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Inclusion of the Cape genus *Anisothrix* in the Namibian-centred genus *Pentatrichia* (Asteraceae, Gnaphalieae) based on a molecular phylogenetic analysis

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Abstract

A phylogenetic analysis of the small genus *Pentatrichia*, containing three species endemic to South Africa and Namibia, was undertaken using nuclear (ITS and 3′ ETS) and chloroplast (*trnT–trnL*) DNA sequence data. Generic circumscription was examined via the inclusion of appropriate outgroup taxa (*Anisothrix* and *Athrixia*). A fully-resolved phylogenetic hypothesis found all *Pentatrichia* species and subspecies to be reciprocally monophyletic based on three sampled specimens of each taxon. A well-supported sister relationship between the radiate *P. rehmii* subsp. *avasmontana* and non-radiate *P. rehmii* subsp. *rehmii* confirmed the results of a previous morphometric study. *Pentatrichia* was found to be non-monophyletic with the exclusion of *Anisothrix kuntzei* and *A. integra*, which were placed as a subclade within *Pentatrichia*, and sister to the type species *P. petrosa*. Morphological synapomorphies supporting the inclusion of *Anisothrix* with *Pentatrichia* are discussed, as well as the evolution of capitulum structure in the group. *Anisothrix* is synonymised with *Pentatrichia* and two new combinations were made. The expanded morphological concept of the genus *Pentatrichia* is presented with a key to all five species.

Keywords: *Anisothrix*; *Athrixia*; ETS; Gnaphalieae; ITS; Molecular systematics; *Pentatrichia*; Phylogeny; Southern Africa; *trnT–trnL* spacer

1. Introduction

The small genus *Pentatrichia* comprises three species of rock-loving shrublets occurring mainly in Namibia, with one species extending into the Northern Cape province of South Africa, and an additional species endemic to the northern Drakensberg region of South Africa. The genus is a member of the daisy tribe Gnaphalieae (immortelles or everlastings), but is unusual in the tribe in its dentate leaves (Fig. 1) as most other gnaphalioid genera have entire leaves.

Understanding of relationships in the Gnaphalieae has changed considerably with the use of DNA sequence data, although a subtribal classification is still lacking (Bayer et al., 2007; Ward et al., 2009). The phylogenetic relationships at the base of the tribe have recently begun to be clarified (Bayer et al., 2000; Bayer et al., 2002; Bergh and Linder, 2009; Ward et al., 2009; Montes-Moreno et al., 2010) and the earliest-diverging lineage has been identified as the "*Relhania* clade". This clade consistently comprises two subclades in all analyses. The first of these, which for clarity we will refer to as the "*Oedera* clade" contains several genera distributed mainly in Southern Africa (*Oedera*, *Relhania* and *Macowania*, amongst others). *Pentatrichia* belongs to the second subclade, which we here refer to by the informal name "*Athrixia* clade". Circumscription of this clade has been clarified in several phylogenetic analyses (Bayer et al., 2000; Bergh and Linder, 2009; Ward et al., 2009; Montes-Moreno et al., 2010). Although Anderberg (1991) grouped the ditypic genus *Philyrophyllum* together with *Pentatrichia* and *Anisothrix* on the basis of morphological characters, Montes-Moreno et al. (2010) found that *Philyrophyllum* is only distantly related. In their analysis, the

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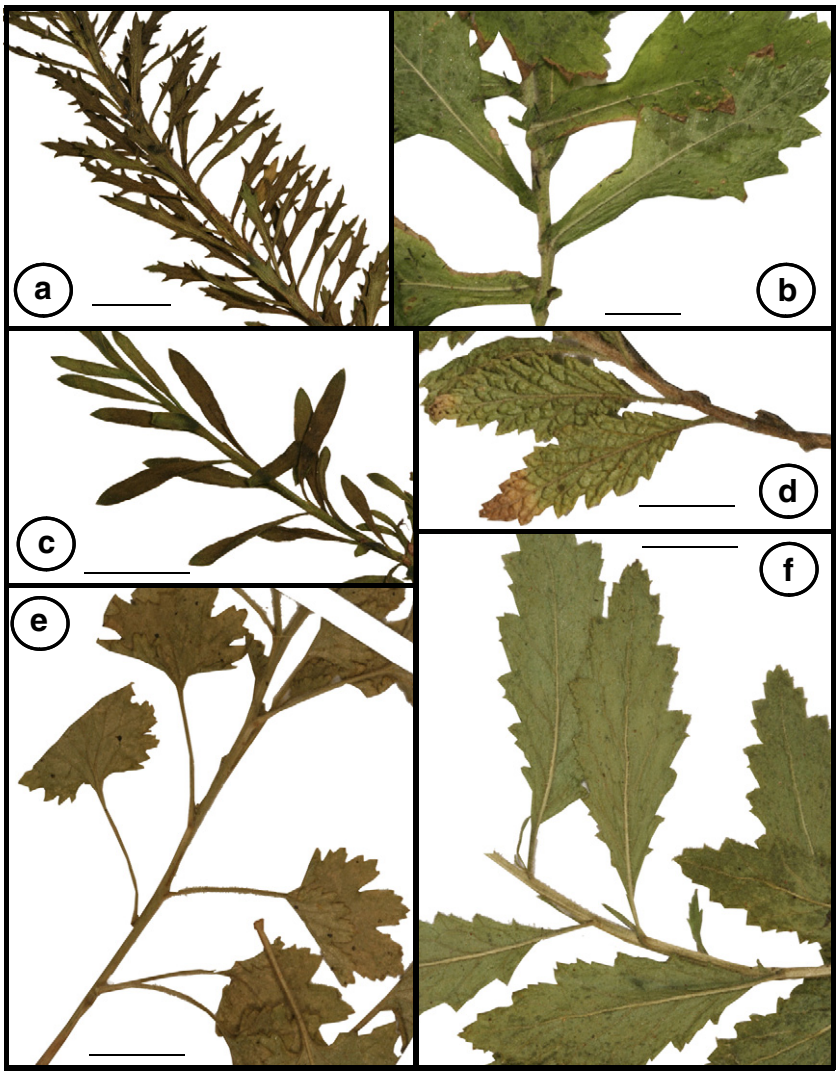

Fig. 1. Photographs of *Pentatrichia* and *Anisothrix* leaves to show different margin dentitions and shapes of the leaf bases. (a) *A. kuntzei*, Bergh 2075; (b) *P. alata*, Bergh 2209; (c) *A. integra*, Bergh 2059; (d) *P. rehmii* subsp. *rehmii*, Klaassen 1752; (e) *P. petrosa*, Williamson s.n. (NBG) and (f) *P. rehmii* subsp. *avasmontana*, Klaassen 1743. All scale bars represent 10 mm.

"*Athrixia* clade" consisted of *Phagnalon*, *Aliella*, *Athrixia*, *Anisothrix* and *Pentatrichia*. Thus the "*Athrixia* clade" comprises, according to current knowledge, *Athrixia* (14 spp., distributed in Southern and East Africa), *Phagnalon* (36 spp., distributed in North-eastern Tropical Africa, Mediterranean basin and the Irano–Turanian region), *Aliella* (4 spp., endemic to Morocco) and *Anisothrix* (2 spp., endemic to the Cape Floristic Region [CFR] of South Africa). Now that the membership of this clade has been defined by molecular data, its morphological synapomorphies can be listed. Member species are perennial herbs or subshrubs with leaf margins generally sparsely or closely dentate; the heads (capitula) are discoid (with all florets tubular and hermaphrodite), disciform (containing two kinds of tubular–filiform florets) or radiate (with central tubular florets and peripheral strap-shaped ray florets). The involucral bracts are imbricate in many rows, and are acute, attenuate, and frequently recurved; ray florets (when present) are pink or white, disc florets are yellow. The stigmatic lines on the style branches are basally separated but apically confluent and the pappus consists of barbellate bristles sometimes alternating with scales. Achenes in the group are sparsely or densely villous. Relationships amongst the genera, however, have not been clearly resolved. *Phagnalon* and *Aliella* were well-sampled and recovered as monophyletic by Montes-Moreno et al. (2010), as was *Athrixia* (with four sampled species). However, these studies are either sparsely-sampled (Bayer et al., 2000) or have focussed mainly on the Northern Hemisphere taxa (Montes-Moreno et al., 2010), and only three representatives of *Pentatrichia* and *Anisothrix* (*P. petrosa*, *P. rehmii* and *A. kuntzei*) have been included in previous analyses. Relationships within *Pentatrichia*, and between these two genera, have thus not been examined in detail.

Anisothrix comprises two species, *A. integra* and *A. kuntzei* that grow in sandstone rock-crevices in the Little Karoo region of the CFR. Both, like the non-radiate species of *Pentatrichia* (Fig. 2), have discoid heads with yellow florets surrounded by numerous linear, acute involucral bracts. They are distinguished