

A NEW SUBFAMILY OF THE ASTERACEAE¹

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ABSTRACT

The Asteraceae are generally divided into two large subfamilies, the Cichorioideae (syn. Lactucoideae; tribes Mutisieae, Cardueae, Lactuceae, Vernonieae, Liabeae, Arctoteae) and the Asteroideae (Inuleae, Astereae, Anthemideae, Senecioneae, Calenduleae, Heliantheae, Eupatorieae). Recent phylogenetic analyses based on morphological and chloroplast DNA data show that the Mutisieae–Barnadesiinae are the sister group to the rest of the family. The Mutisieae–Barnadesiinae are here excluded from the Mutisieae and elevated to the new subfamily Barnadesioideae.

Until the 1970s the tribe Lactuceae was considered to be distinct from all other Asteraceae and it was classified in its own subfamily, the Liguliflorae. The other tribes were placed together in the Tubuliflorae (e.g., Hoffmann, 1890). During the 1970s there was a growing understanding that all the tribes, including the Lactuceae, could be arranged in two large groups (Robinson & Brettell, 1973; Carlquist, 1976; Wagenitz, 1976), foreshadowed by diagrams in Carlquist (1961) and Poljakov (1967). Carlquist (1976) treated these two groups as the subfamilies Cichorioideae and Asteroideae. Their precise circumscription was modified by later authors (Robinson, 1977, 1981, 1983; Thorne, 1983).

Since 1985 cladistic analyses of molecular and morphological data have clarified the phylogeny and classification of the Asteraceae. Jansen & Palmer (1987) reported the presence of a 22 kb cpDNA inversion in *Lactuca* and several other Asteraceae. The inversion was found to be absent in three genera of the Mutisieae–Barnadesiinae, suggesting a basal dichotomy between the Barnadesiinae and the rest of the family. Subsequently, Jansen & Palmer (1988) undertook an analysis of cpDNA restriction site data from 13 genera of the Mutisieae (including the Barnadesiinae) and 9 representatives from other tribes. Later Jansen et al. (1990, 1991a) sampled 57 genera from 15 tribes in an extended study of cpDNA restriction site data. These studies corroborated the sister-group relationship between the Barnadesiinae and the rest of the family. To date, Jansen et al. (1991b) have examined more than 250 Asteraceae genera for the cpDNA inversion, which has proved to be pres-

ent in all genera except those of the Barnadesiinae. The sister-group relationship between the Barnadesiinae and the rest of the family is supported also by analysis of *rbcL* sequences (Kim et al., 1992).

Simultaneously with Jansen & Palmer's cpDNA investigations, Bremer (1987) conducted a cladistic analysis of tribal interrelationships based on morphological data. The study included 27 tribes and subtribes and 47 phylogenetically informative characters, one of them being the cpDNA inversion. The sister-group relationship between the Mutisieae–Barnadesiinae and the rest of the family, revealed by the cpDNA inversion, was supported also by several morphological characters, such as presence of the typical Asteraceae twin hairs on the fruits and spiny pollen.

All available data sets strongly support the sister-group relationship between the Mutisieae–Barnadesiinae and the rest of the family (Jansen & Palmer, 1987, 1988; Bremer, 1987; Jansen et al., 1990, 1991a, b; Karis et al., 1992; Kim et al., 1992). The subtribe Barnadesiinae should now receive formal subfamilial status, as Barnadesioideae. It is a small subfamily of nine genera and nearly 90 species, distributed in South America mainly along the Andes. The Barnadesioideae genera share a number of morphological and molecular synapomorphies. Hence, the subfamily is a strongly supported monophyletic group. Its members are characterized by unique axillary spines and by a unique indumentum of long, unicellular, barnadesioid hairs on the corollas, cypselas, and pappus (Cabrera, 1959, 1961, 1977; Bremer, 1987).

The large subfamily Asteroideae is also a monophyletic group, with synapomorphies both in mor-

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