

MOLECULAR RELATIONSHIPS IN TRIBE BRASSICEAE
(BRASSICA AND ITS WILD ALLIES)

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ABSTRACT

Phylogenetic analyses of chloroplast DNA (cpDNA) restriction site data provided support for the monophyletic origin of the tribe Brassiceae within the Cruciferae and evidence for six major lineages within the tribe. These included: I. Rapa-Oleracea, II. Nigra, III. Crambe, IV. Cakilinae, V. Vellinae, and VI. Zillinae. A comparison of lineages based on molecular data with the morphologically-based subtribes indicated no support for separate subtribal ranking for the Brassicinae, Moricandiinae and Raphaninae, but provided support for subtribes Cakilinae, Vellinae (includes Savignyinae), and Zillinae. The cpDNA data also supported the recognition of Crambe as a separate subtribe.

INTRODUCTION

The tribe Brassiceae (c. 52 genera) is generally considered to represent a natural grouping within the Cruciferae. The latter is distinguished on the basis of having conduplicate cotyledons and (or) two-segmented fruits (Gómez-Campo, 1980; Al-Shehbaz, 1985). Classical taxonomy within the tribe has depended mainly upon fruit characters. Considerable debate has centred on the circumscription and relationships among its subtribes and genera. The last and most comprehensive taxonomic treatment recognized seven subtribes: Brassicinae, Cakilinae, Moricandiinae, Raphaninae, Savignyinae, Vellinae, and Zillinae (Schulz, 1936). Gómez-Campo (1980) proposed a reduction to six subtribes, by including the Savignyinae in the Vellinae. However, the morphologically-based separation of some of the subtribes is not well substantiated (Al-Shehbaz, 1985) and hybridization data have indicated the possibility of genetic exchange among subtribes (Warwick and Black, 1993a).

Molecular studies (Warwick and Black 1991, 1993b) have also indicated artificiality in subtribal separation, i.e. subtribe Brassicinae (nine genera) separated into two main lineages [Rapa-Oleracea and Nigra], with *Raphanus* of the subtribe Raphaninae included in the Rapa-Oleracea lineage.

Using cpDNA restriction site variation, our objectives in the present study were: (i) to test for molecular support for the monophyletic (or natural) status of the tribe Brassiceae and monophyletic lineages within the tribe; and (ii) to compare these molecularly-based lineages with the current taxonomy of the tribe and its morphologically-based subtribal divisions.

MATERIALS AND METHODS

Molecular procedures followed Warwick and Black (1991). DNAs were digested with 17 restriction endonucleases and the presence or absence of 870 restriction sites recorded from the large single copy region of the chloroplast genome. The genera and

species included in the study (total of 24 taxa in the tribe Brassiceae and three outgroup taxa [*Arabis caucasica* and *Barbarea vulgaris* (Tribe Arabideae) and *Capsella bursa-pastoris* (Tribe Lepidieae)] are given in Fig. 1. Phylogenetic analyses, based on 229 informative characters, were conducted using the computer program PAUP (Swofford, 1993). The shortest phylogenetic trees were calculated based on Wagner parsimony and Fig. 1 is the strict consensus tree of the 16 most equally parsimonious trees.

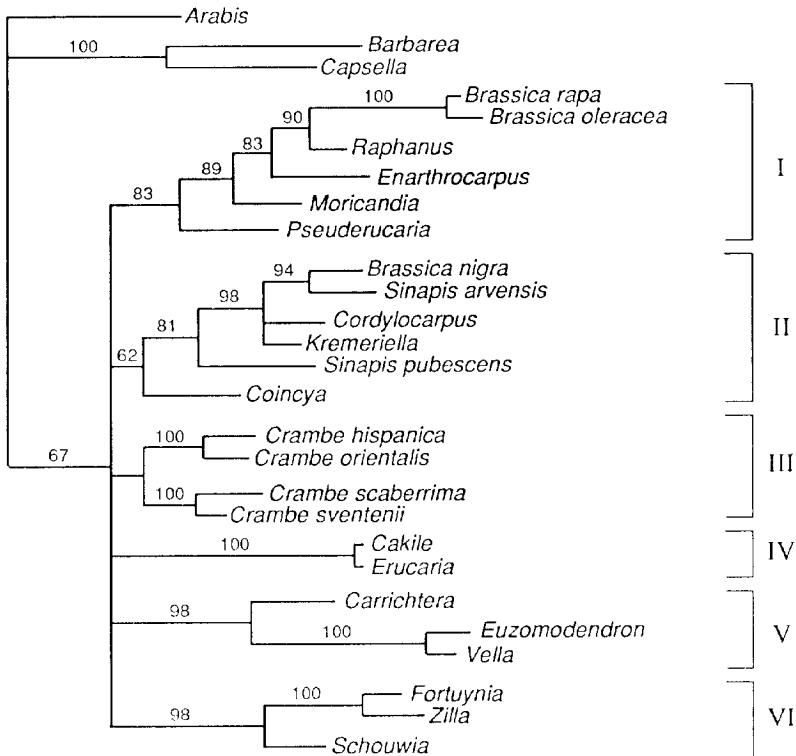
RESULTS AND DISCUSSION

Phylogenetic analysis of molecular data (Fig. 1)

The molecular results indicated that the tribe Brassiceae constituted a single clade supporting its status as a monophyletic or natural group in the Cruciferae.

Six major clades or monophyletic lineages were observed within the tribe (Fig. 1), including: I. Rapa-Oleracea [represented by *Brassica rapa* *Brassica oleracea*, *Raphanus*, *Enarthrocarpus*, *Moricandia*, and *Pseuderucaria*]; II. Nigra [represented by *Brassica nigra*, *Sinapis arvensis*, *Cordylocarpus*, *Kremeriella*, *Sinapis pubescens*, and *Coincya*]; III. Crambe [represented by four *Crambe* spp.]; IV. Cakilineae [represented by *Cakile* and *Erucaria*]; V. Vellinae [represented by *Carrichtera*, *Euzomodendron* and *Vella*]; and VI. Zillinae [represented by *Fortuynia*, *Zilla*, and *Schouwia*].

FIGURE 1. Strict consensus tree for representative taxa of the tribe Brassiceae with six lineages (I to VI). Numbers shown above the branches are percent probability values obtained with bootstrap analysis



Molecular lineages versus taxonomic subtribes

The cpDNA data did not support separate subtribal ranking for the Brassicinae, Moricandiinae and Raphaninae, Savignyinae, but provided support for subtribes Cakilinae, Vellinae and Zillinae, and for the recognition of *Crambe* as a subtribe, as suggested by Gómez-Campo (1980).

The Brassicinae, Moricandiinae and Raphaninae, were instead divided into two lineages (Warwick and Black 1991, 1993b, 1994). The Rapa-Oleracea lineage included *Brassica* (19 spp.), *Diplotaxis* (7 spp.), *Eruca*, *Erucastrum* (6 spp.), and *Sinapis* (1 spp.). The Nigra lineage included *Brassica* (5 spp.), *Coincya*, *Diplotaxis* (12 spp.), *Erucastrum* (8 spp.), *Hirschfeldia*, *Sinapis* (3 spp.), *Sinapidendron*, and *Trachystoma*. Three Moricandiinae genera (*Moricandia*, *Rytidocarpus*, and *Pseuderucaria*) were also included in the Rapa-Oleracea lineage (Warwick and Black, 1994). With the exception of *Crambe*, *Didesmus* and *Crambella*, the remaining Raphaninae genera were split among the same two lineages, with the inclusion of *Enarthrocarpus*, *Morisia*, *Raphanus*, and *Rapistrum* in the Rapa-Oleracea lineage, and *Ceratocnemum*, *Cordylocarpus*, *Guiraoa*, *Hemicrambe*, *Kremeriella*, *Muricaria*, *Otocarpus*, and *Raffenaldia* in the Nigra lineage (Warwick and Black, in prep.).

The cpDNA data were consistent with a monophyletic origin for the Cakilinae, along with two former Raphaninae genera *Didesmus* and *Crambella* (Warwick and Black, in prep.). The recognition of subtribe Vellinae [*Boleum*, *Carrichtera*, *Euzomodendron*, *Psychine*, *Succowia*, and *Vella*] was supported (Warwick and Black, 1994) and the inclusion of *Euzomodendron* consistent with the placement of subtribe Savignyinae in the Vellinae (Gómez-Campo, 1980). The data also supported recognition of subtribe Zillinae and its revision to include: *Foleyola*, *Fortuynia*, *Physorrhynchus*, *Schouwia*, and *Zilla* (Warwick and Black, 1994).

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