Volume 5(1): 13–19
Publication Date: 30 September 1992
dx.doi.org/10.7751/telopea19924955

TELOPEA
Journal of Plant Systematics

The Royal
Botanic Gardens
& Domain Trust

plantnet.rbgsyd.nsw.gov.au/Telopea • escholarship.usyd.edu.au/journals/index.php/TEL • ISSN 0312-9764 (Print) • ISSN 2200-4025 (Online)

In defence of the transfer of *Nablonium* to *Ammobium* (Asteraceae–Gnaphalieae), a reply to Orchard

Arne A. Anderberg

Abstract

Anderberg, Arne A. (Swedish Museum of Natural History, Department of Phanerogamic Botany, P.O. Box 50007, S-104 05 Stockholm, Sweden) 1992. In defence of the transfer of Nablonium *to* Ammobium *(Asteraceae–Gnaphalieae), a reply to Orchard.* Telopea *5(1): 13-19.* The relationship between *Ammobium* (2 species) and *Nablonium* (1 species) has once again been examined. A cladistic parsimony analysis has been undertaken based on the data presented in support of an alternative taxonomic treatment (Orchard this volume). The result of the analysis is illustrated with a cladogram. It is concluded that *Ammobium* is paraphyletic, and the problem with paraphyletic groups is discussed. *Ammobium calyceroides* (= *Nablonium calyceroides*) and *Ammobium craspedioides* are sister species, and most similarities between *A. craspedioides* and *A. alatum* are symplesiomorphies.

Introduction

The systematic position of *Nablonium calyceroides* Cass. (Asteraceae) has been a matter of discussion for many years, but in a recent paper (Anderberg 1990) it was concluded that the genus belongs in the tribe Gnaphalieae subtribe Cassiniinae, being a close relative of *Ammobium* R. Br. The two genera have many characters in common that diagnose them as a derived, monophyletic group within the subtribe (Anderberg 1990, 1991). Apart from *Ammobium*, the Cassiniinae also include genera such as *Ixodia*, *Cassinia* and *Ozothamnus* (Anderberg 1991, cf. Orchard 1981). Based on the results of a cladistic analysis using the paleate genus *Cassinia* as outgroup, I concluded that *Ammobium* is paraphyletic, and that *A. craspedioides* Benth. is the closest relative of *Nablonium calyceroides* (Anderberg 1990). Many of the derived character states found in *Nablonium* were after the analysis interpreted as autapomorphies, integral parts of sets of nested character transformation series leading from the less derived morphology of *Cassinia* via more derived features in *Ammobium* to *Nablonium*. *Nablonium* was therefore transferred to *Ammobium* as *A. calyceroides* (Cass.) A. Anderb. In response to this paper, Telford (in litt.) pointed out that the distribution I gave for *Ammobium alatum* R. Br. was not complete since the species also occurs further south in N.S.W. Although I believe Telford is right, this does not basically change the scenario of vicariance biogeography that was briefly presented in my paper. A similar pattern has also been found in the genus *Telopea* (Weston & Crisp 1987).

My paper on *Nablonium* has also generated a response to the taxonomic conclusions presented therein: an alternative view of the systematics of the two genera has been put forward (Orchard 1992). Orchard accepted most of my conclusions, stating: 'He [Anderberg] has thus performed a valuable service in finally finding a secure tribal resting place for *Nablonium* in the Gnaphalieae', and also: '*Ammobium* and *Nablonium* are in all likelihood indeed closely related'. Orchard presented the results of a detailed morphological investigation of the three taxa, in which a few of the characters I used for my analysis (Anderberg 1990) were reinterpreted and modified to the better. Orchard presented an extensive list of characters together with a corresponding list for *Cassinia*. In spite of our mutual agreement on the systematic position of *Nablonium*, Orchard disagreed with my lumping of *Nablonium* and *Ammobium*. In support of his opinion Orchard stated that: 'the two *Ammobium* species have far more in common with each other than either does with *Nablonium*', and he concluded from these differences that a traditional circumscription of *Ammobium*, with two species, and separate from *Nablonium* would be preferred. I was permitted by the editor to read Orchard's manuscript, and since I do not agree with Orchard's conclusion I am grateful for the opportunity to submit a further paper in response to Orchard.

The choice of outgroup for assessing character polarity was discussed by Orchard. However, lacerate paleae in the two *Ammobium* species and *Nablonium* are unique features, supporting the hypothesis that they form a monophyletic group. Presence of paleae is a rare feature in the tribe, and for an analysis of *Nablonium* and *Ammobium* a paleate taxon should be used as outgroup not to lose information relating to this organ. In this particular case *Cassinia* was chosen, but the differences between *Cassinia* and other paleate genera, e.g. *Ixodia*, are possibly restricted to autapomorphies in the latter. Being a genus belonging outside the *Ammobium-Nablonium* group, *Cassinia* is thus a useful outgroup. In explanation of the topological difference which Orchard observed (between Figs. 8 and 12 in Anderberg 1991), this is the effect always encountered in macrosystematic cladistic analysis, when the most parsimonious character distribution changes as a result of increasing data and an increasing number of taxa.

The additions and reinterpretations offered by Orchard (1992) made it interesting to find out whether the additional information would change the results of my previous paper (Anderberg 1990). Accordingly, I have submitted Orchard's data to a cladistic parsimony analysis. Some included characters are seen to be autapomorphies and will increase the consistency and retention index values, but they are still included here because they were used by Orchard in support of his alternative view. The characters are numbered as they follow in his list, but three entries had to be divided in two since they clearly included more than one character:

1. cypsela shape was divided into 'cylindrical vs. flared cypselas' (character 19 below), and 'not flattened vs. flattened cypselas' (character 20 below).

2. pappus was divided into 'no spines, two tiny spines, two small spines, two large spines' (character 21 below), and 'ligule present, later fusing into cupule, vs. ligule absent' (character 22 below).

3. spine structure was divided into 'subwoody vs. massive woody spines' (character 23 below), and 'rounded vs. 'U- or Y-shaped' spines' (character 24 below).

Lacerate paleae is a character found in all three taxa and thus it is not informative, except for diagnosing the three-taxon group from other paleate genera.

The penultimate entry, the cupule, had to be omitted since Orchard himself considered the fusion in the *Ammobium* species and in *Nablonium* to be non-homologous, as they evolved from different structures. In my earlier paper (Anderberg 1990: character 10 on p. 132) I suggested that the cupules in *Ammobium* and *Nablonium* formed a transformation series. Orchard showed that the two cupules are formed from different kinds of tissue, and concluded that the spines in *Ammobium* and *Nablonium* were non-homologous. Even if the cup-shaped tissues associated with the spines are non-homologous, there is nothing indicating that the spines themselves are not homologous.

Orchard disagreed with my interpretation of a successive transformation in spine-size from no spines at all (outgroup) to massive spines (*Nablonium*), but I cannot see any logical reason for a transformation such as hypothesized by Orchard (no spines-large spines-small spines-tiny spines). The fact that *Nablonium* has a different shape of the spines in transsection is hardly surprising considering all the other unique features of this species.

Here I present only a short summary of the characters involved and their numbers, which correspond to the numbers on the cladogram in Fig. 1, and in Table 1. For details see Orchard (1992) and Anderberg (1990).

1. **Life form**: Shrubs (0) perennial herbs (1).
2. **Vegetative reproduction**: Stolons none (0) stolons present (1).
3. **Vegetative stem branching**: Branching frequent (0) branching none (1).
4. **Branching within inflorescence/scape**: Branched inflorescence (0) unbranched (1).
5. **Scape winged/angled**: Stem at least sometimes winged/angled (0) round stem (1).
6. **Bracts on scape**: Bracts on scape numerous (0) 2–6 (1) none (2).
7. **Leaves decurrent**: Leaves decurrent (0) not decurrent (1).
8. **Leaf hairs, upper surface**: Without multicellular erect hairs (0) with multicellular erect hairs (1).
9. **Leaf hairs, lower surface**: Leaf lower surface cottony (0) not cottony, with erect hairs (1).
10. **Involucral bracts, shape**: Involucral bracts ovate, obtuse, wrinkled (0) involucral bracts acute, smooth (1).
11. **Involucral bracts, texture**: Involucral bracts scarious with small stereome (0) involucral bracts fleshy with large stereome (1).
12. **Involucral bracts, colour**: Involucral bracts showy white or yellow (0) involucral bracts tawny or at least with tawny margins (1).
13. **Paleae**: Paleae scarious (0) woody (1) subwoody (2) herbaceous (3).
14. **Floret colour**: Flowers yellow (0) flowers white (1).
15. **Glandular hairs on corolla tube**: Corolla with glandular hairs (0) corolla without glandular hairs (1).
16. **Papillae on corolla lobes**: Corolla with papillae in the throat (0) corolla without papillae in the throat (1).
17. **Anther appendage**: Anther appendage blunt, as wide as anther (0) anther appendage lanceolate, narrower than anther (1).
18. **Cypsela indumentum**: Cypselas without unicellular papillose hairs (0) cypselas with unicellular papillose hairs (1).
19. **Cypsela shape (outline)**: Cypsela shape cylindrical (0) cypsela shape flared at apex (1).
20. **Cypsela shape (shape in transsection)**: Cypselas not flattened (0) cypselas flattened (1).
21. **Pappus (spines)**: Pappus of bristles, no spines (0) pappus of two tiny spines (1) pappus of two small spines (2) pappus of two large spines (3).
22. **Pappus (ligule)**: Ligule absent (0) ligule present, later fusing into cupule (1).
23. **Spine structure (texture)**: Cypselas with subwoody spines (0) cypselas with massive woody spines (1).
24. **Spine structure (shape in transsection)**: Cypsela with spines round in section (0) spines U- or Y-shaped in section (1).
25. **Preferred habitat**: Inhabiting dry sclerophyll savanna (0) inhabiting maritime interdunal hollows (1).

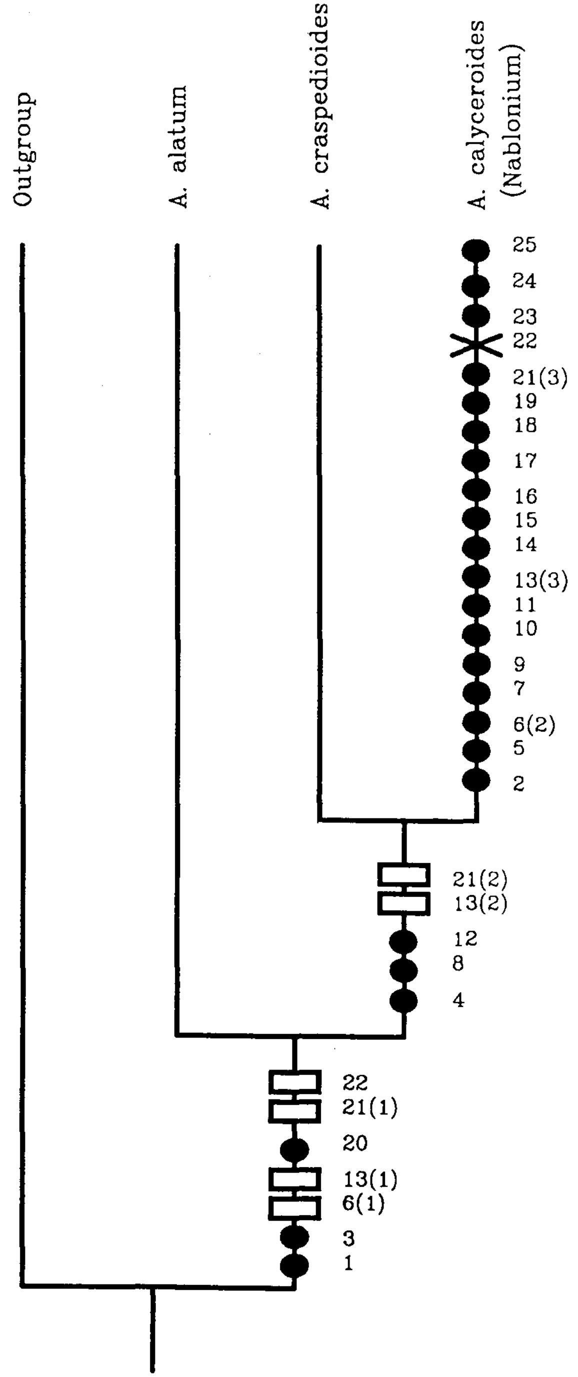

Fig. 1. Cladogram showing the interrelationships between *Ammobium alatum*, *A. craspedioides* and *A. calyceroides (Nablonium)*. The characters are numbered in accordance with Table 1 and with the text.
Black dot = synapomorphy (ci=1), Open box = synapomorphy (ci<1), Cross = reversal.

Cladistic analysis

The data in Table 1 were analysed with the parsimony program Hennig86 (Farris 1988) using the implicit enumeration option 'ie', with the results certain to be of minimal length. All characters were coded as nonadditive except characters 6 and 21, which were coded as an additive transformation series. The analysis of Orchard's data resulted in one cladogram, 31 steps long with a consistency index (ci) of 0.96, a retention index (ri) of 0.75. The most parsimonious character distribution is shown in Fig.1.

The data were also computed with all characters coded as nonadditive, and this analysis gave the same result except for a somewhat lower retention index (ri=0.66). Whether characters are coded as additive or nonadditive the genus *Ammobium* s. str. becomes paraphyletic, and *Nablonium* the sister-species of *Ammobium craspedioides.*

The logical basis of phylogenetic analysis was presented in detail by Farris (1983) pointing out the need for simple scientific hypotheses. Ad hoc hypotheses of parallelisms and reversals must be minimized in number, even if evolution has not proceeded in a simple straightforward maner. One of the fundamentals of phylogenetic systematics is that sister-groups must be placed in taxa of the same rank. Hence, a genus cannot be the sister-group of a species from another genus without the latter being paraphyletic. Generic circumscriptions of 'easily recognizable' groups will inevitably exclude derived relatives, and result in the formation of paraphyletic groups.

In the absence of phylogenetic hypotheses, paraphyletic groups could tentatively be used as taxonomic units during a process of taxonomic work leading from splitting of polyphyletic assemblages to the formulation of hypotheses based on strict monophyly. I have myself separated and reclassified taxa from the large, polyphyletic genera *Helichrysum* and *Gnaphalium* into smaller groups of somewhat uncertain phylogenetic status (Anderberg 1991). Such a pragmatic approach was used, for example, in my transfer of several former *Helichrysum* species to the genus *Ozothamnus.* This latter genus could well prove to be monophyletic when the Cassiniinae are analysed in detail, but intuitively it seemed to be paraphyletic and delimited from *Cassinia* and *Haeckeria* by the mere absence of receptacular paleae. In any case, it is quite clear that the *Ozothamnus* species are only distantly related to *Helichrysum* s. str., and should be removed from their vicinity. Rather than leaving *Helichrysum* as it was, I chose my approach to initiate a process of taxonomic and nomenclatural change intended as one step on the way to a better understanding of the phylogeny of the Gnaphalieae.

Table 1. Data matrix based on the data in the table presented by Orchard (1992). The characters are numbered in accordance with the text, and with Fig. 1.

		1111111111	222222
Character No.	123456789	0123456789	012345
Outgroup	000000000	00?0000000	000??0
A. alatum	101001000	0001000000	111000
A. craspedioides	101101010	0012000000	121000
A. calyceroides (*Nablonium*)	111112111	1113111111	130111

Paraphyletic groups do not represent phylogenetic lineages, and any circumscription of taxa based on paraphyletic groups should be rejected if it is at odds with an available hypothesis of phylogenetic interrelationships based on strictly monophyletic taxa.

Discussion

Orchard presented 14 characters to distinguish *Nablonium* from *Ammobium*, and although the differences are correct it is crucial to remember that 'similarity' can be either symplesiomorphic or synapomorphic. Whereas synapomorphic similarity is diagnostic and useful for hypotheses, symplesiomorphic similarity is not. It can be noted that most differences between the species of *Ammobium* and *Nablonium* are due to specializations in *Nablonium*, either transformations or reversals. A few examples: the presence of stolons is an autapomorphy unique to *Nablonium*, but absence of stolons is not diagnostic of *Ammobium* since stolons are missing also from the related genera. The presence of a ligule forming a cupule with age in the two *Ammobium* species (non-homologous with the similar structure in *Nablonium*) is, for parsimonious reasons, interpreted as lost in *Nablonium* where spines instead form a cupule by fusion of their bases. The occurrence of *Nablonium* in a maritime habitat instead of in sclerophyll savanna is also an autapomorphy, which also has affected the morphology of the plant. The fleshy involucre is probably an adaptation to saline influence, and succulent organs are common in maritime plants, e.g. *Cakile* (Brassicaceae) and *Salicornia* (Chenopodiaceae).

The fact that Orchard amended my data set with reinterpretations of certain characters and by adding more information makes the result of the present analysis more interesting. My original hypothesis was not falsified, but corroborated by a new and larger data set. The most parsimonious hypothesis is that *Nablonium* and *Ammobium craspedioides* have evolved from a common ancestor with unbranched scape, upper leaf surface with multicellular erect hairs, tawny involucral bracts (further transformed into green bracts with tawny margin in *Nablonium*), subwoody paleae (further transformed into herbaceous paleae in *Nablonium*), and prominent spines (even more prominent in *Nablonium*). No single apomorphic character could be found to support a group comprising *A. alatum* and *A. craspedioides* only, and the apparently salient features of *Ammobium* s. str. are also present in *Nablonium* albeit disguised in the form of derived character states and reversals.

The hypothesis is corroborated that *Ammobium (Nablonium) calyceroides* and *Ammobium craspedioides* have evolved from a common ancestor, and that *Ammobium* becomes paraphyletic with *A. calyceroides* placed in a separate genus. *Nablonium* should consequently be included in *Ammobium* to avoid unnatural groupings.

If systematics is to be a science in which biologists other than systematists find the results useful in their own pursuits, we must ensure that taxa are circumscribed in such a way that hypotheses of phylogenetic interrelationships are taken into consideration. Otherwise, taxonomy becomes a concern for taxonomists alone, without explanatory power for disentangling the effects of history and of natural processes in the living world.

Acknowledgements

I would like to thank Joy Everett, Sydney, for valuable comments to improve the presentation of this paper.

References

Anderberg, A. A. (1990) *Nablonium* is a congener of *Ammobium* (Asteraceae–Gnaphalieae). *Telopea* 4: 129–135.

Anderberg, A. A. (1991) Taxonomy and phylogeny of the tribe Gnaphalieae (Asteraceae). *Opera Bot.* 104: 1–195.

Farris, J. S. (1983) The logical basis of phylogenetic analysis. Pp. 7–36 in Platnick, N. I. & Funk, V. A. (eds), *Advances in cladistics 2. Proceedings of the Willi Hennig Society* (Columbia Univ. Press: New York).

Farris, J. S. (1988) *Hennig86 ver. 1.5, reference.* (Port Jefferson Station: New York).

Orchard, A. E. (1981) The generic limits of *Ixodia* R. Br. ex Ait. (Compositae–Inuleae). *Brunonia* 4: 185–197.

Orchard, A. E. (1992) *Ammobium* and *Nablonium* (Asteraceae–Gnaphalieae) – an alternative view. *Telopea* 5: 1–12.

Weston, P. H. & Crisp, M. D. (1987) Evolution and biogeography of the Waratahs. Pp. 17–34 in Armstrong, J. A. (ed.), *Waratahs their biology, cultivation and conservation.* Austral. Natl. Bot. Gard. Occasional Publ. 9.

Manuscript received 30 May 1991
Manuscript accepted 13 March 1992