Available online at www.sciencedirect.com
ScienceDirect
Review of Palaeobotany and Palynology 146 (2007) 169–181
Review of Palaeobotany & Palynology
www.elsevier.com/locate/revpalbo

A search for pollen morphological synapomorphies to classify rogue genera in Compositae (Asteraceae)

Alexandra H. Wortley [a,*], V.A. Funk [b], Harold Robinson [b], John J. Skvarla [c], Stephen Blackmore [a]

[a] *Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, UK*
[b] *US National Herbarium, Smithsonian Institution, Department of Botany, MRC 166, PO Box 37012, Washington DC 20013-7012, USA*
[c] *Samuel Roberts Noble Microscopy Laboratory, Department of Botany — Microbiology, University of Oklahoma, Norman, Oklahoma 73019-6131, USA*

Received 16 November 2006; received in revised form 8 March 2007; accepted 27 March 2007
Available online 1 April 2007

Abstract

Focusing on Compositae, this paper highlights and exemplifies the range of questions to which pollen morphology may contribute in the investigation of problematic taxa. Using a literature survey and new palynological data from LM and SEM studies, the pollen of a number of "rogue genera" was described and compared with that of potential related taxa in Compositae. Rogue genera are defined as taxa that have traditionally been difficult to classify, usually having highly divergent macro-morphological characters compared to the rest of Compositae. They include genera of known tribe but unknown position within that tribe and genera or small tribes of uncertain position in Compositae, as well as taxa that have recently been placed using molecular data but whose morphology continues to intrigue synantherologists.

In the majority of cases, palynology was found to provide new sets of characters which could be compared to the robust hypothesis of relationships shown in the recent DNA-based supertree. Pollen variously provided support and diagnostic characters for some groups (e.g. *Hesperomannia*, *Hoplophyllum*, *Eremothamnus*, Tarchonantheae, Corymbieae and Gymnarrheneae), suggested some possible affinities for taxa currently excluded from phylogenetic studies using DNA (such as *Moquinia*, *Catananche*, *Pacourina* and *Platycarpha*), or to some degree contradicted existing phylogenies (e.g. *Gundelia* and *Warionia*), suggesting areas for future research.

Keywords: classification; molecular data; morphological data; palynology; problem genera; systematics

1. Introduction

The past thirty years have been a time of considerable change and progress in the systematics of Compositae. Throughout that time, it has been recognised that there are a number of problematic ("rogue") taxa which have been difficult to classify to tribe, primarily because of their anomalous morphological features (Carlquist, 1976; Wagenitz, 1976; Bremer, 1994; Jansen and Kim, 1996). These often continue to be the "thorn in the side" of Compositae systematists even as the major questions of phylogenetics and evolution begin to be answered. Rogue taxa (usually genera) are defined as taxa that have proven difficult to place within a higher-level classification, through formal phylogenetic analysis or classification, and using either morphological or molecular data. Often, they are ecologically specialised — apomictic, aquatic,

* Corresponding author. Fax: +44 131 248 2901.
E-mail address: a.wortley@rbge.ac.uk (A.H. Wortley).

0034-6667/$ - see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.revpalbo.2007.03.003

parasitic, xerophytic or woody — and this has resulted in morphological or even molecular-level adaptations that take them outside the realm of the characters most commonly used in classification of the family.

In 1975, at a major conference in Reading, U.K. on *The Biology and Chemistry of the Compositae* (Heywood et al., 1977), Compositae was formally recognised as a natural family with well-defined limits and a diagnostic floral structure. However, the taxonomic arrangement within the family, comprising 13 tribes, remained little different from that of Bentham (1873), a century before. Over the next 20 years, with the rise of phylogenetic systematics (Hennig, 1966), a large number of morphological cladistic analyses were conducted, and molecular sequence data also began to be applied to systematic questions. This growing body of data was collated by Bremer (1987, 1994, 1996) and presented at a second International Compositae Conference at Kew, in 1995. Compositae was by this time classified into some 17 tribes in four subfamilies. However, it was recognised that several genera (such as *Brachylaena*, *Eremothamnus*, *Gundelia*, *Moquinia* and *Tarchonanthus*) were not members of the major tribes in which they had been placed, and were highlighted as clear examples of what we now call rogue genera.

The vast influx of molecular phylogenetic analyses over the decade following the Kew conference has been integrated by Funk et al. (2005) into a Compositae "meta-supertree". During this decade, the work of Baldwin et al. (2002) in Heliantheae and Panero and Funk (2002) in Mutisieae led to the recognition of many more tribes — a total of 34, plus two tribal-level clades — in ten subfamilies. No doubt there will be a few more changes before the classification stabilizes. Some of the new tribes are small, comprising genera that had previously been considered as rogues; and many have not been placed within any of the three traditional subfamilies. Several genera (e.g. *Athroisma*, *Corymbium*, *Cratystylis*, *Gymnarrhena* and *Hecastocleis*) were found to constitute the sister-groups of major evolutionary radiations in Compositae, while yet others remained unplaced at tribal level (e.g. *Catamixis*, *Gladiopappus*). Thus over the past thirty years, while there has been a move towards a more settled phylogeny of Compositae and delimitation of tribes, some problematic taxa have been placed and others thrown out of their traditional positions, leaving a pool of rogue genera that is as large as ever.

1.1. Rogue genera in Compositae

The genera studied here are summarised in Table 1 and can be divided into two categories. Firstly, there are those of known tribe, but whose position within that tribe is in some way unclear. These include *Hesperomannia* A.Gray, a genus of three or four species of small, apomictic trees from Hawaii, traditionally placed in Mutisieae (Cabrera, 1977) but recently transferred to Vernonieae on the basis of molecular sequence data (Kim et al., 1998). In Vernonieae it lies in an uncertain position within a wholly Old World or African clade. In macromorphology, the sweeping hairs of the styles characteristic of the Vernonieae have been reduced to papillae in

Table 1
Summary of genera investigated

Genus	Number of species	Distribution	Best present estimate of systematic position	Reference
Catananche L.	5	Mediterranean	Unplaced in Cichorieae	Blackmore (1976)
Corymbium L.	c. 9	South Africa	Corymbieae, tribe of uncertain position	Funk et al. (2005)
Eremothamnus O.Hoffm.	1	Namibia	Sister to *Hoplophyllum*, unplaced in Arctotideae	Karis et al. (2001)
Fitchia Hook. & Arn.	7	Polynesia	Unplaced in Heliantheae	Ryding and Bremer (1992)
Gundelia L.	1	Mediterranean–Middle East	Possible sister group to *Warionia*, unplaced in Cichorioideae (close to Cichorieae)	(Karis et al., 2001; Panero and Funk, 2002)
Gymnarrhena Desf.	5–6	Middle East	Gymnarrheneae, tribe of uncertain position	Funk et al. (2005)
Hecastocleis A.Gray	1	Nevada, U.S.A.	Hecastoclieae, tribe of uncertain position	Funk et al. (2005)
Hesperomannia A.Gray	3–4	Hawaii, U.S.A.	Unplaced in Vernonieae	Kim et al. (1998)
Hoplophyllum DC.	2	South Africa	Sister to *Eremothamnus*, unplaced in Arctotideae	Karis et al. (2001)
Moquinia DC.	2	Eastern Brazil	Unplaced in Cichorioideae (Vernonieae–Liabeae)	Funk, pers. comm.
Pacourina Aubl.	1	Tropical America	Unplaced in Vernonieae	Jones (1977)
Platycarpha Less.	3	South Africa	Unplaced in Cichorioideae	Wortley et al. (submitted for publication)
Tarchonanthus L.	2	Africa and Middle East	Tarchonantheae, tribe of uncertain position within Cichorioideae	(Keeley and Jansen, 1991; Kim et al., 2002)
Warionia Benth. & Coss.	1	North-western Sahara	Possible sister group to *Gundelia*, unplaced in Cichorioideae (close to Cichorieae)	Panero and Funk (2002)