site: <http://www.biodiversitylibrary.org/bibliography/12561>. This has increased its visibility and resulted in additional citations and submissions. All these things have been accomplished because of the efforts of BERTIL NORDENSTAM and the technical editor GUNNEL WIRÉNIUS NOHLIN (starting with number 24, 1994). For 25 years the journal has been supported by the Department of Phanerogamic Botany, Swedish Museum of Natural History, Stockholm, Sweden (S). Since 1988 they have provided a technical editor, and printed and mailed the journal to over 600 scientists and libraries around the world, free of charge, but from 2013 the museum financial support for technical editing and publishing cannot be maintained. Our colleagues at S have been more than generous for many years and we thank them very much.

The *Compositae Newsletter* has published papers on the taxonomy of many Asteraceae taxa and one of these is Senecioneae, a tribe that is close to the heart of BERTIL NORDENSTAM. His contributions to the Senecioneae date back to the start of his career (e.g., NORDENSTAM 1961) and are continuing until this very day. His papers often reported discoveries resulting from his extensive field work (Fig. 1). In this issue, two new Senecioneae genera are described: *Caputia* B. NORD. & PELSER and *Crassothonna* B. NORD., and we are informed that some more will follow. The Senecioneae publications in *Compositae Newsletter* are among the key literature on the tribe and include the publication of new genera (e.g., NORDENSTAM et al. 1997b, 2009; NORDENSTAM & PELSER 2005) and species (e.g., NORDENSTAM et al. 2002; BELTRAN & BALDEON 2009; NOROOZI et al. 2010), new combinations (e.g., NORDENSTAM 1996, 1997, 1999; BELTRAN 1999; PELSER et al. 2006), discussions of nomenclature and typification (e.g., PÉREZ-MORALES 1997; NORDENSTAM 1997a, 2003, 2007; VELDKAMP & LUT 2009), and morphological treatments (e.g., OTIENO & TADESSE 1992).

Many of us have benefited from the *Compositae Newsletter* and it seems safe to say that without the efforts of BERTIL NORDENSTAM and the support of the Swedish Museum the journal would not exist today. So, from the synantherology community, we say *thank you* to both.





**Fig. 1.** BERTIL NORDENSTAM collecting *Compositae* in Lesotho, close to the Oxbow lodge, above the Tsehlanyane River at ca. 2700 m. Photo: VICKI A. FUNK.

TICA members are currently discussing the future of the *Compositae Newsletter*. So far everyone agrees that it should continue and most think that it will probably have to move to a mainly online journal perhaps similar to *Phytokeys*. No matter what is decided some means of support for the technical editing will have to be found. Also in this issue is a report on the TICA meeting in Montreal and it has additional information. Suggestions and members wishing to volunteer can email TICA ([synantherologist@gmail.com](mailto:synantherologist@gmail.com)).

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**Fig 2.** BERTIL NORDENSTAM collecting *Lamprocephalus* B. NORD. on the Waboosberg, Western Cape. Photo: GUNILLA NORDENSTAM 2006.



## News from The International Compositae Alliance 2012 Meeting

Submitted by VICKI A. FUNK & LUC BROUILLET

The 2012 TICA (The International Compositae Alliance) meeting was held at the Montreal Botanical Garden in Montreal, Canada where it was hosted by Professor LUC BROUILLET (MT). Although the number attending was lower than expected it was a young (mostly) and lively crowd with lots of discussion after most of the talks. Many interesting topics were presented, as you will see from the program and the abstracts that follow this brief message.

During the business meeting we had an open discussion on TICA and there are a few important things to report.

First, we took the opportunity to thank several of our members:

LUC BROUILLET, was thanked for organizing the meeting and field trip.

TORSTEN ERIKSSON (SBT) was recognized for his service as our Webmaster since TICA was started. TORSTEN and his family are moving to Bergen, Norway, for new jobs and he will no longer be able to manage the site. We deeply appreciate his efforts in helping TICA get started and his patience with questions from the members. MAURICIO DIAZGRANADOS (MO) graciously agreed to take over as Webmaster and he will be sending out information to the membership in September when he starts his postdoctoral Fellowship at the Smithsonian Institution.

BERTIL NORDENSTAM (S) has been the editor of the *Compositae Newsletter* (CN) for many years and he has announced that he is stepping down after volume 50 (this volume). Prof. NORDENSTAM was instrumental in changing CN into a proper journal and he pulled together each volume with the help of a Technical Editor. Many of us have benefited from the journal and we owe Prof. NORDENSTAM and The Swedish Museum of Natural History a debt of gratitude. We also thank the long-time Technical Editor GUNNEL WIRÉNIUS NOHLIN (starting with #24 in 1994).

Second, we decided to hold the next TICA meeting in conjunction with the XI Latin-American Botanical Association and the 64<sup>th</sup> Congresso Nacional de Botânica do Brasil, to be held jointly in Salvador, Brazil in 2014. This will be the first time we have met jointly with such a large group and we are all looking forward to it. Our colleagues in Brazil and other Latin American countries are many and several have already volunteered to help. We plan on having one symposium during the Congress that will feature many of our Latin American Colleagues and the work

they have done on understanding the diversity in the family. After the congress we discussed having a one-day meeting of short papers to see what everyone is working on and to encourage collaborations. NADIA ROQUE has offered to organize a field trip to Chapada Diamantia after the meeting.

Third, after a long discussion on the future of the *Compositae Newsletter* we decided that we should explore the possibility of publishing it electronically. Until now the journal has been supported by the Department of Phanerogamic Botany, Swedish Museum of Natural History, Stockholm, Sweden (S). Since 1988 they have provided a technical editor, and printed and mailed the journal to over 600 scientists and libraries around the world, free of charge. Our colleagues at S have been more than generous for many years and we thank them very much. The members present felt that it was unlikely that we would find another institution to take over this responsibility. A suggestion to model the electronic version after *Phytokeys* was discussed and some follow up with the staff at *Phytokeys* has been positive but this would require page charges and/or dues. Right now the journal needs a new editor and nominations are encouraged. All opinions and offers of help are welcome; they will be compiled and circulated to TICA members for comment ([synantherologist@gmail.com](mailto:synantherologist@gmail.com)).

Finally, it with sadness that we mention that ABUNDIO SAGASTEGUI, one of our members, died recently. Below, his colleague MIKE DILLON (F) has provided a few comments.

#### **ABUNDIO SAGÁSTEGUI ALVA (11 July 1932 - 26 May 2012)**

ABUNDIO SAGÁSTEGUI ALVA passed away on 26 May 2012 from complications due to an auto accident in Trujillo, Peru. Born in Guzmango, Cajamarca, SAGÁSTEGUI rose to prominence within the Universidad Nacional de Trujillo (HUT) and later the Universidad Privada Antenor Orrego (HAO). He was one of the most influential and prolific botanists in Peru, having collected well over 18,000 numbers and described nearly 90 species, mostly Asteraceae, including four new genera. No fewer than 30 species commemorate him, having been based upon his collections. His death is a great loss to Synantherology as well as to the botanical community as a whole.



**MONTREAL, JULY 15-19, 2012**

**PROGRAM**

**All activities occur at the Biodiversity Centre, Jardin botanique de Montréal**

**Sunday, 15 July**

17:00 to 19:00 – Biodiversity Centre Auditorium hall, Welcoming reception and registration

**Monday, 16 July**

08:30 registration

09:00 Welcoming to TICA 2012

09:15 BROUILLET, L. – Hommage to LES GOTTLIEB

09:30 BROUILLET, L. – The Evolution of the Compositae: introduction to the symposium

09:45 SCAGLIONE, D. – Progress in genome sequencing of lettuce and other Cichorieae and Cardueae species

10:30 Break

11:00 RENAUT, S. – The extent of genomic divergence among sunflower species with respect to their degree of geographic separation

12:00-13:30 Lunch

13:30 NOYES, R. – Apomixis in the Asteraceae: Still crazy after all these years



14:15 DIAZGRANADOS, M. – Frailejones (Espeletiinae CUATREC.): a recent rapid radiation shaped by the tropical Andes

15:00 Discussion on the Evolution of the Compositae: the future

17:00-21:00 River Cruise and Banquet

### Tuesday, 17 July

09:00 SMISSEN, R. – Using transcriptome data to test reticulate relationships among major clades of Gnaphalieae

09:30 CANTLEY, J. T. – Geoclimatic events of South America influence a west then northward progression of Neotropical Lepidaploinae (Vernoniae: Compositae)

10:00 SCHMIDT-LEBUHN, A. – Testing the monophyly of *Ozothamnus* and *Cassinia* (Asteroideae: Gnaphalieae)

10:30 Break

11:00 FUNK, V. A. – Biogeographic patterns in *Bidens* native to Pacific Oceania

11:30 MAGEE, A. – Systematics of southern African Anthemideae (Asteraceae): unraveling relationships within Pentziinae

12:00-13:30 Lunch

13:30 BENGTON, A. – Phylogeny and evolution of the *Metalasia* clade (Gnaphalieae-Asteraceae)

14:00 GARCÍA, F. – From Andean rainforests to high altitude Paramos: phylogenetic position, molecular dating and insights into the evolution and novel habits of lianescent and arborescent species of *Pentacalia*, *Monticalia*, *Dendrophorbium* and other relatives (Senecioneae)

14:30 Poster session

15:00 TICA meeting (informal discussion) – V. A. FUNK

### Wednesday, 18 July

09:00 URBATSCH, L. – Phylogeny of *Ericameria* and related genera of Astereae (Asteraceae) inferred from nuclear ribosomal and chloroplast sequence data

09:30 FUNK, V. A. – Systematics and Biogeography of the Liabeae (Compositae): an update

10:00 SANCHEZ, G. – A Phylogeny of the Gochnatieae: Understanding a critically placed tribe in the Compositae

10:30 Break

11:00 KEELEY, S. – New Understanding of the Phylogeny and Biogeography of the Vernonieae

11:30 SCHMIDT-LEBUHN, A. – Spatial diversity and collecting activity in the Australian native daisies (Asteraceae)

12:00-12:30 Discussion

12:30-13:30 Lunch

13:30 Guided tour of the Montreal Botanical Garden

## **Botanical Excursion**

### **Thursday, 19 July**

8:00 Departure for Vimy Ridge ultramafic formation

Evening: Supper and lodging in Québec City

### **Friday, 20 July**

9:00 Departure for Chute-Panet bog and return to Montreal

# The International Compositae Alliance (TICA) Montreal, Canada 15-19 July 2012

## ABSTRACTS

Compiled and edited by: LUC BROUILLET & VICKI A. FUNK

### A Tribute to LES GOTTLIEB

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The TICA 2012 meeting is dedicated to the memory of Dr. LES GOTTLIEB, a life-long student of evolution using *Stephanomeria* (Compositae, Cichorieae) and *Gilia* (Polemoniaceae) as models. Born in New York City, he finished his Ph. D. at the University of Michigan in 1969; his topic was speciation in *Stephanomeria*. He spent his entire career as a plant evolutionary biologist at the University of California-Davis. His early studies focused on the process of speciation using *Stephanomeria* as a model system, where he documented homoploid hybrid speciation, polyploid speciation, and sympatric speciation, using isozyme data. The last case was particularly interesting since it involves the diploid *S. malheurensis* GOTTLIEB, which originated within a population of its progenitor, *S. exigua* subsp. *coronaria*. Dr. GOTTLIEB made an outstanding demonstration of this speciation event, investigating numerous aspects of the phenomenon. In addition he published many papers on fundamental issues in evolution and systematics. More recently, he contributed to phylogenetic studies within the tribe Cichorieae in western North America, and he wrote *Stephanomeria* and relatives for the *Flora of North America*. Dr. GOTTLIEB was an outstanding example of an evolutionary scientist who used Compositae as a model system, while contributing to the systematics of the group and so inspired a generation of young systematists to think more broadly and to always strive to understand the context of the morphology they were documenting.



# Symposium: Compositae Evolution

(ALPHABETICAL BY AUTHOR)

## The Evolution of Compositae: an introduction

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The study of the evolution of Compositae has two facets: the study of the evolution of Compositae groups and the study of evolution using Compositae as model organisms. In recent years, while Comps systematists were busy developing a global phylogeny and biogeography of the family, other researchers were making progress in several fields related to their evolution: paleobotany, development, phylogeography, reproduction, speciation and genomics. The need of dated fossils to calibrate Compositae phylogenies has been partly filled recently by the discovery of fossil mutisioid-carduoid heads from the Eocene of Patagonia (BARREDA et al. 2010), as well as pollen of the same age from the southern hemisphere, dating the origin of Comps to about 50 ma. New insights into the origins of the capitulum were provided by a developmental study of Calyceraceae inflorescences, showing the cymose origin of the Comp head (POZNER et al. 2012). On the developmental genetics front, a study of the genes controlling head and floret development in Comps since the late 1990s has resulted in the development of a model of head development in Comps (LAITINEN et al. 2006), as well as in comparative studies. The Compositae are also known for their sporophytic self-incompatibility system, the genetics of which has started receiving attention (e.g. HISCOCK et al. 2003), a major development given its consequences for the evolution of species in the group. Another reproductive system studied well is agamospermy (apomixis), which has been examined in many taxa from genetic and evolutionary standpoints. Phylogeographic studies have been relatively scarce in the family but have provided insights into the evolution of some species or species groups, notably in *Senecio* and relatives. The study of speciation and its genetic aftermaths has been the object of in-depth studies in many genera, most notably in *Helianthus* (RIESEBERG lab) and in *Tragopogon* (SOLTIS lab), including molecular, cytological and genomic approaches. In the genomics field, a new genome size database was developed (<http://www.asteraceae-genomesize.com/>) for the family. But the main

recent progress has been the complete sequencing of the chloroplast genome of lettuce and sunflower (TIMME et al. 2007), as well as the recent sequencing of the nuclear genome of these two organisms (MICHELMORE and RIESEBERG labs), which will soon be made available to the community. Genomics has already shown that the Compositae genome was subjected to multiple polyploidization events (BARKER et al. 2008). These new developments in Compositae research will open the door to new venues of research and new tools for the students of Comp phylogeny, and reciprocally, evolutionary biologists will benefit from better and more detailed phylogenies.

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## **Frailejones (Espeletiinae CUATREC.): a recent rapid radiation shaped by the tropical Andes**

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The páramo ecosystem, located above the tree line in the tropical Andes, has been the setting for some of the most dramatic recent rapid plant radiations. With an estimated age of 2-4 million years, the páramo is the world's most diverse high-elevation ecosystem. Today 141+ species of frailejones (subtribe Espeletiinae CUATREC., Asteraceae) dominate this ecosystem. Frailejones have intrigued naturalists and botanists, not just for their appealing beauty and impressive morphological diversity, but also for their remarkable adaptations to the extremely harsh environmental conditions of the páramo. The most recent classification of the subtribe has eight genera (*Carramboa*, *Coespeletia*, *Espeletia*, *Espeletiopsis*, *Libanothamnus*, *Paramiflos*, *Ruilopezia* and *Tamania*). Previous attempts to reconstruct the evolutionary history of this group failed to resolve relationships among genera and species, and there is no agreement regarding the classification of the group. For this study, sequence data included nrDNA (ITS and ETS) and cpDNA (rpl16), for a total of 2954 aligned bp. Fragment analysis was performed with AFLP data using 28 primer combinations and yielding 1665 fragments. Phylogenies reconstructed suggest that various clades are monophyletic, but the phylogenetic signal may be misled by hybridization and incomplete lineage sorting. The origin of the subtribe in Venezuela is supported. A shallow phylogeny with short branches and the impressive morphological diversity suggest a recent rapid radiation. A Monte Carlo permutation test shows a very strong geographic structure in the phylogeny. Venezuelan páramos show more phylogenetic overdispersion, whereas Colombian páramos generally exhibit phylogenetic clustering, with sympatric species closely related to each other.



## Apomixis in the Asteraceae: Still crazy after all these years

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The Asteraceae is commonly listed as one of the principal families within which asexual reproduction by seed, i.e., apomixis, is prolific. Critical review of the literature indicates that naturally occurring apomixis is robustly indicated for 22 genera in seven tribes of Asteraceae, all but one of which occurs in subfamily Asteroideae. Consideration of 45 additional reports indicates that apomixis for 30 genera is contra-indicated, documenting possible developmental abnormalities in otherwise sexual taxa. Data are strongly indicative or equivocal for effective apomixis for an additional fifteen genera, but thorough documentation is wanting. Thus our state of knowledge of apomixis in the Asteraceae is generally poor. Apomixis has been extensively investigated for three genera of Asteraceae: *Erigeron*, *Hieracium* (*Pilosella*), and *Taraxacum*. Evidence from crossing and developmental studies in these taxa indicates that apomixis in the Asteraceae is generally facultative, resulting from the occasional production of reduced megagametophytes that can participate in biparental reproduction. For instance, for *Erigeron annuus*, data indicates that individual plants, on average, produce >2% ovules that undergo meiotic rather than apomeiotic division of the megasporocyte. Strict apomictic development occurs, but is rare. From a biosystematic perspective, some of the biggest challenges in apomixis biology include 1) understanding why apomixis occurs in some taxa but not in others, 2) interpreting the number of unique origins of apomixis within complexes, 3) elucidating the environmental and demographic conditions that favor the evolution of apomixis in populations, and, 4) determining how the genes for apomixis can spread to sexual populations by pollen.

## **The extent of genomic divergence among sunflower species with respect to their degree of geographic separation**

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Levels of differentiation among populations can be highly variable across the genome. During allopatric speciation, divergence should accumulate across the genome due to the action of both drift and selection. In contrast, during speciation with gene flow, accentuated divergence should be restricted to loci under divergent natural selection. Here, we report on high resolution genomic scans of differentiation among several pairs of sunflowers (*Helianthus* spp.) taxa that vary in their divergence time and degree of geographic separation. We find that in all comparisons, genomic regions of divergence are numerous and small ( $< 1$  centiMorgan). In addition, the proportion of divergent loci fixed by selection was higher in sympatric (43%) than allopatric species pairs (24%), thus confirming the more prominent effect of selection in shaping genomic divergence in sympatry. Lastly, we also find that among independent species pairs, patterns of genomic divergence are surprisingly repeatable, especially in highly differentiated regions. This is due, at least in part, to a repeatable heterogeneous pattern of recombination rates along the genome in independent species pairs. In conclusion, the genomic clustering of highly divergent loci is not influenced by the extent of ongoing gene flow, but probably by other factors such as recombination rates.

## Progress in genome sequencing of lettuce and other Cichorieae and Cardueae species

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The Compositae Genome Project (<http://compgenomics.ucdavis.edu>) is a collaborative project to analyze genetic diversity in the Compositae plant family. Lettuce, an economically important member of this family, is being studied to correlate genotype with phenotypic variation in domestication and agriculturally significant traits. Several resources have been generated including lettuce transcriptome, gene-space, and whole genome assemblies. The whole genome of *Lactuca sativa* cv. Salinas has been sequenced in collaboration with the BGI and a consortium of ten breeding companies. From ~70x coverage with high quality, filtered Illumina reads, 2.5 Gb (93% of the entire genome) was assembled into scaffolds with a N50 of 461,580 bp. Over 11,000 loci from an ultra-dense, transcript-based genetic map was used to assess the quality of the assembly. Over 95% of 3,100 scaffolds that had multiple unigenes were genetically validated and could be ordered in chromosomal linkage groups. The resulting data are displayed using GBrowse. More scaffolds are being assigned to chromosomal linkage groups using genotyping by sequencing of 99 RILs from the reference *L. sativa* cv. Salinas x *L. serriola* mapping population. Chromosomal orders are being refined using population and syntenic information. Approximately, 45,000 gene models have been predicted using several automated annotation pipelines. Manual curation of these models is underway to refine the annotations. The genome sequence is being used to clone and functionally validate genes for disease resistance and development. Generation of ultra-dense maps of chicory and artichoke has also been initiated.



## General Papers

(ALPHABETICAL BY AUTHOR)

### Phylogeny and evolution of the *Metalasia* clade (Gnaphalieae-Asteraceae)

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*Metalasia* is an endemic South African genus of ericoid shrublets in the tribe Gnaphalieae, currently consisting of 57 species with their main distribution in the Cape Floristic Region. Like many other CFR plant clades most species of *Metalasia* have very narrow distributions whereas a few are found over larger areas. Earlier studies based on morphological data alone have tried to disentangle the relationships between *Metalasia* and its allies, but until the present project was initiated, no analyses of molecular data had been performed. Our initial study based on DNA sequence data gave support for a monophyletic *Metalasia* clade comprising eight genera and indicating that some generic realignments may be necessary. The focus of the subsequent work has been a larger study including all currently recognized species of *Metalasia*, utilizing a combination of molecular and morphological data. In contrast to the prevailing cladistic hypothesis from morphological data, our phylogeny show that the species of *Metalasia* form two equally sized, well-supported evolutionary lineages with different distribution, and that *Metalasia* in its current sense is paraphyletic. Biogeographical analyses will reveal more about the evolutionary history of the *Metalasia* clade.

## **Geoclimatic events of South America influence a west then northward progression of Neotropical Lepidaploinae (Vernonieae: Compositae)**

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The historical biogeography of the open canopy dry habitats that cover much of South America remains largely unexplored despite detailed reconstructions of paleogeology and paleoclimatology. To test the floristic biogeographical relationships of these habitats the systematic and biogeographical relationships in the Lepidaploinae were investigated. The Neotropical Lepidaploinae is the largest and most broadly distributed subtribe of tribe Vernonieae: Compositae. A molecular phylogeny was constructed for 91 species of the Lepidaploinae using three chloroplast DNA regions (*trnLc-f*, *ndhF*, *matK*) and the nuclear ITS region. Biogeographic and molecular clock analyses indicate that the Lepidaploinae originated on the Brazilian Shield about 20-12.5 mya. The subsequent diversification of five major lineages is closely tied to geologic and climatic events in South America such as the Andean uplift, periodic lowland marine/freshwater incursions and the development of the Amazon Rainforest as an exclusionary habitat barrier. As new suitable habitat was formed on a changing South American continent, Lepidaploinae lineages advanced westward from the Brazilian Shield to the Andes; and then northward, following the uplift of the Andes Mountains. The timing of diversification of *Lessingianthus* s.s. in Cerrado habitat is correlated to the worldwide rise in C4 grasses. *Lepidaploa* s.s. lineage reached Central America and the West Indies within the last four million years, coincident with the closure of the Isthmus of Panama and long distance dispersals, respectively. Overall, the lineage diversifications of subtribe Lepidaploinae may indicate how South America's complex paleogeoclimatic history have influenced the evolution of Lepidaploinae as well as other angiosperm lineages.

## Biogeographic patterns in *Bidens* native to Pacific Oceania

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The genus *Bidens* (Compositae or Asteraceae: Coreopsideae) has over 200 species and includes 37 species in Pacific Oceania. Most species are from Hawaii or French Polynesia but a few other species are scattered in other parts of the Pacific region. Over one hundred samples from the *Bidens* and related genera of the Coreopsideae have been chosen for testing using specific nuclear and chloroplast markers. Specifically, ITS, ETS, *rpl132trnL*, *psbA*, and *trnQrps6* regions were used. Do all of the *Bidens* found in the Pacific region form a monophyletic group? Yes and No. All species from the Hawaiian Islands, the Marquesas, and the Society Islands form a monophyletic group although relationships among the species found on each islands are still under investigation. But species from Australia, Starbuck Island, and Socorro Island are from independent lineages within the genus. Where are the closest relatives of the *Bidens* in the Pacific region? Previous work indicated that *Bidens* from western North America might be the closest relatives for the Hawaiian species and this is supported by this research. How does the biogeography of *Bidens* compare to other members of the Compositae in Pacific Oceania? Of the 164 species of Compositae native to Pacific Oceania, *Bidens* has the most diverse distribution and is one of the four lineages whose ancestry can be traced to Western North America.

## Systematics and Biogeography of the Liabeae (Compositae): an update

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The tribe Liabeae (Compositae) contains ca. 175 species distributed in 18 genera and its members occupy a variety of habitats in Andes Mountains of South America as well as Mexico, Central America, and the West Indies. The tribe is characterized by a combination of morphological characters, including opposite leaves with white-tomentose pubescence beneath and often with venation strongly trinervate, yellow ray and disk florets, oblong or columnar achenes usually with a biseriate pappus that frequently consists of outer scales and inner scabrous bristles, and the frequent occurrence of latex. DNA sequence data from the nuclear ribosomal ITS region and four chloroplast regions (*trnL-F*, 3' end of *ndhF*, *matK*, *psbA*; a total of more than five kb of sequence data) were used to infer a phylogeny. The data were analyzed using Maximum parsimony, Maximum likelihood, and Bayesian inference posterior probabilities. The results support the monophyly of the tribe and show a consistent placement for all genera except *Cacosmia* (3 species). Four well-supported clades are recovered in the remainder of the tribe, all recognized as subtribes. Liabineae are the sister group of the rest of the tribe. Sinclairineae are the sister group of Munnoziinae plus Paranepheliinae. The genus *Bishopanthus* could not be confidently placed in any of the subtribes; molecular study is not possible. The phylogeny slightly alters the previous assumptions about the biogeography and it seems that the Liabeae originated in the Central and Northern Andes and spread north and south with several independent introductions into Mexico and Central America and one into the Caribbean. With the exception of the Liabeae (Andes) and Moquineae (Brazil), all of the tribes in the subfamily Cichoroideae are either restricted to or have their basal grade in Africa.



**From Andean rainforests to high altitude Páramos:  
phylogenetic position, molecular dating and insights into  
the evolution and novel habits of lianescent and arborescent  
species of *Pentacalia*, *Monticalia*, *Dendrophorbium* and other  
woody relatives (Senecioneae)**

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The high Andes of South America provide a number of geographically and ecologically isolated systems inhabited by plants showing highly modified morphological characters. In this study, sequences from the ITS region of nuclear ribosomal DNA are used to test previous hypotheses about the phylogenetic position of divergent Andean genera, classified in subtribes Tussilaginiinae and Senecionineae. Gene phylogenies based on maximum parsimony and maximum likelihood reveal relationships of arborescent Andean Tussilaginiinae like *Gynoxys*, *Paragynoxys* and *Aequatorium* to Central and North American Tussilaginiinae (*Pittocaulon*, *Robinsonecio*), whereas a genus (*Acrisione*) appears related to a New Zealand clade. We also analyzed the controversial definition of the scandent species of the genus *Pentacalia* in relation to its segregates of erect, high altitude species of *Monticalia* sensu C. JEFFREY. The purpose was to test the hypothesis of a high altitude origin of scandent forms (i.e. *Pentacalia* species) from erect Monticalioid ancestors, with an ulterior process of etiolation, all this resulted in a huge radiation of vine species. Arborescent species of *Dendrophorbium* appear as ancestral forms of another independent vine clade. Viny taxa (e.g. *Cabrieriella*, *Pentacalia cuatrecasana*, *Pentacalia rugosa*) from Sierra Nevada e.g. Santa Marta (a Cretaceous mountain range isolated from the Andes) appear in different clades, but always in an ancestral position related to core representatives of each clade. Also presented is a phylogenetic dating of Senecioneae based on parametric methods (Multidivtime) and six fossil references. The results suggest a vicariant event separating the three clades of the tribe by the end of upper Miocene, coinciding with Miocene Climatic Optimum. Divergence of South American Senecioneae is discussed in the context of Middle Miocene Caribbean and Andean tectonics.

## **New Understanding of the Phylogeny and Biogeography of the Vernoniaeae**

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The tribe Vernoniaeae is among the largest in the Compositae with ca. 1500 taxa. There are two centers of diversity, southern Brazil in the New World and southeastern Africa in the Old World. The previous molecular phylogeny indicated an African/Madagascan origin for the tribe with a basal grade of Old World taxa from which New World species arose. Subtribal/generic relationships within and between hemispheres remained unclear, however. A new phylogeny based on chloroplast and nuclear DNA sequence data of over 300 taxa provides insight into subtribal relationships and dispersal pathways. Africa is confirmed as the ancestral region for the extant members of the tribe and the original source of both New and Old World lineages. Australian and all but one lineage from Southeast Asia (not including India) are of the result of dispersals from African ancestors and suggest a possible route to Hawaii. There was at least one back dispersal from the New to the Old World giving rise to a clade of Southeast Asian taxa. New World Vernoniaeae are monophyletic and apparently the result of a single dispersal from Africa to Brazil. Within the Americas movement can be traced from southeastern Brazil, along the Andes, to Central America and Mexico and the West Indies in several clades including the largest subtribe, the Lepidaploinae. Lineage diversity is limited in eastern North America. Subtribal and generic delimitations will need revision especially in the Old World Erlangeinae, Centrapalinae and Linziinae and the New World Lepidaploinae and Piptocarphinae.

## Systematics of southern African Anthemideae (Asteraceae): unraveling relationships within Pentziinae

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The southern African taxa comprise the earliest diverging lineages within the largely northern hemisphere tribe Anthemideae. Improved understanding of the evolution, diversification and biogeographical history of these southern African lineages is therefore crucial. Generic and species delimitations are, however, far from satisfactory. As a result taxonomic and phylogenetic investigations need to be conducted concurrently. The interesting phylogeographical link between the Pentziinae and the northern hemisphere subtribes and the disjunct north-south distribution of *Pentzia* made this subtribe a clear choice as the starting point for broader systematic studies of southern African Anthemideae. The Pentziinae comprise seven almost-exclusively southern African endemic genera (*Cymbopappus*, *Foveolina*, *Marasmodes*, *Myxopappus*, *Oncosiphon*, *Pentzia* and *Rennera*) and ca. 59 species. Several of the genera in the subtribe were previously united under *Pentzia*. Despite this there remains doubt regarding the monophyly of *Pentzia*, particularly in relation to *Cymbopappus* and *Marasmodes*. It is clear that a re-assessment of generic delimitations within the subtribe should be coupled with a comprehensive taxonomic revision of the central genus *Pentzia*. The genus comprises ca. 27 species and has not been revised since the now outdated synopsis of HUTCHINSON in 1917. Generic delimitations and relationships within the Pentziinae are explored using morphological, anatomical and molecular sequence data (*ndhF*, *psbA-trnH*, *rpl32-trnL*, nrITS). Phylogenetic analyses for 71 accessions (49 species) representing 87% of the subtribe indicates that several of the genera are not monophyletic as currently circumscribed. This is further corroborated by morphological and anatomical characters.

## A phylogeny of the Gochnatieae: Understanding a critically placed tribe in the Compositae

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The Gochnatioideae clade is basal to most Asteraceae, excluding the Barnadesioideae, Stiffitioideae, Mutisioideae, and Wunderlichioideae clades. Gochnatieae, the only tribe of Gochnatioideae comprises four genera: *Cnicothamnus*, *Cyclolepis*, *Gochnatia*, and *Richterago*. The recognition of Gochnatieae was the result of resolving the polyphyly of the Mutisieae suggested on the base of morphology. The tribe Gochnatieae can be defined by a combination of morphological characters, although these features are present in other basal clades. By far, *Gochnatia*, which traditionally includes about 70 species, is the most complex of the tribe and a key taxon to understand Gochnatieae. Within *Gochnatia*, some groups of species, treated as sections, are morphologically well defined and identifiable. Recently, some of the traditional sections of *Gochnatia* have been treated at the genus rank. However, until the present study, a comprehensive and complete phylogenetic analysis including most of its representative species has not been carried out. Our results suggest a paraphyletic *Gochnatia* that is here resolved by the circumscription of segregate genera, some of which are already established and other of which are new. Some morphological characters support these new genera and allow us to present a new comprehensive classification of Gochnatieae.



## Testing the monophyly of *Ozothamnus* and *Cassinia* (Asteroideae: Gnaphalieae)

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The Australian and New Zealand shrubby everlastings of the genera *Ozothamnus* and *Cassinia* and their small satellites represent about 100 species or ca. 10% of the Australian daisy flora. Generic delimitations in the group have long been controversial and subject to revision. In their current circumscription, the two large genera are differentiated based on the presence or absence of paleae and the shape of the phyllaries, although several exceptions exist. It is suspected that at least more heterogeneous *Ozothamnus* is non-monophyletic, and that several of the smaller genera in the group may constitute apomorphic segregates (defined merely by loss of the pappus, etc.), but no comprehensive phylogenetic study had been undertaken. We have produced a molecular phylogeny based on very broad sampling and using nuclear ITS, ETS and chloroplast *psbA-trnH*, *matK-psbA* and *ycf6-psbM* regions. We submitted sequences from the two main genera to Templeton and K-H-Rell tests to compare phylogenies from constrained analyses statistically against the best trees from unconstrained analysis. We found *Ozothamnus* to be non-monophyletic even in a very narrow circumscription, i.e. after the removal of section *Hebelaena* and several other divergent species. *Cassinia*, on the other hand, is likely a natural group. Nuclear data suggest that *Calomeria*, *Cassinia*, *Hackeria* and *Odixia* are nested in *Ozothamnus*; chloroplast data provide poorer resolution and a somewhat contradictory topology but the results of the constraint tests are identical for both datasets.

## Spatial diversity and collecting activity in the Australian native daisies (Asteraceae)

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Australia is home to ca. 1,000 currently recognized species of native Asteraceae, 50% of them Gnaphalieae, 30% Astereae, 10% Senecioneae. We conducted spatial analyses at the 1° scale to examine the distribution of species richness, collecting activity and various measures of phylogenetic diversity. In a first step, we queried all Asteraceae specimen data from Australia's Virtual Herbarium, removed duplicates and deleted all specimens lacking point data and all geographic outliers. The final dataset comprised 114,537 collections of 968 species. Three different approaches of inferring species diversity were compared; the results were broadly equivalent, with the twenty hotspots found in the south-east of the continent and Tasmania in all cases. Reliance on documented species numbers is direct but leads to a distorted perception of the relative local diversity due to very uneven collecting efforts. The Chao 1 estimator of species richness corrects those distortions but is unavailable for about 50% of Australia due to insufficient local collections. Finally, a distribution modelling approach provides inferences for all of Australia but overestimates species numbers across the board. To obtain branch lengths for phylogenetic diversity, a molecular phylogeny (ITS, *psbA-trnH*, *matK*, *trnL-trnF*) was generated with 159 of the 164 genera as OTUs. Phylogenetic diversity was inferred to be high in the south-west and south-east, and phylogenetic endemism to be high in the tropical north, the south-west, Tasmania and in border ranges between Queensland and New South Wales.

## **Using transcriptome data to test reticulate relationships among major clades of Gnaphalieae**

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Previously we have postulated ancient allopolyploid origins for several diverse and widely distributed clades of Compositae tribe Gnaphalieae on the basis of low copy number nuclear gene phylogenies. Presently we are making use of massively-parallel sequencing technology to further test and elaborate our hypotheses. Using the Roche GS-Junior platform we have generated between 38 and 52 Megabases of sequence for four species of Gnaphalieae, two putative allotetraploids and two putative diploids. We are employing two approaches to incorporate these data into our research. Firstly, we are using assembled cDNA sequences to characterise additional genes for amplification by PCR and phylogenetic analysis. Secondly, we are attempting to identify orthologous sequences from the transcriptome assemblies and conduct phylogenetic analyses of these directly. Although preliminary results are consistent with our hypothesised allopolyploid relationships, at the level of phylogenetic divergence across the tribe, both approaches are proving difficult to implement. As is the case in most phylogenetic studies using nuclear genes, establishing orthology/paralogy relationships among sequences is a major problem. This talk will present an update of evidence suggesting the importance of allopolyploidy in the phylogeny of the tribe Gnaphalieae and discuss challenges posed by phylogenetic analysis of genome scale data sets.

## The *ycf1* and other chloroplast gene regions for phylogenetic assessment of tribe Astereae

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Species centered about *Ericameria* and their derivatives are abundant in western North America especially in the California Floristic Province, the Great Basin, and Rocky Mountains. The *ycf1* chloroplast region was sequenced in approximately 100 representative taxa. Datasets were aligned using T-Coffee and manually adjusted. Variable and parsimony informative sites were obtained using MEGA 5. Models were chosen for each using the AIC criterion implemented in jModelTest, and all analyses were run using the GTR model. The analyses were run using MrBayes on the CIPRES portal. Trees represent a 50% majority-rule consensus tree of post-burnin trees from 4 independent runs constructed using the sumt command in MrBayes. The great success story in these investigations has been *Ericameria*. Various workers have shown it to be comprised of species traditionally accommodated in *Chrysothamnus*, *Macronema*, *Haplopappus* sect. *Asiris*, and *Stenotopsis*. ITS, ETS, and chloroplast markers robustly support this clade. *Chrysothamnus*, a long recognized genus, is not supported by any of the data sets. Comparisons between the ITS/ETS and chloroplast regions among the other entities investigated will be made. Data from *ycf1* sequences of basal Astereae and taxa from different geographic regions suggests that it is an appropriate candidate DNA region for further testing the phylogeny for tribe Astereae.



## Posters

(ALPHABETICAL BY AUTHOR)

### **Taxonomic revision of *Baccharis* subgen. *Tarchonanthoides* (Compositae: Astereae): a group from the South American grasslands and savannahs**

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*Baccharis* L. is a New World genus with about 400 species and broadly characterized by the tufted indumentum of trichomes with a single adjoining basal cell and the unisexual florets, mostly in different specimens (dioecy). Five subgenera are currently recognized: *Baccharis* (180 species), *Molina* (PERS.) HEERING (130 species), *Pteronioides* HEERING (60 species), *Stephananthus* (LEHM.) HEERING (four species), and *Tarchonanthoides* HEERING (23 species). A taxonomic revision and a phylogenetic analysis of *Baccharis* subgen. *Tarchonanthoides* are underway. This work summarizes the first results of the taxonomic revision. *Baccharis* subgen. *Tarchonanthoides* is characterized by the corollas of female florets with five papillose teeth and by the nearly fully cleft style apex of male florets; moreover this subgenus lacks the tufted indumentum characteristic of most *Baccharis* species. The subgenus occurs in the South American grasslands and savannahs from Southeastern Brazil to Western Bolivia, south to Central and Eastern Argentina, with the greatest diversity in Southeastern Brazil and Uruguay. Currently, 23 species and 10 synonyms are recognized within the subgenus, as a result of the revision of the 33 names previously published, the description of three new species and the proposition of a new combination and status. Additionally seven lectotypes are chosen. Morphologically, the species of the subgenus are classified into four sections: *Canescentes* GIULIANO (nine species), *Coridifoliae* GIULIANO (nine species), *Curitybensis* GIULIANO (three species), and *Tarchonanthoides* (HEERING) CUATREC. (two species). However, changes in the circumscription and composition of the sections may take place when results of the forthcoming molecular phylogenetic studies will be completed.

**Within-population variation of floral morphology in  
*Aster hispidus* var. *tubulosus*: its relationship to microhabitat  
and to pollinators**

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Within-population variation in floral morphology provides an ideal study system to understand plant diversification through adaptive evolution. *Aster hispidus* var. *tubulosus*, an endemic variety of *A. hispidus* complex in Japan, shows extreme within-population variation in floral morphology, from ligulate to long tubular ray florets in the outermost wheel of the capitulum. In this study, we examined whether this variation can be attributed to environmental factors of their habitats. The study population was subdivided into small patches alongside the river, which differed in the micro-environment and the frequency of floral types. According to a two-year survey, we found that the frequency of individuals with long tubular ray florets is negatively correlated with the degree of coverage of the patches. We hypothesized that the observed correlation was due to different selection pressures acting on floral morphology (presumably genetically controlled), which might depend on the degree of coverage of the patches. We also investigated whether morphology of outermost florets affects pollinator attraction in the field. As a result, we found that the ligulate ray florets have an advantage in attracting pollinators over the long tubular ray florets. We will discuss possible adaptive significance of long tubular ray florets and a mechanism of maintaining continuous floral variation in this species.

**Phylogenetic study of *Mikania* WILLD.  
(Compositae – Eupatorieae):  
a preliminary analysis**

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*Mikania* WILLD. contains ca. 450 species, it is the largest genus of Eupatorieae and one of the greatest of Compositae. It has a pantropical distribution, but its richness is concentrated in South America. The species of the genus are vines or shrubs, with heads composed of four florets and four phyllaries. Because of its size, taxonomic revisions are difficult to be performed. Infrageneric classifications have been proposed since the nineteenth century, mainly based on species habits, leaf shape and arrangement of the heads. Although there are few doubts about the monophyly of the genus, phylogenetic studies have never been performed to evaluate whether suggested infrageneric taxa are monophyletic. The present work is a preliminary analysis towards a more comprehensive molecular phylogeny of the genus. Sequences of approximately 900 bp of the Internal Transcribed Spacer (ITS) were obtained for 20 species of *Mikania*. The parsimony analysis resulted in four cladograms in which two main clades with high jackknife support emerged, each one comprising species of different habits and types of inflorescence. However, it is necessary to include more terminals and to analyze additional molecular markers in order to have a clearer picture of the relationships within *Mikania*.

# On the identity of *Pluchea incisa* ELMER, with notes on the genera *Blumea* and *Pluchea* (Asteraceae-Inuleae)

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## Abstract

The species *Pluchea incisa* ELMER is discussed after investigation of floral micro-characters of the stamens and style. It is concluded that it is not a member of *Pluchea* or the Inuleae-Plucheinae, but instead belongs in the genus *Blumea* of the Inuleae-Inulinae.

## Introduction

The species *Pluchea incisa* was described by ELMER (1908) as belonging to CANDOLLE'S *Pluchea* section *Hebephora* (CANDOLLE 1836), a small group with two species (*P. hirsuta* and *P. scabrida*). The notion that *Blumea* and *Pluchea* are two closely related genera of the Inuleae is a traditional view founded on the fact that in both, the outer female florets are tubular or filiform, whereas the inner ones are male or bisexual. To MERRILL & MERRITT (1910) *Pluchea incisa* instead appeared to be a species of *Blumea* related to *B. chinensis* (L.) DC., and it was moved to that genus as *B. incisa* (ELMER) MERR. No characters in particular were put forward in support of this opinion, other than an impression of overall similarity. In a revision of *Pluchea*, KING-JONES (2001) mentioned that ELMER'S *Pluchea incisa* was likely belonging to another genus but without giving any statement of an alternative placement. Among other things she put forward the yellow flowers, subscaudent growth habit and capitula arranged in a racemose fashion as characters indicating a placement outside of *Pluchea*. In this context it may be worthwhile to recapitulate the difference between the two genera *Blumea* and *Pluchea*.



### Taxonomic background

In the first cladistic study of the Inuleae, ANDERBERG (1989) concluded that *Blumea* and *Pluchea* belonged to different major lineages. The analyses were based on morphological characters, several of which were floral micro-characters. Among other things, the styles of *Pluchea* were found to have sweeping-hairs that were rather long and distinctly obtuse, and also distributed a long distance down the shaft below the bifurcation of the style. In *Blumea*, the well-developed sweeping-hairs were more or less acute and confined to the style branches or sometimes diminishing in size and extending down to the bifurcation or just below. Acute sweeping-hairs like in the *Blumea* kind of styles were found in genera of the subtribe Inulinae in e.g. *Inula* and *Pulicaria*, whereas the *Pluchea* kind of style was typical of genera such as *Epaltes*, *Laggera*, *Nicolasia*, and *Sphaeranthus*. The stamen filament collars in many *Pluchea* species have characteristically swollen cells, whereas the filament collars in stamens of *Blumea* are always of a flat, quadrangular shape. An interesting discovery was that the *Pluchea* kind of styles was also found in two African species of *Blumea* (*B. cafra* and *B. bovei*), and the genus *Doellia* was later described to accommodate these two species (ANDERBERG 1995). In some modern African flora treatments, *Doellia* has not been accepted and its species are still included in *Blumea* (BEENTJE 2002, 2006), disregarding the difference in style morphology. The conclusion that *Blumea* and *Pluchea* belonged to different evolutionary lineages, and that *Doellia* belonged in the Plucheinae clade together with *Pluchea* rather than with *Blumea*, has been corroborated by analyses of DNA sequence data by ANDERBERG et al. (2005) in which two major clades of genera were identified, corresponding to the subtribes Inuleae-Inulinae and Inuleae-Plucheinae, respectively. All genera of the Inulinae clade also showed a 3 bp insertion in *ndhF* that was not present in any genus of the Plucheinae clade. Interestingly, *Doellia* with its plucheoid stilar sweeping-hairs (ANDERBERG 1995, Fig. 1 F) also lacked this 3 bp DNA insertion. The distinction between *Blumea* and *Pluchea* is clear-cut, and if DNA sequences of *ndhF* are not obtainable, the shape of the stilar sweeping-hairs and filament collar cells may give a good indication of which genus a plant belongs to.

A first detailed investigation of styles in loose flowers from the type specimen of *Pluchea incisa* could either give support to MERRILL's opinion, or indicate that the plant belongs to another genus as suggested by KING-JONES (2001).

### Methods, Results & Discussion

Flowers were soaked in water, dissected and mounted in Hoyer's solution (ANDERSON 1954) for microscope investigation of floral micro-characters. The

anthers have almost unbranched tails, the endothelial tissue has radial wall thickenings and the filament collar is well developed and formed by slightly elongated quadrangular cells, and they are not swollen. The stylar sweeping-hairs are acute at the distal and median part of the style-branches but become shorter and more obtuse towards and just below the bifurcation where they disappear. Judging from the overall morphology of the plant, and by investigation of the floral micro-characters, I feel convinced that MERRILL & MERRITT (1910) were right in assuming that *Pluchea incisa* is a species belonging in *Blumea*.

### Investigated material

Philippines. Benguet, Island Luzon, Baguio. ELMER 8396 (K, L).

### Acknowledgements

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# Ray-florets in *Chiliadenus* (Asteraceae-Inuleae), discovered. An epigenetic phenomenon?

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## Abstract

Two specimens of *Chiliadenus rupestris* (Asteraceae, Inuleae) having capitula with one or two ray-florets have been discovered. The genus *Chiliadenus* is one of few in the Inuleae-Inulinae where capitula are consistently consisting of hermaphroditic disc-florets only. A discussion of the trait is presented, and the morphology and characteristics of the ray-florets are described and illustrated.

## Introduction

The species of *Chiliadenus* CASS. have formerly been included in either *Jasonia* CASS. or *Varthemia* DC., but the genus was again recognized as distinct from these two by BRULLO (1979), who e.g. stated that one difference between *Jasonia* and *Chiliadenus* was that the former has radiate heads with distinct ray-florets whereas the latter has discoid heads with hermaphroditic tubular disc-florets only. The genus *Chiliadenus* has nine species distributed around the Mediterranean, and has consistently (e.g., QUEZEL & SANTA 1963, TUTIN 1976, FEINBRUN-DOZHAN 1978, ALAVI 1983, BOLÓS & VIGO 1995, BOULOS & HIND 2002, VOGT 2002, ANDERBERG & ELDENÄS 2007, BLANCA 2009) been presented as a genus with discoid capitula composed of hermaphroditic tubular disc-florets only. In taxonomic treatments and determination keys, there is no information on variation in this character and to my knowledge there is no reference in the literature mentioning presence of ray-florets in species today placed in *Chiliadenus*. Two specimens of *Chiliadenus rupestris* (POMEL) BRULLO have now been found, both with capitula provided with ray-florets.

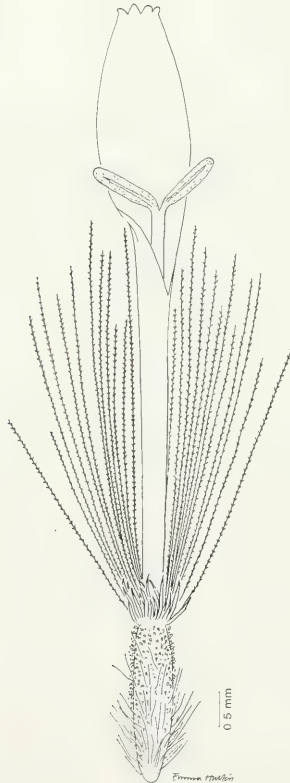


## Material and methods

The two radiate specimens were both collected at Beni-Snassen in Northern Morocco [JURY 13031 (BC, RNG, S) and JURY 15481 (RNG)]. Ray-florets were soaked in water and mounted in Hoyer's solution (ANDERSON 1954) for microscope investigation.

## Results

In the cladistics analysis of the Inuleae of ANDERBERG (1991), which was based on morphological data, three characters relating to heterogamous capitula and their marginal florets were coded as "unknown" in *Chiliadenus*, i.e. the shape of marginal florets, the sex of marginal florets, and the shape of ray-floret epidermis cells. In the light of the new discovery additional and more complete data can be provided.



**Fig. 1.** Ray-floret from *Chiliadenus rupestris*. Voucher: JURY 13031 (RNG).

**Description of ray-florets.** Ray-florets when present (Fig. 1), 1–2 per capitulum, ca. 10 mm long, pistillate; lamina short, elliptic, 5 x 2 mm, in-rolled (at least on herbarium specimens), 4–5-veined, apically with three or four short lobes; epidermis cells elongated in outline, with surface striations and minute marginal denticulations, without linear crystals, not crested; tube ca. 4 mm. Style bifid; style-branches elongated, flattened, somewhat wider distally, adaxially with two distally confluent bands of stigmatic tissue. Pappus pale yellowish-red, consisting of several barbellate bristles in one row surrounded by a series of free, narrowly triangular scales. Cypselas (immature) 2 mm long, ellipsoid, glandular-hairy, proximally with elongated twin-hairs. Carpodium small.

### Discussion

Not all capitula on the radiate specimens of *Chiliadenus rupestris* seem to have them, and in those capitula where there are rays they are only one or two per capitulum. The ray-florets have a distinct lamina about half as long as the ray-floret (lamina in-rolled on the dried herbarium specimens) and well-developed styles.

The largest analysis of molecular data from the Inuleae-Inulinae is that of *ndhF* sequences from 160 species by ENGLUND et al. (2009). In this study, *Chiliadenus* was found to be the sister-group of *Dittrichia*, and the two genera were part of a larger clade comprising also *Jasonia* CASS. and *Pulicaria* GAERTN. These genera have capitula with ray-florets, but in *Jasonia* they are neuter without any style. Apart from *Jasonia*, a few other genera of the Inuleae also have ray florets without a style, i.e. *Anvillea* DC., *Perralderia* COSS., and *Iphiona* CASS., but these all belong to different monophyletic lineages and apparently the style has been lost in ray-florets on at least three different occasions. As concluded by BRULLO (1979), *Jasonia* and *Chiliadenus* are not congeners, and it is also clear from DNA analysis that they do not form a monophyletic group, as the latter is more closely related to *Dittrichia* GREUTER than to *Jasonia*. *Dittrichia* rays are pistillate, like the *Chiliadenus* specimens found here. Discoid capitula and loss of ray-florets probably evolved in the ancestor of *Chiliadenus* after it had differentiated from the ancestor of *Dittrichia*. The apomorphic trait was then inherited by the offspring as they evolved into the nine discoid species of today. ENGLUND et al. (2009) included five of the nine species of *Chiliadenus*, and found a trichotomy with the Algerian *C. hesperius* (MAIRE & WILCZEK) BRULLO and the Spanish *C. saxatilis* (LAM.) BRULLO unresolved in relation to a clade formed by the Maltese *C. bocconeii* BRULLO, the Libyan-Egyptian *C. candicans* (DELILE) BRULLO, and the Moroccan *C. rupestris*. Therefore it can be concluded that the radiate specimens of *C. rupestris* are not representing an archaic part of the genus retaining its rays

as a symplesiomorphy, but they belong to a more derived group of taxa and the rays have apparently reappeared secondarily.

Normally radiate species may have individuals, populations or subspecific taxa without rays, e.g. *Anvillea garcinii* DC. (ANDERBERG 1982), *Senecio vulgaris* L. (CHATER & WALTERS 1976). Rays may be lost due to adaptation to arid environments like in some south Algerian representatives of *Anvillea garcinii* ssp. *radiata* (COSS. & DUR.) ANDERB., or species may be polymorphic for other reasons. In *Senecio vulgaris* it has been shown that the radiate condition is dominant over the discoid, and that a change from homozygous for dominant alleles or heterozygous for dominant alleles to homozygous for recessive alleles may result in the loss of rays. Two gene loci (RAY1, RAY2) and a number of modifier genes seem to be active in the presence /absence of rays in *Senecio vulgaris* (GILLIES et al. 2002). Homozygotic dominant alleles give long rays, heterozygotic dominant give short rays, and homozygotic recessive results in loss of ray-florets. There seems to be one or two genes regulating the formation of ray-florets also in other Compositae, such as *Gerbera* L. (LAITINEN et al. 2006) and *Layia* HOOK. & ARN. (FORD & GOTTLIEB 1990), but the absence of rays in a plant does not mean it has lost the necessary regulatory genes (BALDWIN 2005). GILLIES et al. (2002) tested the hypothesis that CYCLOIDEA (CYC) gene homologues were involved in the formation of ray-florets in *Senecio*. This gene family is known to be involved in formation of the capitulum, and according to CARLSON et al. (2011) there have been several rounds of duplication of CYC-like genes in the Asteraceae, to some extent involved in the formation of zygomorphic flowers, with radiate species having more copies than discoid species. CHAPMAN et al. (2012) presented evidence for several paralogues of CYC2-like genes being present in the Asteraceae.

Situations where genera with only discoid species where some suddenly display individuals with ray-florets are apparently very unusual and I have not been able to find any discussion of this phenomenon in the literature. Nothing is known about the genetic mechanisms at work specifically in *Chiliadenus*, but it is reasonable to believe that it follows the same general patterns as described for other Asteraceae. If it conforms to *Senecio vulgaris*, where also the heterozygotic condition for dominant alleles result in presence of rays, one would expect the ancestor of *Chiliadenus* to be homozygotic recessive as no rays are formed. If so, there would not be any dominant ray-floret alleles present, and the mechanisms behind the occurrence of ray-florets in *C. rupestris* would have to be explained in some other way. One bold and perhaps far-fetched hypothesis could be that all *Chiliadenus* have the ray-floret genes, but that epigenetic suppression of these regulator or associated modifier genes has inhibited ray-floret development until some circumstance made ray-florets reappear in the Beni-Snassen population. Apparently this phenomenon may have many different causes and the mechanisms

behind them are far from clear. Perhaps these plants may one day be used for genetic research to shed more light on the issue on why ray-floret phenotypes are formed.

### Acknowledgements

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# The genus *Cavea*, an addition to the tribe Gymnarrheneae (Asteraceae-Gymnarrhenoideae)

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## Abstract

The systematic position of the yet unplaced *Cavea tanguensis* was investigated by analysis of DNA sequences from the plastid gene *ndhF*. It is concluded that *Cavea tanguensis* is the sister of *Gymnarrhena micrantha*, and that the genus *Cavea*, which has been notoriously difficult to place with any certainty, is a second member of tribe Gymnarrheneae (Asteraceae-Gymnarrhenoideae).

## Introduction

The present paper is one in a series of studies aiming at finding the systematic position for aberrant and odd representatives of the Asteraceae, such as *Caesulia* ROXB. (ANDERBERG et al. 2005), *Dipterocome* FISCH. & C. A. MEY. (ANDERBERG et al. 2007), *Feddea* URB. (CARIAGA et al. 2008), *Gymnarrhena* DESF. (ANDERBERG et al. 2005), *Nanothamnus* THOMSON (ANDERBERG & PANDEY 2008), *Pseudotrachia* HIERN (ANDERBERG & KARIS 1995), and *Rhodogeron* GRISEB. and *Sachsia* GRISEB. (HONG et al. 2004).

One remaining systematic enigma in the family is the monotypic genus *Cavea* W. W. SM. & J. SMALL from the Himalayas (Fig. 1). It is one of the last rogue genera of the Asteraceae, i.e. genera for which the systematic position is unclear and yet unsolved and not tested in a phylogenetic framework based on DNA sequence analyses. In some more recent treatments of the family (JEFFREY 2009, PELSER & WATSON 2009, CHEN & ANDERBERG 2011) *Cavea* has been treated as a *genus incertae sedis*, either belonging to the Cichorioideae or the Asteroideae, and its tribal relationship has also earlier been much discussed. Most authors have been eager to exclude it from the group they have been studying, but none willing to

accept it.

The morphological features of *Cavea* have made it difficult to place in relation to other genera. BREMER (1994), who listed *Cavea* among the Asteroideae unassigned to a tribe, noted that its filament collars were poorly developed and its endothelial tissue thickenings inconspicuous or absent like in the Cichorioideae tribes. He also stated that its style had stigmatic lines in two bands unlike the Cichorioideae, but typical of the Asteroideae. JEFFREY (2007) regarded *Cavea* as most likely related to the Inuleae in spite of its Carduoid facies, and later (JEFFREY 2009) pointed out its breeding system as being unique with both dioecious and monoecious plants in the same population.

In spite of all the detailed morphological investigations, the systematic position of *Cavea* has remained unsolved. Therefore it was the more intriguing to try and shed light on these issues by analysis of DNA sequence data. The results were surprising.

### Taxonomic history

The species *Saussurea tanguensis* J. R. DRUMM. was described in 1910 and placed in Cynaroideae-Carduineae (DRUMMOND 1910). Later the new genus *Cavea* was described based on DRUMMOND's species (SMITH & SMALL 1917), and with great hesitation placed near *Pluchea* of the Inuleae. The authors discussed the tendency in *Cavea* towards dioecy (large amount of capitula with no male florets), and that the Inuleae in their pollen presentation mechanism were closer to the Cynareae and Mutisieae, and also that the style and stamens would place *Cavea* nearer to Gochnatineae of the Mutisieae, than to *Saussurea*.

LING & CHEN (1965) agreed with SMITH & SMALL in that the genus belonged in the Inuleae-Pluchinae but provided an amplified and much more detailed description of the genus. Among other things, they noted that the plants showed different breeding systems in the same population and that some were smaller in size, sometimes even stemless (LING & CHEN 1965, pl. 19 fig. 14).

DITTRICH (1977) as well did not accept *Cavea* in the Cardueae and instead suggested it to have an uncertain position in the Inuleae. This view was not shared by MERXMÜLLER et al. (1977) who excluded it from the Inuleae because of aberrant pollen morphology with infratectal bacules [“infrategillar bacules”] (MERXMÜLLER et al. 1977, p. 579). Based on his thorough experience of Inuleae pollen ultrastructure, LEINS (1971) concluded that *Cavea* pollen was sufficiently different from what he had seen in the Inuleae to merit its exclusion from that tribe. ANDERBERG (1991) also kept *Cavea* out of the Inuleae s.str., and from his Plucheeae. This opinion was based on the presence in *Cavea* of a deeply lobed

corolla, undifferentiated anther filament collar, indistinct or missing endothelial thickenings, and also supported by the infratectal pollen wall (see above).

### Material and methods

DNA was extracted from leaves taken from herbarium specimens of *Cavea tanguensis* [Vouchers: ROCK 16868 (S); SINCLAIR & LONG 5423 (E); LUDLOW, SHERRIFF & HICKS 16309 (E); LUDLOW, SHERRIFF & HICKS 20793 (E)]. To test the tribal position of *Cavea tanguensis* in the family, four obtained *ndhF* sequences were analyzed together with the data set (184 taxa) from ANDERBERG et al. (2005) and with an additional number of unpublished sequences, mainly from the Inuleae, a total of 258 sequences of taxa representing all Asteraceae tribes.

**Molecular methods.** DNA extraction was carried out with the QIAGEN DNeasy Plant Mini Kit using the manufacturer's protocol. PCR reactions were performed with PuReTaq Ready-To-Go PCR Beads. Amplification was performed under the following settings: 95°C 5 min, followed by 4 cycles of 95°C 30 sec, 54°C 30 sec, 72°C 1 min 15 sec; 4 cycles of 95°C 30 sec, 52°C 30 sec, 72°C 1 min 15 sec and 36 cycles of 95°C 30 sec, 49°C 30 sec, 72°C 1 min 15 sec, with a final extension step at 72° 8 min. Purification of PCR products was done with the ExoFast enzymatic purification kit (Fermentas Life Sciences) following the manufacturer's protocol. Sequencing reactions were made with the same primers as in the amplification, using the BigDye Terminator v.3.1 Cycle Sequencing Kit. Unincorporated dye terminators were removed using QIAGEN's DyeEx 96 Kit. Fragments were separated and analyzed on an ABI 3130xl Genetic Analyzer. Primers used for PCR and sequencing of *ndhF* are presented in Table 1. The four new sequences have been submitted to GenBank (Accession numbers JQ922540-JQ922543).

**Alignment.** Alignment of *ndhF* was performed with the BioEdit software (HALL 1999) ver. 6.0.5. The aligned *ndhF* data set included 258 sequences with several representatives of each tribe of the Asteraceae.

**Phylogenetic analyses.** The alignment of the 258 *ndhF* sequences resulted in a data matrix with 2289 sites which was analyzed with parsimony jackknifing using the software XAC (FARRIS 1997) with the following settings: 1000 replications, each with branch-swapping and 10 random-additions of sequences. For the analysis, *Boopis* (Calyceraceae) was used as outgroup (FARRIS 1972).

### Results

The results of the parsimony jackknife analysis (Fig. 2) showed that 703 of the 2289 sites were informative, and that the four sequences of *Cavea* formed a



monophyletic group (100 % jackknife support), with *Gymnarrhena micrantha* as their sister group. The position of the *Gymnarrhena - Cavea* clade was congruent with the position of the former in the Cichorioid tribal complex in ANDERBERG et al. (2005).

## Discussion

The strongly supported close relationship between *Cavea* and *Gymnarrhena* was unexpected as the two have no obvious similarities.

*Gymnarrhena micrantha* is a small rosulate, stemless herb with linear lanceolate entire leaves and two kinds of capitula. One kind being female, cleistogamous and subterranean, the other kind is situated in the soil surface and provided with both female and male florets. FUNK & FRAGMAN-SAPIR (2009) reported that *Gymnarrhena* can survive quite harsh environmental changes and that its amphicarpny may be an autapomorphic adaptation to desert life. The genus has a distribution over large parts of North Africa and the Middle East. *Gymnarrhena* was once placed in the Inuleae (BENTHAM 1873, HOFFMANN 1890), just like *Cavea*, but later authors have not accepted it in treatments of that tribe (e.g. LEINS 1973, MERXMÜLLER et al. 1977, ANDERBERG 1991). The genus *Gymnarrhena* has been difficult to place, but DNA analysis has shown it to take a rather isolated position in the Cichorioideae (ANDERBERG et al. 2005). Earlier FUNK & PANERO (2002) had described a new tribe and subfamily (Gymnarrhenoideae-Gymnarrheneae) to accommodate this small monospecific evolutionary lineage, and placed it outside of the Cichorioideae-Corymbieae-Asteroideae. *Gymnarrhena* has an unusual aspect and its habit, gross morphology and its micromorphology have not provided any clues as to what its closest relative may be. The pollen was investigated by WORTLEY et al. (2007) in search of synapomorphies that could support its position in the Asteraceae phylogeny as evidenced by molecular data, but the study was not very conclusive as they found the ultrastructure not matching that of the Cichorioideae, but with some features approaching those in *Corymbium* (Corymbieae) stated to be the sister group of the Asteroideae.

The results of the present investigation placing the likewise enigmatic genus *Cavea* as sister to *Gymnarrhena* are of course interesting. Although they are both autapomorphic and without any obvious relatives as judged from their morphological characters, they must both have some taxon to which they are more related than to others. An explicit hypothesis of a close generic relationship between the two has never been presented before, and it must be noted that the presence in *Cavea* of two kinds of capitula with a tendency towards dioecism, and the presence of two growth forms, one with distinct stem and the other acaulescent are striking given a position as sister to the likewise acaulescent *Gymnarrhena*.

The latter also has two kinds of capitula, one with only female florets, and the other with male and female florets mixed, which FUNK & FRAGMAN-SAPIR (2009) suggested to be possible clusters formed by reduction of several capitula sitting close together. The pollen of *Cavea tanguensis* has yet to be investigated, but it would be some support for its position if it could be shown to have infrategillar baculae like *Gymnarrhena micrantha*.

In biogeographical terms, the two genera are allopatric. *Gymnarrhena* grows in deserts from North Africa to the Middle East, and *Cavea* on alpine meadows and gravelly places beside streams and glaciers on high altitudes in the Himalayas much further to the East. Both plants inhabit environments that are known to promote adaptations and morphological specialization. This distribution is the remains of a once continuous range of their ancestor, and the morphological characteristics of each of the two genera the result of long isolation in an eastern and western distribution. The addition of *Cavea* to the tribe Gymnarrheneae contributes to the understanding of the origin of that clade. From being an isolated Saharo-Sindian taxon, the origin of the tribe now seems to be in Asia, in an area that later broke up and formed the present day distributions of the two genera.

### Conclusion

The present analysis of *ndhF* sequence data indicates with strong support that the genus *Cavea* is sister to the Saharo-Sindian genus *Gymnarrhena*. Both genera have an unusual morphology and several unique features that have made them difficult to place. It is concluded that *Cavea* is not a member of the Asteroideae as previously assumed, but part of the Cichorioideae tribal complex, likely a second genus in the small tribe Gymnarrheneae, and thus yet another Asteraceae *genus incertae sedis* may have found a secure resting place.

### Investigated material of *Cavea tanguensis*

Tibet, Melong Gompa, 2.VII.1939, GOULD 2233 (K); Tibet, Rama to Melong Gompa, 1.VII.1939, GOULD 2326 (K); Eastern Himalaya, Nam La, 23.I.1924, KINGDON WARD 5977 (K); East Himalaya, Chumoleri, 12.IX.1912, LEPCHA 455 (E); Bhutan, Lingshi Dzong, 25. V. 1949, LUDLOW, SHERRIFF & HICKS 16309 (E); Bhutan, Gafoola, Upper Pho Chu, 7.VII.1949, LUDLOW, SHERRIFF & HICKS 16763 (E); Tibet, Cho La, North side, 4. VII. 1949, LUDLOW, SHERRIFF & HICKS 20793 (E). China, Szechuan, Mont Konka, Risonquemba, Konkaling, V-VIII 1928, ROCK 16868 (E, S); Bhutan, Upper Mo Chu District, valley SW of Lingshi Dzong, SINCLAIR & LONG 5423 (E, K); Tibet, Yanthang, 16.VII.1906, WHITE s.n. (K).

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Table 1.

Primer sequences (5'-3') for *ndhF*.

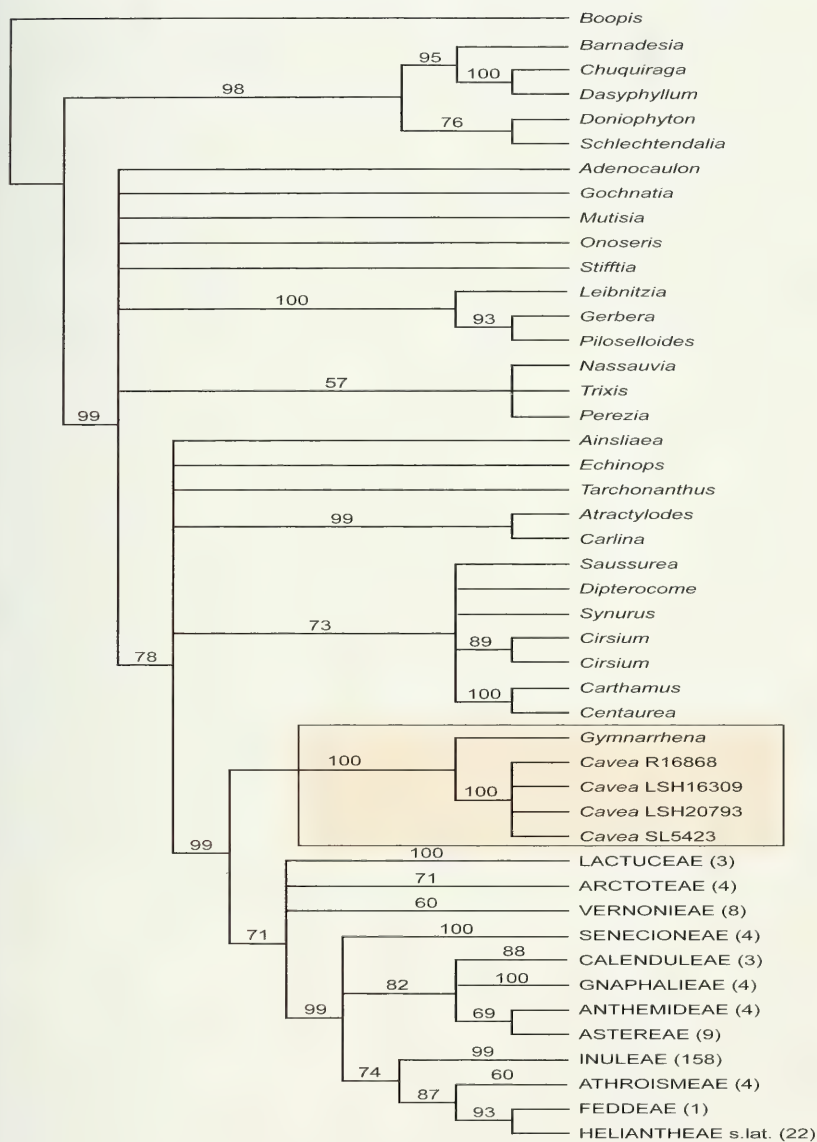
F = forward, R = reverse.

Name	Direction	Primer sequence
RJ1	F	AGG TAA GAT CCG GTG AAT CGG AAA C
5	F	GTC TCA ATT GGG TTA TAT GAT G
5B	F	GGA GCT ACT TTA GCT CTT G
16	R	GTT AAA CCT CCC ATAAGC ACC ATA TTC TGA C
1650-Ast	F	TAT GAT CCA ACC CTT TMT TTM TAT TCC
1700	R	CAT AGT ATT ATC TGA TTC ATA AGG ATA
10B	R	CCT ACT CCA TTT GGA ATT CCA TC

All primers except were published in KÄLLERSJÖ et al. (2000), except for primers 520 and 1750 that were published by ANDERBERG & SWENSON (2003). Primers RJ1 and RJ14 were designed by KI-JOONG KIM and ROBERT JANSEN.



Fig. 1. *Cavea tangensis*. Scanned herbarium specimen. - Rock 16868 (S).



**Fig. 2.**

Parsimony jackknife tree based on *ndhF* sequence data showing the position of *Cavea* among the Asteraceae tribes, as sister group of *Gymnarrhena*. Support values > 50 % are shown for each clade.

# *Caputia*, a new genus to accommodate four succulent South African Senecioneae (Compositae) species

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## Abstract

The new genus *Caputia* B. NORD. & PELSER is described, with four species confined to South Africa. Its members are succulent perennial herbs or shrubs with more or less fleshy tomentose or glabrescent leaves. The genus has tussilaginoïd as well as senecioid morphological characters, and takes strongly supported incongruent phylogenetic positions in nuclear and plastid phylogenies: sister to subtribe Brachyglottidinae or sister to the Synotoid group of Senecioninae, respectively. This suggests that the genus is potentially of hybrid origin. The four species are *Caputia medley-woodii* (HUTCH.) B. NORD. & PELSER (type), *C. tomentosa* (HAW.) B. NORD. & PELSER, *C. scaposa* (DC.) B. NORD. & PELSER and *C. pyramidata* (DC.) B. NORD. & PELSER.

## Introduction

One of the most interesting of the generic entities identified in our phylogenetic survey of the tribe Senecioneae (PELSER et al. 2007, 2010, NORDENSTAM et al. 2009) is the *Senecio medley-woodii* group. There is no available generic name for this distinct assemblage of four succulent species, confined to South Africa, and some of which are quite spectacular and well known in cultivation (ROWLEY 1994, CULLEN et al. 2000, EGGI 2002). We here suggest the new generic name *Caputia* for this assemblage, an allusion to their geographical origin. The name has provisionally already been used, e.g. in PELSER et al. (2010). The old geographical name *Caput bonae spei* was often applied not only to the Cape of Good Hope





**Fig.1.** *Caputia medley-woodii*.

From Flow. Pl. S. Afr. Plate 83 (1923), "*Senecio Medley-Woodii*".

itself, but to the Cape Province or even the whole of South Africa. The generic name also alludes to *Capelio*, one of the early-diverging genera in the tribe, and herbaria with alphabetical generic order will then conveniently file these two genera close together.

## Discussion

The members of *Caputia* used to be treated under *Senecio* L. (HARVEY 1865, HUTCHINSON 1923, ROWLEY 1994, 2002) and one of them sometimes in *Kleinia* MILL. (DE CANDOLLE 1838, HARVEY 1865, MARLOTH 1932). In phylogenies derived from nuclear as well as plastid DNA sequences the genus is only distantly related to *Senecio* s.str. In an ITS phylogeny of the tribe (PELSETER et al. 2007), three *Caputia* species (included as *Senecio medley-woodii*, *S. scaposus* and *S. pyramidatus*) form a clade that is sister to subtribe Brachyglottidinae. This subtribe (which is not yet formally published) has a majority of genera in Australasia (*Brachyglottis*, *Bedfordia*, *Dolichoglottis*, *Haastia*, etc.), but also extensions into New Guinea (*Papuacalia*) and Chile (*Acrisione*). However, the plastid phylogeny presented by PELSETER et al. (2007) indicates a close relationship between *Caputia* and the Asian genus *Synotis* in subtribe Senecioninae. This phylogenetic incongruence was later confirmed in a study that used a more extensive sampling of Senecioneae genera and characters (PELSETER et al. 2010). The ITS/ETS phylogeny in the latter study places *Caputia* sister to the Brachyglottidinae (100% parsimony bootstrap support [BS]; 1.0 posterior probability [PP]). Again, plastid DNA sequence data suggest closer affinities with the Senecioninae and resolved *Caputia* sister to the Synotoid group (95% BS; 1.0 PP), which is composed of *Austrosynotis* (Tropical Africa), *Cissampelopsis* (Asia), *Dauresia* (Namibia), *Humbertacalia* plus a few related genera (Madagascar and Mascarenes), *Mikaniopsis* (Africa), and *Synotis* (E Asia especially Sino-Himalayan region).

PELSETER et al. (2010) suggested that ancient hybridization is the most likely explanation for the incongruent phylogenetic position of *Caputia*. Morphology provides some, although admittedly limited, support for this hypothesis. Subtribe Brachyglottidinae is characterized by ‘tussilaginoïd’ features and among these are anthers with a cylindrical filament collar and polarized endothelial cell walls. In subtribe Senecioninae, however, mostly ‘senecioid’ features are found and these include balustriform filament collars and radial endothelial cell walls. The anthers of *Caputia* appear to be somewhat intermediate. Their filament collar is subcylindrical or weakly balustriform and the endothecium is transitional with radial and polarized thickenings. The disc-floret styles have continuous stigmatic areas, a feature characteristic of tussilaginoïd genera and less common among the senecioid taxa.

## Taxonomy and Descriptions

### *Caputia* B. NORD. & PELSER, gen. nov.

Erect branching shrubs, shrublets or thick-stemmed herbs. Leaves alternate, sessile, subcarnose to strongly succulent, flattened and thickish to terete, entire or coarsely dentate, mostly thinly to densely tomentose, sometimes glabrescent, sometimes persistently silvery white-felted. Capitula large, solitary or few to many in corymbose or thyrsoid synflorescences, radiate or discoid. Involucre cupshaped; phyllaries 8–13, uniseriate. Receptacle flat, glabrous, alveolate. Ray-florets absent or 8–13(–14), female, yellow; lamina strapshaped. Style bilobed. Cypsela ellipsoid-oblong, glabrous or with few scattered trichomes, sometimes more densely puberulous basally. Pappus bristles numerous, barbellate, white, persistent. Disc-florets numerous, hermaphroditic; corolla tubular, somewhat widening distally, 5-lobed; lobes triangular-ovate, midlined, apically subcucullate and somewhat papillate. Anthers basally obtuse to shortly sagittate; endothecium transitional with radial and polarized thickenings; filament collar subcylindrical or weakly balustriform; apical appendage ovate, flat. Style bifurcate with continuous stigmatic area inside the branches, apically subtruncate with few and short sweeping-hairs. Cypsela fusiform-ellipsoid, glabrous or puberulous. Pappus bristles numerous, white, persistent. Chromosome no.  $2n = 20$  ( $x = 10$ ) with large chromosomes.

Four species, distributed in mostly arid parts of Western and Eastern Cape Province, KwaZulu-Natal and Swaziland.

Type species: *Caputia medley-woodii* (HUTCH.) B. NORD. & PELSER.

### Key to the species of *Caputia*

- 1a. Stems and leaves with a dense silvery-white persistent tomentum. Capitula discoid ..... 2. *C. tomentosa*
- 1b. Plants araneose-tomentose, glabrescent. Capitula radiate ..... 2
- 2a. Leaves flattened, obovate—rhomboid ..... 1. *C. medley-woodii*
- 2b. Leaves terete (cylindrical, fusiform, sometimes apically flattened) ..... 3
- 3a. Stemless or short-stemmed shrublets. Capitula few (1–6) in racemose synflorescence ..... 3. *C. scaposa*
- 3b. Shrubs up to 180 cm high. Capitula numerous in conical or elongated synflorescence ..... 4. *C. pyramidata*



**Fig. 2.** *Caputia tomentosa*, flowering in National Botanic Gardens, Kirstenbosch, South Africa. Photo: B. NORDENSTAM 2007.





**Fig. 3.** *Caputia tomentosa*. From Curtis Bot. Mag. 6063 (1873), "*Senecio Haworthii*".

### 1. *Caputia medley-woodii* (HUTCH.) B. NORD. & PELSNER, comb. nov.

Basionym: *Senecio medley-woodii* HUTCH., Fl. Pl. S. Afr. Plate 83 (1923).

A branched shrub 0.5–2 m tall; stems thick, fleshy, often red or purplish, white-felted when young, glabrescent. Leaves sessile, obovate to rhomboid, 3–6 cm long, 1.5–3 cm wide, flattened but carnosely, margins entire to coarsely dentate especially distally and somewhat undulate, apically mucronate-apiculate, basally somewhat cuneate, white-tomentose when young, becoming glabrous. Peduncle 10–20 cm long with 1–4 capitula in corymbose arrangement, with small scattered bracts. Capitulum large, radiate. Involucre campanulate, with a few minute calyculus bracts; phyllaries 8–13, uniseriate, lanceolate–elliptic-ovate, 12–15 mm long, 3–6 mm wide, somewhat woolly, subcoriaceous, obtuse. Receptacle flat to somewhat convex, minutely alveolate with shortly fringed margins and a small central pit. Ray-florets ca. 12 (10–14), tube cylindric, 5–6 mm long, glabrous or with scattered short trichomes, lamina 1.5 cm long, bright yellow, 6–8-veined. Disc-florets 30–70, corolla 12 mm long, yellow or brownish-yellow, gradually widening upwards; lobes 1.5 mm long with a median resin duct. Style branches 2 mm long, apically truncate and minutely penicillate. Cypsela 6–7 mm long, fusiform, glabrous, 5-ribbed. Pappus bristles 9–10 mm long, white, persistent. Chromosome no.  $2n = 20$  (AFZELIUS 1967). – Fig. 1.

#### Selected collections (herbarium abbreviations as in HOLMGREN et al. 1990):

SOUTH AFRICA, NATAL: /2930DA Pietermaritzburg/, Craiglea, opposite Monteseel to the E and Table Mountain to the W, edge of escarp, 19.VI.1977, P. C. V. DE TOIT 2437 (K); Oribi Flats, top of Oribi Gorge, IV.1937, A. P. D. McCLEAN 563 (K); Ngotshe, Lebombo Mts, Majezind area, 1750 ft, 8.VII.1962, C. J. WARD 4183 (K); /3030 Port Shepstone/, granite hill 4 miles inland Umtentweni, 6.VIII.1967, R. G. STREY 7617 (K, S); Natal, Port Shepstone, Fairacres Estate on Oribi Flats, krans overlooking deep Umzimkulwana Valley, 22.VII.1953, R. A. DYER 5416 (K); near Murchison, recd. X.1884, MEDLEY-WOOD 3065 (K); Krantz Kloof, 23.VIII.1915, J. M. WOOD 13247, "*Medley-Woodii* HUTCHINSON n.sp." (K 1 specimen, annotated by HUTCHINSON, syntype); Natal, Inanda, comm. VIII.1879, J. M. WOOD 555, "*S. Medley-Woodii* HUTCH." (HUTCHINSON scripsit, K several specimens, syntypes).

*C. medley-woodii* is near-endemic in KwaZulu-Natal, occurring also in neighbouring Eastern Cape and Swaziland. The habitats are granite and other rocky outcrops, river gorges etc. at lower altitudes up to 600 m.s.m. (HILLIARD 1977).

HUTCHINSON (1923) named it for JOHN MEDLEY WOOD (1827–1915), a Natal botanist of distinguished repute. The species is widely cultivated as a handsome succulent in greenhouses (ROWLEY 1994, 2002).



**Fig. 4.** *Caputia scaposa*. From Curtis Bot. Mag. 4011 (1843), "*Senecio calamifolius*".



**Fig. 5.** *Caputia pyramidata*. From Curtis Bot. Mag. 5396 (1863), "*Senecio pyramidatus*".



## 2. *Caputia tomentosa* (HAW.) B. NORD. & PELSER, comb. nov.

Basionym: *Kleinia tomentosa* HAW., Syn. Pl. Succ.: 314 (1812).

Syn.: *Cacalia tomentosa* HAW. Misc. 189 (1803) non JACQ. 1775 (= *Adenostyles alba*) nec non VILL. 1779 nec non L.fil. 1782.

*Cacalia canescens* WILLD., Enum. Hort. Berol. Suppl. 427. (1814).

*Cacalia haworthii* SWEET, Hort. Brit. (Loudon): 336 (1830).

*Kleinia haworthii* DC., Prodr. 6: 338 (1838); HARVEY, Fl. Cap. 3: 318 (1865).

*Kleinia cana* DC., Prodr. 6: 338 (1838), HARVEY, Fl. Cap. 3: 319 (1865).

*K. cana* was said to be allied to *haworthii* but with shorter leaves, ca. 17–19 mm long (HARVEY 1865). ROWLEY (1994) noted that the type of *K. cana* DC. has flattened leaves which are narrowly elliptic to obovate and have rounded or pointed tips. MARLOTH in Flora of South Africa (1932: 269) remarked that difference in foliage “does not count” and synonymized *K. cana* with *K. haworthii*.

*Senecio quinquangulatus* SCH.BIP., Flora 28: 500 (1845).

*Senecio haworthii* (DC.) SCH.BIP., Flora 28: 500 (1845) (STEUDEL, Nomencl. Bot., ed. 2, 2: 561, 1841, nomen).

Because of its discoid capitula this species was treated in *Kleinia* by several authors (HAWORTH, DE CANDOLLE, HARVEY, MARLOTH). *Kleinia tomentosa* HAW. is here regarded as a new name dating from 1812, not a new combination since the earlier potential basionym is illegitimate.

An erect succulent sparingly branched shrublet densely silvery-white-tomentose throughout. Leaves 2–6–10) cm long, 6–12 mm thick, terete, fusiform to cylindrical, apiculate, rarely slightly flattened with a few minute lobes near the apex. Capitula solitary on an erect scape 8–10 cm long and with a few small bracts, discoid. Involucre cupshaped, phyllaries 8–9. Disc-florets 30–40, yellow. Floral details as in generic description. Style branches truncate. Pappus bristles ca. 15 mm long, white. Cypsela puberulous. Chromosome no.  $2n = 20$  (AFZELIUS 1967). – Figs. 2, 3.

This species has a complicated nomenclatural history, which is only partly described by BUTTERFIELD (1954) and ROWLEY (1994). Very popular in cultivation because of its fleshy terete or fusiform leaves with a dense silvery or snow-white tomentum, but rarely flowering. A photograph of a flowering specimen in Kirstenbosch was published in NORDENSTAM et al. (2009) and here (Fig. 2). Curtis Bot. Mag. Plate 6063 was based on a flowering specimen from Sir THOMAS

HANBURY's garden in Italy (Palazzo Orengo near Mentone), where it flowered in 1873.

The native habitat is in Namaqualand in the Northern Cape, e.g. in the Richtersveld, where the largest-leaved and whitest form has been found (cultivar 'Hans Herre' in ROWLEY 1994, 2002). Also recorded from the Great Karoo (W and E Cape), e.g. near Laingsburg and Camdeboo (MARLOTH 1932).

**3. *Caputia scaposa* (DC.) B. NORD. & PELSER, comb. nov.**

Basionym: *Senecio scaposus* DC., Prodr. 6: 403 (1838).

Syn.: *Senecio calamifolius* HOOK., in Curtis Bot. Mag. 69, Plate 4011 (1843).

Stemless shrubs (var. *scaposus*), or erect branching short-stemmed shrub up to 0.4 m high (var. *caulescens*); stems and branches pale green and somewhat downy. Leaves alternate, fascicled (subrosulate) in basal bunches, cylindrical, up to 12 cm long and 0.5–1 cm thick, somewhat curved, terete and obtuse or apically flattened and spoon-like and lobed (var. *addoensis*), cobwebby-tomentose or white-felted, glabrescent. Capitula several or rarely solitary, terminal in a long-pedunculate capitulescence with reddish, sparsely tomentose, nude or shortly bracteate peduncles. Capitula heterogamous, radiate, yellow-flowered. Involucre cupshaped, calyculate; phyllaries 8–12, araneose. Ray-florets 7–13, female; lamina strap-shaped. Disc-florets hermaphrodite, corolla distally campanulate, 5-lobed. Floral details as in generic description. Cypselas puberulous or subglabrous. Chromosome no.:  $2n = 20$  (AFZELIUS 1967). – Fig. 4.

This Eastern Cape species ranges from the Gamtoos River in Humansdorp eastwards to Grahamstown and Victoria East, where it grows in arid lands. It was introduced to Kew from a collection by BOWIE (likely collected in 1820–1822), where it thrived anonymously for many years until it was named in 1843 by HOOKER as *Senecio calamifolius*. However, it was published earlier as *Senecio scaposus* in 1838 by DE CANDOLLE, who is the name-bringing author.

**Selected collections:**

CAPE PROVINCE: Uitenhage, Zwartkops River, J. F. DRÈGE, ZEYHER 2983 (BM, K, S), ECKLON & ZEYHER 519 (K); between Bethelsdorp and Uitenhage, 27.XII.1813, BURCHELL 4405 (herb. HOOKER, K); Tambukiland, righthand side of Keyrivier between Windvogelberg and Zwartkey, ECKLON & ZEYHER 572 (S); Prope Grahamstown, 2000 ft, IX.1869, MACOWAN 1490 (BM, K); Uitenhage, 200 ft, 13.I.1933, F. R. LONG 895 (K); Humansdorp, 2 m. W of Gamtoos River drift on road from Humansdorp to Hankey, 100 ft, III.1928, FOURCADE 3623 (K); Uitenhage, on the Capetown road hill, I.1840 A. PRIOR s.n. (K); farm Naudes Hoek near Kieskama River, Victoria East, H. GIFFEN 725 (K).

HARVEY recognized two varieties, viz. var. *acaulis*, with very short or scarcely any stem and var. *caulescens*, with a developed stem up to 40 cm and branched (= *S. calamifolius* HOOK.). A third variety is var. *addoensis* (ROWLEY 1994), based on *Senecio addoensis* COMPTON. This differs by the flattened and lobed leaf-tips. Because of their morphological distinction and popularity in cultivation, the varieties deserve valid names as follows.

**3a. *Caputia scaposa* (DC.) B. NORD. & PELSER var. *scaposa*.**

Syn.: *Senecio scaposus* var. *acaulis* HARV., Fl. Cap. 3: 406 (1865).

**3b. *Caputia scaposa* (DC.) B. NORD. & PELSER var. *caulescens* (HARV.) B. NORD. & PELSER, comb. nov.**

Basionym: *Senecio scaposus* DC. var. *caulescens* HARV., Fl. Cap. 3: 406 (1865).

Syn.: *Senecio calamifolius* HOOK. in Curtis Bot. Mag. Plate 4011 (1843).

**3c. *Caputia scaposa* (DC.) B. NORD. & PELSER var. *addoensis* (COMPTON) B. NORD. & PELSER, comb. nov.**

Basionym: *Senecio addoensis* COMPTON, J. Bot. 72: 48 (1934).

Syn.: *Senecio scaposus* DC. var. *addoensis* (COMPTON) G. D. ROWLEY, Cact. Succ. J. (Los Angeles) 62(6): 283 (1990).

**4. *Caputia pyramidata* (DC.) B. NORD. & PELSER, comb. nov.**

Basionym: *Senecio pyramidatus* DC., Prodr. 6: 402 (1838).

A succulent short-stemmed suffrutex or shrub up to 1.8 m high with araneose-tomentose glabrescent stems and branches, becoming glaucous. Leaves alternate, mostly crowded basally, sessile, cylindrical and succulent, entire, 8–15 cm long, about 0.5(–1) cm thick, acute. Capitula numerous in thyrsoid elongated or conical synflorescence, large, heterogamous, radiate, yellow-flowered, on bracteolate pedicels. Involucre hemispherical–cupshaped; phyllaries uniseriate, white-tomentose with brownish tips and margins. Ray-florets ca. 13 (10–14), female; style bilobed. Disc-florets numerous, hermaphrodite; corolla tubular, distally widening, 5-lobed; lobes narrowly ovate. Cypselas glabrous. Pappus bristles numerous, white. Chromosome no. unknown. – Fig. 5.

**Selected collections:**

CAPE PROVINCE: Uitenhage, BOWIE 3 (BM); Uitenhage, ZEYHER 941 (BM); Zoutpanshoogde, BURKE s.n. (BM); Uitenhage, XII.1847, A. PRIOR s.n. (K); Somerset Div., mtn. above the spring at Commadagga, 6.VII.1813, BURCHELL 3341 (K); Peddie Div., begin River Valley opposite Wooldridge, 1000 ft, 15.X.1945, ACOCKS 11852 (K); Peddie Div., near Peddie, dry *Euphorbia* scrub, 1800 ft,

7.VIII.1953, L. E. CODD 1977 (K); Algoa Bay, St. George's Strand, 20.XI.1932, F. R. LONG 862 (K); Port Elizabeth, recd. 9.III.1906, ETHEL WEST 20 (K); Albany, Pluto's Vale, 3–4 miles N of Botha's Hill, 1500 ft, X.1027, R. A. DYER 1058 (K).

This is a very striking species, as testified e.g. by HARVEY (1865): "A very fine species" and HOOKER in Bot. Mag. Plate 5396 stated: "perhaps among the most ornamental of the genus" (i.e. *Senecio*).

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# *Crassothonna* B. NORD., a new African genus of succulent Compositae-Senecioneae

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## Abstract

The new genus *Crassothonna* B. NORD. is described with 13 species transferred from the large and polymorphic genus *Othonna* L. *Crassothonna* species are perennial herbs, shrublets or shrubs with terete succulent leaves. The genus is mainly South African with a centre in Little Namaqualand and adjacent parts of the Western Cape, but is also represented by a few species in the eastern Cape Province, Natal and southern Namibia. Several species belong to the Gariiep floristic element.

## Introduction

The genus *Othonna* L. (Compositae-Senecioneae) comprises about 120 species (NORDENSTAM 2007) with a marked centre in southern Africa. The taxonomy of this genus is notoriously difficult, and further revisional work remains to be done especially on the specific level. On the generic level one major change is necessary, viz. to remove a group of highly succulent terete-leaved taxa out of the genus. They are here recognized as a new genus *Crassothonna* B. NORD. with (provisionally) 13 species. The remaining *Othonna* s.str. comprises tuberous herbs and shrubby perennials with quite a variety of life-forms and adaptations to extreme climatic conditions.

Molecular data support the segregation of this group from *Othonna*, although only a few species have been investigated so far. However, it has been demonstrated that *O. sedifolia* and *carnosa* (now *C. cacalioides*) form a clade closer to *Gymnodiscus* LESS. (a small genus of annual herbs) than to the core of *Othonna* (DEVOS et al. 2010, NORDENSTAM et al. 2009, PELSER et al. 2010).

***Crassothonna* B. NORD., gen. nov.**

Glabrous shrubs or shrublets or perennial herbs. Stems terete, thin to thickened, sometimes bottle-shaped and carnose, little- to much-branched. Leaves alternate, simple, terete, subterete or ovoid to fusiform, highly succulent, green or glaucous or pruinose or minutely papillose, sessile or shortly petiolate, apically rounded to obtuse, sometimes mucronate. Capitula heterogamous, radiate or disciform, terminal, pedunculate on thin and sometimes long peduncles with one or a few minute bracts, solitary or few to several or many in corymbose synflorescence. Involucre soft, campanulate (not cup-shaped), phyllaries uniseriate, 5–8, basally shortly connate, herbaceous, 3–5-veined, with membranaceous margins. Receptacle flat or somewhat convex, glabrous, minutely alveolate. Ray-florets female, fertile, tube shortly cylindrical, lamina strap-shaped, yellow or more rarely white, sometimes tubular and eligulate. Style bifurcate, truncate or obtuse, with short apical sweeping-hairs. Cypselas fusiform–oblong–obovoid, 2–5 mm long, 1–3 mm wide, veined or ribbed, glabrous or puberulous or covered with a dense silvery-white tomentum of appressed trichomes becoming mucilaginous when soaked. Pappus bristles numerous, minutely barbellate, white, persistent or caducous. Disc-florets hermaphrodite but often female-sterile (functionally male), with style in central florets undivided with a conical tip, but in some taxa marginal disc-floret styles fertile, bifurcate with separate stigmatic areas on the inside of style branches and tip shortly conical or subtruncate with short sweeping-hairs; corolla tubular-campanulate, 5-lobed, lobes midveined, sometimes only faintly so. Anthers basally obtuse, ecaudate, endothecium radial; apical appendage flat, ovate-oblong; filament collar balustriform. Cypselas, usually not developing, narrowly oblong, glabrous or puberulous. Pappus bristles few to several, white, caducous.

Type: *Crassothonna cylindrica* (LAM.) B. NORD.

13 species recognized here, South Africa, Namibia. A few more taxa remain to be described, and a revision of the genus is in preparation. The members of the genus have a characteristic look. The terete succulent leaves are usually long and uniformly thick, but variable in size and shape. They may be short and almost grape-like as in *C. clavifolia* or small and somewhat larva-like as in *C. sedifolia*, and in *C. opima* very large and sausage-like.

Most species are diploid with  $2n=20$ . This number has been counted in *C. alba*, *cacalioides* (2 collections), *capensis* (2 collections), *clavifolia*, *cylindrica*, *floribunda*, *opima*, *patula*, *protecta* (6 collections), *sedifolia* (3 collections) and *sparsiflora* (AFZELIUS 1924, 1967, CZEIKA 1957, NORDENSTAM 1967, 1969a, 1971, ORNDUFF et al. 1967, RATLER & MILNE 1973). Only *C. rechingeri* differs by the hexaploid number  $2n=60$  (NORDENSTAM 1971).

**1. *Crassothonna alba* (COMPTON) B. NORD., comb. nov.**

Basionym: *Othonna alba* COMPTON, Trans. Roy. Soc. South Africa 19: 321 (1931).

Similar to *C. cylindrica* and *C. cacalioides* but easily recognized by the white rays. ROWLEY (1994), also in EGGLE (2002), did not recognize it as a distinct species but cited it in synonymy of *Othonna carnosa* LESS., which is now *Crassothonna cacalioides*. The status of this white-rayed taxon will be further investigated. It has been recorded from the Western Cape, in karroo, but is nowhere common or abundant.

**2. *Crassothonna cacalioides* (L.f.) B. NORD., comb. nov.**

Basionym: *Cineraria cacalioides* L.f., Suppl. Pl.: 374 (1782).

Syn.: *Othonna carnosa* LESS., Syn. Gen. Compos.: 88 (1832).

LESSING published the new name *Othonna carnosa* for a taxon cited as *Cineraria cacalioides* THUNB. and for the obvious reason that the specific epithet was not available under *Othonna* (*O. cacalioides* L. fil. is a quite different species and a true *Othonna*; cf. NORDENSTAM 1969b). This nomenclature was adopted by HARVEY in *Flora capensis* (HARVEY 1865). However, under *Crassothonna* the earliest epithet *cacalioides* is available, so this species has to change its name completely - from *Othonna carnosa* to *Crassothonna cacalioides*. The white-rayed related taxon from the Western Cape is distinguished as *C. alba* (cf. above), and a rayless taxon in KwaZulu-Natal Province is recognized as *C. discoidea* (cf. below).

Coastal areas from Humansdorp in the Eastern Cape north to KwaZulu-Natal border.

**3. *Crassothonna capensis* (L. H. BAILEY) B. NORD., comb. nov.**

Basionym: *Othonna capensis* L. H. BAILEY, Cycl. Amer. Hort.: 1180 (1901).

Syn.: *Othonna crassifolia* HARV., Fl. Cap. 3: 336 (1865), non *O. crassifolia* L., Syst. Nat. ed. 12, 2: 579; Mant. Pl.: 118 (1767) = *Othonna othonnites* (L.) DRUCE.

Very popular and common in cultivation, and unfortunately sometimes still under the invalid name from HARVEY's *Flora capensis*, viz. *Othonna crassifolia* HARV.

The plants in cultivation easily form green mats of succulent leaves and a profusion of yellow flowerheads, which makes it a favourite in rock gardens or green-houses in many parts of the world. With reference to the leaf-shape it is often called 'Little Pickles'.

Distributed in the Western Cape.

**4. *Crassothonna clavifolia* (MARL.) B. NORD., comb. nov.**

Basionym: *Othonna clavifolia* MARLOTH, Trans. Roy. Soc. South Africa 2: 38 (1910).

Short thickened stems and leaves grape-like or ovoid-fusiform and mucronate.

This species is endemic to the area around the lower Orange River, i.e. southernmost Namibia and the Richtersveld in northern Namaqualand, a region phytogeographically known as the Gariep Centre, home of the Gariep floristic element (NORDENSTAM 1966, 1969c, VAN WYK & SMITH 2001).

The species is sought after by succulent growers and makes a nice impression with its low habit and grape- or olive-like leaves in small bunches.

**5. *Crassothonna cylindrica* (LAM.) B. NORD., comb. nov.**

Basionym: *Cacalia cylindrica* LAM., Encycl. Méth. Bot. 1: 529 (1785).

Syn.: *Othonna cylindrica* (LAM.) DC., Prodr. 6: 477 (1838).

A branching erect shrub up to one m high, with elongate terete leaves and several (mostly 2–4) yellow-flowered capitula in small synflorescences.

This is a shrubby species widely distributed in the Western Cape north to southern Namibia. The succulence of the leaves has been questioned (cf. ROWLEY 1994: 170), but there is no doubt that the leaves are terete and succulent, like in all congeners.

**6. *Crassothonna discoidea* (OLIV. in HOOK.) B. NORD., comb. et stat. nov.**

Basionym: *Othonna carnosa* var. *discoidea* OLIV. in HOOK. Icon. Plant. 18 t. 1713 (1887–1888).

This is sufficiently distinct from *C. cacalioides* to be regarded as a separate species (cf. HILLIARD 1977, who expressed the same opinion). Apart from the disciform (not discoid, in spite of the epithet) capitula it has a distinctive habit with rather large and long leaves (up to 15 cm long and 1 cm wide), many-flowered capitulescences with long peduncles, and other characteristics to be discussed in my forthcoming revision of the genus. It seems to be confined to KwaZulu-Natal, where it is found in coastal areas, forming colonies in sand dunes or sandy grassland.

**7. *Crassothonna floribunda* (SCHLTR) B. NORD., comb. nov.**

Basionym: *Othonna floribunda* SCHLTR, Bot. Jahrb. Syst. 27(1-2): 214 (1899).

This is close to *C. cylindrica* with which it is partly sympatric, distributed in the Western Cape, from Malmesbury northwards into Namaqualand, but has not yet been recorded from Namibia. It is more richly flowering (= ‘floribund’) than

*C. cylindrica* with rays deeper yellow or even orange-coloured.

**8. *Crassothonna opima* (MERX.) B. NORD., comb. nov.**

Basionym: *Othonna opima* MERX., Mitt. Bot. Staatssamml. München 5: 636 (1965).

A robust erect branching shrub up to one m high with thickish stems and branches. Leaves very long and thick, terete, sausage-like, up to 15 cm long and 1.5 cm thick.

Perhaps the most striking species in the genus, because of its large sausage-like leaves. It is confined to the Richtersveld in northern Namaqualand and southernmost Namibia, i.e. a typical Gariep element. It is hybridizing occasionally with one or two other species of *Crassothonna*, viz. *C. cylindrica* and *C. floribunda* (cf. also ROWLEY 1994: 185). I have seen and collected intermediate specimens growing with the presumed parent species in parts of the Richtersveld.

**9. *Crassothonna patula* (SCHLTR) B. NORD., comb. nov.**

Basionym: *Othonna patula* SCHLTR, J. Bot. 36: 26 (1898).

A stemless herbaceous succulent with stolons, forming new plants from rooting nodes.

This was described from the Eastern Cape, but is apparently distributed more widely with scattered occurrences also in the Western Cape and Namaqualand. The stoloniferous habit is shared with *C. rechingeri* (cf. below). The latter is a hexaploid rayless species, whereas *C. patula* is a radiate diploid with  $2n=20$ , counted on plants originating from Vanrhynsdorp Div., 15 miles E of Vanrhynsdorp (NORDENSTAM 1971).

**10. *Crassothonna protecta* (DINTER) B. NORD., comb. nov.**

Basionym: *Othonna protecta* DINTER, Repert. Spec. Nov. Regni Veg. 19: 141 (1923).

Syn.: *Othonna crassicaulis* COMPTON, Trans. Roy. Soc. South Africa 19: 322 (1931).

A characteristic species with a bottle-shaped or sausage-like swollen short stem up to 15–20 cm high, little-branched with weak branches. Leaves subterete and succulent, but often somewhat flattened or grooved on the upper side, rather narrow and elongate, apically mucronate; leaf-axils woolly. Ray-florets numerous (13–22), with light yellow or greenish lamina, often becoming rolled back.

The species is distributed in arid areas of the Western and Northern Cape from the Witteberg and Karoo Poort through Namaqualand into southern Namibia.



**11. *Crassothonna rechingeri* (B. NORD.) B. NORD., comb. nov.**

Basionym: *Othonna rechingeri* B. NORD., Ann. Naturhist. Mus. Wien 75: 139 (1971 publ. 1972).

This one of the few rayless species of the genus. The stoloniferous habit is shared with *C. patula*, which is a diploid with radiate capitula. *C. rechingeri* is hexaploid with  $2n=60$  (NORDENSTAM 1971). The species is easily cultivated and tends to spread to other pots by the rooting tuberous nodes formed on the runners.

The species may be confined to the Northern Cape (type locality in Calvinia Div.).

**12. *Crassothonna sedifolia* (DC.) B. NORD., comb. nov.**

Basionym: *Othonna sedifolia* DC., Prodr. 6: 479 (1838) [1837 publ. early Jan 1838].

A small erect branching shrub up to 50–60 cm high with mostly single capitula. Leaves short and thick, obovoid or terete, less than 1 cm long and shortly petiolate to sessile, smooth or minutely papillose. Rays pale or richly yellow.

There is some interesting variation within this species especially in leaf shape and texture, and it is possible that *Othonna papillosa* DTR may be recognized as a separate taxon. Further studies on this issue are ongoing.

Fairly widespread in the Western Cape and Namaqualand into southern Namibia.

**13. *Crassothonna sparsiflora* (S. MOORE) B. NORD., comb. nov.**

Basionym: *Euryops sparsiflorus* S. MOORE, Bull. Herb. Boissier Ser. 2, 4: 1023 (1904).

*Othonna sparsiflora* (S. MOORE) B. NORD., Mitt. Bot. Staatssamml. München 4: 125 (1961).

This species was first described as a member of *Euryops*, but moved to *Othonna* by NORDENSTAM (1961). It is similar to *C. cylindrica* and *C. cacalioides* but easily recognized on its disciform heads with tubular-campanulate hermaphroditic marginal florets. The plant is a branching shrub ca. 0.5 to 0.8 m tall and the capitula are borne singly on peduncles up to 7 cm long.

Restricted to the Richtersveld in northern Namaqualand and southern Namibia, i.e. a typical Gariep element (cf. spp. 4 & 8).

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# Diversity of trichomes from mature cypselar surface of some taxa from the basal tribes of Compositae

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## Abstract

Structure and distribution of trichomes are important from the taxonomic point of view. The distribution and structure of trichomes appear to be genetically controlled and are more or less stable and have paramount taxonomic significance.

It has been observed by many workers that trichomes from the vegetative as well as reproductive parts can be used successfully for the delimitation of genera and species within the family Compositae (Asteraceae). However, broad comparative studies of cypselar trichomes are scarce or lacking. The present study indicates that trichome structure is highly variable. Trichomes from the outer surface of mature cypselas of 44 genera and 71 species belonging to 7 tribes of the four subfamilies Mutisioideae, Carduoideae, Pertyoideae and Cichorioideae were studied by light microscopy and SEM. Number of studied genera and species in each tribe is indicated in parentheses: Mutisieae (1/3), Dicomeae (1/1), Cardueae (9/17), Pertyeae (1/3), Cichorieae (14/23), Arctoteae (3/3) and Vernonieae (12/21). Both glandular and non glandular trichomes are divided into seven major types.

Presence of 'twin' or 'duplex' cypselar hairs is one of the characteristic features of the family Compositae and is prevalent in the tribes Cichorieae, Dicomeae, Pertyeae, Mutisieae and Vernonieae. This type of trichomes is less common in the tribes Arctoteae and Cardueae. Distribution and structure of trichomes have taxonomic significance at the generic and infrageneric level. However, their value



as taxonomic markers will be greatly increased when combined with other cypselar characters such as structure of carpopodium, stylopodium and pappus, as well as surface features of cypselar wall, etc. Certain taxa have unique types of trichomes regarded as apomorphies. Fusiform twin hairs have been noted in *Gerbera piloselloides*, whereas papillose twin hairs were noticed in *Actites megalocarpa*. Sometimes papillate hairs united to form a scale-like structure e.g. in *Crepis* and *Hypochaeris*. Multicellular non-glandular acroscopic hairs have been noticed in *Echinops sphaerocephalus*. In *Carlina*, glandular twin hairs were observed.

**Keywords:** Trichomes, twin hairs, mature cypselas, Compositae.

### Introduction

The Compositae (Asteraceae) family is nested in the order Asterales of Campanulids according to the APG III classification (The Angiosperm Phylogeny Group 2009). The family has largest number of accepted species, ca. 24,000, among angiosperm plant families and is distributed throughout the globe except Antarctica (FUNK et al. 2009, FUNK 2010). The genera number 1600–1700. All available evidence indicates that the family is monophyletic (e. g., SMALL 1919, BREMER 1987, JANSEN & PALMER 1987, 1996, BREMER et al. 1992, HANSEN 1990, 1991a, b).

After the long outdated classifications of BENTHAM (1873 a, b) and HOFFMANN (1890), the new classification of the Compositae by BREMER (1994) was the first approach at a modern phylogenetic analysis of this family. BREMER'S classification was morphologically based, but with subsequently rapidly developing molecular data a new picture of the family phylogeny emerged, first summarized by KADEREIT & JEFFREY (2007) and their associates. This modern approach culminated in the seminal and epoch-making work of FUNK et al. (2009). At present, the basal groups of Compositae are recognized as subfamilies like Barnadesioideae, Mutisioideae, Hyalideae, Wunderlichieae, Carduoideae, Pertyoideae and Cichorioideae. The present study includes some members of four basal subfamilies (Mutisioideae, Carduoideae, Pertyoideae and Cichorioideae).

Trichomes or hairs have long been of much importance in systematic investigation of angiosperms. Anatomically, a trichome or hair is an epidermal outgrowth of diverse form, structure and function (UPHOF 1962, ESAU 1965, FAHN 1986, 1988). Despite the great variety of systems proposed for the classification of trichome types, they are basically classified as either glandular with a secretory function or as covering hairs (non-glandular) without a secretory function (CUTTER 1978). Hairs originate from epidermal cells and develop on the outer surface of various plant organs (WERKER 2000). The hairs offer a rich field of investigation for a micro-morphologist because of their common occurrence and great diversity,

simplicity in structure and easy availability for observation due to their superficial position (SAHU 1982 a, b, c, 1983).

The types of hairs (epidermal outgrowths) have been reviewed and classified in early works, such as by DE BARY (1884) who recognized four major categories, viz., (i) Bladders, (ii) Hairs, (iii) Scales and (iv) Shaggy hairs. DE BARY (l.c.) also noted that the presence of hairs in plant organs is a universal character in vascular plants. Later COWAN (1950) merged the 'Shaggy hairs' into the category of 'hairs' and various other categorizations of trichome type have been put forward. Similar approaches have been made in various plant families. For example, GOEBEL (1900) was the first to discuss the significance and relationships of trichomes in the tribe Rhinanthae of the family Scrophulariaceae.

One pioneer in the study of role and importance of hairs in taxonomy and their phylogenetic evolution was SOLERADER (1908) in his work entitled "Systematic Anatomy of the Dicotyledons". He again divided the hairs into two major categories, viz. (i) the clothing hairs and (ii) the glandular hairs. SOLERADER (op.c.) described the hairs present on the ovary of *Spilanthes oleracea* (now *Acmella oleracea*) as follows: "they consist of two long hair cells which are jointed together lengthwise along one side, but diverse apically so as to resemble swallows tail." Such types of hair are characteristic of the ovary or cypsela (achene) in the family Compositae (RAMAYYA 1962 a, b, c) and these hairs were designated variously; e.g., 'Zwillingshaare' (KRAUS 1866, HESS 1938), translated to 'twin hairs' (e.g., VAUGHAN 1970, GRAU 1977, DITTRICH 1977), or 'biseriate forked hair' (NARAYANA 1979), simply 'achene hair' (SMALL 1919, HESS 1938, RAMAYYA 1962 a, b, c, 1963, 1969, 1972, MANILAL 1963, SAHU 1976, 1978, 1979, 1980, 1982 a, b, 1983, 1984, FREIRE et al. 2002), or sometimes 'duplex hair' (e.g., MACLOSIE 1883, NICHOLS 1893, NORDENSTAM 1977). Primarily a twin hair consists of two triangular or rectangular and usually short basal cells, completely or partly united with each other along their longitudinal walls (SANCHO & KATINAS 2002). NORDENSTAM (1968 b) described the twin hairs of *Euryops* as consisting of two parallel, short to elongate cells plus a smaller basal cell, i.e. three cells altogether.

Early records of the hairs of Compositae are usually brief and sometimes fragmentary, e.g. as reported by NICHOLS (1893), LLOYD (1901), KUPFER (1903), CAVILLIER (1907, 1911), HOLM (1908, 1913, 1917 & 1926), SABNIS (1921), BRIQUET (1916, 1930), DIETERT (1938), ARTSCHWAGER (1943), VOLLE & HETZGER (1949) and MIRASHI (1955, 1956). Later more detailed accounts have been made such as the descriptions of glandular hairs of the subtribe Madinae presented by CARLQUIST (1958, 1959 a, b, c).

Another significant contribution regarding the hairs of Compositae has been documented by RAMAYYA (1962 a, b, c, 1963 & 1969). He described the structure,

variation and distribution of 35 types of hairs in some Compositae and their mode of development. He also recognized four distinct "Systems of hairs" in this family, viz., (i) Filiform Trichome System; (ii) Macroform Trichome System; (iii) M-Multiseriate Trichome System and (iv) P-Multiseriate Trichome System.

METCALFE & CHALK (1950, 1979, 1989) have stated that trichomes possess taxonomic value, that both glandular and non-glandular hairs are present in the Compositae, and that the non-glandular hairs are of various morphological types, whereas the glandular hairs are more or less homogeneous with a uniform structure.

Structures of hairs are greatly variable among different taxa. For example, SPRING (2000) has described more than 300 forms of plant trichomes.

Many workers have contributed on the systematic value of hairs in the genus *Vernonia* s.lat., like HUNTER & AUSTIN (1967) and FAUST & JONES (1973) in North American species, and NARAYANA (1979) on 15 South Indian species. In the latter 18 types of hairs were noted by NARAYANA (l.c.), out of which three types (biseriate vesicular glandular hair, biseriate non-forked hair and biseriate forked) were found on the ovary wall. Twenty Indian species of *Vernonia* were studied by SAHU (1984), who mentioned that the frequency distribution of cypselar (= achenial) hairs is highest (57%) among all the hairs observed. Five among the six cypselar hair types noted are of glandular type, viz. (i) biseriate glandular hair, (ii) biseriate vesicular glandular hair, (iii) biseriate capitate glandular hair, (iv) biseriate vesicular capitate glandular hair, and (v) multiseriate glandular hair, and one (vi) non-glandular hair type.

NORDENSTAM (1968b, 1977, 1978, 2006a, 2007) noted that the duplex hairs are widespread in the tribe Senecioneae but not in Calenduleae. He found that such hairs show various modifications and occasionally (e.g. in species of *Euryops*, *Mesogramma*, *Bolandia*, *Dauresia*, *Lomanthus*) exude mucilage when treated in water (NORDENSTAM & PELSNER 2005, 2009). Similar type of duplex hairs has been observed by MACLOSIE (1883), JAMES (1883), NICHOLS (1893), DRURY & WATSON (1965) and SAHU (1983), mainly in the Senecioneae, e.g. species of *Senecio*, *Othonna*, and *Euryops*. MACLOSIE (1883) and SAHU (1976, 1978, 1979, 1980, 1982 a, b) also observed similar trichomes in other taxa of Compositae.

KING & ROBINSON (e.g., 1969, 1970, 1979) have used the hair structure along with other epidermal features in determining many generic circumscriptions in the Compositae, especially in the Eupatorieae.

In the systematic review of Cynareae, DITTRICH (1977) reported that cypselas in subtribe Echinopsinae (*Echinops* and *Acantholepis*) are densely covered by multicellular stiff hairs. In all members of the subtribe Carlininae, cypselas hairs

are 'twin hair' type. Members of the Cardueae have been studied in some detail by PETIT (1987, 1997).

NAPP-ZINN & EBLE (1980) studied the glandular and non glandular hairs of 20 genera of the Anthemideae. On the basis of differences of glandular hairs, three species of *Artemisia* are clearly separated, i.e., *A. nova*, *A. arbuscula* and *A. tridentata* (KELSEY & SHAFIZADEH 1980, KELSEY 1984).

The types of hairs may be considered as valuable accessory characters in plant taxonomy, particularly at infrageneric levels (STEBBINS 1953, FAUST & JONES 1973, NAPP-ZINN & EBLE 1980, SAHU 1978, 1979, 1980, 1982 a, b, 1984, HOOT 1991, KOROLYUK 1997).

SANCHO & KATINAS (2002) have shown the presence of typical twin type of hairs from the corollas of Mutisieae. In addition to that corollas also bear four other types of hairs. They have also indicated that the ontogenies of cypselar twin hairs and twin hairs of corollas were identical.

NORDENSTAM (1968a, 1978, 2006 b) and LUNDIN (2006) have pointed out that some members of the tribe Senecioneae possess more complex, stellate or substellate types of hairs, e.g., *Aequatorium* B. NORD. and *Nordenstamia* LUNDIN and rarely in *Euryops*, although not on the cypselas, which are glabrous (or glandular-puberulous). Substellate or T-shaped hairs occur also in *Dresslerothamnus* H. ROB. of the same tribe (ROBINSON 1989).

Microcharacters of glandular hairs from 34 species belonging to 7 tribes of the subfamily Asteroideae, have been studied by CICCARELLI et al. (2007) who discussed the usefulness of the glandular hairs of the ovary.

Leaves of the industrial oilseed *Vernonia galamensis* ssp. *galamensis* var. *ethiopica* GILBERT, contain glandular hairs, which are actually 10-celled peltate biseriolate glandular hairs (cf. also below). Along with these hairs this taxon has awl-shaped glandular hairs and non-glandular hairs (FAVI et al. 2008).

The detailed structure of trichomes from stem and leaves of 135 species belonging to 53 genera in tribe Lactuceae was studied by KRAK & MRÁZ (2008). They recognized eight types and several subtypes, and they have focused on the utility of hairs in the infratribal classification with the help of both light and scanning electron microscopy.

ANDREUCCI et al. (2008) studied critically the histochemistry and morphology of multicellular biseriolate glandular hairs of *Matricaria chamomilla*. These hairs are composed of 10 cells, viz. two basal cells, two peduncle cells and a secretory head containing six cells. Ten-celled biseriolate glandular hairs also have been reported by MONTEIRO et al. (2001) from the leaves of *Stevia rebaudiana* (tribe Eupatorieae).



Similar type of stalked glandular hair and two types of non-glandular hairs have been noted from the cypselas of *Stevia rebaudiana* by CORNARA et al. (2001).

ADEDEJI (2004) and ADEDEJI & JEWoola (2008) stated that hairs can be fruitfully used for the delimitation of genera within the family Compositae and they have mentioned different types of glandular and non-glandular hairs. The genus *Vernonia* can be delimited from other genera by the presence of T-shaped hairs and *Chromolaena* has amoeboid-shaped hairs.

Diversity of leaf hairs and phylogenetic relationships on the basis of such hairs in different taxa of *Artemisia* have been discussed by HAYAT et al. (2009a, b, c) using both light microscopy and scanning electron microscopy. Eight major types of hairs were distinguished in their study.

ROBINSON (2009) has correlated some hair characters with their chemical components. Glandular hairs may have different types of defensive components, viz. sesquiterpene lactones, monoterpenoids, gelatinous material with clerodane and labdane derivatives, which are usually common in Eupatorieae and Heliantheae. These two tribes are also characterized by the absence of T-shaped hairs. He has also emphasized the use of non-glandular hairs in different degrees. Hair characters support the separation of *Critoniopsis* SCH.BIP. from *Tephrothamnus* SCH.BIP. and *Eremosis* (DC.) GLEASON as proposed by KEELEY et al. (2007) on the basis of DNA studies.

Adding to the great variation in cypselar hairs, the tribe Gochnatieae (previously in Mutisieae) has three types of hairs, viz., two-armed, obliquely septate, and biseriate glandular (FREIRE et al. 2002). VENTOSA & HERRERA (2011 a, b) report the presence of biseriate glandular hairs with vesicle and simple biseriate non-glandular hairs on the cypselas of several species of *Anaetha* D. DON (formerly in genus *Gochmatia*).

The present study deals with the cypselas of 44 genera and 71 species of 7 tribes (Mutisieae, Dicomeae, Cardueae, Pertyeae, Cichorieae, Arctoteae and Vernonieae) under four subfamilies (Mutisioideae, Carduoideae, Pertyoideae and Cichorioideae). We thus briefly survey and summarize the variation of hairs from the mature cypselas belonging to the subfamily Cichorioideae sensu BREMER (1994), or the basal subfamilies and tribes sensu PANERO & FUNK (2002), FUNK et al. (2009) and FUNK (2010).

The objectives of this study are as follows:

- i) to elucidate the presence or absence of hairs on cypselar surface.
- ii) to present the types of hairs and location of hairs on the cypselar surface.
- iii) to describe the comparative morphological features of cypselar hairs in different genera and species.



- iv) to facilitate an accurate and rapid identification of taxa along with other cypselar features.
- v) to verify the potential usefulness of cypselar hairs for taxonomic or phylogenetic studies.
- vi) to investigate affinities among the analyzed taxa based on the distribution of hairs types.

Since micro-morphological features of hairs from different plant parts play such a significant role in plant taxonomy, particularly at the generic and specific levels, many plant anatomists and taxonomists have been attracted and fascinated by this subject and tried to prove the relationships of taxa on the basis of hair characters. Only a fraction of the rich literature has been summarized here. But knowledge about cypselar hairs and their taxonomic significance is still incomplete. Therefore, some additional information based on both light microscopy (LM) and scanning electron microscopy (SEM) is provided here.

### **Materials and Methods**

This study is based on the mature cypselas from collections in AD, BRI, LISC, NSW, RB, SRGH, TAI and Z herbaria as designated in Index Herbariorum (HOLMGREN et al. 1990). Some cypselas were collected by the first author indicated as S. MUKHERJEE from some parts of India also and deposited in the Herbarium of the Department of Botany, University of Kalyani, Kalyani – 741235, India as indicated by the new herbarium acronym, KAL. A list of all studied taxa and their source of origin is given in Appendix I. Studied taxa were classified in tribes according to FUNK et al. (2009), with nomenclature updated to current knowledge (mostly according to the online version of THE INTERNATIONAL PLANT NAMES INDEX, Harvard University databases) and the genera and species are enumerated in alphabetical sequence.

For microscopic examination, mature dry cypselas were observed after boiling with water and fixed in FAA solution (JOHANSEN 1940). Some FAA preserved cypselas were boiled in saturated solution of chloral hydrate solution for 1–3 minutes and washed with water. Whole cypselas (both treated and untreated) were stained in 0.5% aqueous safranin solution and were mounted in 70% phenol glycerine solution for microscopic observation.

Camera lucida drawings were done using a compound trinocular research microscope. For each species, at least five randomly selected cypselas were examined.

For scanning electron microscopy (SEM) studies dry cleaned cypselas were placed directly on the stubs with double coated adhesive tape and coated with gold. The

cypselar surface with or without hairs was scanned and photographed in a Philips Electron Microscope at 15 KV in the Regional Sophisticated Instrumentation Centre of Bose Institute at Kolkata, West Bengal, India. A few SEM photographs were taken in Hitachi SEM at the University Scientific Instrumentation Centre (USIC) of the University of Burdwan, Burdwan, West Bengal, India.

Descriptive terminology for trichomes follows RAMAYYA (1962 a, b, c), NARAYANA (1979), PAYNE (1978) and CICCARELLI et al. (2007). However, simple self explanatory terms are included to identify the specific type of hair.

### Discussion

Out of 71 studied species, 53 species (75%) have hairs on the mature cypselar surface and 18 species (25%) lack hairs. Of those possessing cypselar hairs, only six taxa (11%) possess only glandular hairs (G), 33 species (62%) have non-glandular hairs (NG), and remaining 14 species (26%) have both glandular and non-glandular hairs.

As indicated above the classification of Compositae has been recently thoroughly revised, but is still in some groups in a state of flux. BREMER (1994) in his cladistic classification of Compositae mentioned that in spite of the beginning accumulation of modern molecular data, a continued detailed study of morphological characters is necessary for the construction of robust phylogenies. This statement is still valid today.

Detailed morpho-anatomical studies of cypselas have been performed at least since the time of SCHULZ-BIPONTINUS (1844 a, b), and important pioneering work by BERKHEY (1761). GAERTNER (1790) and numerous contributions by HENRI CASSINI (1781 – 1832) must also be acknowledged. In later times, many workers (e.g., BRIQUET 1916, 1930, BLAKE 1918, GIROUX 1930, KYNČLOVÁ 1970, GRAU 1977, 1980, SAENZ 1981, VALEZ 1981, PANDEY et al. 1982, MUKHERJEE 2000, 2001 a, b, 2008, DAS & MUKHERJEE 2008) have clearly indicated that diacritical features of cypselas could be used for the delimitation, characterization and phylogenetic relationships among the taxa of Compositae. Important features of cypselas include general morphology, presence or absence of ribs, carpodium, stylopodium, pappus, surface trichomes, phytomelanin layer, calcium oxalate crystals, and tissue organization of pericarp and testa. All these characters are genetically controlled (LANE 1985, CRAWFORD et al. 2001). These micro-characters of cypselas are used for characterization of taxa at the generic and specific level and also for improvement of existing system of classification. (cf. KÄLLERSJÖ 1985, MUKHERJEE 2000, 2001 a, b, MUKHERJEE & SARKAR 2001a,b,c, MUKHERJEE & NORDENSTAM 2004, 2008, 2010). Therefore, cypselar hairs are part of the set of

microcharacters which all play similar roles along with other features.

Basic structure, distribution and apical part of hairs are all significant at the specific level. Morphological similarity in such details often reflects taxonomic closeness as pointed out by ANDERBERG (1989, 1991 a, b) and ELDENÄS et al. (1996). An example from the present study is provided by *Crepis* and *Hypochaeris* which have identical types of hairs. Both genera belong to the tribe Cichorieae and they are related (Clade 4 in KILLIAN et al. 2009).

HESS (1938) has argued that the principal function of 'twin hairs' is absorption of water, particularly those which have thickened walls. According to him, this type of hairs has sufficient amount of pits which facilitate the absorption of humidity from surrounding atmosphere. Therefore plants with such type of cypselar hair can thrive in arid and semiarid regions. Myxogenic 'twin hairs' keep the moisture around the cypselas as a mucilaginous layer, thus facilitating germination and/or perhaps contribute to seed dispersal. Present study indicates that phylogenetically widely separated tribes (e.g., Mutisieae and Cichorieae) possess twin type of hairs, which are also recorded in literature from many different groups of the family. So, this phenomenon may represent a convergent evolution in different tribes in response to similar environmental conditions.

Secretory substances within the glandular hairs are thought to protect plants against herbivores and pathogens, and at the same time they might reduce the loss of water through cuticular transpiration as well as maintaining the temperature of the leaves (DELL & MCCOMB 1975, 1977, KELSEY & SHAFIZADEH 1980, WERKER & FAHN 1981, DUKE et al. 1994, TATTINI et al. 2000). Glandular trichomes of *Stevia rebaudiana* contain sesquiterpene lactones, which are widespread throughout the family in various organs. Presence of such compounds, which have a bitter taste and may be toxic to grazing animals, should be of importance in the protection of plants against herbivores.

According to MAYEKISO et al. (2008), the non-glandular trichomes "appeared to originate from the epidermal layer by periclinal division. This process continued by periclinal division until several cells which formed the uniseriate trichomes, was produced".

Hairs are directly attached to, or in close contact with the surrounding environment, so their role must be largely protection from adverse biological, chemical and physical conditions. Absorbing and secretory activity of hairs also influence pollination and seed dispersal (cf. above, and UPHOF 1962, WERKER 2000).

Presence of 'twin hairs' indicates that the studied subfamilies (Mutisioideae, Cardioideae, Pertyoideae, Cichorioideae) are apomorphic in relation to the primitive subfamily Barnadesioideae, characterized by its 'barnadesioid hairs'

(CABRERA 1959, 1977, BREMER 1987, BREMER & JANSSEN 1992, KATINAS & STUESSY 1997, GRUENSTAEUDL et al. 2009). These are generally three-celled trichomes often with a long apical cell, a basal isodiametric cell, and an attached epidermal cell (two parallel cells).

Variation of 'twin hair' structure was indicated already by HESS (1938) and further discussed by FREIRE & KATINAS (1995). Present study also shows the variation of twin hairs in different taxa.

Biseriate (usually 10-celled) glandular hairs are common in Compositae (CARLQUIST 1958, 1959a, b, c, 1961), but not observed in mature cypselas. Such hairs have been reported from various tribes of several subfamilies, e.g. Mutisieae (CASTRO et al. 1997); Vernonieae (NARAYANA 1979, CASTRO et al. 1997) and Cardueae (SCHNEPF 1969). Peltate glands are very prominent in different species of *Vernonia*. These are visible with simple dissecting microscope. Such glandular hairs were termed as 'bilobed hairs' by FAUST & JONES (1973), and they are apparently common in the tribe Vernonieae.

Our study also confirmed that mature cypselar hairs of Compositae are often good taxonomic markers and can be utilized to resolve the taxonomic affinity of a group. For example, the tribe Vernonieae is mainly characterized by the presence of both glandular and non-glandular hairs in many studied genera, e.g. *Centrapalis*, *Lepidaploa*, *Polydora*, *Vanillosmopsis*, *Vernonanthura* and *Vernonia*. Previously almost all these taxa have been included in the genus *Vernonia* (e.g., JONES 1977).

CICCARELLI et al. (2007) discussed the distribution of hairs on the ovary surface in different taxa of Compositae. The distribution of hairs is perhaps remaining constant within a species. Shape of the hair tip is greatly variable and sometimes species specific according to the documentation by CICCARELLI et al. (l.c.). Our findings agree with these observations.

Examination with the SEM revealed the presence of two types of hairs, corresponding to the two general types recognized in many previous works (cf. above). The non-secreting or non-glandular type is abundant and responsible for covering or protecting the cypselar surface. Secreting hairs are usually club-shaped or spheroidal glandular structures of varying size and shape. The cuticular striations are either smooth or reticulate in nature. On the basis of this character two species of *Cicerbita* (*C. cyanea* and *C. macrorhiza*) can be easily distinguished.

NARAYANA (1979) has reported three types of trichomes from the cypselas of *Vernonia*. He designated the 'twin hair' as 'biseriate forked hair'. His other two types of hairs have not been observed in the present study. Out of six hair types from 20 species of *Vernonia* reported by SAHU (1984), only the 'twin hair' was observed in the present study (by SAHU designated as "achenial hair"). The peltate



gland is usually found mainly on the leaves of *Vernonia* spp. This type of gland was designated as 'bilobed trichome' by FAUST & JONES (1973), and also found on the mature cypselas of different taxa of Vernonieae. Actually this gland is composed of 10 cells (cf. above). Such type of trichome has been noted by FAVI et al. (2008) from *Vernonia galamensis* ssp. *galamensis* var. *ethiopica*.

In *Arctotheca*, the entire cypselas is completely embedded in white indumentum formed by filiform, entangled hairs with simple obtuse apex but not 'twin' type, while in *Arctotis*, the major portion of cypselar surface is glabrous, except near the base, where it possesses numerous, white, 3–5.5 mm long 'twin hairs', whereas in *Berkheya* the entire cypselar surface bears 'twin hairs' of varying size. On the basis of these hair characters these three genera of Arctoteae can be easily distinguished.

According to BREMER (1994) and earlier system of classifications (BENTHAM 1873a,b, CABRERA 1977) *Ainsliaea*, *Gerbera* and *Dicoma* belonged to the tribe Mutisieae. But on the basis of recent studies (PANERO & FUNK 2002, KADEREIT & JEFFREY 2007, FUNK et al. 2009) these three genera have been included in three distinct tribes. *Gerbera* remains in Mutisieae (subfamily Mutisioideae), whereas *Dicoma* (and *Macledium* CASS. now recognized as separate) belong in the tribe Dicomeae of the subfamily Carduoideae and *Ainsliaea* in the tribe Pertyeae under the subfamily Pertyoideae. If we look into structure of hairs on cypselas, these three taxa each have a distinct type of hairs as well as a distinct type of cypselar tissue organization (MUKHERJEE 2001a). These findings support the separation of these and related taxa into three different tribes.

In Cardueae, cypselar surface is often bossed, seldom cross rugose (*Arctium*), covered by unicellular hairs (*Centaurea cyanus*), possessing scabrous multicellular hairs (*Echinops*) or carrying 'twin hairs' (*Carlina*) or glabrous in others. Majority of aforesaid types except unicellular hairs have been mentioned by DITTRICH (1977) from this tribe. The unicellular hair on the cypselar surface of *Centaurea* has been reported by BRIQUET (1930), however. A small swollen and glandular hair-like outgrowth is seen at the base of each side of the cypselas in *Cirsium japonicum*. Such type of hair has not been found in other studied species of this tribe. PETIT (1997) has used cypselar trichomes along with other morphological characters to elucidate relationships in Cardueae.

In mature cypselas, variation of hairs is significantly less than in the young cypselas or in the vegetative organs. Only seven basic types of hairs have been observed in the present study, whereas numerous and various types of trichomes have been noted by different workers either from the vegetative part or from the young reproductive parts in other taxa. The basic types of hairs observed by us are as follows:



1. Twin hairs; 2. Papillate hairs; 3. Vesicle-like capitate glandular hairs;
4. Non-glandular filiform hairs; 5. Multicellular non-glandular acroscopic hairs;
6. Simple hairs; 7. Unicellular hairs.

Among these the twin hairs, papillate types and vesicle-like capitate glandular hairs are predominant. This is perhaps due to their persistent nature as compared to the deciduous nature of other types of hairs. Similarly detailed cellular configuration of hairs is not clearly visible in mature state of the cypselas. Therefore the detailed cellular structure of hairs has not been included here.

### 1. Twin type of hairs

These are prevalent in studied tribes Dicomeae, Pertyeae, Mutisieae, Cichorieae and Vernonieae, but less common in the tribes Arctoteae and Cardueae. Twin hairs again can be broadly categorized on the basis of shape of the terminal and basal cells into the following subtypes:

- i) Long twin hairs : consisting of long laterally adpressed cells: *Ainsliaea latifolia*, *A. reflexa*, *Berkheya zeyheri*, *Carlina vulgaris*, *Catananche caerulea*, *Macledium sessiliflorum*, *Vernonanthura diffusa*, *Vernonia scorpioides*,
- ii) Short twin hairs : arm or apical cells are short in length: *Gerbera jamesonii*, *Vernonia glabra*.
- iii) Apical ends of the arm or apical cells at distinctly unequal levels: *Ainsliaea latifolia*, *Baccharoides calvoana* ssp. *meridionalis*, *Vernonanthura diffusa*, *Vernonia cistifolia*.
- iv) Apical ends of the arm or apical cells more or less in equal plane: *Catananche caerulea*, *Elephantopus scaber*, *Lepidaploa gracilis*, *Polydora bainesii*, *Polydora poskeana*, *Vernonia glabra*, *Vernonia scorpioides*.
- v) Free portion of arm cells or apical cells greater in length than the basal united portion: *Baccharoides anthelmintica*, *Centrapalis kirkii*.
- vi) Papillate twin hairs: two papilla-like cells united to form twin hair: *Cicerbita cyanea* (only found in ribs region).
- vii) Fusiform twin hairs: arm cell thin-walled, more or less equal in length with abruptly attenuated tips, usually coloured (pink): *Piloselloides hirsuta*.
- viii) Base of twin hairs bilobed: *Gerbera jamesonii*.
- ix) Basal cells of twin hairs distinctly recurved: *Macledium sessiliflorum*.

On the basis of orientation or distribution of twin hairs on the cypselar surface,

hairs may be following types.

- i) Densely distributed throughout the cypselar surface, e.g., *Carlina acanthifolia*, *Vernonia cistifolia*, *Vernonia glabra*, *Vernonia scorpioides*.
- ii) Sparsely distributed throughout the cypselar surface, e.g., *Lepidaploa gracilis*.
- iii) Restricted (mainly) to furrow region, e.g., *Linzia melleri*.
- iv) Restricted (mainly) to ribs region, e.g., *Polydora bainesii*, *Vernonia petersii*.
- v) Mainly concentrated towards the lower part of cypselar, e.g., *Gerbera jamesonii*.
- vi) Mainly concentrated towards the apical part of cypselar, e.g., *Cicerbita macrorhiza*.

## 2. Papillate hairs

Papillate hairs are usually present in the majority of studied taxa of the tribe Cichorieae. On the basis of structure of other types of hairs and distribution of papillate hairs on the cypselar surface, the members of Cichorieae can be grouped into the following types:

- i) Papillate hairs moderately long with granule-like micro-projections as secondary sculpture, e.g., *Cicerbita cyanea*, *Lactuca serriola*.
- ii) Papillate hairs without micro-projections, e.g., *Actites megalocarpa*, *Cicerbita macrorhiza*, *Taraxacum officinale*.
- iii) Papillate hairs extremely minute and randomly dispersed, e.g., *Hieracium villosum*.
- iv) Numerous minute papillate hairs arranged in several transverse tires and forming a transversely muricate surface, e.g., *Scorzonerooides autumnalis*.
- v) Papillate hairs free at the furrows, but on the ribs papillate hairs laterally connate with each other and forming multicellular scale-like structures. Based on the shape of these scale-like structures there are three subtypes:
  - a) Apex of the scale nearly flat, e.g., *Crepis vesicaria*.
  - b) Apex of the scale nearly triangular, e.g., *Hypochoeris glabra*.
  - c) Apex of the scale nearly rounded, e.g., *Hypochoeris radicata*.
- vi) Papillate hairs with wide bifurcate base and pointed apex, e.g., *Taraxacum officinale*.

- vii) True papillate hairs absent, but surface squamosely muricate. Muricae vertically elongated with rounded broad elevation. Epidermal cells form obscurely papilla-like structures with obtuse apex, e.g., *Tragopogon porrifolius*.
- viii) Cypselar surface with papillate hairs at the furrows and moderately long papillate twin hairs on the ribs, e.g., *Actites megalocarpa*, *Cicerbita cyanea*.
- ix) Cypselar surface without papillate hairs but with long twin hairs, e.g., *Catananche caerulea*.
- x) Cypselar surface without any type of hairs but cross rugose or cross marked, e.g., *Sonchus brachyotus*.

### 3. Vesicle-like capitate glandular hairs

These are prevalent in the tribe Vernonieae. On the basis of distribution and structure of these hairs on the cypselar surface the following categories are recognized:

- i) Glandular hairs uniformly distributed throughout the cypselar surface, e.g., *Vernonia colorata*.
- ii) Glandular hairs sparsely distributed on the furrows only, and cypselar hairs may be of two types:
  - a) Glandular hairs homomorphic, e.g., *Centrapalis kirkii*, *Gymnanthemum amygdalinum*, *Lepidaploa gracilis*, *Polydora bainesii*, *Vanillosmopsis capitata*, *Vernonanthura diffusa*, *Vernonia cistifolia*, *Vernonia petersii*, *Vernonia scorpioides*. In *Polydora bainesii* each glandular hair has three distinct zones and in *Polydora poskeana* each glandular hair has two semi-lunar hyaline spaces at the two opposite sides (visible after clearing).
  - b) Glandular hairs dimorphic, e.g., *Rolandra fruticosa*, *Vernonia colorata*.
- iii) Glandular hairs densely distributed on the furrows of cypselar. There are three subcategories:
  - a) Glandular hairs arranged in 4–9 vertical zones, e.g., *Bothriocline laxa*, *Centrapalis kirkii*, *Polydora bainesii*, *Vernonia cistifolia*.
  - b) Glandular hairs arranged in 1–3 vertical rows, e.g., *Gymnanthemum amygdalinum*, *Lepidaploa gracilis*, *Vanillosmopsis capitata*, *Vernonanthura diffusa*.
  - c) Glandular hairs arranged in 1–2 vertical rows in two sides of each furrow, e.g., *Baccharoides calvoana*, *Linzia melleri*, *Vernonia glabra*.

4. **Multicellular non-glandular acroscopic hairs.** This type is found in only one species, viz., *Echinops sphaerocephalus*.
5. **Unicellular hairs.** This unbranched non-glandular hair type was observed in *Centaurea cyanus* and *Cirsium vulgare*.
6. **Simple hairs**, i.e. unbranched multicellular non-glandular hair type, e.g., *Arctotheca calendula*, *Arctotis venusta*, *Centrapalis kirkii*, *Lactuca serriola*, *Tragopogon porrifolius*.
7. **Non-glandular filiform hairs.** These hairs have a basal bulbous portion and a long filiform terminal part, e.g., *Linzia melleri*.

### Conclusion

From the above discussion it is obvious that micro-morphological characters of hairs along with other microcharacters of cypsela or other vegetative or floral morphological characters can be used for taxonomic and phylogenetic studies in the Compositae. There is a need to develop better universal terminology and perform detailed comparative studies of these micro-morphological features to improve Compositae taxonomy. An intensive morphological and ultrastructural study of cypsela hairs of cypsela along with other features of cypsela will make it possible to identify species in the fruiting state even when plants in flower are not available.

The present study also suggests that the value of hairs as a taxonomic criterion will be greatly increased when combined with other lines of evidence.

Table 1. Types and distribution of hairs in mature cypselas of Compositae in the present study.

SSL no. (1)	Taxa (2)	Presence (+) or absence (-) of hairs (3)	Types of hairs: glandular (G) or non glandular (NG) hairs (4)	Morphological nature of hairs on the mature cypselar surface (5)
	Tribe Mutistieae			
1)	<i>Gerbera jamesonii</i> (Figs. 1, 2)	+	NG	Cypselar surface sparsely covered by thin-walled short stiff persistent twin hairs more or less identical in structure. Base of the twin hairs bilobed. Tips of hair cells situated more or less on same plane.
2)	<i>Leibnitzia nepalensis</i>	+	NG	Structure and distribution of hairs more or less identical with the previous one.
3)	<i>Piloselloides hirsuta</i> (Fig. 3)	+	NG	Short fusiform thin-walled pink coloured twin hairs densely distributed throughout the surface. Tips of the twin cells abruptly attenuate and situated in equal plane.
	Tribe Dicomeae			
4)	<i>Maclodium sessiliflorum</i> ssp. <i>sessiliflorum</i> (Figs. 4, 5, 6, 108)	+	G	Cypselar surface densely covered by slender stiff white about 1.0 – 1.5 mm long twin hairs. Length of the hairs variable. Basal cells of the glandular hairs much wider than the base of the body cells of the hair and basal glandular cells contain brown coloured substances. Basal portion of hairs often recurved. Hairs also observed in SEM photographs.



	Tribe Cardueae			
5)	<i>Arctium lappa</i> (Figs. 7, 88)	-	-	Cypselar surface glabrous, i.e. without hairs, but cross rugose by numerous black patches throughout.
6)	<i>Carduus defloratus</i>	-	-	Cypselar surface somewhat bossed and finely striated and glabrous.
7)	<i>Carlina acanthifolia</i> ssp. <i>cynara</i> (Figs. 8, 9, 96)	+	G	Cypselar surface densely covered by acroscopic stiff light yellow to light brown long shortly forked twin hairs. Foot cell of each glandular hair deep brown in colour.
8)	<i>Carlina vulgaris</i> ssp. <i>vulgaris</i> (Figs. 10, 11)	+	G	Same as preceding.
9)	<i>Centaurea cyanus</i> (Figs. 12, 13, 97, 98)	+	NG	Cypselar surface sparsely covered by soft short fine pale yellow unicellular shiny hairs.
10)	<i>Centaurea macrocephala</i>	-	-	Cypselar surface glaucous glabrous.
11)	<i>Centaurea maculosa</i>	-	-	Same as preceding.
12)	<i>Cirsium arvense</i>	-	-	Cypselar surface glaucous glabrous.
13)	<i>Cirsium falconeri</i>	-	-	Cypselar surface glaucous like in <i>C. arvense</i> .
14)	<i>Cirsium japonicum</i> (Fig. 14)	+	G	Cypselar surface somewhat bossed without twin hairs, but two sides near the base bear two glandular hair like outgrowths.
15)	<i>Cirsium vulgare</i> (Fig. 15)	-	-	Cypselar surface somewhat bossed with numerous vertically elongated discrete black patches.

16)	<i>Echinops sphaerocephalus</i> (Figs. 16, 17, 101)	+	NG	Cypselar surface densely covered by multicellular, acroscopic hairs with sharply pointed apex.
17)	<i>Ptilostemon diacantha</i>	-	-	Cypselar surface glabrous, but with many large blackish brown somewhat bossed patches.
18)	<i>Rhaponticum scariosum</i> ssp. <i>rhaponticum</i>	-	-	Cypselar surface glabrous.
19)	<i>Saussurea abnormis</i>	-	-	Cypselar surface glabrous.
20)	<i>Saussurea deltoidea</i> (Fig. 18)	-	-	Cypsela surface with scale-like projections but without hairs.
21)	<i>Saussurea heteromalla</i>	-	-	Cypsela surface having cross rugosity with fringed margins.
	Tribe Pertyeae			
22)	<i>Ainsliaea aptera</i>	+	NG	Cypsela surface sparsely covered by soft short silky thin-walled dark coffee-coloured twin hairs with equally sized arms.
23)	<i>Ainsliaea latifolia</i> (Figs. 19, 20, 36)	+	NG	Cypsela surface very densely covered by slender stiff persistent acroscopic twin hairs. Basal cell of twin hairs more or less same in diameter throughout the length of the hair. Tips of the apical cells of the hair situated in prominently distant planes.
24)	<i>Ainsliaea reflexa</i> var. <i>nimborum</i> (Fig. 87)	+	NG	Twin hairs densely distributed on the entire cypselar surface except carpodial region. Twin hairs more or less same as preceding.
	Tribe Cichorieae			

25)	<i>Actites megalocarpa</i> (Figs. 21, 85)	+	NG	Cypselar surface minutely papillate throughout except at the top of the ribs region, where papillate twin hairs are present. Cypselar surface not cross rugose.
26)	<i>Catananche caerulea</i> (Fig. 22)	+	NG	Cypselar surface sparsely covered by long persistent twin hairs with more or less equal tips.
27)	<i>Cicerbita cyanea</i> (Fig. 23)	+	NG	Cypselar surface densely covered by numerous short papillate hairs with sharply pointed apex. Papillate type of twin hairs found in the ribs region.
28)	<i>Cicerbita macrorhiza</i> (Figs. 24, 25, 26, 27, 28, 99)	+	NG	Cypselar surface densely covered by numerous short papillate hairs with blunt ends. Surface with two types of twin hairs: one with distinctly unequal tips, other with more or less equal blunt tips. In addition papillate twin hairs and long unicellular hairs also present - altogether five types of hairs present on cypselar surface.
29)	<i>Crepis pyrenaica</i>	-	-	Cypselar surface glabrous.
30)	<i>Crepis vesicaria</i> (Figs. 29, 100)	+	NG	Cypselar surface densely covered by two types of hairs. At the ribs, papillate hairs laterally connate with each other forming a multicellular (4-9 cells) scale-like structure almost flat at the apex; whereas papillate hairs are discrete and free at the furrows. Entire cypselar surface or hair surface with numerous micro-projections.
31)	<i>Hieracium villosum</i> (Figs. 30, 102)	+	NG	Entire cypselar surface with conspicuously small acroscopic randomly distributed papillate hairs.
32)	<i>Hypochoeris glabra</i> (Figs. 31, 103)	+	NG	Cypselar surface more or less identical with <i>Crepis vesicaria</i> except at the apical part of multicellular scale-like structure nearly triangular in shape. Secondary sculpture of hairs and surface somewhat micro-warty.

33)	<i>Hypochoeris radicata</i> (Figs. 32, 33, 104)	+	NG	Cypselar surface nearly similar to <i>Crepis vesicaria</i> except the apical part of the multicellular scale-like structure more or less rounded. Secondary sculpture micro-warty like <i>C. vesicaria</i> and <i>Hypochoeris glabra</i> .
34)	<i>Lactuca dissecta</i>	+	NG	Cypselar surface densely covered by minute papillate hairs evenly distributed.
35)	<i>Lactuca graciliflora</i>	+	NG	Cypselar surface densely covered by light brown to dirty white papillate evenly distributed hairs.
36)	<i>Lactuca serriola</i> (Figs. 34, 105)	+	NG	Cypselar surface densely covered by numerous moderately long papillate hairs with acuminate apex. Hairs more conspicuous near the apical part of cypselar. Cypselar surface including hairs possess granule-like micro-projections.
37)	<i>Launaea acanthis</i>	-	-	Cypselar surface glabrous.
38)	<i>Launaea asplenifolia</i>	-	-	Cypselar surface glabrous.
39)	<i>Launaea procumbens</i>	-	-	Cypselar surface glabrous.
40)	<i>Launaea sarmentosa</i>	-	-	Cypselar surface glabrous.
41)	<i>Scorzoneroideis autumnalis</i> (Figs. 35, 106)	+	NG	Cypselar surface with numerous short triangular papillate hairs arranged in different vertical planes and surface appears as transversely muricate. Apical part of each papilla possesses pigmented substances.

42)	<i>Picris hieracioides</i>	+	NG	Cypselar surface transversely rugose with free papillate hairs on the furrows and papillate twin hairs on the ribs.
43)	<i>Prenanthes khasiana</i>	+	NG	Cypselar surface minutely papillate throughout and with papillate twin hairs on the ribs only.
44)	<i>Sonchus brachyotus</i> (Fig. 113)	-	-	Cypselar surface glabrous and finely cross rugose or cross marked at the ribs.
45)	<i>Sonchus schweinfurthii</i>	+	NG	Cypselar surface with numerous randomly distributed minute papillate hairs having pigmented substances inside. Cypselar surface not cross rugose.
46)	<i>Taraxacum officinale</i> (Fig. 36)	+	NG	Cypselar surface densely covered by numerous papillate hairs with obtuse apex and bifurcate base.
47)	<i>Tragopogon porrifolius</i> (Figs. 37, 114)	+	NG	Major portion of cypselar surface squamosely muricate at the ribs (not papillate or hairy). Murica vertically elongated with rounded broad elevation. Apical part of cypselar adjacent to pappus with numerous long filiform simple hairs.
	Tribe Arctoteae			
48)	<i>Arctotheca calendula</i> (Figs. 38, 89)	+	NG	Entire cypselar densely and completely covered by numerous persistent very fine and slender white filiform woolly hairs with single obtuse apex. Basal end of cypselar with tail-like similar tufted long hairs.
49)	<i>Arctotis venusta</i> (Figs. 39, 90)	+	NG	Cypselar surface glabrous except at the basal end, which bears numerous silky very fine white 3.5 – 5 mm long tufted hairs with rounded apex, but not twin type.



50)	<i>Berkheya zeyheri</i> ssp. <i>zeyheri</i> (Figs. 40, 93)	+	NG	Cypselar surface sparsely to densely covered by numerous fine short to long variable thin-walled persistent twin hairs with apical ends in equal plane.
	Tribe Vernoniaeae			
51)	<i>Baccharoides anthelmintica</i> (Figs. 41, 91)	+	G + NG	Cypselar surface with capitate glandular hairs sessile ellipsoid vesicle-like arranged in 1–2 rows in each furrow region, and upwardly directed 'twin hairs' present throughout the surface with more or less equal apical cells. Outer surface of the vesicle-like capitate glandular hairs smooth without reticulate cuticular striations.
52)	<i>Baccharoides calvoana</i> ssp. <i>meridionalis</i> (Figs. 42, 43, 92)	+	NG	Ridges of cypselar surface densely covered by long chocolate brown persistent twin hairs with nearly equal tips. Hairs more conspicuous towards the base of cypsela.
53)	<i>Bothriocline laxa</i> (Figs. 44, 45, 94, 95)	+	G	Hairs sessile capitate ellipsoid vesicle-like arranged in 4–9 vertical rows in each furrow from the base to apex. These are thick-walled, filled with secretory substances. Hairs pentangular to hexangular in outline in SEM with reticulate cuticular striations.
54)	<i>Centropetalis kirkii</i> (Figs. 46, 47, 48)	+	G + NG	Cypselar surface sparsely covered by many long very narrow thin-walled twin hairs. Free portion of terminal cells of the twin hair always longer than the basal united portion. Also large number of free heteromorphic vesicle-like capitate glandular hairs irregularly arranged on the furrows.
55)	<i>Elephantopus scaber</i> (Fig. 49)	+	G + NG	Glandular hairs vesicle-like thick-walled capitate sessile obovoid to ellipsoid, found in furrows, distributed sparsely. Twin hairs sparsely distributed in the furrows with more or less equal cells.

56)	<i>Gymnanthemum amygdalinum</i> (Figs. 66, 67)	+	G + NG	More or less identical with <i>Polydora bainesii</i> , but tip cells situated in distinctly unequal level. Capitate sessile glandular hairs free not coalesced with each other.
57)	<i>Lepidaploa gracilis</i> (Figs. 50, 51, 52)	+	G + NG	Furrow region of cypselar surface densely covered by acroscopic long thin-walled persistent twin hairs with more or less equal terminal ends. Many circular to elliptic vesicle-like capitate glandular hairs usually coalesced, sometimes free, distributed in furrows.
58)	<i>Linzia melleri</i> (Figs. 53, 54, 55, 107)	+	G + NG	Furrow regions of cypselar surface possess both twin hairs and capitate vesicle-like glandular hairs. Glandular hairs arranged uniseriately, occasionally biseriately in each side of furrow. Seldom 2-celled glandular filiform hairs present at the apical part of cypselata.
59)	<i>Polydora bainesii</i> (Figs. 56, 57, 58, 109, 110)	+	G + NG	Sessile capitate vesicular glandular hairs irregularly arranged in the furrow region, free or coalesced. Each glandular hair differentiated into 3 distinct zones: outer transparent, middle compact, and inner semitransparent zone. Twin hairs long, distributed throughout the surface but more numerous near ribs. In SEM, glandular trichome obovoid, with smooth surface, with terminal tubercle like short outgrowth.
60)	<i>Polydora poskeana</i> (Figs. 59, 60, 61)	+	G + NG	Ribs 3–5 times narrower than furrows and densely covered by thick-walled persistent twin hairs with more or less equal terminal cells. Furrows possess numerous ellipsoid to globose free large oriented capitate glandular hairs. Each glandular hair characterized by the presence of 2 semi-lunar hyaline spaces at the two opposite sides (after clearing).

61)	<i>Pseudoclephantopus spicatus</i>	+	NG	Basal portion of cypselar surface and ribs region densely covered by long narrow thin-walled twin hairs with more or less equal tips.
62)	<i>Rolandra fruticosa</i> (Figs. 62, 63, 111, 112)	+	G	Hairs sessile thick-walled bilobed subglobose sparsely distributed throughout the surface. In SEM these appear homomorphic napiform bilobed and conspicuously depressed or notched at the middle with smooth cuticular striations. After clearing surface shows dimorphic glandular hair-like structure in 3-8 vertical rows.
63)	<i>Vanillosmopsis capitata</i> (Figs. 64, 65, 115)	+	G	Hairs sessile ellipsoid thick-walled, free in pairs and arranged in 2-3 vertical rows, found in furrow regions only, containing yellow substances.
64)	<i>Vernonanthura diffusa</i> (Figs. 68, 69, 70)	+	G + NG	Similar to <i>Gymnanthemum amygdalinum</i> but vesicle-like capitate glandular hairs arranged in groups or singly in 1-4 vertical rows. Twin hairs with distinctly unequal tips.
65)	<i>Vernonia cinerea</i>	+	G + NG	Cypselar surface sparsely covered by moderately long thin-walled twin hairs with slightly unequal tips. Furrow region possesses many vesicle-like ovoid glandular hairs, usually arranged in 1-3 vertical rows.
66)	<i>Vernonia cistifolia</i> (Figs. 71, 72, 73, 116)	+	G + NG	Capitate glandular hairs free sessile ellipsoid to circular from the top view and triangular from side view, distributed randomly on the furrows. Twin hairs short, distributed throughout the surface but more concentrated near ribs. In SEM glandular trichome with rounded apex and one deep wide circular depression at the centre, with smooth surface.

67)	<i>Tarlmounia elliptica</i>	+	G	Twin hairs not found on the cypselar surface, but multicellular vesicle-like glandular hairs found on the furrow regions arranged in 3-4 vertical rows.
68)	<i>Vernonia colorata</i> ssp. <i>colorata</i> (Figs. 82, 83, 84, 120)	+	G	Ribs usually wider than furrows and covered by numerous coalesced very small globose thick-walled glandular hairs. Furrow regions with free large ellipsoid to subglobose and unevenly distributed vesicle-like glandular hairs. Twin hairs absent. Capitulate glandular hairs distinctly dimorphic.
69)	<i>Vernonia glabra</i> (Figs. 74, 75, 76, 117)	+	G + NG	Both ribs and furrow region of the cypselar surface covered by short twin hairs. Capitulate vesicle-like glandular hairs arranged in 1 or 2 vertical rows on both sides of the furrow and coalesced with each other and each hair has a large central cavity.
70)	<i>Vernonia petersii</i> (Figs. 77, 78, 118)	+	G + NG	Ribs 2-3 times narrower than furrows. Cypselar surface densely covered by long stiff twin hairs in many rows with more or less equal tips. Capitulate vesicle-like glandular hairs arranged in 1-3 rows in transverse plane to form horizontal strip-like structure. Glands usually coalesced with each other.
71)	<i>Vernonia scorpioides</i> (Figs. 79, 80, 88, 119)	+	G + NG	Cypselar surface, especially furrow regions, covered by slender long persistent twin hairs with slightly unequal tips. Furrows region possesses capitulate vesicle-like glandular hairs in many rows, usually coalesced.

## Appendix 1. Taxa studied and specimen location.

Sl. No.	Name of the Species	Tribe	Source of Origin
1.	<i>Actites megalocarpa</i> (HOOK.f.) LANDER (syn. <i>Sonchus megalocarpus</i> (HOOK.f.) J. M. BLACK)	Cichorieae	AD; A.A. MUNIR 5512
2.	<i>Ainsliaea aptera</i> DC.	Pertyeae	KAL ; S. MUKHERJEE 25
3.	<i>Ainsliaea latifolia</i> (D. DON) SCH.BIP.	Pertyeae	KAL ; S. MUKHERJEE 17
4.	<i>Ainsliaea reflexa</i> MERR. var. <i>nimborum</i> HAND.-MAZZ.	Pertyeae	TAI; YUH FONG CHEN 3300
5.	<i>Arctium lappa</i> L.	Cardueae	Z ; Nr. 343
6.	<i>Arctotheca calendula</i> (L.) LEVYNS	Arctoteae	AD; N. N. DONNER 8541
7.	<i>Arctotis venusta</i> T. NORL.	Arctoteae	Z; Nr. 345
8.	<i>Baccharoides anthelmintica</i> (L.) MOENCH	Vernonieae	KAL; S. MUKHERJEE 1
9.	<i>Baccharoides calvoana</i> (HOOK.f.) ISAWUMI, EL-GHAZALY & B. NORD. ssp. <i>meridionalis</i> (WILD) ISAWUMI, EL-GHAZALY & B. NORD.	Vernonieae	SRGH; G. POPE 1930
10.	<i>Berkheya zeyheri</i> (SOND. & HARV.) OLIV. & HIERN ssp. <i>zeyheri</i>	Arctoteae	LISC; A.R. TORRE 6907
11.	<i>Bothriocline laxa</i> N. E. BR. ssp. <i>laxa</i>	Vernonieae	SRGH; M. MAVI 11
12.	<i>Carduus defloratus</i> L.	Cardueae	Z; Nr. 359
13.	<i>Carlina acanthifolia</i> ALL. ssp. <i>cynara</i> (POURRET ex DUBY) ROUY	Cardueae	Z; Nr. 360
14.	<i>Carlina vulgaris</i> L. ssp. <i>vulgaris</i>	Cardueae	Z; Nr. 361
15.	<i>Catananche caerulea</i> L.	Cichorieae	Z: Nr. 363
16.	<i>Centaurea cyanus</i> L. (syn. <i>Cyanus segetum</i> HILL)	Cardueae	Z; Nr. 364
17.	<i>Centaurea macrocephala</i> MUSS. PUSCHK. ex WILLD.	Cardueae	Z; Nr. 366



18.	<i>Centaurea maculosa</i> LAM. ssp. <i>maculosa</i>	Cardueae	Z; Nr. 369
19.	<i>Centrapalis kirkii</i> (OLIV. & HIERN) H. ROB.	Vernonieae	LISC; F.A. MENDONCA 2033
20.	<i>Cicerbita cyanea</i> (D. DON) P. BEAUV.	Cichorieae	KAL; S. MUKHERJEE 18
21.	<i>Cicerbita macrorhiza</i> (ROYLE) P. BEAUV.	Cichorieae	KAL; S. MUKHERJEE 19
22.	<i>Cirsium arvense</i> (L.) SCOP.	Cardueae	KAL; S. MUKHERJEE 23
23.	<i>Cirsium falconeri</i> (HOOK.f.) PETR.	Cardueae	KAL; S. MUKHERJEE 12
24.	<i>Cirsium japonicum</i> DC.	Cardueae	Z; Nr. 378
25.	<i>Cirsium vulgare</i> (SAVI) TEN.	Cardueae	BRI; s.n., s.coll.
26.	<i>Crepis pyrenaica</i> (L.) GREUTER	Cichorieae	Z; Nr. 383
27.	<i>Crepis vesicaria</i> L.	Cichorieae	AD; N.N. DONNER 8607
28.	<i>Echinops sphaerocephalus</i> L.	Cardueae	Z; Nr. 386
29.	<i>Elephantopus scaber</i> L.	Vernonieae	RB; SN 257
30.	<i>Gerbera jamesonii</i> BOLUS ex HOOK.f.	Mutisieae	Z, Nr. 397
31.	<i>Gymnanthemum amygdalinum</i> (DELILE) SCH.BIP. ex WALP. (syn. <i>Vernonanthura condensata</i> (BAKER) H. ROB.)	Vernonieae	RB ; SN 249
32.	<i>Hieracium villosum</i> JACQ.	Cichorieae	Z; Nr. 404
33.	<i>Hypochaeris glabra</i> L.	Cichorieae	AD; A. A. MUNIR 8601
34.	<i>Hypochaeris radicata</i> L.	Cichorieae	BRI; s.n., s.coll.
35.	<i>Lactuca dissecta</i> D. DON	Cichorieae	KAL; S. MUKHERJEE 43
36.	<i>Lactuca graciliflora</i> DC. (syn. <i>Stenosseris graciliflora</i> (WALL. ex DC.) C. SHIH)	Cichorieae	KAL; S. MUKHERJEE 52
37.	<i>Lactuca serriola</i> L.	Cichorieae	BRI; s.n., s.coll.
38.	<i>Launaea acaulis</i> (ROXB.) BABC. ex KERR	Cichorieae	KAL; S. MUKHERJEE 39
39.	<i>Launaea aspleniifolia</i> (WILLD.) HOOK.f.	Cichorieae	KAL; S. MUKHERJEE 54

40.	<i>Launaea procumbens</i> (ROXB.) RAMAYYA & RAJAGOPAL	Cichorieae	KAL; S. MUKHERJEE 46
41.	<i>Launaea sarmentosa</i> (WILLD.) SCH.BIP. ex KUNTZE	Cichorieae	KAL; S. MUKHERJEE 37
42.	<i>Leibnitzia nepalensis</i> (KUNZE) KITAM.	Mutisieae	KAL ; S. MUKHERJEE 44
43.	<i>Lepidaploa gracilis</i> (KUNTH) H. ROB.	Vernonieae	RB; SN 250
44.	<i>Linzia melleri</i> (OLIV. & HIERN) H. ROB.	Vernonieae	LISC; R. SANTOS 2051
45.	<i>Macledium sessiliflorum</i> (HARV. in HARV. & SOND.) S. ORTIZ ssp. <i>sessiliflorum</i>	Dicomeae	LISC ; A. R. TORRE 13
46.	<i>Picris hieracioides</i> L.	Cichorieae	KAL; S. MUKHERJEE 29
47.	<i>Piloselloides hirsuta</i> (FORSSK.) C. JEFFREY ex CUFOD.	Mutisieae	KAL; S. MUKHERJEE 28
48.	<i>Polydora bainesii</i> (OLIV. & HIERN) H. ROB.	Vernonieae	SRGH ; G. POPE 1929
49.	<i>Polydora poskeana</i> (VATKE & HILDEBRANDT) H. ROB.	Vernonieae	LISC; A. R. TORRE & PAIVA 11332
50.	<i>Prenanthes khasiana</i> C. B. CLARKE	Cichorieae	KAL ; S. MUKHERJEE 67
51.	<i>Pseudelephantopus spicatus</i> (JUSS.) C. F. BAKER	Vernonieae	KAL; S. MUKHERJEE 21
52.	<i>Ptilostemon diacantha</i> (LABILL.) GREUTER	Cardueae	Z; Nr. 377
53.	<i>Rhaponticum scariosum</i> LAM. ssp. <i>rhaponticum</i> (L.) GREUTER (syn. <i>Leuzea</i> <i>rhapontica</i> (L.) J. HOLUB)	Cardueae	Z; Nr. 413
54.	<i>Rolandra fruticosa</i> (L.) KUNTZE	Vernonieae	RB; SN 255
55.	<i>Saussurea abnormis</i> LIPSCH. (syn. <i>Himalaiella abnormis</i> (LIPSCH.) RAAB-STRAUBE, should prob. be treated in <i>Jurinea</i> )	Cardueae	KAL; S. MUKHERJEE 32
56.	<i>Saussurea deltoidea</i> (DC.) SCH. BIP.	Cardueae	KAL; S. MUKHERJEE 22

57.	<i>Saussurea heteromalla</i> (D. DON) HAND.-MAZZ.	Cardueae	KAL; S. MUKHERJEE 27
58.	<i>Scorzonerooides autumnalis</i> (L.) MOENCH (syn. <i>Leontodon autumnalis</i> L.)	Cichorieae	Z; Nr. 409
59.	<i>Sonchus brachyotus</i> DC.	Cichorieae	KAL; S. MUKHERJEE 20
60.	<i>Sonchus schweinfurthii</i> OLIV. & HIERN	Cichorieae	SRGH; M. MAVI 8
61.	<i>Taraxacum officinale</i> WEBER	Cichorieae	AD; A. A. MUNIR 5500
62.	<i>Tarlmounia elliptica</i> (DC.) H. ROB., S. C. KEELEY, SKVARLA & R. CHAN (syn. <i>Vernonia elliptica</i> DC.)	Vernonieae	KAL; S. MUKHERJEE 57
63.	<i>Tragopogon porrifolius</i> L.	Cichorieae	AD; N. N. DONNER 8606
64.	<i>Vanillosmopsis capitata</i> (SPRENG.) SCH. BIP.	Vernonieae	RB; SN 248
65.	<i>Vernonanthura diffusa</i> (LESS.) H. ROB.	Vernonieae	RB; SN 254
66.	<i>Vernonia cinerea</i> (L.) LESS.	Vernonieae	KAL; S. MUKHERJEE 55
67.	<i>Vernonia cistifolia</i> O. HOFFM.	Vernonieae	SRGH; G. POPE 1931
68.	<i>Vernonia colorata</i> (WILLD.) DRAKE ssp. <i>colorata</i> (syn. <i>V. senegalensis</i> LESS.)	Vernonieae	LISC; SCHLIEBEN 2457
69.	<i>Vernonia glabra</i> (STEETZ) VATKE	Vernonieae	SRGH ; M. MAVI 12
70.	<i>Vernonia petersii</i> OLIV. & HIERN ex OLIV.	Vernonieae	LISC; A. R. TORRE 118
71.	<i>Vernonia scorpioides</i> (LAM.) PERS.	Vernonieae	RB; SN 251



**Figs. 1–38.** The structure and distribution of hairs from mature cypselas in different taxa.

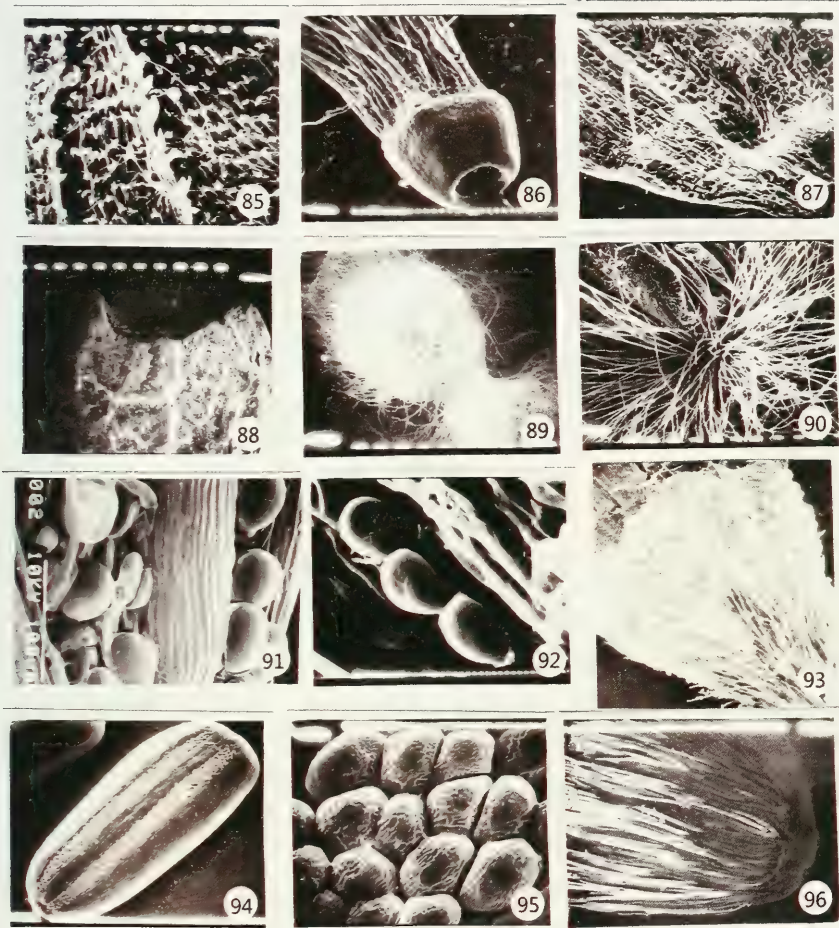
- Figs. 1,2: *Gerbera jamesonii*.  
Fig. 3: *Piloselloides hirsuta*.  
Figs. 4, 5, 6: *Macledium sessiliflorum* ssp. *sessiliflorum*.  
Fig.7: *Arctium lappa*.  
Figs.8, 9: *Carlina acanthifolia* ssp. *cynara*.  
Figs. 10, 11: *Carlina vulgaris* ssp. *vulgaris*.  
Figs.12, 13: *Centaurea cyanus*.  
Fig. 14: *Cirsium japonicum*.  
Fig. 15: *Cirsium vulgare*.  
Figs. 16, 17: *Echinops sphaerocephalus*.  
Fig. 18: *Saussurea deltoidea*.  
Figs. 1–9, 20: *Ainsliaea latifolia*.  
Fig. 21: *Actites megalocarpa*.  
Fig. 22: *Catananche caerulea*.  
Fig. 23: *Cicerbita cyanea*.  
Figs. 24–28: *Cicerbita macrorrhiza*.  
Fig. 29: *Crepis vesicaria*.  
Fig.30: *Hieracium villosum*.  
Fig. 31: *Hypochaeris glabra*.  
Figs. 32, 33: *Hypochaeris radicata*.  
Fig. 34: *Lactuca serriola*.  
Fig. 35: *Scorzoneroide autumnalis*.  
Fig. 36: *Taraxacum officinale*.  
Fig. 37: *Tragopogon porrifolius*.  
Fig. 38: *Arctotheca calendula*.





**Figs. 39–84.** The structure and distribution of hairs from mature cypselas in different taxa.

- Fig. 39: *Arctotis venusta*.  
Fig. 40: *Berkheya zeyheri* ssp. *zeyheri*.  
Fig. 41: *Baccharoides anthelmintica*.  
Figs. 42, 43: *Baccharoides calvoana* ssp. *meridionalis*.  
Figs. 44, 45: *Bothriocline laxa* ssp. *laxa*.  
Figs. 46–48: *Centrapalis kirkii*.  
Fig. 49: *Elephantopus scaber*.  
Figs. 50–52: *Lepidaploa gracilis*.  
Figs. 53–55: *Linzia melleri*.  
Figs. 56–58: *Polydora bainesii*.  
Figs. 59–61: *Polydora poskeana*.  
Figs. 62, 63: *Rolandra fruticosa*.  
Figs. 64, 65: *Vanillosmopsis capitata*.  
Figs. 66, 67: *Gymnanthemum amygdalinum*.  
Figs. 68–70: *Vernonanthura diffusa*.  
Figs. 71–73: *Vernonia cistifolia*.  
Figs. 74–76: *Vernonia glabra*.  
Figs. 77, 78: *Vernonia petersii*.  
Figs. 79–81: *Vernonia scorpioides*.  
Figs. 82–84: *Vernonia colorata* ssp. *colorata*.



Figs. 85–96. SEM photographs showing the structure and distribution of cypselar hairs.

Fig. 85: *Actites megalocarpa*,  $\times 400$ . Fig. 86: *Ainsliaea latifolia*,  $\times 200$ .

Fig. 87: *Ainsliaea reflexa*,  $\times 100$ . Fig. 88: *Arctium lappa*,  $\times 50$ .

Fig. 89: *Arctotheca calendula*,  $\times 50$ . Fig. 90: *Arctotis venusta*,  $\times 50$ .

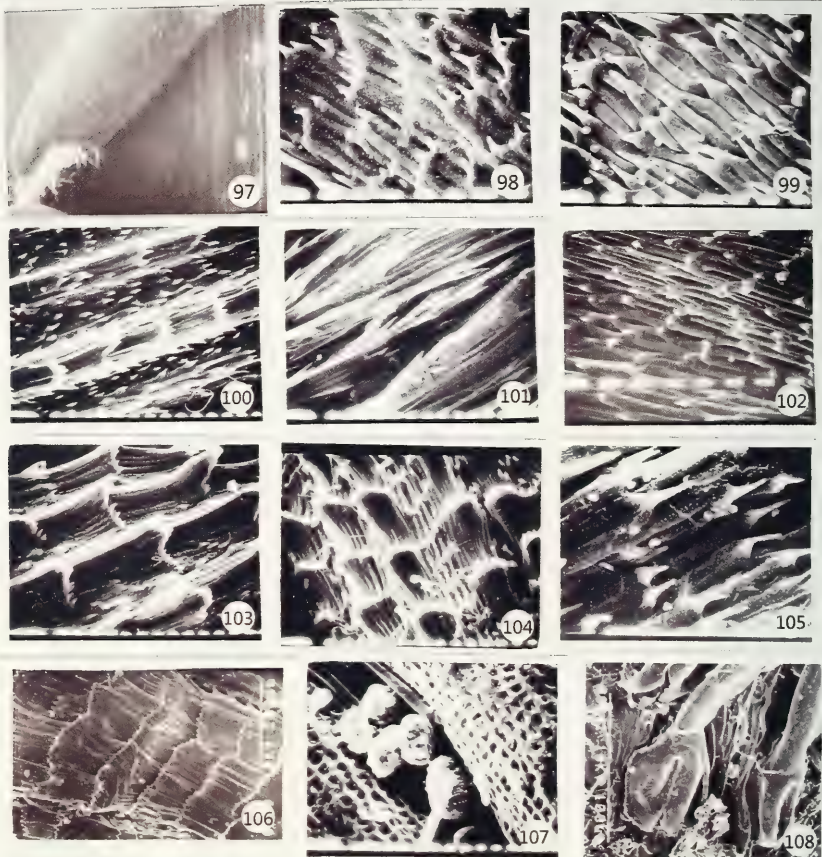
Fig. 91: *Baccharoides anthelmintica*.

Fig. 92: *Baccharoides calvoana* ssp. *meridionalis*,  $\times 1600$ .

Fig. 93: *Berkheya zeyheri*,  $\times 50$ .

Figs. 94, 95: *Bothriocline laxa*,  $\times 100$ ;  $\times 1600$ .

Fig. 96: *Carlina acanthifolia*,  $\times 100$ .



**Figs. 97–108.** SEM photographs showing the structure and distribution of cypselar hairs.

- Fig. 97: *Centaurea cyanus*,  $\times 25$ . Fig. 98: *Cicerbita cyanea*,  $\times 800$ .  
 Fig. 99: *Cicerbita macrorrhiza*,  $\times 800$ . Fig. 100: *Crepis vesicaria*,  $\times 400$ .  
 Fig. 101: *Echinops sphaerocephalus*,  $\times 400$ . Fig. 102: *Hieracium villosum*,  $\times 800$ .  
 Fig. 103: *Hypochaeris glabra*,  $\times 400$ . Fig. 104: *Hypochaeris radicata*,  $\times 400$ .  
 Fig. 105: *Lactuca serriola*,  $\times 1600$ . Fig. 106: *Scorzonerooides autumnalis*,  $\times 400$ .  
 Fig. 107: *Linzia melleri*,  $\times 400$ . Fig. 108: *Macledium sessiliflorum* ssp. *sessiliflorum*,  $\times 400$ .





**Figs. 109–120.** SEM photographs showing the structure and distribution of cypselar hairs.

Figs. 109, 110: *Polydora bainesii*,  $\times 50$ ;  $\times 400$ . Figs. 111, 112: *Rolandra fruticosa*.

Fig. 113: *Sonchus brachyotus*,  $\times 400$ . Fig. 114: *Tragopogon porrifolius*,  $\times 400$ .

Fig. 115: *Vanillosmopsis capitata*,  $\times 50$ . Fig. 116: *Vernonia cistifolia*,  $\times 800$ .

Fig. 117: *Vernonia glabra*,  $\times 200$ . Fig. 118: *Vernonia petersii*,  $\times 400$ .

Fig. 119: *Vernonia scorpioides*,  $\times 100$ . Fig. 120: *Vernonia colorata* ssp. *colorata*,  $\times 400$ .



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