

A typological analysis of the inflorescences of the genus *Nassauvia* (Asteraceae)

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Summary

The inflorescences of the genus *Nassauvia* are analyzed following Troll's comparative-morphological approach. Eight types of synflorescences are recognized, each defined by a particular combination of six developmental processes: truncation, proliferation, shortening of internodes, homogenization of paraclades, suppression of paraclades and shortening of peduncles. Decomposing each inflorescence type into six characters, each referring to a hypothesized developmental process, makes the data suitable for cladistic analysis. The synflorescence patterns described in the present analysis mostly correlate with currently accepted infrageneric classifications; discrepancies are discussed. Inflorescences currently described as „pseudocephalia“ are shown to be strongly condensed panicles or stachyoids of heads. Sister group inspection suggests the condensed panicle of heads to be the basal inflorescence condition within the genus *Nassauvia*.

Key words: *Nassauvia*, inflorescences, Troll/Weberling typological system

Introduction

Kellogg (2000), following Bradford (1998), stated that the Troll/Weberling typological system has limitations both for describing inflorescences and for applying to cladistic studies. Therefore, she proposed a new model, compatible with cladistic approaches, which considers inflorescence traits as products of a series of developmental switches, performed by meristem-identity genes. She argued that each switch at each node in the inflorescence can be considered as a phylogenetic character.

Nevertheless, the typology-based system developed by Troll & Weberling (Troll 1964/69; Weberling 1989, 1998) has proved to be useful for describing inflorescences (Rua 1999 and references therein; Judziewicz et al. 1999) as well as for providing characters for cladistic analysis (Nickol 1995; Agesen 1999; Rua & Aliscioni 2002).

In the present paper we analyzed the inflorescences of genus *Nassauvia* following Troll's typological system, enriched with concepts of Weberling, Sell and other authors (Rua 1999), considering hypothesized developmental processes as “switches”, with the aim of finding relationships among the different models observed in its species and defining characters for cladistic studies, capable to describe the whole variation observed.

Nassauvia is a South American genus of **Asteraceae** (**Mutisieae, Nassauviinae**) with 38 species (Cabrera 1982; Kalin Arroyo & Marticorena 1988), remarkable by the variability in the structure of the inflorescences. The 3–5 flowered heads were described by Cabrera (1982) as solitary or grouped in dichasial or pleiochasial partial inflorescences. Freire et al. (1993), in a cladistic study of the genus, coded the distribution of heads as follows: 0) grouped in paniculate, spicate or corymbose synflorescences, 1) conforming a pseudo-

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cephalium, or 2) solitary at the end of stems. These authors considered an evolutionary change from pseudocephalia to solitary capitula as more parsimonious. In *Triptilion*, the sister genus of *Nassauvia*, heads are arranged in lax to condensed panicles (Freire et al. 1993).

Materials and methods

Inflorescences were studied and dissected on herbarium samples of different species of *Nassauvia* at BAA and SI. Specimen determinations were verified by the authors, following Cabrera (1971, 1982). In some cases descriptions were taken from bibliography (Cabrera 1982; Kalin Arroyo & Marticorena 1988).

Descriptions of inflorescences were made according to Troll's typological system (Troll 1964/1969; Weberling 1989, 1998), enriched with some concepts of Sell, Briggs & Johnson, and other authors (Rua 1999 and references therein). Nevertheless, a simplified terminology is applied by naming synflorescences on the base of their branching patterns, regardless of the flowering units are heads (capitula, florescences) instead of single flowers.

Cross sections of heads were obtained using a rotary microtome, stained with safranin/fast-green, and observed with a light microscope.

Results

Heads are found at the end of the main axis (terminal) or in the axil of bracts (lateral). Each head is composed of 2–4 (in lateral heads) or 0–6 (in terminal heads) small phyllaries (bracts around the base of the inflorescence) and 3 or 5 pales forming a false involucre, each pale subtending a flower, each pale-flower pair at a different level on the receptacle (Fig. 1).

In some species heads are solitary (Fig. 2C) or conforming dichasia at the end of stems (Fig. 2B) or at an axillary position (Fig. 2D, 2E and 2H), whilst in other species solitary heads or dichasia are grouped into panicle-like branching systems (Fig. 2A, 2F and 2G). In the last case, some species have 5–3 heads at the basal nodes, 2 heads at the middle nodes, and 1 head at the upper nodes (Fig. 2A), while others have the paraclades homogenized so that only one head is found at each node (Fig. 2F and 2G). Heads or dichasia may have conspicuous peduncles (Fig. 2A) or be sessile (Fig. 2F and 2G). The internodes of the main axis are usually short (Fig. 2A and 2G) but may be long (Fig. 2F).

Condensed panicles of heads (Fig. 2A) were observed in *Nassauvia aculeata* (Less.) Poepp. et Endl., *N. darwinii* (Hook. et Arnott) Hoffmann et Dusén and *N. looseri* Cabrera. Shortening of peduncles leads to “pseudocephalia”, which can retain the paniculate

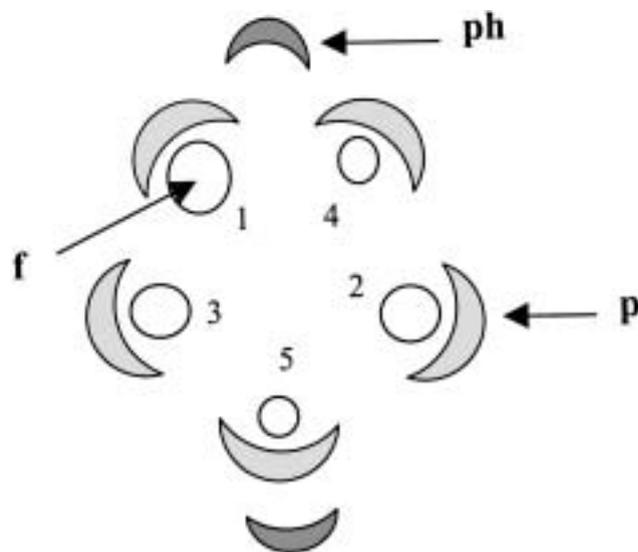


Fig. 1. Diagram of the cross section of a head of *Nassauvia ulicina* (BAA 5796). References: **f** = flower, **p** = pale, **ph** = phyllary. Numbers indicate the position of flowers on the receptacle, from proximal to distal.

structure, as observed in some specimens of *N. argyrophylla* Cabrera and *N. darwinii*. In most cases, however, pseudocephalia are **condensed stachyoids of heads** because of the complete homogenization of paraclades (Fig. 2G), as it occurs in *Nassauvia argentea* Phil., *N. argyrophylla*, *N. coronopipappa*, *N. cumingii* Hook. et Arnott, *N. dentata* Griseb., *N. digitata* Wedd., *N. dusenii* O. Hoffm., *N. glomerata* (Don) Wedd., *N. lagascae* (Don) F. Meigen, *N. latissima* Skottsb., *N. magellanica* J. F. Gmel., *N. pinnigera* Don, *N. planifolia* Wedd., *N. pulcherrima* Cabrera, *N. pygmaea* (Cass.) Hook. f., *N. pyramidalis* Meyen, *N. ramosissima* DC., *N. revoluta* Don, *N. ruizii* Cabrera, *N. sceptrum* Dusén, *N. serpens* D'Urv., *N. sprengeioides* DC., and *N. sublobata* Cabrera.

In *N. chubutensis* Speg. the synflorescences are **stachyoid** (Fig. 2F) or **thyrsoid of heads** with long internodes, with one or two heads at each node respectively.

Nassauvia fuegiana (Speg.) Cabrera, *N. glomerulosa* (Lag.) Don, *N. axillaris* (Lag.) Don, and *N. ulicina* (Hook. f.) Macloskie have **truncate proliferating synflorescences** in which a terminal head does not develop and the apical meristem resumes vegetative growth after production of axillary heads or dichasia. In *N. fuegiana* the synflorescence axis has long internodes and the heads are solitary and short pedunculated to sessile (Fig. 2D). Such spike- or raceme-like synflorescences have been usually described as “solitary, axillary heads in the nodes of a vegetative axis” in the current taxonomic literature.

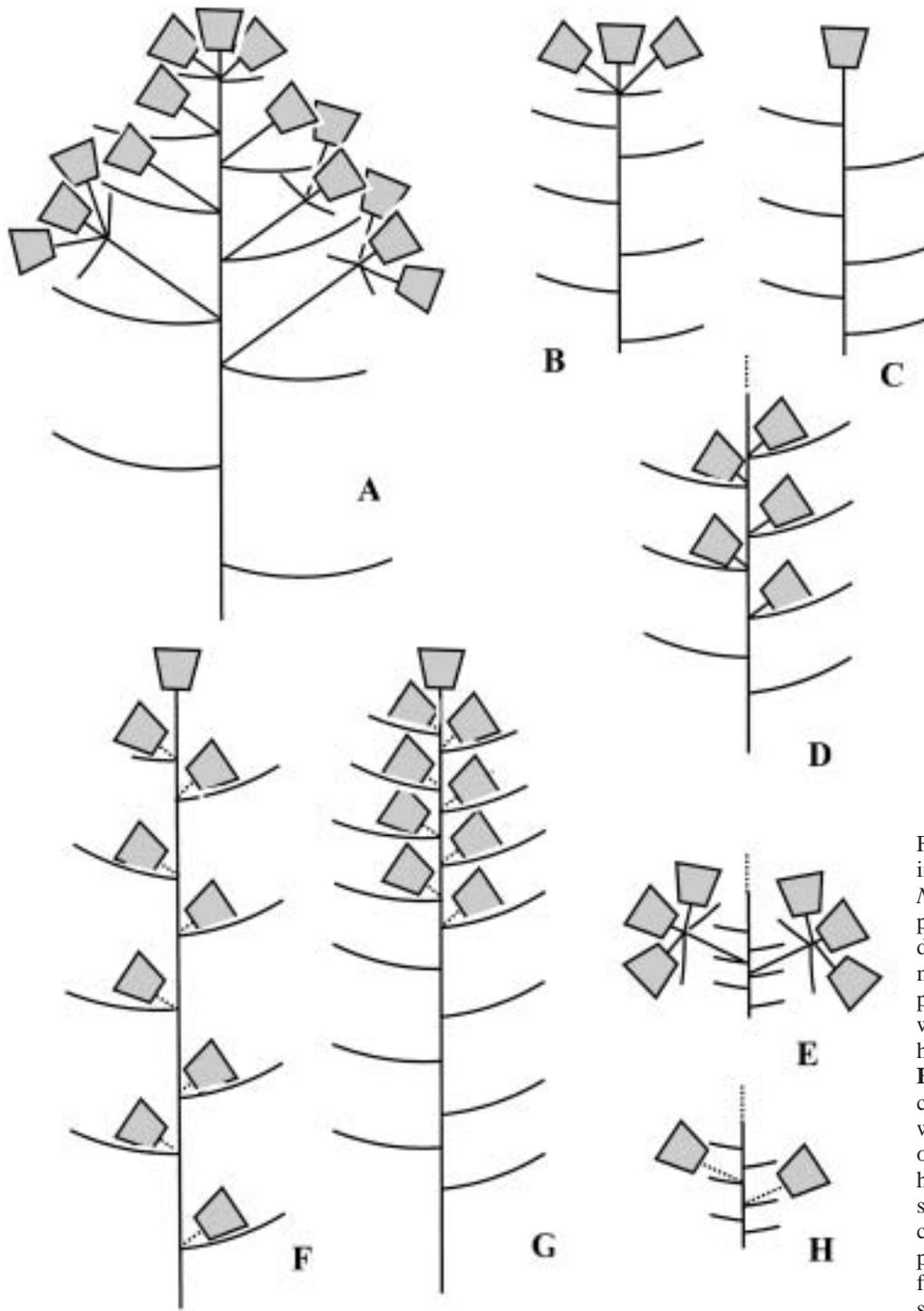


Fig. 2. Different models of inflorescences in the genus *Nassauvia*. **A**: condensed panicle of heads. **B**: terminal dichasium. **C**: solitary terminal head. **D**: truncate proliferating synflorescence with long internodes and homogenized solitary heads. **E**: truncate proliferating condensed synflorescence with pedunculated dichasia of heads. **F**: stachyoid of heads. **G**: condensed stachyoid of heads (pseudocephalium). **H**: truncate proliferating condensed synflorescence with solitary sessile heads.

The synflorescences of *N. axillaris*, *N. glomerulosa* and *N. ulicina* are condensed into brachyblasts with reduced leaves and rhythmic growth, which generally bear one or a few paraclades, represented by a **sessile head** (Fig. 2H) or a **pedunculated dichasium** (Fig. 2E).

Repression of paraclade development leads to synflorescences only consisting of a **terminal head** (main florescence), as it occurs in *N. darwinii*, *N. gaudichaudii* (Cass.) Gaudich., *N. hillii* Cabrera, *N. juniperina* Skottsb. and *N. meviae* Cabrera (Fig. 2C). In *N. ameghinoi* Speg., *N. pentacaenoides* Speg. and

N. uniflora (Don) Hauman terminal heads may be either solitary or accompanied by 2 distal axillary heads forming a **dichasial** pattern (Fig. 2B). Such reduced synflorescences may be formally derived from any of the models with terminal head, but the occurrence of solitary terminal heads (Fig. 2C) as well as stachyoidal pseudocephalia (Fig. 2G) and condensed panicles of heads (Fig. 2A) in *Nassauvia darwinii* suggests that solitary terminal heads represent an extremely reduced case of a condensed panicle.

Discussion

Differences among the models of inflorescences present in the genus *Nassauvia* may be explained in terms of the following processes: truncation with proliferation, shortening of internodes, homogenization of paraclades, suppression of paraclades, and shortening of peduncles. As no developmental evidence is currently available supporting correlations between such processes in *Nassauvia*, each of them would be treated as an independent character in cladistic studies. The treatment of the inflorescence type as a single compound character (cf. character 12 in Freire et al. 1993) seems to be somewhat hazardous, since inflorescence configurations may have resulted from the combination of several characters developmentally independent.

In the analysis of Freire et al. (1993), the inflorescence type (character 12) has three states: 0 = conflorescence cymose (paniculate, spicate, or corymbose); 1 = pseudocephalum; 2 = solitary, and is treated as additive following Cabrera (1982). Nevertheless, their condition '0' includes very dissimilar inflorescence structures, corresponding to the models represented in our figures 2A, D, E, F, and H. Likewise, the state '1' comprises both paniculate and stachyoidal pseudocephalia, as represented in our figures 2A and 2G. Considering that cladistic characters are hypotheses of homology, such assignment of character states results unsatisfactory.

Our inflorescence characters can be mapped onto Freire's cladograms as follows:

(1) truncation accompanied of proliferation is synapomorphic of the **Strongyloma** clade, except *N. maeviae*; (2) short internodes are plesiomorphic, internode elongation being autapomorphic in *N. chubutensis* and *N. fuegiana*; (3) homogeneous paraclades are plesiomorphic, heterogeneous branching occurs in representatives of sect. **Panargyrum** and in *N. argyrophylla* (sect. **Nassauvia**); (4) suppression of paraclades is synapomorphic of the **Calopappus** + **Caloptilium** + **Mastigophorus** + **Panargyrum** clade (CCMP clade thereafter), with one internal reversion; (5) condensed peduncles

are plesiomorphic, the elongated condition being synapomorphic of the clade including all representatives of CCMP clade except *N. pygmaea*. Thus, the phylogenetic hypothesis of Freire et al. (1993) does not support the multiple origin of pseudocephalia, (i.e. stachyoidal or thyrsoidal branching systems condensed as a result of internode and peduncle shortening), which would rather be considered plesiomorphic within the genus. Nevertheless, such a conclusion would be regarded as preliminary because of the low support of most groups in Freire's analysis. Further character evidence as well as a more comprehensive sampling of outgroups is necessary in order to test the hypothetical course of inflorescence evolution against a stable phylogenetic background.

As stated above, some authors criticized the "typological" approach of Troll/Weberling for describing inflorescences (Grimes 1992; Bradford 1998; Kellogg 2000). Nevertheless, they seem to be more troubled by the terminology than by the very concept underlying the Troll/Weberling approach. In fact, the fundamental contribution of Troll was highlighting the necessity of a comparative morphological approach for discovering homology, what in turn he considered central for assessing phylogenetic relationships (Troll 1951). In spite of them themselves, the authors cited above agree with Troll both in criticizing traditional descriptive terms for describing inflorescences and in proposing a homology-based system. What they seem to feel as new personal contributions are in most cases only new names for old things. At this respect Tomlinson (1984) advised: "Do not eschew typology, it is the first step in any morphological analysis".

As has been demonstrated in this study of *Nassauvia* inflorescences, a typological approach not only can be compatible with a cladistic treatment of characters, but may be a necessary first step for constructing hypotheses of primary homology (de Pinna 1991) suitable for testing through cladistic analysis (cf. Rua 1999). Although progress in biology gives us new tools for understanding plant morphology, this must not dazzle our sight and lead us to throw away classical approaches that have proved to be useful in explaining morphological variation.

The synflorescence patterns described in the present analysis mostly correlate with the infrageneric taxa recognized by Cabrera (1982) in his revision of the genus *Nassauvia*. Such a subdivision of the genus was also supported to a great extent by the morphology-based cladistic analysis performed by Freire et al. (1993).

With the exception of *N. maeviae*, the species of the subgenus **Strongyloma**, one of the two subgenera in which *Nassauvia* is divided, show homothetic (truncate) synflorescences, represented in Fig. 2D, 2E and 2H.

The remaining models are all represented in subgenus *Nassauvia*. The case of *N. maeviae*, with solitary heads at the end of branchlets, is difficult to understand in the light of this analysis.

Sect. **Panargyrum**, of the subgenus *Nassauvia*, is characterized by condensed panicles of heads (*N. darwinii*, *N. aculeata* and *N. looseri*, Fig. 2A), with a reduced condition in *N. uniflora* and sometimes in *N. darwinii* (Fig. 2C). The presence of more or less condensed panicles in the genus *Triptilium*, which has been postulated as the sister taxon of *Nassauvia* (Freire et al. 1993), suggests that condensed panicles may be basal in the genus.

In the subgenus *Nassauvia* sect. **Nassauvia** all species present stachyoids of heads usually condensed into pseudocephalia (Fig. 2G), with the exception of *N. chubutensis* in which the stachyoid (or thyrsoid) internodes are elongated (Fig. 2F). Interestingly, this species appears as sister taxon of the remainder of the sect. **Nassauvia** in some of the trees shown by Freire et al. (1993).

In sect. **Mastigophorus** all species but one (*N. pygmaea*) have terminal dichasia of heads or solitary terminal heads (*N. ameghinoi*, *N. gaudichaudii*, *N. hilli*, *N. juniperina*, and *N. pentacaenoides*, Fig. 2B and 2C); in turn, *N. pygmaea* bears pseudocephalia. Remarkably, it was shown that sect. **Mastigophorus** is paraphyletic when including this species (Freire et al. 1993).

Sect. **Caloptilium** includes only *N. lagascae* characterized by the presence of pseudocephalia and the pappus made up of several plumose hairs. This species, placed in sect. **Panargyrum** by Freire et al. (1993), is very similar to those of sect. **Nassauvia**, from which it differs in the characters of the pappus, the last being composed by few caducous paleae. The observation of one specimen (*Boelcke 1879*, BAA) affined to *N. revoluta* (sect. **Nassauvia**) with both pseudocephalia with paleaceous and plumose pappus, leads us to consider that there is a great affinity between *N. lagascae* and the species of section **Nassauvia**, and to doubt both on the validity of the section **Caloptilium** and on the inclusion of *N. lagascae* in sect. **Panargyrum**.

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