

TAXONOMIC STATUS OF *NARDOPHYLLUM SCOPARIUM* (ASTERACEAE:
ASTEREAE) WITH OBSERVATIONS ON THE DEFINITION OF
NARDOPHYLLUM

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ABSTRACT

Nardophyllum scoparium Philippi from northwestern Chile was transferred to *Hinterhubera* by Cabrera but it is here retained in the original position proposed by Philippi. The species is characterized by green-glutinous stems with small, widely spaced leaves and small, nearly discoid heads. The disc flowers are hermaphroditic with fertile ovaries, the few peripheral flowers are pistillate and apparently derived from hermaphroditic ones. Two other taxa also appear to be best placed within *Nardophyllum*, the southern Argentinian, monotypic genera *Aylacophora* and *Paleaepappus*. Two new combinations are proposed: *Nardophyllum* [*Aylacophora*] *deserticola* and *Nardophyllum* [*Paleaepappus*] *patagonicum*. As recognized here, *Nardophyllum* comprises ten species.

KEY WORDS: *Nardophyllum*, *Hinterhubera*, *Aylacophora*, *Paleaepappus*, Asteraceae, Astereae, South America

Nardophyllum scoparium Philippi was described by Philippi in 1894 from a collection near Coquimbo in northwestern Chile, where it apparently is endemic. The plants of this species produce green-glutinous, thornless, and nearly leafless stems, small and nearly discoid heads, central flowers relatively few (7-12) and with fertile ovaries, glandular achenes, and disc style branches with long, minutely papillate collecting appendages. In his conspectus of the genus *Nardophyllum* Hook. & Arn., Cabrera (1954; also see 1971, 1978) excluded *N. scoparium* on the basis of its pistillate peripheral flowers, as the seven species of *Nardophyllum* accepted by Cabrera produce discoid heads with only hermaphroditic flowers. In most respects, however, *N. scoparium* is similar to other species of *Nardophyllum* but distinctly different from the genus

Hinterhubera Schultz-Bip. ex Weddell (see below), where Cabrera placed *N. scoparium*. Reiche (1902) suggested that *N. scoparium* is a synonym of *Baccharis* (*Heterothalamus*) *spartioides* (Hook. & Arn. ex DC.) Remy but their resemblance is primarily restricted to similarity in habit.

Characteristics of *Nardophyllum*

Plants of all species of *Nardophyllum* are small shrubs; *N. chiliotrichoides* (Remy) A. Gray and *N. armatum* (Weddell) Reiche produce thorny branches. The leaves of *Nardophyllum* tend to be widely separated and quickly caducous (*N. bryoides* [Lam.] Cabrera and *N. obtusifolium* Hook. & Arn. are exceptional in their more densely arranged and persistent leaves). Heads are solitary, discoid (without ray flowers), relatively few-flowered (mostly 5-20), and those of *N. bracteolatum* Hauman, *N. bryoides*, and *N. chiliotrichoides* produce receptacular paleae. Phyllaries are ovate-triangular, strongly graduated in length, and strongly and evenly indurated. The collecting appendages of the style branches are as long or longer than the stigmatic portions (*N. armatum* is unusual in its short collecting appendages), and the collecting hairs are reduced to obovoid papillae densely and evenly set along the appendages. The achenes are plump to nearly terete and mostly 5-8 nerved but vary to 2-nerved and flattened; they are commonly sessile-glandular but otherwise densely strigose-sericeous to sparsely strigose with non-glandular hairs. The pappus occurs in 2-4 (or more) series commonly graduated in length but without a distinctly shorter, outer series. The pappus elements vary from slender and nearly terete (in *N. obtusifolium* and *N. armatum*) to broad and prominently flattened (in *N. chiliotrichoides*, *N. lanatum* (Meyen) Cabrera, *N. bracteolatum*, and *N. bryoides*); the more slender pappus elements tend to be dilated near the apex.

The species of *Nardophyllum* (as recognized here, see list below) occur from the Tierra del Fuego region northward along the coast of southern Argentina and through Chile into northeastern Argentina and Bolivia. The generitype is *N. lanatum*.

Characteristics of *Hinterhubera*

Hinterhubera differs from *Nardophyllum* in a number of significant features: the leaves are densely arranged on the stems; the phyllaries are persistent, subequal in length, and portions are distinctly herbaceous rather than evenly indurated; the flowers are more numerous, the pistillate in an outer zone of several series; the central flowers are pseudohermaphroditic (with sterile ovaries); and the pappus is composed of a single inner series with a few, short bristles or setae in an outer series.

Hinterhubera is endemic to the northern Andes, its seven species restricted to Colombia and Venezuela (Cuatrecasas & Aristeguieta 1956; Aristeguieta 1964; Cuatrecasas 1969). The generitype is *H. columbica* Schultz-Bip. ex Weddell. Other genera of the subtribe *Hinterhuberinae* also produce pseudohermaphroditic flowers and pistillate flowers with 5-lobed corollas, and they have been hypothesized to be closely related to *Hinterhubera*: *Aztecaster* Nesom and *Parastrephia* Nutt. (Nesom 1993a, 1993c) and a group of more highly specialized genera of the northern Andes: *Flosmutisia* Cuatrecasas, *Laestadia* Kunth ex Less., *Floscaldasia* Cuatrecasas, and *Westoniella* Cuatrecasas (Nesom 1993b).

Nardophyllum scoparium or *Hinterhubera scoparia*?

Nardophyllum scoparium is similar to accepted species of *Nardophyllum* in its widely spaced, caducous leaves, small, few-flowered heads, the morphology of its phyllaries, collecting appendages, and pappus, and in its geographic position. The open, loosely paniculate capitulescence, punctate glands, resinous covering and complete lack of tomentum on the stems and leaves, and the flat, 2-4 nerved achenes of *N. scoparium* are unusual, but *N. chiliotrichoides* also produces flattened achenes, and the vestiture of *N. scoparium* is approached by the glandular vegetative parts of *N. genistoides* (Philippi) A. Gray, also a rare species of central Chile. Cabrera (1954) noted that *N. genistoides* differs from the rest of the genus in "aspect," presumably referring at least partly to its vestiture.

The peripheral flowers of *Nardophyllum scoparium* are pistillate with fertile ovaries, but they are very few in number, ranging from none to one or two. The corollas of these flowers are narrowly tubular with five apical lobes ca. 0.5 mm long, and their style branches are ca. 2.5 mm long, each bearing lateral stigmatic lines but also a papillate apical appendage 0.5 mm long. Pistillate style branches with apical appendages are otherwise unknown in the *Astereae* but are typical in morphology for fertile hermaphroditic (disc) flowers. Because of the overall similarity of *N. scoparium* to other species of *Nardophyllum*, it is probable that these sporadically occurring peripheral flowers are homologous with the hermaphroditic flowers of *Nardophyllum* (sensu Cabrera) and derived from them. A similar origin for the peripheral pistillate flowers of the genus *Aztecaster* has also been postulated (Nesom 1993a), and this also is probably true for the peripheral flowers in *Hinterhubera*, *Parastrephia*, and other related genera (see below).

Nardophyllum scoparium is isolated in *Hinterhubera*, but it is reasonably accepted as a member of *Nardophyllum*. The unusual features of *N. scoparium* can be regarded as specializations within the genus, and the production of secondarily derived, peripheral pistillate flowers is viewed here as a tendency

in parallel with species of genera in the *Hinterhubera* group. If the peripheral flowers were absent, *N. scoparium* surely would have been accepted as *Nardophyllum*. If not treated within that genus, *N. scoparium* would have to be segregated as a monotypic genus.

Nardophyllum scoparium Philippi, Anal. Univ. Chile 87:435. 1894. *Hinterhubera scoparia* (Philippi) Cabrera, Notas Mus. La Plata [Univ. Eva Peron, Bot.] 17:65. 1954. TYPE: CHILE. Prov. Coquimbo, "in parte superiore vallis de Huanta," *F. Philippi* (HOLOTYPE: SGO, *vide* Cabrera 1954).

Specimens examined: CHILE. Prov. Coquimbo, Huanta, valley S of Juntas, ca. 3000 m, 4 Jun 1975, *Grau 1656* (MO,UC).

Phylogenetic position of *Aylacophora* and *Paleaepappus*

Two monotypic genera of southern Argentina, *Aylacophora* Cabrera (endemic to Prov. Neuquen) and *Paleaepappus* Cabrera (endemic to Prov. Chubut), are closely similar to *Nardophyllum*. As noted by Cabrera (1969), plants of both are similar in habit to *N. chilotrichoides*, *N. armatum*, and other *Nardophyllum*. *Aylacophora* and *Paleaepappus* produce solitary, discoid heads with paleate receptacles and phyllaries that are caducous and similar in other respects to those in *Nardophyllum*. The morphology of the style branch collecting appendages also is similar to that of *Nardophyllum*, and the pappus occurs in several series.

The pappus of both *Aylacophora* and *Paleaepappus* is reduced to flattened paleate or subpaleate elements. Cabrera (1969, 1971) noted explicitly that *Paleaepappus* differs from *Nardophyllum chilotrichoides* principally in its paleaceous pappus; in fact, the two appear so similar in other aspects that it is conceivable that they may be sister species. There is a strong tendency for flattening of pappus elements in accepted species of *Nardophyllum*, and various degrees of pappus reduction and modification occur and are accepted within many genera of Astereae.

Aylacophora has flattened and strongly shortened pappus elements (ca. 1.0-1.5 mm long) and differs further from most *Nardophyllum* in its achenes, which are 2-nerved, flattened, and sericeous along the margins, the faces glabrous. An extra nerve, however, is occasionally produced on the faces, and *N. scoparium* also produces flattened, 2-nerved achenes. Other species of *Nardophyllum* produce achenes with a densely strigose-sericeous vestiture of long, ascending-appressed hairs. Parallel variability in achene shape and nervation occurs within the closely related genus *Ericameria* (Nesom 1990; Nesom & Baird 1993), as well as within *Oritrophium* (Kunth) Cabrera, and the exclusion of *Aylacophora* from *Nardophyllum* on such a basis appears to be artificial.

The narrow, internally tomentose, cauline sulcae emphasized by Cabrera (1953) as a distinctive feature of *Aylacophora* appear to be homologous with ribbing found in most species of *Nardophyllum*. In *Nardophyllum*, the stems have broad, tomentose strips alternating with narrow, glabrous-viscid ribs. Young stems of *Aylacophora*, however, are identical to those of *Nardophyllum*, but on older stems of the former, the glabrous portions broaden and the tomentose bands become correspondingly narrower and appear as depressed sulcae between the raised, glabrous-viscid portions.

While *Aylacophora* is further removed phenetically than *Paleaepappus* from the morphology of most species of *Nardophyllum*, both of the former elements, along with *N. scoparium*, are more reasonably treated as specialized elements within *Nardophyllum* than as monotypic genera. *Nardophyllum*, even without these species, is heterogeneous, and if the peculiarities of *Nardophyllum* species (*sensu* Cabrera) are emphasized, yet others might justifiably be segregated at generic rank.

***Nardophyllum patagonicum* (Cabrera) Nesom, *comb. nov.* BASIONYM:**
Paleaepappus patagonicus Cabrera, Bol. Soc. Argent. Bot. 11:273. 1969.
TYPE: ARGENTINA. Prov. Chubut: Río Chico, 1900, C. Ameghino
s.n. (HOLOTYPE: LP).

***Nardophyllum deserticola* (Cabrera) Nesom, *comb. nov.* BASIONYM:**
Aylacophora deserticola Cabrera, Bol. Soc. Argent. Bot. 4:268. 1953.
TYPE: ARGENTINA. Neuquen, Plaza Huinul, A.L. Cabrera 11053
(HOLOTYPE: LP; Isotype: US!).

With the inclusion of these two species, *Nardophyllum* comprises ten species:

- N. armatum* (Weddell) Reiche
- N. bracteolatum* Hauman
- N. bryoides* (Lam.) Cabrera
- N. chiliotrichoides* (Remy) A. Gray
- N. deserticola* (Cabrera) Nesom
- N. genistoides* (Philippi) A. Gray
- N. lanatum* (Meyen) Cabrera
- N. obtusifolium* Hook. & Arn.
- N. patagonicum* (Cabrera) Nesom
- N. scoparium* Philippi

Excluded from *Nardophyllum*:

Nardophyllum paniculatum Philippi = *Baccharis philippii* Heering

Phylogenetic position of *Nardophyllum*

Asa Gray (1862) suggested that the closest relative of *Nardophyllum* might prove to be the North American taxon widely known as *Chrysothamnus nauseosus* (Pallas) Britt. but recently placed instead as a species of *Ericameria* Nutt. sect. *Macronema* (Nutt.) Nesom (Nesom & Baird 1993). Correspondingly, Gray suggested that the closest relative of the South American *Lepidophyllum* Cass. (including *Parastrephia* in Gray's view) might be *Ericameria* sect. *Ericameria*. Before learning of Gray's much earlier hypothesis, I also suggested that *Ericameria* (sensu Nesom 1990) should be investigated for polyphyly, based on an understanding of its relationships in a broader context (Nesom 1993a). Gray's ideas regarding the interrelatedness of these South American taxa with *Ericameria* as well as the African genus *Pteronia* L. were evidently corroborated by Bentham (in Bentham & Hooker 1873) and by Cabrera (1954).

The nature of the relationship among *Nardophyllum*, *Pteronia*, and *Ericameria* remains obscure. The first two genera both produce glandular achenes, apparently a primitive feature within the subtribe; achenes are consistently eglandular in *Ericameria*. The heads in *Nardophyllum* and *Pteronia* are discoid (vs. variably radiate in *Ericameria*), but the loss of rays can only be tenuously interpreted as homologous in the two southern genera, since the loss apparently has occurred independently within *Ericameria*. *Parastrephia*, *Aztecaste*, and *Hinterhubera* also have become rayless independently of *Nardophyllum* and *Pteronia*. The only genera of *Hinterhuberinae* with paleate receptacles occur in South America (see Nesom 1993a). Some species of *Nardophyllum* are paleate, and the loss of pales is interpreted here as a specialization within the genus. The closest relationships of *Nardophyllum* almost certainly lie with radiate South American genera that have paleate receptacles and a similar habit, *Chiliophyllum* Philippi, *Chiliotrichum* Cass., and *Chiliotrichopsis* Cabrera. Further investigation of phylogenetic relationships within the subtribe will have to proceed in the context of these taxa.

It is clear that the *Hinterhuberinae* originated in the Southern Hemisphere, and most of the diversity of the subtribe remains centered in South America. *Pteronia* is geographically isolated in Africa and is more closely similar to South American genera than to its Madagascan relatives, while *Ericameria*, *Aztecaste*, and *Westoniella* Cuatrecasas represent independent introductions of the tribe into North America. The latter two represent northward intrusions of the specialized, primarily north Andean group of genera related to *Hinterhubera*, but *Ericameria* appears to be more primitive, perhaps most closely related to *Nardophyllum*, and its origin in North America must have been relatively earlier and via a different pathway. *Ericameria*, like *Pteronia*, can be divided into infrageneric subgroups, but the morphological overlap among the subgroups and the geographical coherence of each of these two genera, as well as within *Nardophyllum*, indicate that all can reasonably be considered

monophyletic.

ACKNOWLEDGMENTS

I thank Billie Turner and Mark Mayfield for their reviews of the manuscript, the staffs of GH and UC for loans of specimens, the staffs of MO and US for their help during recent visits, and Barney Lipscomb (BRIT) for help in securing literature.

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