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MADAGASTER (ASTERACEAE: ASTEREAE), A NEW GENUS OF SUBTRIBE HINTERHUBERINAE

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ABSTRACT

The five, white-rayed, Madagascan species previously identified as *Aster* are outside the morphological and phyletic bounds of *Aster*. In contrast, they are closely similar to another endemic genus of Madagascar, the yellow-rayed *Rochonia*, as well as to the white-rayed *Diplostephium* of South America and the Australasian genus *Olearia*. Although the classification is problematic, the white-rayed Madagascan species are here recognized as the new genus **Madagaster** Nesom. *Madagaster* and *Rochonia* are the only Madagascan representatives among the 22 genera that constitute the subtribe Hinterhuberinae, which extends from Madagascar into South Africa, South America, North America, and Australasia.

KEY WORDS: *Madagaster*, *Aster*, *Olearia*, *Diplostephium*, Astereae, Asteraceae, Madagascar

Aster L. in Madagascar (Humbert 1960) has been recognized as five species that are shrubs to small trees with large, coriaceous leaves and a persistent, close, tomentose ("pannose") vestiture often produced on the leaves, young branches, and petioles. The heads are relatively large, produced singly or in a corymbiform to paniculate capitulescence, and the receptacles are epaleate. The ray flowers are in a single series and have long, conspicuous, white to bluish ligules. The achenes are strigose but eglandular, narrowly oblanceolate, (4-)5-8-ribbed, and nearly terete to slightly compressed (but not strongly flattened). The pappus is "sub-biseriate," with an inner series of apically dilated, barbellate bristles and an outer group of bristles unequal in length but all somewhat shorter than the inner. The plants apparently are scattered and relatively uncommon, occurring on rocky ridges and summits, often in ericoid vegetation. These species, which have been described and illustrated in detail (Humbert 1960), clearly constitute a monophyletic assemblage.

Humbert (1923) described the second species of this group as *Diplostephium madagascariense* Humbert, emphasizing its similarity to the South American genus *Diplostephium* Kunth, but he also observed its resemblance to the Australasian genus *Olearia* Moench. "La separation de ces trois genres basee en grande partie sur des considerations d'ordre geographique, est difficilement justifiable" (1960, p. 318). He later took an even more conservative approach (1932) in identifying these white-rayed Madagascan species as *Aster* and concurrently transferring the four species of the yellow-rayed, Madagascan endemic *Rochonia* DC. to *Aster*, noting that the only difference between the two species groups was their ray color and emphasizing his observation of the absence of decisive characters to separate *Diplostephium* and *Olearia* from *Aster*. He did specifically note that *Aster* was necessarily considered "sensu lato" in this context, as it is almost completely restricted to the Northern Hemisphere. Humbert resegregated *Rochonia* in 1960, "ayant observe dans la nature toutes les especes malgaches connues de ce groupe, ...malgre la difficulte de constater en herbier l'homochromie ou l'heterochromie, et tout en maintenant les reserves enoncees [in 1932]" (p. 315). Zhang & Bremer (1993) placed *Rochonia* with *Psiadia* Jacq., *Psiadiella* Humbert, *Microglossa* DC., and others, presumably because of their yellow rays (although *Rochonia* is misplaced there on the basis of several other characters scored by Zhang & Bremer). In my view, *Psiadia* and its closest relatives are part of the Baccharidinae (Nesom 1993). Zhang & Bremer did not consider the white-rayed Madagascan species under discussion apart from *Aster*.

Both white- and yellow-rayed species occur within American Hinterhuberinae (Nesom 1993), but all genera (as currently treated) of the subtribe produce either one color of rays or the other. *Chiliophyllum* Phil. (yellow-rayed) and *Chiliotrichum* Cass. (white-rayed) are relatively similar in overall morphology but differ in features of the achenes and other technical characters that indicate they are separate clades. There is no general reason that yellow- and white-rayed species cannot be accepted within a single genus, and both colors are known within other genera of Astereae, but it is clear that the shrubby, yellow-rayed species of Madagascar constitute a lineage separate from the white-rayed species. Even if these should prove to be sister groups, they are justifiably regarded as separate taxa.

If these white-rayed Madagascan species must be placed in a pre-established genus, *Aster* is the least acceptable of the choices considered by Humbert. In true *Aster*, the plants are herbaceous, without a pannose indument, the leaves are sometimes thickened but never strongly coriaceous, and the achenes are obovate, flat, and 2-ribbed. The only native African species of *Aster* are those centered around *A. bakeranus* C.A. Smith and *A. harveyanus* O. Kuntze of South Africa (Lippert 1973), and the Madagascan species are not related to these (Nesom in prep.). Nor is there any other group of *Aster* in any sense to which the Madagascan species might be closely related.

Rochonia, Madagascan *Aster*, *Diplostephium*, and *Olearia*, are members of the subtribe Hinterhuberinae, which is now redefined to include 22 genera that extend from Madagascar into Africa, South America, North America, and Australasia (Nesom 1993). The identity of both groups of the Madagascan species with this more inclusive subtribe is clear, particularly in their shrubby habit, large, coriaceous leaves, production of a pannose tomentum, and plump, oblanceolate, multinerved achenes. The occurrence of plants of relatively similar, generalized morphology (*i.e.*, in *Olearia*, *Diplostephium*, *Rochonia*, and Madagascan *Aster*) across the whole geographic range of the subtribe suggests that they may be close to the primitive form for the group. The only continental African taxon of the Hinterhuberinae is the South African genus *Pteronia* L. (Hutchinson & Phillips 1917), in which specializations appear to eliminate it from consideration in hypotheses regarding the immediate ancestry and closest relatives of the Madagascan species. The heads in *Pteronia* are discoid (lacking ray flowers), the involucres elongated, the pappus accrescent, and there is a tendency for the production of opposite leaves and beaked achenes.

Diplostephium is primarily northern Andean in distribution, ranging from northern Chile and Bolivia to Colombia and Venezuela, with one species in Costa Rica of Central America. It appears to be monophyletic, and its common ancestry with other South American genera of Hinterhuberinae is indicated by the tendency for production of receptacular pales and disc flowers with sterile ovaries, specialized features not found in the Madagascan species.

Olearia is an Australasian genus (primarily Australia, New Zealand, and New Guinea) of about 100 species highly variable in habit, capitulescence, vestiture, and other technical features. Two separate groups of the genus are closely but independently related to *Celmisia* Cass. and three other, much smaller Australasian genera (*e.g.*, Drury 1968; Given 1969, 1973). All of these are white-rayed and all have unusually high levels of polyploidy (12-ploid or 24-ploid, see comments in Nesom 1992) in addition to their common morphology that indicate that the whole group is monophyletic. Many, if not most, of the other New Zealand species of *Olearia* also have similar levels of ploidy, but many of the Australian species for which reports exist are diploid or tetraploid. The generitype of *Olearia* is an Australian species (*O. tomentosa* [J.C. Wendl.] DC. = *O. dentata* Moench) with alternate leaves and a vestiture of bifurcate, basifixed trichomes; the chromosome numbers of two species of the group that includes *O. tomentosa* have been reported as 10-ploid and 12-ploid (*O. pannosa* Hook. and *O. argophylla* F. Muell., respectively). Species of another group produce stellate trichomes and have diploid chromosome numbers. Species of yet other groups have simple trichomes and diploid numbers. The specialized trichomes are restricted within the subtribe to these Australasian species. Aspects of this variation have been described earlier by botanists who divided the genus into sections based primarily on

trichome morphology (Archer 1861; Bentham 1866; and others mostly following Bentham's modification of Archer's original treatment). Recent studies, however, have unequivocally noted that *Olearia* is polyphyletic (*e.g.*, Drury 1968; Given 1973), and it appears that some of the diploid *Olearia* species with unbranched trichomes may be more closely related to genera outside of the subtribe Hinterhuberinae than to any within it (pers. observ.).

Taxonomy within the *Olearia-Celmisia* complex is highly unsettled, even with regard to the definition and limits of *Olearia* itself. The taxonomic position of the white-rayed Madagascan species relative to *Olearia* sensu lato is equally obscure, but there is no group of *Olearia* to which they might have an unequivocally close relationship. There are no published chromosome counts for the Madagascan species of *Aster* or *Rochonia*; all reports for *Pteronia* as well as the South American species of Hinterhuberinae, however, are diploid (n=9).

The white-rayed "asters" of Madagascar can no longer be formally treated as *Aster*. Instead, they are members of the Hinterhuberinae, where they should be placed either within *Rochonia*, within *Olearia*, or as a genus distinct from both. A position for these species apart from *Rochonia* is consistent with current views of variation and associated taxonomy within the subtribe, as noted above. With regard to *Olearia*, the only native Australasian genus of Astereae that also occurs outside of that region is *Lagenifera* Cass. The latter has additional species and its closest relatives in South America, and the relationships of many other Australasian Astereae also lie in that direction. The Australian species of *Erigeron* L. do not belong in that genus; Given (1973) has already made this observation for *E. pappochroma* Labill. Baccharidinae of Africa and Madagascar have their closest relatives in South America (Nesom 1993), and African grangeoid herbs with relatives in Australasia have even more closely related intermediaries in South America (Nesom in prep.). In view of these and the considerations in the preceding paragraph, I believe there is no justification for treating Australasian *Olearia* as congeneric with the Madagascan "asters." A decision to recognize the latter as a separate genus certainly reflects the conclusion that such a treatment has the greatest probability of remaining stable.

Madagaster Nesom, *gen. nov.* TYPE SPECIES: *Madagaster mandrarensis* (H. Humb.) Nesom

Speciebus *Rochoniae* DC., *Diplostephii* Kunth, *Oleariae* Moench, ac generibus ceteris subtribus Hinterhuberinae habitu fruticoso, capitulis amplis, foliis amplis coriaceis, et tomento persistenti similis. Differt a *Rochonia* ligulis albis, setis pappi dilatatis ad apices, et acheniis majoribus. Differt a *Astro* L. habitu, vestimento, et morphologia foliorum ac acheniorum.

1. **Madagaster madagascariensis** (H. Humb.) Nesom, *comb. nov.* BASIONYM: *Diplostephium madagascariense* H. Humb., Mem. Soc. Linn. Norm. 25:53. 1923. *Aster madagascariensis* (H. Humb.) H. Humb., *Fl. Madag.*, Composeés 1:318. 1960.

2. **Madagaster mandrarensis** (H. Humb.) Nesom, *comb. nov.* BASIONYM: *Aster mandrarensis* H. Humb., Bull. Mus. Paris, ser. 2, 4(8):1017. 1932.

3. **Madagaster saboureaui** (H. Humb.) Nesom, *comb. nov.* BASIONYM: *Aster saboureaui* H. Humb., *Fl. Madag.*, Composeés 1:320. 1960.

4. **Madagaster senecionoides** (Baker) Nesom, *comb. nov.* BASIONYM: *Rochonia senecionoides* Baker, J. Linn. Soc. 25:326. 1890. *Aster baronii* H. Humb., Bull. Mus. Paris, ser. 2, 4(8):1018. 1932. Not *Aster senecionoides* Franch. 1896.

5. **Madagaster andohahelensis** (H. Humb.) Nesom, *comb. nov.* BASIONYM: *Aster andohahelensis* H. Humb., Bull. Mus. Paris, ser. 2, 4(8):1016. 1932.

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