

A cladistic analysis of *Nassauvia* Comm. ex Juss. (Asteraceae, Mutisieae) and related genera

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FREIRE, S. E., CRISCI, J. V. & KATINAS, L., 1993. **A cladistic analysis of *Nassauvia* Comm. ex Juss. (Asteraceae, Mutisieae) and related genera.** *Nassauvia* and the most closely related genera *Calopappus* and *Triptilion* from the southern Andes and Patagonia of South America, form a monophyletic group diagnosed by the following synapomorphies: cypsela trichomes single two-celled, cypsela testa with strengthened cells, pollen grains spheroidal to spheroidal-oblate, colpi membrane with sexine processes, pappus bristles two to six, and pappus deciduous. Furthermore, *Nassauvia*, *Triptilion*, and *Calopappus* form a group with two other Andean genera, *Moscharia* and *Polyachyrus*, diagnosed by occurrence of pseudocephalia and a reduction in the number of flowers to five, three or one. A cladistic analysis of the group was undertaken using 35 characters from morphology, anatomy, and palynology. The monophyletic terminal taxa were the 38 species of *Nassauvia*, the genus *Triptilion*, the monotypic genus *Calopappus*, the genus *Polyachyrus*, and the genus *Moscharia*. Character polarity was based on outgroup comparison using *Cephalopappus*. The analysis resulted in 223 equally parsimonious cladograms, each with 70 steps and a consistency index of 0.57. A successive weighting procedure was applied, resulting in 15 cladograms with a consistency index of 0.82. Results of the cladistic analysis support most of the current systematic classification of *Nassauvia*, with three exceptions: (1) *Nassauvia* (excluding *Calopappus*) is paraphyletic; (2) section *Mastigophorus* appears to be a polyphyletic group (*N. pygmaea* does not cluster with the remaining species of the section); (3) section *Panargyrum* (without *N. lagascae* = section *Caloptilium*) appears to be a paraphyletic group. The capitula arranged in cymose conflorescences in *Triptilion* are regarded as a primitive condition which gave rise to all stages present in *Nassauvia* (conflorescence spicate, pseudocephalium, capitula solitary). The capitula arranged in pseudocephalia in *Moscharia* and *Polyachyrus* are regarded as a parallel development to the pseudocephalium found in *Nassauvia*. *Nassauvia*, subgenus *Strongyloma* appears as the most primitive taxon, with its spicate conflorescence, whereas section *Mastigophorus* with its solitary capitulum is thought-derived. These results correspond well with cytological data where species of the subgenus *Strongyloma* have $n = 11$ and the species of section *Mastigophorus* are tetraploids ($n = 22$).

ADDITIONAL KEY WORDS:—Cytology – evolution of heads – phylogeny.

CONTENTS

Introduction	294
Material and methods	294
Results	298
Discussion	304
Placement of <i>Calopappus</i>	304
Evolution of flowering heads	305
Pappus	305
Cytology	307
Geographic distribution and ecology	307

Acknowledgements	308
References	308

INTRODUCTION

Nassauvia Comm. ex Juss. is found in the southern Andes and Patagonia of South America. The 38 species of *Nassauvia* (Arroyo & Marticorena, 1988; Cabrera, 1982) have been divided into two subgenera and four sections based on plant growth habit, cypsela morphology, pappus, and leaf shape (Cabrera, *l.c.*). Although some hypotheses of relationships between species have been postulated (Cabrera, 1982; Hunziker *et al.*, 1991; Stuessy *et al.*, 1988), their genealogy is still unclear.

Nassauvia, with *Triptilion*, *Calopappus*, *Moscharia* and *Polyachyrus*, represent an interesting group within the subtribe Nassauviinae (Crisci, 1974a, 1980) because of the several disjunct distribution patterns of closely related species and advanced characters within the family, such as the occurrence of secondary capitula or pseudocephalia in several species. Nevertheless, *Nassauvia*, *Triptilion* and *Calopappus* form a monophyletic group based on several synapomorphies (cypsela trichomes single two-celled, cypsela testa with strengthened cells, pollen grains spheroidal to spheroidal-oblate, colpi membrane with sexine processes, pappus bristles two to six, pappus deciduous).

This paper presents a cladistic analysis of *Nassauvia* using a Wagner parsimony algorithm (Farris *et al.*, 1970). To test the monophyly of *Nassauvia*, we have included the most closely related genera *Triptilion*, *Calopappus*, *Polyachyrus*, and *Moscharia* as part of the ingroup. All of them have been recently monographed (*Nassauvia*: Cabrera, 1982; *Calopappus*: Crisci & Freire, 1986; *Triptilion*: Katinas *et al.*, 1992; *Polyachyrus*: Ricardi & Weltdt, 1974; *Moscharia*: Crisci, 1974b).

MATERIAL AND METHODS

Nassauvia, *Triptilion*, *Calopappus*, *Moscharia* and *Polyachyrus* belong to the subtribe Nassauviinae (Crisci, 1974a), which is delimited from the rest of the Mutisieae by the following three characters: disc florets bilabiate and style branches truncate at the apex with a crown of collector hairs.

The monophyletic terminal taxa of this analysis are: (1) the genus *Polyachyrus* (seven species), which is characterized as a monophyletic group by the presence of pseudocephalia composed of up to ten heads disposed at different levels; (2) the genus *Moscharia* (two species), which can be also delimited from all other genera of the subtribe by the pseudocephalia composed of eight to ten heads attached at the same level; (3) the genus *Triptilion* (seven species) which is characterized as a monophyletic group by a pappus formed of four to five paleae plicate along the median line, and expanded and laciniate in the upper part; (4) the monotypic genus *Calopappus*; (5) the 38 species of *Nassauvia*. Table 1 shows their geographical distribution.

Data from 35 characters were derived from plant habit, leaf morphology, growth characteristics, capitula arrangement, capitula morphology, cypsela morphology, pappus morphology and pollen grain type (Cabrera, 1982; Grau, 1980; Parra & Marticorena, 1972). Table 2 shows the characters and character states used in the cladistic analysis.

TABLE 1. Taxa studied, acronyms, and geographical distributions

Taxa	Acronym	Geographical distribution (Cabrera, 1982; Crisci, 1974a)
<i>Calopappus</i>	CAL	central Chile
<i>Cephalopappus</i>	CEP	northeastern of Brazil (Bahia)
<i>Macrachaenium</i>	MAC	<i>Nothofagus</i> forest
<i>Moscharia</i>	MOS	central Chile
<i>Nassauvia</i>		
Subgen. <i>Nassauvia</i>		
Sect. <i>Caloptilium</i>		
<i>N. lagascae</i>	LAG	Argentina (S Mendoza to Santa Cruz), Chile (Aconcagua to Cautín, and Magallanes)
Sect. <i>Mastigophorus</i>		
<i>N. ameghinoi</i>	AME	Argentina (S Chubut and Santa Cruz)
<i>N. gaudichaudii</i>	GAU	Argentina (Falkland Islands = Islas Malvinas)
<i>N. hillei</i>	HIL	Argentina (Neuquén)
<i>N. juniperina</i>	JUN	Argentina (Chubut, Santa Cruz)
<i>N. pentacaenoides</i>	PEN	Argentina (Santa Cruz)
<i>N. pygmaea</i>	PYG	Argentina (Neuquén to Tierra del Fuego, Isla de los Estados), Chile (Ñuble to Magallanes)
Sect. <i>Nassauvia</i>		
<i>N. argentea</i>	AGE	Argentina (Neuquén), central Chile
<i>N. argyrophylla</i>	AGY	Argentina (Neuquén to Chubut)
<i>N. coronipappa</i>	COR	Chile (Ultima Esperanza)
<i>N. chubutensis</i>	CHU	Argentina (Chubut)
<i>N. cumingii</i>	CUM	Argentina (S San Juan to Mendoza), Chile (Coquimbo to Santiago)
<i>N. dentata</i>	DEN	Argentina (Neuquén, Rio Negro, Chubut), Chile (Llanquihue, Magallanes)
<i>N. digitata</i>	DIG	Argentina (Neuquén), Chile (Talca to Bio-Bío)
<i>N. dusenii</i>	DUS	Argentina (Rio Negro to S Chubut)
<i>N. latissima</i>	LAT	Argentina (S Tierra del Fuego, Isla de los Estados)
<i>N. magellanica</i>	MAG	Argentina (Santa Cruz, Tierra del Fuego)
<i>N. pinnigera</i>	PIN	Argentina (Mendoza, Neuquén), Chile (Santiago to Curicó)
<i>N. planifolia</i>	PLA	Argentina (S Mendoza, N Neuquén)
<i>N. pulcherrina</i>	PUL	Argentina (S Neuquén, NW Rio Negro)
<i>N. pyramidalis</i>	PYR	Argentina (Mendoza, N Neuquén), Chile (Santiago to Bio-Bío)
<i>N. ramosissima</i>	RAM	central Chile (Linares)
<i>N. revoluta</i>	REV	Argentina (Mendoza to Santa Cruz), Chile (Aconcagua to Magallanes)
<i>N. ruizii</i>	RUI	Argentina (Mendoza)
<i>N. sceptrum</i>	SCE	Argentina (Santa Cruz)
<i>N. serpens</i>	SER	Argentina (Falkland Islands = Islas Malvinas)
<i>N. sprengelioides</i>	SPR	Chile (Curicó to Malleco), Argentina
<i>N. sublobata</i>	SUB	Argentina (S Mendoza, N Neuquén)
Sect. <i>Panargyrum</i>		
<i>N. aculeata</i>	ACU	Argentina (Mendoza to Tierra del Fuego), Chile (Aconcagua to Magallanes and Aisen)
<i>N. darwinii</i>	DAR	Argentina (Neuquén to Tierra del Fuego), Chile
<i>N. glomerata</i>	GLT	Argentina (N Mendoza, N Neuquén), Chile (Santiago to Talca)
<i>N. looseri</i>	LOO	Chile (Santiago)
<i>N. uniflora</i>	UNI	Argentina (S San Juan, N Mendoza), Chile (Aconcagua)
Subgen. <i>Strongyloma</i>		
<i>N. axillaris</i>	AXI	S Bolivia to central Chile and Argentina (N Chubut)
<i>N. fuegiana</i>	FUE	Argentina (S Mendoza to N Tierra del Fuego)
<i>N. glomerulosa</i>	GLS	Argentina (S Mendoza to Santa Cruz)
<i>N. maeveae</i>	MAE	Argentina (S Santa Cruz)
<i>N. ulicina</i>	ULI	Argentina (Rio Negro to Santa Cruz)
<i>Polyachyrus</i>	POL	S Perú, central Chile
<i>Triptilion</i>	TRI	central Chile, Argentina (Neuquén to Santa Cruz)

TABLE 2. Characters and character states used in cladistic analysis of *Nassauvia* and allied genera

Characters	Character states
1 Habit	0. Herbs; 1. Shrubs
2 Life cycle	0. Perennial; 1. Annual
3 Limb of leaves multicostate	0. Absent; 1. Present
4 Brachyblast	0. Absent; 1. Present
5 Leaves	0. Entire; 1. Partite
6 Shape of leaf	0. Obovate, ovate; 1. Linear-subulate
7 Shape of leaf base	0. Non-vaginate; 1. Vaginate
8 Auricles	0. Absent; 1. Present
9 Cross section of leaf	0. Aplanate; 1. Circular
10 Basal leaves in rosettes	0. Present; 1. Absent
11 Phyllotaxy	0. Spreading; 1. Crowded
12 Type of inflorescence	0. Conflorescence cymose (paniculate, spicate or corymbose); 1. Pseudocephalium; 2. Solitary
13 Pseudoinvolucre	0. Absent; 1. Present
14 Receptacle of the pseudocephalium	0. Conical; 1. Convex
15 Capitula of the pseudocephalium	0. Monomorphic; 1. Dimorphic
16 Type of pseudocephalia	0. In branched cyme; 1. Solitary
17 Number of series of involucre	0. 2; 1. 1; 2. 3
18 Length of involucral bracts	0. Outer bracts longer than inner; 1. All the same length
19 Number of bracts of involucre	0. More than 5; 1. Less than 5
20 Height of involucre	0. Less than 15 mm; 1. More than 17 mm
21 Number of flowers per capitulum	0. 5 (rarely 4); 1. 1-2 (rarely 3)
22 Colour of corollas	0. White; 1. Violet or pink
23 Cypselas pubescent	0. Present; 1. Absent
24 Cypselas hairs	0. Double trichomes 'Zwillingshaare'; 1. Single trichomes two-celled
25 Cross-section of cypselas testa	0. External layer of the testa with epidermal cells not strengthened; 1. Lateral and basal walls of the testa epidermis strengthened
26 Shape of pollen grains	0. Subprolate to prolate-spheroidal; 1. Spheroidal to spheroidal-oblate
27 Colpus membrane	0. Smooth; 1. With sexine processes
28 Tectum and infratectum	0. Infratectum thickness; 1. Tectum and infratectum equal thickness
29 Margin of pappus bristles	0. Plumose; 1. Entire or ciliate
30 Pappus plumose	0. Completely plumose; 1. Plumose on the distal half
31 Number of pappus bristles	0. 10 or more; 1. 2-6
32 Surface of pappus bristles	0. Flat; 1. Plicate
33 Type of pappus	0. Hairy (less than 0.1 mm wide); 1. Chaffy (0.2 to 1 mm wide); 2. Paleaceous (more than 1.5 mm)
34 Pappus duration	0. Persistent; 1. Deciduous
35 Length of bristles pappus	0. Pappus and corollas (upper lip) equal; 1. Pappus shorter than corollas (upper lip); 2. Pappus reduced or absent

Character polarity was determined by outgroup comparison (Humphries & Funk, 1984; Maddison *et al.*, 1984; Watrous & Wheeler, 1981) with *Cephalopappus* as the outgroup which, according to Crisci (1980), appears at the base of the tree branch of *Nassauvia*, *Triptilion*, *Calopappus*, *Moscharia* and *Polyachyrus*. *Nassauvia*, related genera and *Cephalopappus* form a monophyletic group diagnosed by a reduction in the size of capitula and the reduction in the size or number of pappus bristles. Because the pappus is absent in *Cephalopappus*, we used *Macrachaenium* as a second outgroup (Karis *et al.*, 1992). However, identical results were obtained by using 'question marks' for these characters involving the pappus in *Cephalopappus*.

Table 3 contains the data matrix used in this analysis. Four of the 35 characters (12, 17, 33 and 35) had more than two character states. Characters

TABLE 3. Data matrix

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35			
1 OUT	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
2 CAL	1	0	0	0	0	1	1	0	0	1	1	2	?	?	?	?	2	0	0	1	0	0	1	?	1	1	0	1	1	?	0	0	1	0	0			
3 MOS	0	1	0	0	1	?	0	1	0	0	0	1	1	1	1	0	1	?	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	2			
4 POL	0	1	0	0	1	?	0	1	0	0	0	1	0	0	0	0	1	?	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	1			
5 TRI	0	1	0	0	1	?	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
6 ACU	0	0	0	0	0	1	0	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
7 AGE	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	?	1	1	1	1	?	1	0	1	1	1		
8 AGY	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	1	?	1	1	1	1	1	?	1	0	1	1	1	1		
9 AME	0	0	0	0	0	1	1	0	1	1	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
10 AXI	1	0	0	1	0	1	1	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
11 COR	0	0	?	0	0	0	0	?	1	1	1	0	0	0	1	0	0	0	0	0	1	0	1	?	1	1	1	1	1	?	1	1	2	0	1			
12 CUM	0	0	?	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	?	1	1	1	1	?	1	0	1	1	1	1		
13 CHU	0	0	1	0	1	0	0	0	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
14 DAR	0	0	0	0	0	1	0	0	1	?	1	0	0	0	1	0	0	0	0	0	0	0	0	1	?	1	1	1	1	0	0	0	0	0	0	0	1	
15 DEN	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	?	1	1	1	1	?	1	0	1	1	1	1	1	
16 DIG	0	0	1	0	1	?	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	?	1	1	1	1	1	?	1	0	1	1	1	1	1	
17 DUS	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	?	1	1	1	1	1	?	1	0	1	1	1	1	
18 FUE	1	0	0	1	0	1	1	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
19 GAU	0	0	0	0	0	1	1	0	1	1	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
20 GLS	1	0	0	1	0	1	1	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
21 GLT	0	0	?	0	1	?	0	0	?	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	?	1	1	1	1	1	?	0	0	0	0	0	0	
22 HIL	0	0	0	0	0	1	1	0	1	1	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
23 JUN	0	0	0	0	0	1	1	0	1	1	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
24 LAG	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	?	1	1	1	1	0	0	0	0	0	0	0	0	
25 LAT	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	?	1	1	1	1	1	?	1	0	1	1	1	1	1
26 LOO	0	0	?	0	0	1	0	0	?	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	?	1	1	1	1	1	?	0	0	0	0	?	?	
27 MAE	1	0	0	1	0	1	1	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
28 MAG	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	?	1	1	1	1	?	1	0	1	1	1	1	1	
29 PEN	0	0	0	0	0	1	1	0	1	1	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
30 PIN	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	?	1	1	1	1	?	1	0	1	1	1	1	1	1
31 PLA	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	?	1	1	1	1	?	1	0	1	1	1	1	1	1
32 PUL	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	?	1	1	1	1	1	?	1	0	1	1	1	?	?
33 PYG	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	?	1	1	1	1	1	?	1	0	1	1	1	0	0
34 PYR	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	?	1	1	1	1	1	?	1	0	1	1	1	1	1
35 RAM	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	?	1	1	1	1	1	?	1	0	1	1	1	?	?
36 REV	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	?	1	1	1	1	1	?	1	0	1	1	1	1	1
37 RUI	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	?	1	1	1	1	1	?	1	0	1	1	1	1	1
38 SCE	0	0	1	0	0	?	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	?	1	1	1	1	1	?	1	0	1	1	1	1	1
39 SER	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	?	1	1	1	1	1	?	1	0	1	1	1	1	1
40 SPR	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	?	1	1	1	1	1	?	1	0	1	1	1	1	1
41 SUB	0	0	1	0	1	?	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	?	1	1	1	1	1	?	1	0	1	1	1	1	1
42 ULI	1	0	0	1	0	1	1	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
43 UNI	0	0	0	0	1	?	0	0	0	1	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

17, 33 and 35 were treated as non-additive (equivalent to 'unordered' in other analyses). Character 12 (type of inflorescence) was treated as additive. Despite the fact that for some authors (e.g. Hauser & Presch, 1991) the hypothesis of order in character changes is unnecessary, we believe that character 12 should be treated as ordered because as was pointed out by Cabrera (1982) the changes from cymose conflorescence to solitary capitula seem to be more parsimonious when it has a transformation series through the pseudocephalium. Characters 6, 13–16, 24, 30 are related to characters 5, 12, 23 and 29, respectively. Therefore we have coded those taxa with partite leaves (character 5, state 1), without a pseudocephalium (character 12, state 0 or 2), with glabrous cypselas (character 23, state 1), with entire or ciliate pappus bristles (character 29, state 1) as '?' in characters 6, 13–16, 24 and 30.

The data were analysed using Farris's phylogenetic program, Hennig86 version 1.5 (Farris, 1988), applying the options 'mhennig' for constructing multiple initial cladograms, followed by 'bb*' (branch breaker), an heuristic for determining the shortest tree. We also used the successive approximations weighting procedure in Hennig86, which calculates weights from the last fits to the prior round of most parsimonious trees. The weights are based on the rescaled consistency index (rc), which is the product of character consistency (c) and character retention index (r). The value is rescaled to lie within a range of 0–10. The weighting procedure is repeated on successively produced trees until the trees no longer change (Farris, 1989). When the analysis yielded more than one tree, we constructed a strict consensus tree using the Nelsen option of Hennig86.

RESULTS

Two hundred and twenty three equally parsimonious cladograms were generated from our data matrix. All have 70 steps and a consistency index of 0.57. If we exclude the autapomorphies for the genera *Moscharia* (characters 13, 14, 15, 19), *Triptilion* (characters 18, 30), and *Calopappus* (character 20), the length is 63 steps and the consistency index is 0.50. The strict consensus tree of the 223 cladograms (Fig. 1) shows that six monophyletic groups appear in all of them: (1) MOS-POL (annual, leaves partite, auricles, pseudocephalium, involucre one-seriate, flowers one to three, corollas violet); (2) all taxa except MOS and POL (cypselas hairs single two-celled, testa epidermis strengthened, pollen grains spheroidal to spheroidal oblate, colpi membrane with sexine processes, pappus bristles two to six, pappus deciduous); (3) all taxa except MOS-POL and TRI (basal leaves not in rosette, leaves crowded, pappus bristles entire or ciliate); (4) UNI-GLT-LOO (LAG-DAR-ACU) (leaves non-vaginate, hairy pappus); (5) LAG-DAR-ACU (pappus bristles plumose); (6) AXI-FUE-GLS-MAE-ULI (shrubs, brachyblasts, leaves linear-subulate, leaves vaginate).

When the successive approximations weighting procedure was applied, 15 minimum length trees were obtained after the third round of weighting, with a length of 292 steps (the high value for the length is a function of the weight being scaled up to a value of 10), and the consistency improved to 0.82. The values of the range and number of steps and consistency indices (c), retention indices (r), and weights ($rc \times 100$) for each character are listed in Table 4. After the procedure, the maximum weight of 10 was assigned to characters 4, 8–11, 13–20, and 23–26; a weight of 4 to characters 3, 29 and 35; a weight of 3 to character 33; a weight of 2 to characters 2, 6–7, 12, 21–22, 31 and 34; a weight of 0 to characters 1, 5, 27 and 32. The strict consensus tree of the 15 cladograms (Fig. 2) shows seven additional monophyletic groups not included in the strict consensus tree of the 223 cladograms, listed with their synapomorphies: (1) all taxa except MOS-POL, TRI and the species of the subgenus *Strongyloma* (pseudocephalium solitary, cypselas glabrous); (2) PYG (((HIL-JUN-AME) GAU-PEN) (CAL(UNI(GLT-LOO(LAG-DAR-ACU)))))) (leaves vaginate, pappus and corolla of equal long); (3) (((HIL-JUN-AME)GAU-PEN(CAL(UNI(GLT-LOO(LAG-DAR-ACU)))))) (leaves linear-subulate, capitula solitary and bristles pappus 10 or more); (4) (HIL-JUN-AME)GAU-PEN (cross section of leaf circular); (5) HIL-JUN-AME (pappus bristles two to six); (6) CAL(UNI-GLO-

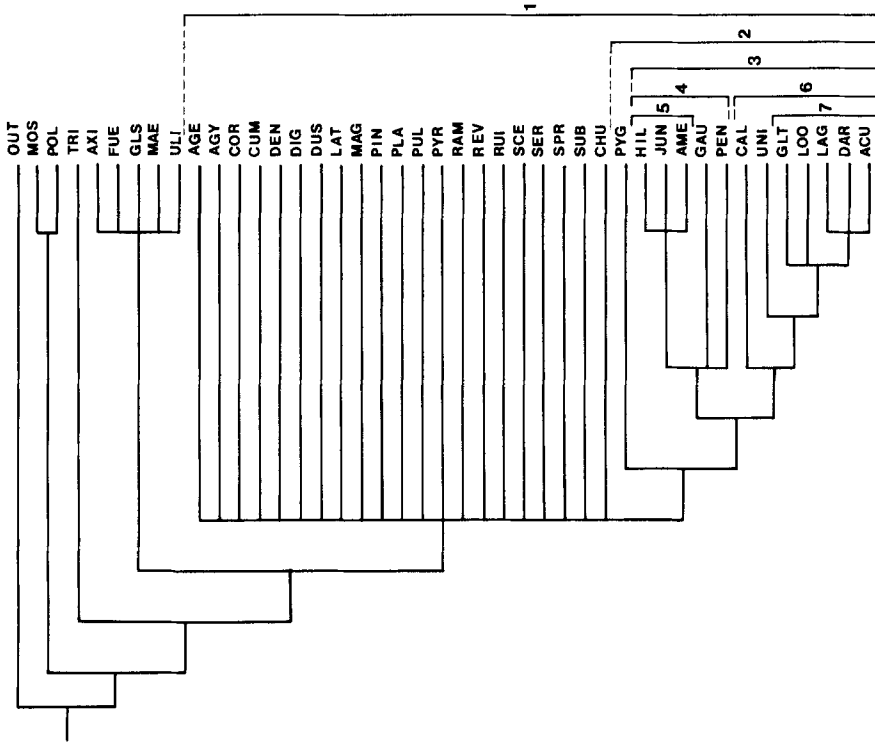


Figure 2. Strict consensus cladogram from 15 most parsimonious cladograms after applying the successive weighting procedure. Numbers 1-7 show seven additional monophyletic groups not included in Fig. 1. Refer to Table 1 for acronyms.

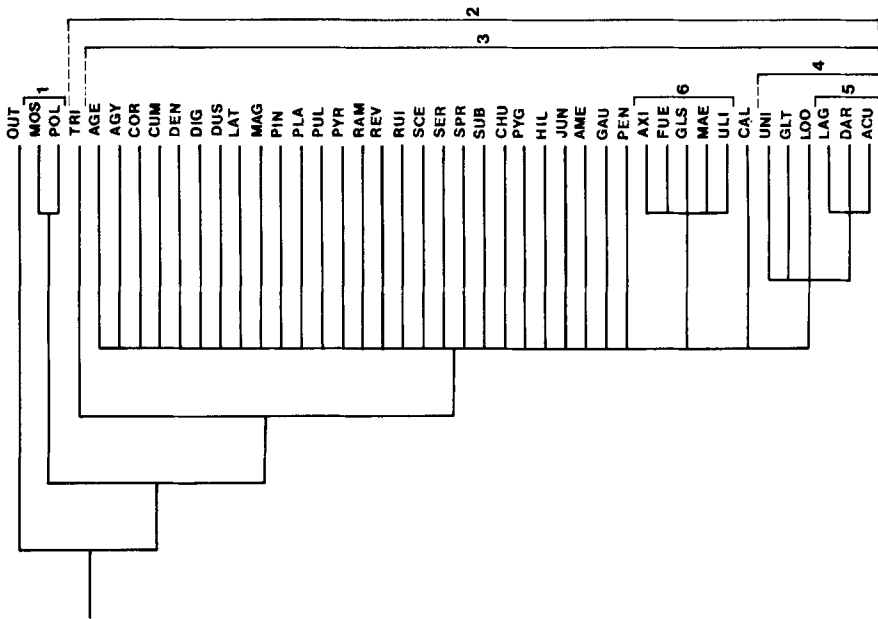


Figure 1. Strict consensus cladogram from the 223 most parsimonious cladograms. Numbers 1-6 show six monophyletic groups that appear in all of the 223 cladograms. Refer to Table 1 for acronyms.

TABLE 4. Character consistencies (c) and retention indices (r) as the best fits on the 15 equally parsimonious trees from Hennig86, used to calculate weights. Final weights were obtained after the third round of the successive weighting procedure in Hennig86. Weights were scaled to integers

Character	Range of step	Number of step	Consistency index (c)	Retention index (r)	Weight ($rc \times 10$)	Final weight
1	1	2	0.50	0	0	0
2	1	2	0.50	0.50	2	2
3	1	2	0.50	0.92	4	4
4	1	1	1	1	10	10
5	1	7	0.14	0.14	2	0
6	1	3	0.33	0.77	4	2
7	1	3	0.33	0.71	4	2
8	1	1	1	1	10	10
9	1	1	1	1	10	10
10	1	1	1	1	10	10
11	1	1	1	1	10	10
12	2	6	0.33	0.60	2	2
13	1	1	1	1	10	10
14	1	1	1	1	10	10
15	1	1	1	1	10	10
16	1	1	1	1	10	10
17	2	2	1	1	10	10
18	1	1	1	1	10	10
19	1	1	1	1	10	10
20	1	1	1	1	10	10
21	1	2	0.50	0.50	2	2
22	1	2	0.50	0.50	2	2
23	1	1	1	1	10	10
24	1	1	1	1	10	10
25	1	1	1	1	10	10
26	1	1	1	1	10	10
27	1	2	0.50	0	0	0
28	1	1	1	1	10	10
29	1	2	0.50	0.83	4	4
30	1	1	1	1	10	10
31	1	3	0.33	0.81	4	2
32	1	3	0.33	0	0	0
33	2	4	0.50	0.71	3	3
34	1	3	0.33	0.80	2	2
35	2	4	0.50	0.81	4	4

LOO(LAG-DAR-ACU))) (pappus persistent); (7) GLT-LOO(LAG-DAR-ACU) (pseudocephalium).

The 15 trees obtained after successive weighting can be further simplified to ten topologies without loss of parsimony. The reason for this is that the Hennig86 regards trees as distinct if there are any different character interpretations to distinguish them and producing extra branches in some cladograms (Carr *et al.*, 1990). In five of our 15 cladograms appear simultaneously two groups: (GAU-PEN) and (HIL-JUN-AME), which cannot be supported at the same time in the same cladogram.

Figure 3 illustrates one of ten equally parsimonious cladograms. Figure 4 shows the ten different configurations for the positions of *N. coronipappa*, *N. chubutensis* and HIL-JUN-AME-GAU-PEN for the middle of the cladogram.

The differences in the positions of *N. coronipappa* and *N. chubutensis* (Fig. 3) result from changes in character 3 (presence or absence of leaves multicostate) and character 12 (presence of pseudocephalium). Character 3 is missing for *N. coronipappa* (i.e. '?'), so the presence of this character is assumed in Figure 4a, c, e, i, whereas absence is assumed in Figure 4b, d, f-h, j. We have no

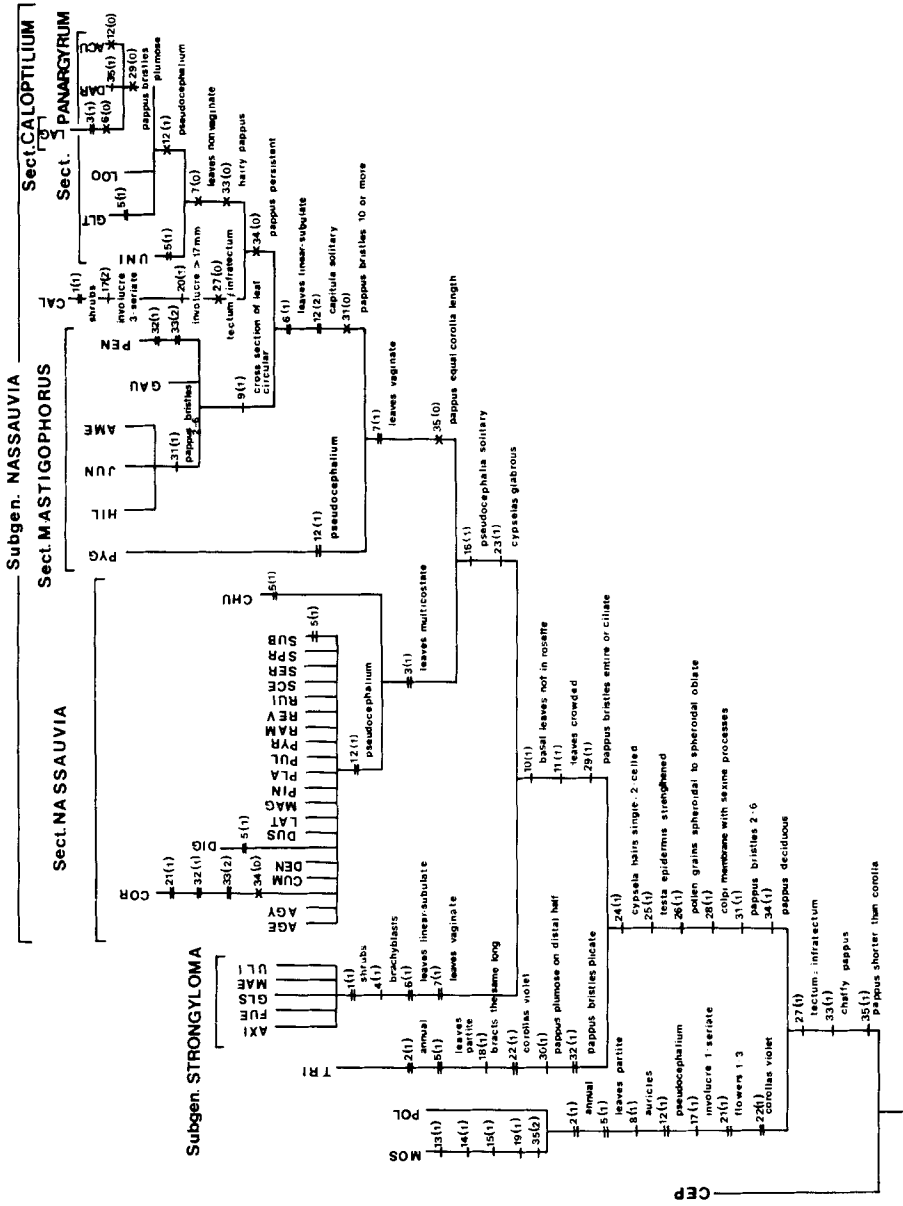


Figure 3. One of the ten most parsimonious cladograms found after applying the successive weighting procedure. Consistency index = 0.82. Character state changes are superimposed onto the cladograms; single lines = synapomorphies; double lines = homoplasies (parallel or convergent evolution), X = reversals. Refer to Table 1 for acronyms.

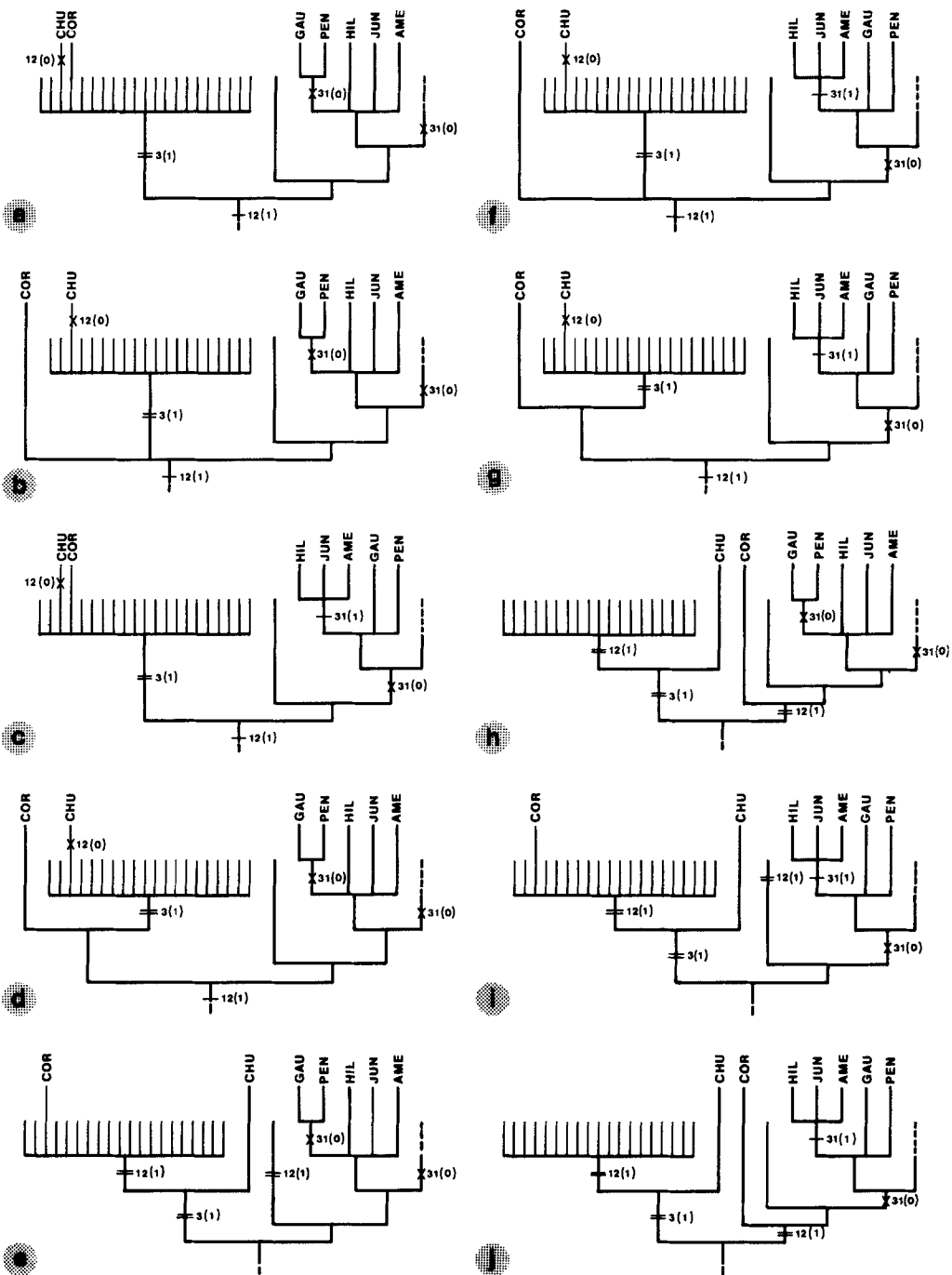


Figure 4. Variation in the topologies of the middle of the ten most parsimonious trees found after applying the successive weighting procedure. The ten configurations show the different positions of *N. coronipappa* (COR), *N. chubulensis* (CHU), *N. gaudichaudii* (GAU), *N. pentacenooides* (PEN), *N. hillii* (HIL), *N. juniperina* (JUN), and *N. ameghinoi* (AME), resulting from the changes in characters 3, 12 and 31.

Character number	As coded	After cladogram construction
1	0 → 1	1 ← 0 → 1
2	0 → 1	1 ← 0 → 1
3	0 → 1	1 ← 0 → 1
5	0 → 1	
6	0 → 1	1 ← 0 → 1 → 0
7	0 → 1	1 ← 0 → 1 → 0
12	0 → 1 → 2	
17		1 ← 0 → 2
21	0 → 1	1 ← 0 → 1
22	0 → 1	1 ← 0 → 1
27	0 → 1	0 → 1 → 0
29	0 → 1	0 → 1 → 0
31	0 → 1	0 → 1 → 0 → 1
32	0 → 1	
33		
34	0 → 1	
35		

Figure 5. Character transformation for selected characters as coded and after cladogram construction.

reason to choose between the alternative patterns found in character 3. In character 12, the hypothesis that the pseudocephalium is lost (Fig. 4a–d, f–g) requires a developmentally more complex pattern of changes than the alternative of two parallel presences (Fig. 4e, h–j). We have chosen the last case where *N. chubutensis*, is isolated from the remaining species of the section *Nassauvia*, because it is the only species that inhabits the Patagonian steppe, whereas the other species of section *Nassauvia* are present in the High Andean steppe.

The different positions of HIL-JUN-AME-GAU-PEN complex are the result of changes in character 31. Character 31 (number of pappus bristles) show two patterns: one reversal to ten or more pappus bristles with one reduction to two to six pappus bristles (Fig. 4c, f–g, i–j) and independent reversals to ten or more pappus bristles (Fig. 4a–b, d–e, h). We have chosen to illustrate in the reversal followed by reduction in Figure 3.

The cladogram chosen (Fig. 3) shows that 18 characters remain as originally coded (characters 4, 8–11, 13–16, 18–20, 23–26, 28, and 30). Of the remaining 17 characters (Fig. 5), seven show parallelisms (characters 1–3, 5, 21, 22 and 32), five show parallelisms and reversals (characters 6, 7, 12, 33 and 34) and four show reversals (characters 27, 29, 31 and 35).

DISCUSSION

Our analysis suggests that *Nassauvia*, is a paraphyletic group. However, if *Calopappus* is included within the genus, *Nassauvia* is likely to be monophyletic.

The monophyletic groups found in the cladograms of our analysis correspond to those of the current infrageneric classification of *Nassauvia* (Cabrera, 1982) with two exceptions: (1) section *Mastigophorus* is polyphyletic because *N. pygmaea* does not cluster with the remaining species; and (2) section *Panargyrum* is paraphyletic because *N. lagascae* (= section *Caloptilium*) is not included within the section *Panargyrum*.

The major section of the subgenus *Nassauvia*, section *Nassauvia*, is a monophyletic group diagnosed by multicostate leaves. Within section *Nassauvia*, there is no resolution among the species in this analysis. The other monophyletic group is subgenus *Strongyloma* defined by four synapomorphies: shrubs with brachyblasts, leaves linear-subulate and vaginate.

Placement of Calopappus

In two studies of the subtribe Nassauviinae (Crisci, 1974a, 1980) *Calopappus* is considered as a valid genus separated from *Nassauvia*. According to Crisci (*l.c.*), *Triptilion* and *Nassauvia* form the sister group of *Calopappus*, and these three genera together form the sister group of *Polyachyrus* and *Moscharia*. *Calopappus* was recognized as a distinct genus (Crisci & Freire, 1986) based on capitula length, 17–25 mm long, pollen morphology ('type *Calopappus*', Crisci, 1974a) and three rows of involuclral bracts. However, in light of the results obtained here, *Nassauvia* constitutes a monophyletic genus only when *Calopappus* is included in it, diagnosed by the presence of entire or ciliate pappus bristles, crowded and basal cauline leaves not occurring in a rosette. The distinctive appearance of

Calopappus is due to the possession of several derived characters (autapomorphies) mentioned above.

Within *Nassauvia*, *Calopappus* is related to species of subgenus *Nassauvia* by its glabrous cypselas. Within this large subgenus, *Calopappus* combines the species of section *Mastigophorus* (excluding *N. pygmaea*) and the species of section *Panargyrum* (including section *Caloptilium*). These three groups have linear-subulate leaves, solitary capitula, and ten or more pappus bristles.

Calopappus was previously included in subgenus *Mastigophorus* (Weddell, 1855) and compared with *N. pentacaenoides* of section *Mastigophorus* by Cabrera (1982). *Nassauvia pentacaenoides* possesses pollen grains of intermediate size as compared with *Calopappus* and other species of *Nassauvia*. On the other hand, *Calopappus* appears to be related to members of section *Panargyrum* by its persistent pappus.

Evolution of flowering heads

Evolution of capitula in Asteraceae has been the subject of several investigations during the 1960s and 70s (Burt, 1961, 1977; Leppik, 1960, 1970, 1977; Zohary, 1950). Often observed is a reduction in the number of flowers in the capitula and the aggregation of capitula into capitate secondary inflorescences (pseudocephalum, Troll, 1928). Approximately 70 genera (7% of the genera in the family) have pseudocephalia, and occur in nine tribes (Crisci, 1974b; Good, 1931; Stuessy, 1978). Within the Nassauviinae, *Nassauvia* and related genera show a trend towards reduction of the number of flowers in the capitula and the aggregation of capitula into capitate secondary inflorescences, as pseudocephalia (Crisci, 1974a). In *Nassauvia* all stages are found between a cymose conflorescence and a solitary capitulum or pseudocephalum.

In our cladistic analysis (Fig. 6) the corymbose conflorescence in *Triptilion* is regarded as primitive, from which three different degrees of head condensation were derived: (1) spicate conflorescence (subgenus *Strongyloma*, and *N. chubutensis*); (2) heads arranged in pseudocephalum in cymose or racemose clusters (*Moscharia* and *Polyachyrus*); (3) solitary pseudocephalum (section *Nassauvia* except *N. chubutensis*, *N. pygmaea*, *N. lagascae*, section *Panargyrum* except *N. uniflora* and *N. aculeata*). Within the context of the cladogram presented, the solitary capitula (*N. uniflora*, *Calopappus*, section *Mastigophorus* except *N. pygmaea*) are regarded as derived, originating by a reduction in the total number of the capitula from a cymose conflorescence. By the same context, the occurrence of secondary heads in *Moscharia* and *Polyachyrus* is regarded as a parallel development from the pseudocephalia found in *Nassauvia*.

Pappus

From the cladogram variation in the pappus can be examined as an evolutionary scenario (Fig. 6). From the condition in *Macrachaenium* of plumose hairy and numerous pappus bristles, there is an increase in the width of pappus bristles (*Moscharia*, *Polyachyrus*), followed by a reduction in size (in *Moscharia*) or number of pappus bristles, becoming deciduous (dysfunctional) in the latter case. From the chaffy pappus composed of two to six pappus bristles, two evolutionary lines evolved: one (culminating in *Triptilion*) where the pappus bristles are plumose only in the upper part, and a second major line that begins with ciliate

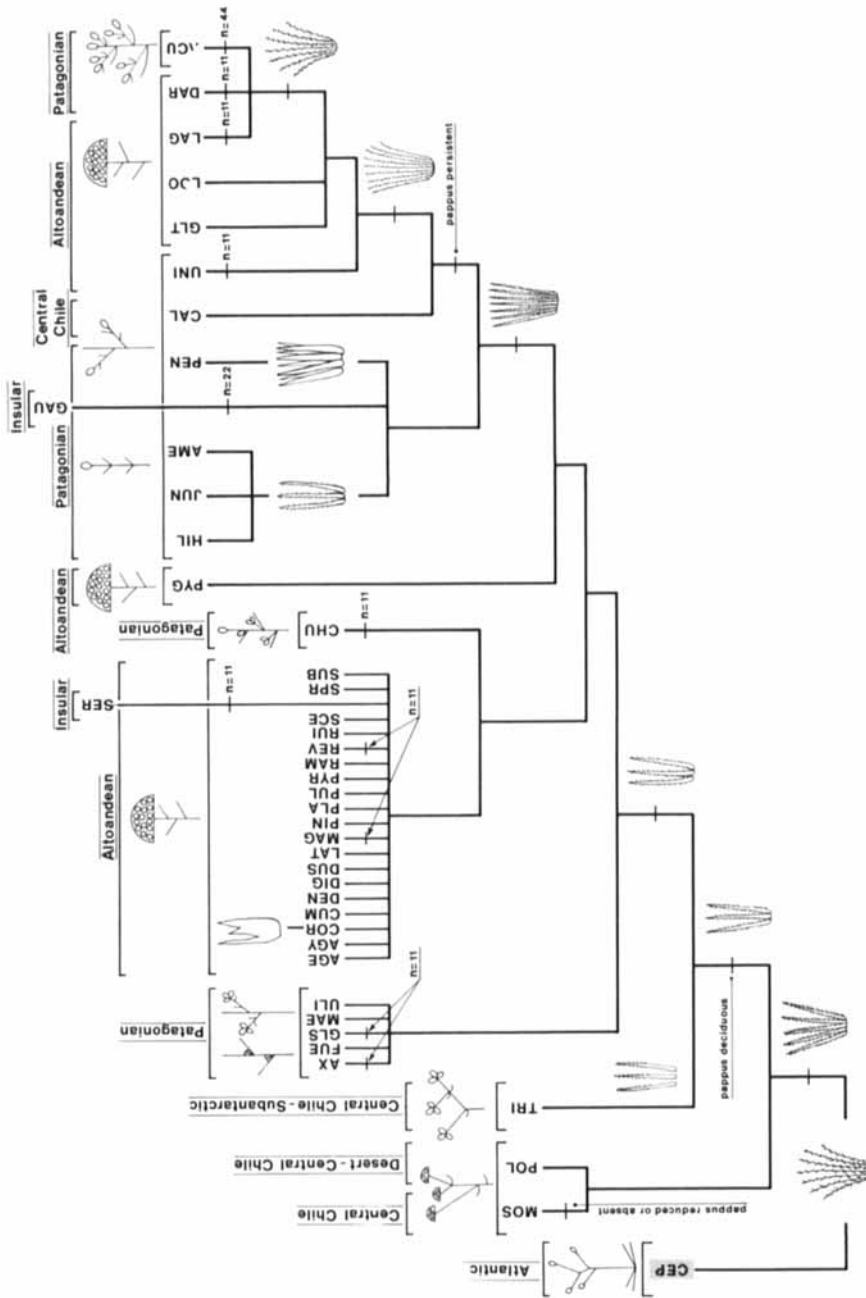


Figure 6. Exemplar cladogram showing the evolution of pappus, flowering heads, and chromosome numbers (the latter not included in the data matrix). The occurrence of taxa according to biogeographic provinces (Cabrera and Willink, 1973) are also included. Refer to Table 1 for acronyms.

or entire pappus bristles (subgenus *Strongyloma*, section *Nassauvia*, *N. pygmaea*) and culminates in the plesiomorphic condition (as reversals, i.e. hairy and numerous pappus bristles) becoming again persistent (section *Panargyrum* including *Caloptilium*). The paleaceous pappus occurs twice on the cladogram in *Nassauvia*, in *N. coronipappa* and *N. pentacaenoides* and presumably evolved from a chaffy pappus. Within *Nassauvia*, Cabrera (1982) considered the hairy plumose pappus as the most primitive type and the chaffy or paleaceous pappus as the result of the union of many hairs. Accordingly, he suggested section *Panargyrum* as the basal complex of the genus *Nassauvia* which has given rise to sections *Mastigophorus*, *Caloptilium* and *Nassauvia*. In contrast, the results of our analysis shows the section *Panargyrum* (including *Caloptilium*) as the most derived group.

Cytology

Within the tribe Mutisieae only about 10% of the c. 1000 species have been examined cytologically (Crisci, 1976). Both Crisci (1976) and Cabrera (1977) reported that counts are available for 26 of the 89 genera in the tribe. In the subtribe Nassauviinae, chromosome numbers have been published for 37 of the 300 species (12%) and ten for the other 22 genera (Crisci, 1976).

On the basis of our results we can assess some cytological data within *Nassauvia* and related genera (Fig. 6). In this group chromosome numbers are known for *Moscharia* ($n = 20$, Crisci, 1974a), and 11 species of *Nassauvia* (*N. darwinii* $n = 11$, Moore in Crisci, 1974a; *N. gaudichaudii* $n = 22$, Moore, 1967; *N. magellanica* $n = 11$, Moore in Crisci, 1974a; *N. serpens* $n = 11$, Moore, 1967; *N. axillaris* $n = 11$, Hunziker *et al.*, 1991; *N. chubutensis* $n = 11$, Hunziker *et al.*, 1991; *N. glomerulosa* $n = 11$, Hunziker *et al.*, 1991; *N. lagascae* $n = 11$, Hunziker *et al.*, 1991; *N. revoluta* $n = 11$, Hunziker *et al.*, 1991; *N. uniflora* $n = 11$, Hunziker *et al.*, 1991; *N. aculeata* $n = 44$, Hunziker *et al.*, 1991).

The basic number in *Nassauvia* is $x = 11$; species are reported at three ploidy levels: $2x$, $4x$ and $8x$ (Hunziker *et al.*, 1991). Our results correspond well with this interpretation. If the trend of evolution within *Nassauvia* has been from an ancestral type such as *Cephalopappus* (with paniculate conflorescence), then subgenus *Strongyloma* (with its spicate conflorescence), would presumably be closer in morphology to the ancestral stock than any other extant group within the genus. The presence of diploid chromosome number of $n = 11$ in *N. axillaris* and *N. glomerulosa* supports the hypothesis that subgenus is primitive. According to its solitary capitula the tetraploid *N. gaudichaudii* ($n = 22$) belongs to an advanced section of *Nassauvia*. *Nassauvia aculeata* ($n = 44$) is placed as the most derived species on the cladogram.

Geographic distribution and ecology

The distribution of the taxa (Table 1, Fig. 6) shows that four genera, *Moscharia*, *Polyachyrus*, *Triptilion* and *Calopappus*, are restricted to central Chile (The 'Chilean Province' mentioned in Cabrera and Willink, 1973). However, *Polyachyrus* encroaches northern Chile and extreme southern Peru (The 'Desert Province' of Cabrera and Willink, *l.c.*) and *Triptilion* is found also in the western part of Patagonia (The 'Subantarctic Province' of Cabrera and Willink, *l.c.*). Excluding *Nassauvia*, they do not form a monophyletic group in any of our

cladograms. These four genera present several apomorphic character states, such as the annual life cycle (*Triptilion*, *Moscharia*, *Polyachyrus*), compacted head clusters or pseudocephalia (*Moscharia*, *Polyachyrus*) or monocephalous flowering stems (*Calopappus*), basally branched scrub shrub (*Calopappus*), linear-subulate shaped leaves (*Calopappus*), and succulent leaves (*Polyachyrus*).

Nassauvia is found in two biogeographic provinces (Cabrera, 1982), Patagonian and Altoandean provinces, with different ecological requirements. The Patagonian steppe species of *Nassauvia* (subgenus *Strongyloma*; *N. chubutensis*; section *Mastigophorus* excluding *N. pygmaea* and *N. gaudichaudii*; *N. darwinii* and *N. aculeata* of section *Panargyrum*) grow under dry conditions and most of them possess linear-subulate leaves. Within the Patagonian steppe species there are two species groups, subgenus *Strongyloma* which is relatively primitive because of its spicate confluence and pubescent cypselas, and section *Mastigophorus* with advanced characters, such as solitary capitula. The Altoandean steppe species of *Nassauvia* (*N. pygmaea*; *N. lagascae*; section *Nassauvia* except *N. chubutensis* and *N. serpens*; section *Panargyrum* except *N. darwinii* and *N. aculeata*) grow under more humid conditions. They have aggregations of capitula into secondary clusters or pseudocephalia (Fig. 6). This head condensation is probably correlated with an increase in elevation and shortening of flowering season (Stuessy *et al.*, 1988).

Only two species of *Nassauvia* grow in the Insular Province. According to the cladogram, one of them (*N. serpens*) is related to the Altoandean species, and the other (*N. gaudichaudii*) is closely related to the Patagonian species. The complexity of the biota inhabiting the Falkland Islands was pointed out by Morrone (1992), who identified them as a panbiogeographic node (*sensu* Croizat, 1958).

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