

MESEMBRYANTHEMACEAE

A NEW TRIBE AND ADJUSTMENTS TO INFRAFAMILIAL CLASSIFICATION

Recently the tribal classification of Mesembryanthemaceae Fenzl has been the focus of attention in contributions based on both morphological (Chesselet *et al.* 2001, 2002) and molecular (Klak *et al.* 2003) evidence. Molecular data provides an independent character set for testing the congruence of morphological characters. When contrasting these data sets we find that molecular data largely support the broad infrafamilial classification based primarily on nectary type proposed by Chesselet *et al.* (2002), except in the case of tribe Delospermeae (Figure 15).

Delosperma N.E.Br. (\pm 163 species) and *Drosanthemum* Schwantes (\pm 120 species) are the largest of several genera placed by Chesselet *et al.* (2002) in the Delospermeae. Klak *et al.* (2003), however, do not maintain

the Delospermeae, but place all taxa assigned to this tribe in an expanded concept of Ruschieae (Chesselet *et al.* 2002). Although the molecular phylogeny of Klak *et al.* (2003) is not fully resolved, four distinct clades do emerge for subfamily Ruschioideae, three of which are formally recognized taxonomically by these authors. The fourth clade includes all investigated members of *Drosanthemum* and a single species of *Delosperma*, namely *D. asperulum* (Salm-Dyck) L.Bolus (= *Drosanthemum asperulum* (Salm-Dyck) Schwantes). The latter taxon has since been transferred back to *Drosanthemum* by Klak (2003) on the grounds that it resolves with *Drosanthemum* in a distinct evolutionary lineage within the tribe Ruschieae (Klak *et al.* 2003). This clade is, however, not given any formal taxonomic status despite it having 95% bootstrap support in a strict

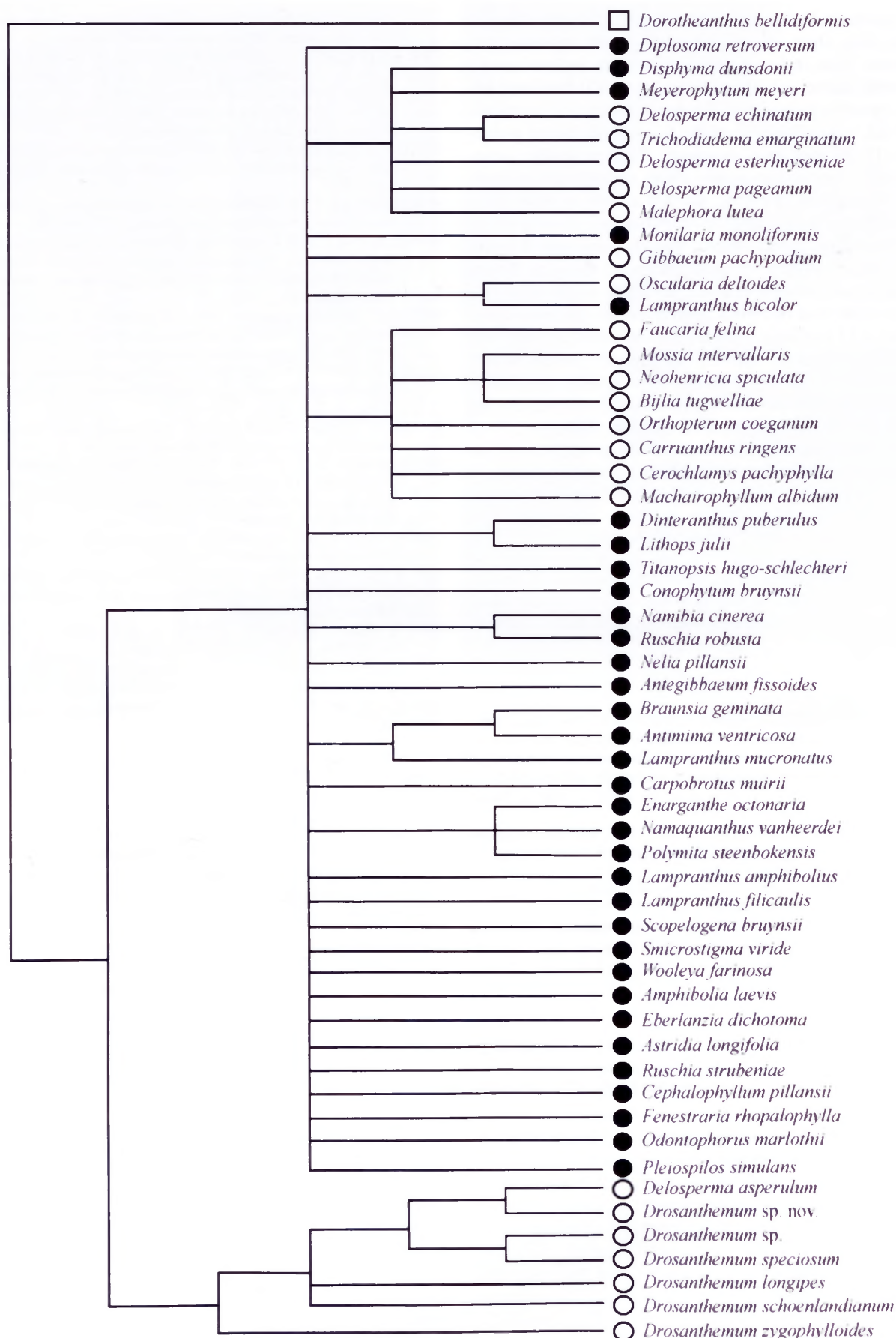


FIGURE 15.—Nectary characters from Chesselet *et al.* (2002) plotted on molecular phylogeny for mesembs from Klak *et al.* (2003). The most striking result is that the *Delosperma* Group of Hartmann (1991, 1993) is polyphyletic. Note the molecular resolution obtained for members of the newly described tribe Drosanthemeae in contrast to polytomy obtained for the Ruschieae, indicating the greater age of the former group. Members of the *Bergeranthus* and *Stomatium* groups of Hartmann (1991, 1993) resolve as a distinct clade within Ruschieae and are characterized by a lophomorphic meronectary. Key: □, broad flat meronectary; ○, lophomorphic meronectary; ●, lophomorphic holonectary.

consensus tree of the 5000 most parsimonious trees based on a four-gene-region analysis. Here we propose the latter clade as a distinct new tribe, the *Drosanthemeae*. The molecular phylogeny nevertheless shows that some other *Delosperma* species as well as several other genera included in *Delospermeae* by Chesselet *et al.* (2002) are clearly better placed in *Ruschieae*.

The most unexpected result of the molecular phylogeny provided by Klak *et al.* (2003) is that the '*Delosperma* group' of Hartmann (1991, 1993) is polyphyletic. Since Schwantes (1947), in his *System der Mesembryanthemaceen*, defined Subtribe *Delospermatinae*, *Delosperma* and *Drosanthemum* have been uncritically associated with each other. Despite the simple hygrochastic fruit, papillate epidermis, often broad, flat mesophytic leaves, and an exceptionally wide (for mesembs) distribution range that extends from southern Africa to East Africa and the Indian Ocean islands of Reunion and Madagascar, the genus *Delosperma* is not as 'primitive' as has been widely accepted. In contrast, *Drosanthemum*, with its characteristic basally-free leaves that bear large, water-filled bladder cells, emerges as being more basal than hitherto surmised. The wide distribution range of *Drosanthemum* and its strong presence in the Fynbos Biome supports this hypothesis. Recently, Chesselet *et al.* (2003) argued that basal tribes in *Ruschioideae* have their origins in the Fynbos Biome, which is considered the older biome in relation to the Succulent Karoo (Stuckenberg 1998).

At present the distinct clade named here as tribe *Drosanthemeae* contains the single genus *Drosanthemum*. Following extensive work on the flowers and fruit of *Drosanthemum* (Hartmann & Bruckmann 2000; Rust *et al.* 2002) a single possible synapomorphy involving the fruit stalk was found for the genus. *Drosanthemum* is a large and morphologically heterogeneous taxon characterized by no less than 13 different fruit types and five floral types. Congruence between these character sets exists in only three cases. The genus remains one of the most problematic in terms of identification. The fact that some *Drosanthemum* species tend to show free leaves, supports their more primitive position in the phylogeny. This characteristic is shared with other more primitive *ruschioid* taxa in tribes *Apatesieae* and *Dorotheanthaeae* and it can thus be regarded as a symplesiomorphic feature. *Enarganthe* N.E.Br. is reported to have basally-free leaves (Brown 1930), although examination of leaf material does not confirm this unambiguously. We therefore consider basally fused leaves as a possible synapomorphy for tribe *Ruschieae* (Figure 16). Those species of *Drosanthemum* that appear to have leaves that are fused at the base may indicate convergence with taxa in *Ruschieae*.

Both *Delosperma* and *Drosanthemum* are characterized by flowers with a 'lophomorphic meronectary' and were placed by Chesselet *et al.* (2002) in *Delospermeae* together with all other genera with this type of nectary. The inclusion, into this tribe, of the *Bergeranthus* and *Stomatium* groups of Hartmann (1991, 1993), was counter-intuitive, though justified according to the principle of parsimony, in the absence of other character sets at the time. The molecular study of Klak *et al.* (2003) has shown that taxa belonging in the latter two groups are

better placed in tribe *Ruschieae*. The presence of a lophomorphic meronectary indicates a possible reversal, switching of major genes or the persistence of the plesiomorphic condition in genera allied to *Bergeranthus* and *Stomatium*.

Following the reassessment of the tribal classification based on nectary types and together with insights gained from molecular data, we propose the following nomenclatural adjustments. For a comprehensive tribal classification refer to Chesselet *et al.* (2002).

***Drosanthemeae* Chesselet, Gideon F.Sm. & A.E.van Wyk, trib. nov. Type: *Drosanthemum* Schwantes**

Plantae perennes. Paria foliorum plerumque basi discreta; folia saepeque caules plerumque cum cellulis vesicariis prominentibus vel pilis. Flores semper cum meronectariis lophomorphis. Capsulae hygrochasticae, plerumque 5(6)-carpellatae, interdum cum locellis seminalibus basalibus.

Plants perennial. *Leaf pairs* mostly basally free, leaves and often stems, usually with prominent bladder cells or hairs. *Flowers* always with crested or lobed (lophomorphic) separate nectaries (meronectary). *Capsules* hygrochastic, usually 5(6)-carpellate sometimes with basal seed chambers.

Includes tribe *Delospermeae* Chesselet, Gideon F.Sm. & A.E.van Wyk p.p.

Includes subtribe: *Delospermatinae* Schwantes p.p.

Comprises the *Delosperma* Group of Hartmann (1991, 1993) p.p.

Genera: *Drosanthemum* [at least as to species investigated by Klak *et al.* (2003)]. Note: the inclusion of additional species currently placed in *Delosperma* and/or *Mestoklema* is uncertain at this stage, as is the possible exclusion of some species currently placed in *Drosanthemum*.

***Ruschieae* Schwantes in Ihlenf., Schwantes & Straka in Taxon 11: 54 (1962), emend. Klak, Khunou, Reeves & Hedderson: 1443 (2003). Type: *Ruschia* Schwantes. Note: the spelling of '*Ruschiae*' in Klak *et al.* (2003) is an orthographic error.**

Plants perennial, sometimes with enlarged rootstock. *Leaves* mesomorphic or xeromorphic, always basally fused, with or without prominent bladder cells and/or hairs or with homocellular or heterocellular xeromorphic surfaces. *Flowers* with crested or lobed (lophomorphic) separate nectaries (meronectary) or annular nectaries (holonectary). *Capsules* hygrochastic, rarely with reduced expanding keels, and breaking up when dry (schizocarpic); *fruit* rarely a berry.

Comprises the *Bergeranthus*, *Delosperma* p.p., *Dracophilus*, *Eberlanzia*, *Lampranthus*, *Leipoldtia*, *Mitrophylum*, *Ruschia*, *Stomatium* and *Titanopsis* Groups of Hartmann (1991, 1993).

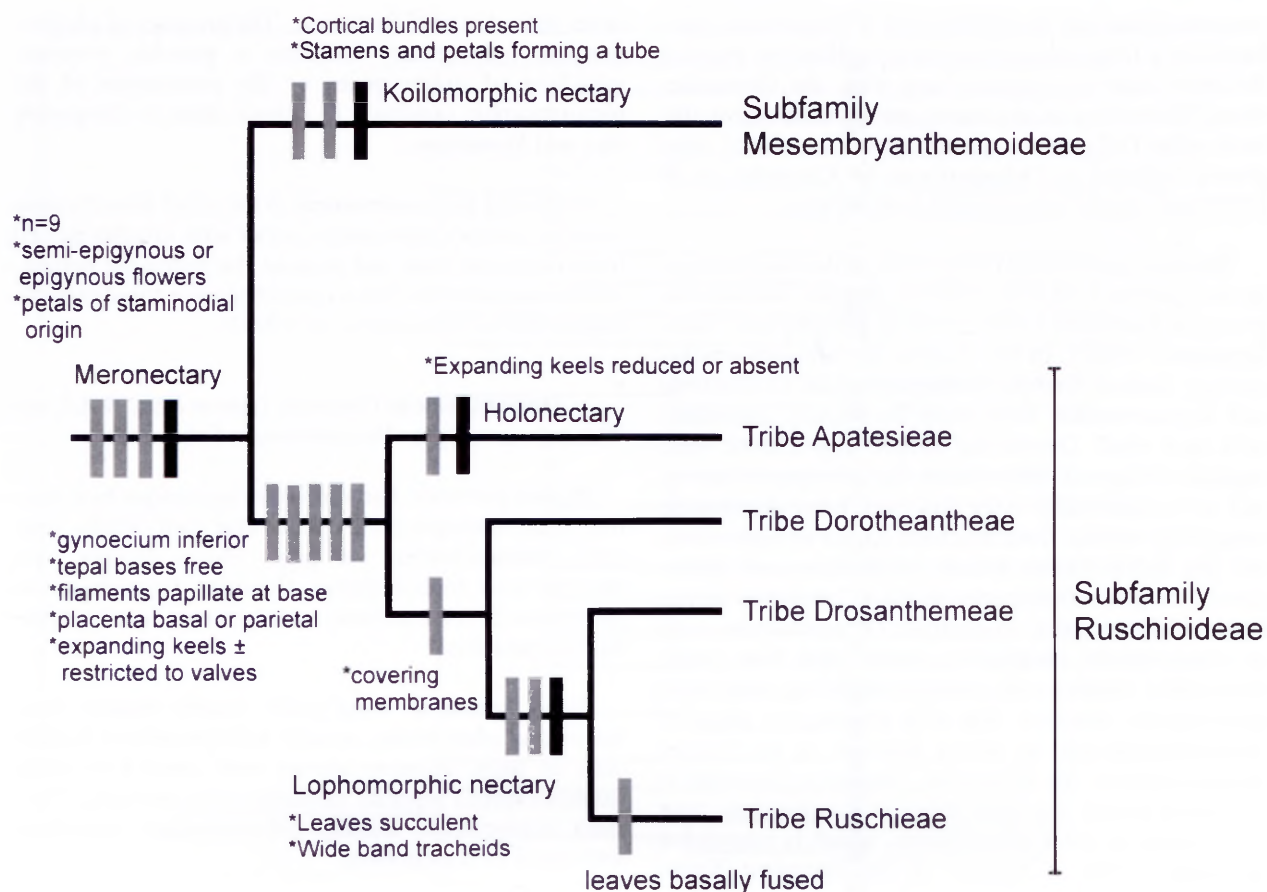


FIGURE 16.—Cladogram of the basal groups of Mesembryanthemaceae. The previously named tribe Delospermeae has been replaced with Tribe Drosanthemeae. Genera previously included in Delospermeae have been redistributed in Drosanthemeae and Ruschieae. From Chesselet *et al.* (2002), with modification. Note: characters of the floral nectary indicated as black bars.

Includes subtribes: Carpobrotinae Schwantes, Conophytinae Schwantes, Delospermatinae Schwantes p.p., Dracophilinae Schwantes, Erepsinae Schwantes, Faucariinae Schwantes, Frithiinae Schwantes, Gibbaeinae Schwantes, Jacobseniinae Schwantes, Jensenobotryinae Schwantes, Leipoldtiinae Schwantes, Lithopinae Schwantes, Lampranthinae Schwantes, Malephorinae Schwantes, Mitrophyllinae Schwantes, Nananthinae Schwantes, Pleiospilinae Schwantes, Psammophorinae Schwantes, Ruschiinae Schwantes, Stoeberiinae Friedrich, Stomatinae Schwantes.

Genera: *Acrodon*, *Aloinopsis*, *Amphibolia*, *Antegibbaeum*, *Antimima*, *Arenifera*, *Argyroderma*, *Astridia*, *Bergeranthus*, *Bijlia*, *Braunsia*, *Carpobrotus*, *Carruanthus*, *Cephalophyllum*, *Cheiridopsis*, *Cerochlamys*, *Chasmato-phyllum*, *Circandra*, *Conophytum*, *Corpuscularia*, *Cylindrophyl-lyllum*, *Deilanthus*, *Delosperma*, *Dicrocaulon*, *Didymaotus*, *Dinteranthus*, *Diplosoma*, *Disphyma*, *Dracophilus*, *Eberlanzia*, *Ebracteola*, *Ectotropis*, *Enarganthe*, *Erepsia*, *Esterhuysenia*, *Faucaria*, *Fenestraria*, *Frithia*, *Gibbaeum*, *Glottiphyllum*, *Hallianthus*, *Hammeria*, *Hartmanthus*, *Hereroa*, *Ihlenfeldtia*, *Jacobsenia*, *Jensenobotrya*, *Jordaaniella*, *Juttadinteria*, *Khadia*, *Lampranthus*, *Lapidaria*, *Leipoldtia*, *Lithops*, *Machairophyl-lyllum*, *Malephora*, *Marlothistella*, *Mestoklema*, *Meyerophyllum*, *Mitrophyllum*, *Monilaria*, *Mossia*, *Muiria*, *Namaquan-thus*, *Namibia*, *Nananthus*, *Nelia*, *Neohenricia*, *Octopoma*, *Odontophorus*, *Oophytum*, *Orthopterum*, *Oscularia*, *Ottosonderia*, *Pleiospilus*, *Polymita*, *Psammophora*, *Rabiea*, *Rhinephyllum*, *Rhombophyllum*, *Ruschia*, *Ruschi-*

anthemum, *Ruschianthus*, *Schlechteranthus*, *Schwante-sia*, *Scopelogenia*, *Smicrostigma*, *Stayneria*, *Stoeberia*, *Stomatium*, *Tanquana*, *Titanopsis*, *Trichodiadema*, *Vanheer-dea*, *Vanzijlia*, *Vlokia*, *Wooleya*, *Zeuktophyllum*.

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