

SYNOPSIS AND CLADISTICS OF THE GENUS

Misodendrum (Misodendraceæ, Santalales)

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Keywords: Cladistics, Taxonomy, *Misodendrum* (*Misodendraceæ, Santalales*).

Summary. *Misodendrum* Banks ex DC., exclusively parasitic on *Nothofagus* (*Nothofagaceæ*) and the single representative of the family *Misodendraceæ* (*Santalales*), is a monophyletic group defined by its achlamydeous perianth. It comprises eight species endemic to the Subantarctic province in southern South America. A synopsis of *Misodendraceæ* is provided, including a diagnoses, a key to the species, and distributional and host plant information. The cladistic analysis of *Misodendrum* was carried out using 18 characters of its external morphology and anatomy. The eight species of *Misodendrum* and the closely related families *Eremolepidaceæ* and *Viscaceæ* were used as terminal taxa. Plesiomorphic character states were identified with *Loranthaceæ* as outgroup. The analysis yielded one cladogram with the following phylogenetic sequence: (*Loranthaceæ*, (*Viscaceæ*, (*Eremolepidaceæ*, ((*Misodendrum linearifolium*, (*M. quadriflorum*, (*M. brachystachyum*, *M. oblongifolium*)), ((*M. gayanum*, *M. punctulatum*), (*M. angulatum*, *M. macrolepisMisodendrum* correspond closely to the subgenera and sections previously proposed by other authors.

Resumen. *Misodendrum* Banks ex DC., parásito exclusivo de *Nothofagus* (*Nothofagaceæ*) y único representante de la familia *Misodendraceæ* (*Santalales*), es un grupo monofilético caracterizado por su perianto aclamídeo. Este género comprende ocho especies, todas endémicas de la provincia Subantártica, en el sur de Sudamérica. Se presenta una sinopsis de las *Misodendraceæ*, que incluye diagnóstico, clave para las especies más información sobre su distribución y plantas huéspedes. El análisis cladístico fue realizado sobre 18 caracteres morfológicos y anatómicos. Las ocho especies de *Misodendrum* y las familias *Eremolepidaceæ* y *Viscaceæ* fueron consideradas como táxones terminales. Los estados plesiomórficos de los caracteres fueron identificados usando *Loranthaceæ* como grupo externo. En el análisis se obtuvo un único cladograma con la siguiente secuencia filogenética: (*Loranthaceæ*, (*Viscaceæ*, (*Eremolepidaceæ*, ((*Misodendrum linearifolium*, (*M. quadriflorum*, (*M. brachystachyum*, *M. oblongifolium*)), ((*M. gayanum*, *M. punctulatum*), (*M. angulatum*, *M. macrolepisMisodendrum* se corresponden con los subgéneros y secciones propuestos por otros autores con anterioridad.

INTRODUCTION

Misodendrum Banks ex DC. is the only genus of the family *Misodendraceæ*, order *Santalales*. The genus comprises eight species, traditionally classified in two subgenera and five sections (table I). The species of *Misodendrum* are strict parasites of *Nothofagus*, the single genus of the family *Nothofagaceæ*, which is dominant in forests of the Austral region (southern South America, Australia, Tasmania, New Zealand, New Guinea, and New Caledonia). In contrast with other *Nothofagus* parasites, e. g., the scale insect family *Eriococcidae*, HUMPHRIES & AL. (1986) or the fungus genus *Cyttaria*, CRISCI & AL. (1988), *Misodendrum* is endemic to southern South America.

Our objectives are to contribute to the taxonomy of *Misodendrum*, by providing a synopsis and a key to its species, and undertaking a cladistic analysis, in order to elucidate its phylogenetic placement and analyze the relationship among its species.

MATERIAL AND METHODS

Taxa. *Misodendrum* forms a monophyletic group distinguished by its achlamydeous perianth. The units of the analysis (table II) are the eight species of this genus. In order to test the monophyly of the genus and establish its cladistic relationships, we included also as terminal units the closely related families *Eremolepidaceæ* and *Viscaceæ*.

Characters. For the cladistic analysis, 18 characters were derived from examination of 284 specimens deposited in the collections HAC, LP, LPG, and SI, see HOLMGREN & AL. (1990) for herbarium acronyms. Multistate characters were treated as nonadditive. Plesiomorphic character states were identified by outgroup comparison with *Loranthaceæ*, which is closely related to *Misodendraceæ* according to CANDOLLE (1830), AGARDH (1858), and ORFILA (1978).

Analysis. Data matrix (table III) was analyzed using the branch and bound parsimony algorithm and tree analysis options of PAUP 3.1, SWOFFORD (1991), on a Macintosh IIxi computer, and Hennig86, FARRIS (1988) on a PC IBM compatible, applying the implicit enumeration (ie*) option for calculating cladograms. Consistency, KLUGE & FARRIS (1969) and retention, FARRIS (1989) indices were calculated. CLADOS 1.1, NIXON (1992) was used for examination of character distributions.

To test for nonrandom structure in the data, the frequency distribution of the lengths of 10,000 trees randomly selected by PAUP from the set of all possible trees was evaluated for left-handed skewness, HILLIS (1991), HUELSENBECK (1991), KÄLLERSJÖ & AL. (1992), MAYER & SOLTIS (1994). The significance of skewness was measured by comparing the observed distribution with that of the random data, using the g1 statistics and the models of HILLIS & HUELSENBECK (1992). A decay analysis was performed to measure the relative robustness of the clades in the most parsimonious trees, MISHLER & AL. (1991), DONOGHUE & AL. (1992). This was done by constructing a strict consensus tree for all trees that were up to one step longer than the most parsimonious trees, then doing the same for trees up to two steps longer, and continuing to add steps until the strict consensus tree collapsed to an unresolved shrub. The number of extra steps required to collapse each particular clade (i. e. the decay index) can be interpreted as a measure of the relative robustness of that clade, DONOGHUE & AL. (1992). In addition, support for each branch was estimated using bootstrap analysis, FELSENSTEIN (1985). The decay and bootstrap analyses were undertaken using PAUP.

RESULTS

Misodendraceæ Agardh, Theor. syst. pl. fam. phan.: 336 (1858)

Dioecious shrublets, hemiparasitic, more or less green, and chlorophyllous; plants with thickened haustoria that promote overgrowth of the host at the contact zone. Leaves alternate, small and simple, sometimes reduced and scale-like, stipules wanting. Flowers small, unisexual, in catkin-like compound racemes or spikes; staminate flowers lacking perianth, consisting of 2-3 stamens around a small lobed nectary-disk; anthers bisporangiate and monothecal, opening by a terminal slit; pollen grains 4-12 colporate; pistillate flowers without perianth, with crescent staminodes; gynoecium syncarpic, 3-carpellate; ovary unilocular, with very short, stout style with three stigmas; ovules 3, pendulous from the top of the free central placental column, not differentiated into nucellus and integument. Fruit an achene, crowned by strongly accrescent, feathery staminodes; seeds solitary, without testa.

This monotypic family of *Santalales*, CRONQUIST (1988), is based on the genus *Misodendrum* Banks ex DC., originally assigned to *Loranthaceæ*, CANDOLLE (1830), subsequently transferred to *Santalaceæ*, BENTHAM & HOOKER (1880), and treated as a distinct family by AGARDH (1858), ORFILA (1976, 1978), ROSSOW (1982, 1984), and CARLQUIST (1985).

Misodendrum Banks ex DC., Coll. mém. 6 (Loranthacées): 12 (2-X-1830)

SPECIES TYPICA: *M. punctatum* Banks ex DC.

Misodendrum comprises eight species endemic to the Subantarctic province of the Andean subregion, MORRONE (1994, 1996), of South America. This genus was previously studied by HOOKER (1847), BENTHAM & HOOKER (1880), HIERONYMUS (1889), VAN TIEGHEM (1896), ENGLER (1897, 1914), SPEGazzini (1902), SKOTTSBERG (1913), RUIZ (1974), ORFILA (1976, 1978), ROSSOW (1982, 1984), and CARLQUIST (1985). According to the revisionary studies of ORFILA (1978) and ROSSOW (1982), species of *Misodendrum* are classified in two subgenera and five sections (table I). The number of valid names, however, differs between both authors. ORFILA (1978) recognizes twelve species, whereas ROSSOW (1982) reduces them to eight. In this analysis the concept of the latter author was confirmed.

KEY TO THE SPECIES OF *MISODENDRUM*

- | | | |
|----|--|----------------------|
| 1a | Stem with warty cortex; male flowers with two stamens | 2 |
| 1b | Stem with smooth or fissured-folded cortex; male flowers with three stamens | 5 |
| 2a | Female inflorescence composed of compact spikes with scale-like bracteoles; flowers 2, sessile, at base of each bracteole | 3 |
| 2b | Female inflorescence composed of lax spikes of umbellets or glomerules with foliaceous bracteoles; flowers 4-6, pedicellate, in each bracteole | 4 |
| 3a | Floral buds under foliar buds; female inflorescence with deciduous tectrix bract; basal bracteole of inflorescence usually sterile | <i>M. punctatum</i> |
| 3b | Floral buds over foliar buds; female inflorescence with basal tectrix bract; basal bracteole of inflorescence fertile | <i>M. gayanum</i> |
| 4a | Stems cylindric; leaves ovate-lanceolate | <i>M. macrolepis</i> |
| 4b | Stems angled and winged; leaves linear, the basal ones bract-like | <i>M. angulatum</i> |

- 5a Leaves obovate, spatulate, and petiolate; floral buds under foliar buds; bristles of achene plumose up to the middle, with apical hooks *M. quadriflorum*
- 5b Leaves linear or oblong, and sessile; floral buds over foliar buds; bristles of achene plumose up to the non-hooked apex 6
- 6a Stem swollen at base, cortex with minute waxy incrustations; bracteoles broader at base; male flowers numerous; ovary glabrous; achene bristles incurved at apex 7
- 6b Stem not swollen at base, cortex without waxy incrustations; bracteoles broader at apex; male flowers 1-2; ovary glabrescent or puberulous; achene bristles straight at apex *M. linearifolium*
- 7a Leaves usually glabrous; achene bristles <4 cm *M. brachystachyum*
- 7b Leaves pubescent; achene bristles >4 cm *M. oblongifolium*

1 *Misodendrum punctulatum* Banks ex DC., Coll. mém. 5: tab. IIA (1830)

- = *Misodendrum punctulatum* var. *subumbellatum* DC., Coll. mém. 6: tab. IIB (1830)
- = *Misodendrum commersonii* Tiegh., Bull. Soc. Bot. France 43: 557 (1896)
- = *Misodendrum recurvum* Tiegh., Bull. Soc. Bot. France 43: 557 (1896)

Plants glabrous. Stem cylindric with a warty cortex. Leaves widely cordate, subpetiolate and ciliate.

Floral buds under foliar buds; male flowers composed of compact spikes, each flower protected by a scale-like bracteole, stamens 2; basic female inflorescence composed of compact spikes with scale-like bracteoles, each bracteole enclosing 2 sessile flowers, stigma 3, ovary glabrous. Aquene with straight bristles plumose up to the apex. Fig. 1.

DISTRIBUTION. Widespread from Bio-Bío to Isla de los Estados, Tierra del Fuego (fig. 3).

HOST PLANTS. *Nothofagus antarctica*, *N. betuloides*, *N. dombeyi*, *N. nitida*, and *N. pumilio*.

MATERIAL EXAMINED. ARGENTINA. Neuquén: «lago Hermoso», Quintana & Balbiano (SI 28269). «parque nacional Lanín, lago Curruhué Grande», Gutiérrez 252 & Zavarce (HAC); Gutiérrez 254 & Zavarce (HAC); Gutiérrez 255 & Zavarce (HAC). «lago Lolog», Gutiérrez 256 & Zavarce (HAC). «camino a Huahum», Delucchi 580 (LP); Delucchi 581 (LP). «parque nacional Nahuel Huapi, colonia Cortinario, puerto Manzano», Diem 3160 (SI); Diem 3161 (SI). «lago Espejo», Cabrera 5999 (LP); Gutiérrez 189 & Zavarce (HAC); Gutiérrez & Zavarce 215 (HAC). Gutiérrez & Zavarce 238 (HAC). «Villa la Angostura», Gutiérrez 176 & Zavarce (HAC); Gutiérrez 180 & Zavarce (HAC). Gutiérrez 181 & Zavarce (HAC). «paso Córdoba», González 315 (LP). «Rahue», Cabrera 18704 (LP). «San Martín de los Andes», Bridarolli 2222 (LP). «colonía Chapelco», Stuessy & al. 10084 (LP). «lago Lácar», Schajovskoy (LP). Río Negro: «El Bolsón», Illin (LP); Martínez Crovetto 3247 (SI). «lago Roca», Boelcke 6028 & Correa (SI). «parque nacional Nahuel Huapi», Orfila (LPAG); Fabris & Solbrig 5995 (LP). «arroyo Castafio Otero», Fabris & Solbrig 487 (LP). «Bariloche, colonia Runge», Cabrera 83 & Job (LP 21369). «colonía Otto», Neumeyer 321 (LP); Stuessy 6777 & al. (LP). «colonía Santa Elena», Fabris 1191 & Solbrig (LP). «colonía Tronador», Burkart 26478 & Troncoso (SI). «Colonia Suiza», Gutiérrez 157 & Zavarce (HAC). «lago Mardari», Fabris 1248 & Solbrig (LP); Gutiérrez 92 & Zavarce (HAC); Gutiérrez 128 & Zavarce (HAC). «Río Machete», Rothkügel (SI 26746). Chubut: Spegazzini 17552 (LP). «Carrenleufú», Illin (LP). «colonía Piedra», Hogberg (SI 26764). «Cordillera», Burmeister (LP). «Corcovado», Casabón (LPAG); Illin 1 (SI). Santa Cruz: «lago Argentino», Dimitri (LPAG); Cabrera 25880 & al. (LP); Spegazzini 17553 (LP); James 38 (SI); Hicken & Hauman 223 (SI). «glaciar norte del colonia Mayor», Dimitri 1036 (LPAG). «península Avellaneda», Hicken 208 (SI). «lago Roca, Calafate», Birabén & Birabén 210 (LP). «lago San Martín, isla Lobble», Hogberg 11 (SI). «lago Viedma», Dimitri (LPAG). «Río Turbio, valle del arroyo Santa Flavia», Romero 36 (LP). Tierra del Fuego: Spegazzini 19694 (LP). «isla de los Estados, puerto Cook», Torres 1184 (LP); Nicora 7281 (SI). «lago Roca», Boetto 8462 (LPAG). «Río Varela», Goodall 626 (LP). «Ushuaia», Alboff (LP 21365); Alboff 698 (LP); Alboff 700 (LP); Alboff 701 (LP); Gebhard 72 (LP); Pennington 248 (SI); Hicken (SI 26777); Goodall 669 (LP). CHILE. Bío-Bío: «salto del Trubunleo», Burkart 27472 (SI). Los Lagos: «Chiloé», Belfreund (LP 33190); Spegazzini 17563 (LP). Piruquina, potrero el Manzano, Junge 8 (SI). Llanquihue, cerca del volcán Osorno, Morrison 17549 (SI). «Valdivia», Hollermayer 314 (SI). «cordillera de la Pelada», Gunckel 3024 (LP). Aisén: «estancia Coihaique», Maldonado 228 (LP). «valle Coihaique», Burkart 1516

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| 3b | Floral buds over foliar buds; female inflorescence with basal tectrix bract; basal bracteole of inflorescence fertile | <i>M. gayanum</i> |
| 4a | Stems cylindric; leaves ovate-lanceolate | <i>M. macrolepis</i> |
| 4b | Stems angled and winged; leaves linear, the basal ones bract-like | <i>M. angulatum</i> |

(LPAG). **Magallanes:** «Fuerte Buines», Pisano 2683 (LPAG). «isla Dawson», Benove 89 (SI). «isla Navarino», Alboff (LP 21363). «Punta Arenas», Pastore (SI 26759). «salto Grande del Paine», Pisano 2339 (LPAG); Pisano 2340 (LPAG). «Sección Lazo, colonia Toro», Pisano 4100 (LPAG). «Seno Skyring, estancia María», Rigg 24 (SI). «Última Esperanza, colonia Dorotea, puerto Natales», Eyerman & al. 24214 (SI). **Without precise data:** Dimitri (LPAG).

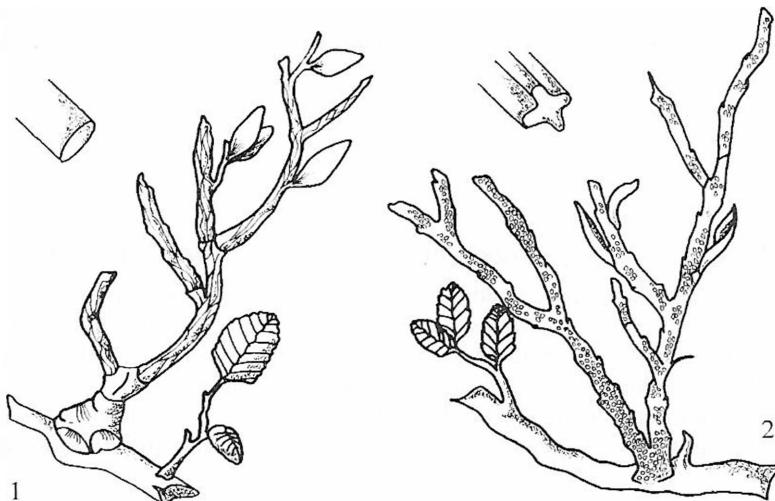


Fig. 1, 2. Habit of *Misodendrum*. 1) *M. punctulatum* Banks ex DC. 2) *M. angulatum* Phil.

2 *Misodendrum gayanum* Tiegh., Bull. Soc. Bot. France 43: 557 (1896)

- = *Misodendron imbricatum* Hook. fil., Fl. antarct. 1: 549 (1847), non Poepp. & Endl.
- = *Misodendron patagonicum* Spegg., Anales Mus. Nac. Hist. Nat. Buenos Aires 7: 161 (1902)
- = *Misodendron diemii* Ruiz, Bol. Soc. Argent. Bot. 16(1-2): 79-82 (1974)

Plants glabrous. Stem cylindric with a warty cortex. Leaves lineal-lanceolate, sessile, ciliate, entire or minutely denticulate up to the apex. Floral buds over foliar buds; male flowers composed of compact spikes, each flower protected by a scale-like bracteole, stamens 2; basic female inflorescence composed of compact spikes with scale-like bracteoles, each bracteole enclosing two sessile flowers, stigma 3, ovary glabrous. Aquene with straight bristles plumose up to the apex.

DISTRIBUTION. From southern Neuquén and northern Río Negro in Argentina to Los Lagos, Aisén, and Magallanes in Chile (fig. 4).

HOST PLANTS. *Nothofagus antarctica*, *N. dombeyi*, and *N. nitida*.

MATERIAL EXAMINED. ARGENTINA. Neuquén: «parque nacional los Arrayanes», Greenstone (SI 26982). «parque nacional Nahuel Huapi, isla Victoria», Corte 24 (LP); Boelcke 1767 (SI). «lago Espejo», Cabrera 6002 (LP). «lago Nahuel Huapi, brazo Huemul», Lanza 3365 (LP). «colonia Cortinario, puerto Manzano», Diem 3060 (SI). «Quetrihué», Diem 89 (LP). RÍO NEGRO: «parque nacional Nahuel Huapi, Bariloche, bahía López», Maldonado 28 (LP). «lago Mascardi», Orfila 629 (LPAG). «lago Nahuel Huapi», Spegazzini 17564 (LP). «Llao Llao», Maldonado 599 (LP). CHILE. LOS Lagos: «Ensenada, lago Llanquihue», Barros 1900 (SI). «Valdivia», Hollermayer 664 (LP). «volcán Villarrica», Hollermayer 408 (LP). AISÉN: «istmo de Ofqui, San Rafael», Hicken (SI 20792, SI 26767).

3 *Misodendrum macrolepis* Phil., Anales Univ. Chile 27(3): 316 (1865)

Plants glabrous. Stem cylindric with a warty cortex. Leaves ovate-lanceolate, sessile, ciliate, entire. Floral buds over foliar buds; male flowers composed of compact spikes, each bracteole protecting 2 flowers, stamens 2; basic female inflorescence composed of lax spikes of umbellets or glomerules, each umbellet with 4-6 flowers protected by a foliaceous bracteole, the basal bracteole usually sterile, flowers minutely pedicellate, stigma 3, ovary glabrous. Fruit unknown.

DISTRIBUTION. Restricted to Valdivia, Los Lagos, Chile (fig. 5).

HOST PLANTS. *Nothofagus dombeyi*.

MATERIAL EXAMINED. CHILE. Los Lagos: «Valdivia, cordillera de la Pelada», Hollermayer 672 (LP).

4 *Misodendrum angulatum* Phil., Anales Univ. Chile 27(3): 315 (1865)

Plants glabrous. Stem angled and usually winged with a warty cortex. Leaves lineal, entire, sessile, glabrous. Floral buds over foliar buds; male flowers composed of compact spikes, each bracteole protecting 2 flowers, stamens 2; basic female inflorescence composed of lax spikes of umbellets or glomerules, each umbellet with 4-6 flowers protected by a foliaceous bracteole, the basal bracteole usually sterile, flowers minutely pedicellate, stigma 3, ovary glabrous. Aquene with straight bristles plumose up to the apex. Fig. 2.

DISTRIBUTION. Widespread from Neuquén to Magallanes (fig. 6).

HOST PLANTS. *Nothofagus antarctica*, *N. betuloides*, and *N. dombeyi*.

MATERIAL EXAMINED. ARGENTINA. Neuquén: «parque nacional los Arrayanes», Greenstone (SI 26778). «San Martín de los Andes», Rasp. 19 (SI). Río Negro: «parque nacional Nahuel Huapi, Paso de las Nubes», Fabris & Solbrig 482 (LP); Boelcke & Correa 5482 (SI). Santa Cruz: «colonia Fitz Roy, lago Azul», Dimitri (LPAG). CHILE. Los Lagos: «Valdivia, cordillera de la Pelada», Beldf'reund (LP 33165, LP 33192). Magallanes: «Seno Skyring, Río León», Pisano 2686 (LPAG); Pisano 2699 (LPAG).

5 *Misodendrum quadriflorum* DC., Coll. mém. 6: tab. 12, 1 (1830); Prodr. 4: 286 (1830)

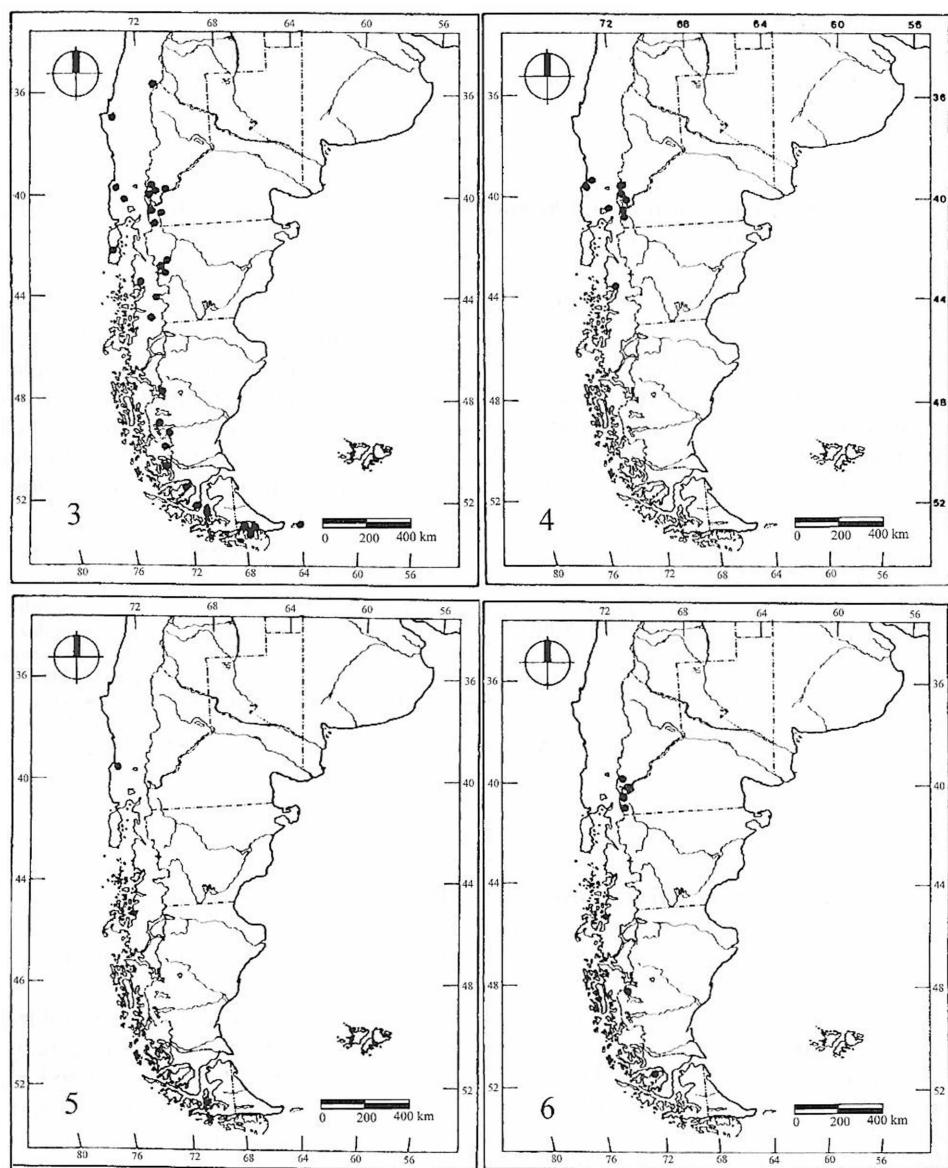
= *Telophyllum quadriflorum* (DC.) Tiegh., Bull. Soc. Bot. France 43: 558 (1896)

Plants pubescents. Stem cylindric, swollen at base, with a smooth or fissured-folded cortex and waxy incrustations. Leaves obovate-spatulate, entire, minutely pedicellate, glabrous. Floral buds under foliar buds; male flowers composed of compact spikes, each bracteole protecting 2(3) flowers, stamens 3; basic female inflorescence composed of lax spikes, flowers 6, opposite, ebracteolate but with a apical bracteole in the floral axis, flowers sessile, stigma 3, ovary glabrous. Aquene with claviform bristles plumose up to the middle with apical hooks

DISTRIBUTION. Widespread in the Subantarctic province (fig. 7).

HOST PLANTS. *Nothofagus pumilio*.

MATERIAL EXAMINED. ARGENTINA. Neuquén: «lago Hermoso», Diem 3168 (SI). «lago Meliquina», Birabén & Birabén 715 (LP). «lago Paz», Spegazzini 17554 (LP). «parque nacional Nahuel Huapi, colonia Cortinario, puerto Manzano», Diem 3182 (SI). «San Martín de los Andes», Rasp. 21 (SI). Río Negro: «parque nacional Nahuel Huapi, lago Mardaris», Orfila 533 (LPAG); Orfila 609 (LPAG); Orfila 621 (LPAG); Orfila 622 (LPAG); Orfila 695 (LPAG). Chubut: Spegazzini 17555 (LP). «lago General Vintter», Orfila 694 (LPAG); Orfila 695 (LPAG); Orfila 755 (LPAG); Orfila 800 (LPAG). Santa Cruz: «arroyo Toso», Hicken 515 & Hauman (SI). «colonia Cazador», Centilli 398 (LP). «colonia Fitz Roy, lago Azul», Dimitri (LPAG).



Figs. 3-6. Geographic distribution of *Misodendrum*. 3) *M. punctulatum*. 4) *M. gayanum*. 5) *M. macrolepis*.
6) *M. angulatum*

«lago Viedma», *Orfila* (LPAG); *Penibertun* (SI 26682). **Tierra del Fuego**: «Brown», *Goodall* 275 (LP). «lago Roca», *Orfila* 582 (LPAG); *Orfila* 591 (LPAG). «parque nacional Tierra del Fuego, Ensenada», *Orfila* 593 (LPAG). «Ushuaia», *Gebhard* 71 (LP); *Hicken* (SI); *Hicken* 20 (SI); *Goodall* 87 (LP); *Goodall* 588 (LP). **CHILE. Magallanes**: «isla Navarino», *Alboff* 703 (LP); *Alboff* 705 (LP); *Alboff* 706 (LP); *Alboff* 708 (LP); *Alboff* 709 (LP, LP 21375). «Mina Carota», *Donat* 297 (SI).

**6 *Misodendrum brachystachyum* DC., Coll. mém. 6: 14, tab. 12: 1 (1830);
Prodr. 4: 286 (1830)**

- = *Archiphyllum brachystachyum* (DC.) Tiegh., Bull. Soc. Bot. France 43: 557 (1896)
- = *Archiphyllum macrophyllum* (Phil.) Tiegh., Bull. Soc. Bot. France 43: 557 (1896)

Plants pubescents. Stem cylindric swollen at base, with a smooth or fissured-folded cortex and waxy incrustations. Leaves lineal-oblongate, entire, sessile, glabrous or glabrescents. Floral buds over foliar buds; male flowers composed of compact spikes, each bracteole protecting many flowers, stamens 3; basic female inflorescence composed of lax spikes, with a bracteole at the base of the floral axis, flowers numerous, alternate, minutely pedicelate, ebracteolate, stigma 3, ovary glabrous. Aquene with incurvate bristles plumose up to the apex.

DISTRIBUTION. From Bío-Bío (Chile) to Isla de los Estados in Tierra del Fuego, Argentina (fig. 8).

HOST PLANTS. *Nothofagus antarctica*, *N. betuloides*, *N. dombeyi*, and *N. pumilio*.

MATERIAL EXAMINED. **ARGENTINA. Río Negro**: «parque nacional Nahuel Huapi, lago Mardari», *Orfila* 641 (LPAG); *Orfila* 642 (LPAG). **Chubut**: «Corcovado», *Casaubón* (LPAG). «lago Menéndez», *Neumayer* 386 (LP 41030). **Santa Cruz**: «lago Argentino», *James* 2261 (SI). **Tierra del Fuego**: *Spegazzini* 17570 (LP); *Spegazzini* 19693 (LP). «isla de los Estados, puerto Cook», *Torres* 1134 (LP). «puerto Ferrari», *Iter Patagonicum* 224 (SI). «Ushuaia», *Hicken* (SI 26749). **CHILE. Bío-Bío**: «laguna del Laja, Los Barros», *Burkart* 27473 (SI). **Los Lagos**: «Valdivia», *Buchtien* (SI 26762). «Valdivia, Purulou», *Hollermayer* 312 (SI). **Aisén**: «istmo de Osqui», *Hicken* (SI 20824). **Magallanes**: «isla Dawson», *Benoit* 88 (SI). «Punta Arenas», *Bonarelli* (SI 26745); *Hicken* 137 (SI). «Río Blanco», *Kunkel* 2220 (SI). «Río Seco», *Donat* 296 (SI). Without precise data: *Hicken* 72 (SI).

7 *Misodendrum oblongifolium* DC., Prodr. 4: 671 (1830)

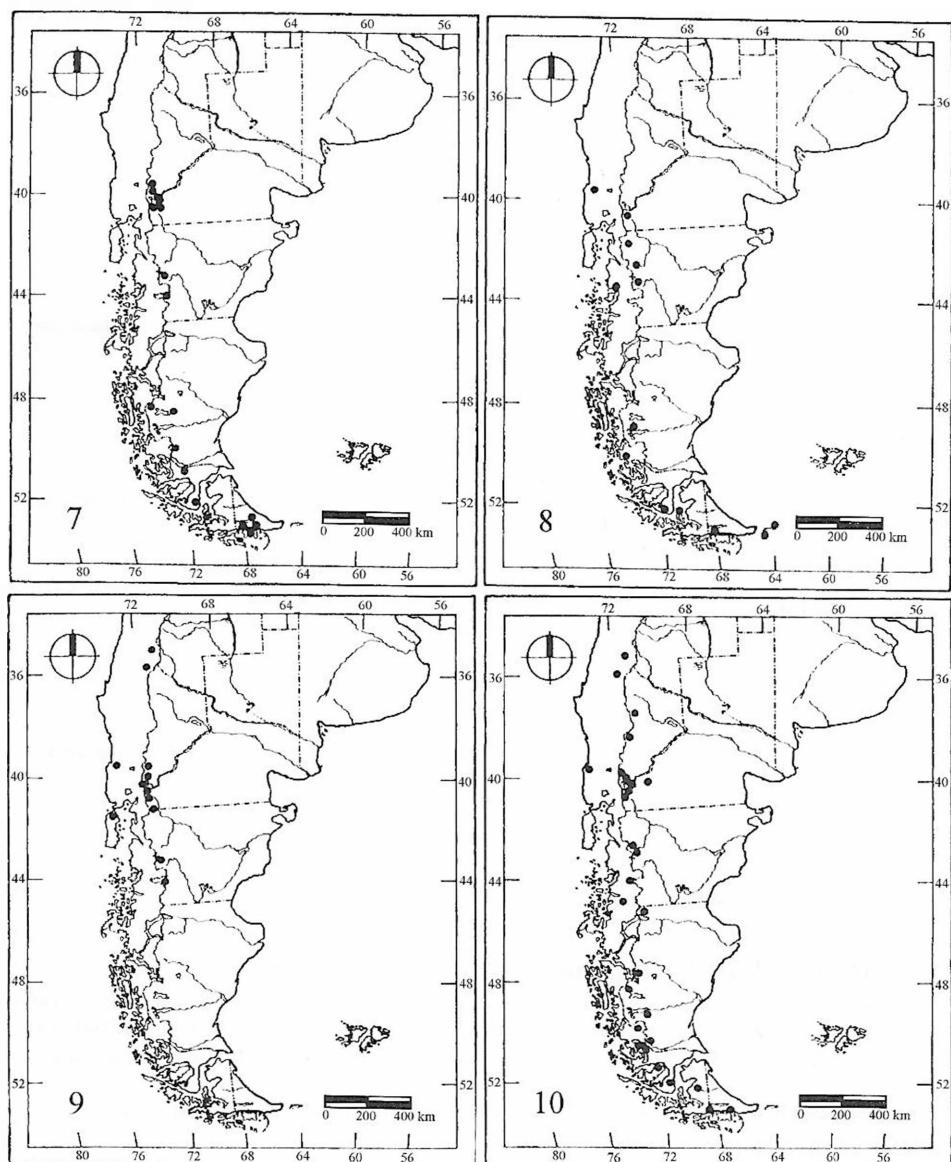
- = *Archiphyllum oblongifolium* (DC.) Tiegh., Bull. Soc. Bot. France 43: 557 (1896)
- = *Misodendron oblongifolium* DC. var. *lilacinum* *Orfila*, Revista Fac. Agron. Univ. Nac. La Plata, ser. 2, 52(1-2): 51 (1976)

Plants pubescents. Stem cylindric swollen at base, with a smooth or fissured-folded cortex and waxy incrustations. Leaves lineal-oblongate to elliptic, entire, sessile, usually pubescents. Floral buds over foliar buds; male flowers composed of compact spikes, each bracteole protecting many flowers, stamens 3; basic female inflorescence composed of lax spikes, with a bracteole at the base of the floral axis, flowers numerous, alternate, minutely pedicelate, ebracteolate, stigma 3, ovary glabrous. Aquene with incurvate bristles plumose up to the apex.

DISTRIBUTION. From Bío-Bío, Araucanía, and Los Lagos (Chile) to Chubut in Argentina (fig. 9).

HOST PLANTS. *Nothofagus antarctica*, *N. betuloides*, and *N. pumilio*.

MATERIAL EXAMINED. **ARGENTINA. Neuquén**: «lago Hermoso», *Diem* 3170 (SI). «parque nacional Nahuel Huapi, colonia Bayo», *Dolly* 112 & *Jones* (LP). «colonia Cortinario, puerto Manzano», *Diem* 3081 (SI). «Río Estancado», *Diem* 3097 (SI). «Pulmarí», *Comber* 383 (LP). **Río Negro**: «El Bolsón, colonia Pilquitrón», *Cabrera* 23064 & al. (LP). «parque nacional Nahuel Huapi, colonia Catedral», *Cabrera* 11498 pp. (LP). «colonia Otto», *Neumeyer* 323 (LP). «colonia Tronador», *Burkart* 26477 (SI); *Burkart* 26476 pp. & *Troncoso* (SI). «lago Mardari», *Orfila* 606 (LPAG); *Orfila* 638 (LPAG); *Orfila* 713 (LPAG). «puerto Blest»,



Figs. 7-10. Geographic distribution of *Misodendrum*. 7) *M. quadriflorum*. 8) *M. brachystachy whole*. 9) *M. oblongifolium*. 10) *M. linearifolium*

Orfila 706 (LPAG). «valle del Rio Ouleuc», *Fabris* 86 & *Solbrig* (LP). **Chubut:** *Spegazzini* (LP). «Carrenleufú», *Spegazzini* 17571 (LP). «lago Fontana», *Kozlowsky* (LP 21360). «lago General Paz», *Gerluis* (SI 20828). «lago General Vinter», *Orfila* 640 (LPAG); *Orfila* 698 (LPAG); *Orfila* 703 (LPAG); *Orfila* 704 (LPAG); *Orfila* 753 (LPAG); *Orfila* 754 (LPAG); *Orfila* 759 (LPAG); *Orfila* 763 (LPAG); *Orfila* 764 (LPAG); *Orfila* 765 (LPAG). **CHILE.** *Bío-Bío:* «Terma de Chillán», *MacHerboru* (SI 26772); *Cabrera* 3627 (LP). **Araucanía:** «Cautín, volcán Llaima», *Werdermann* 1218 (SI). **Los Lagos:** «Valdivia, cordillera Pelada», *Hollermayer* 681 (LP).

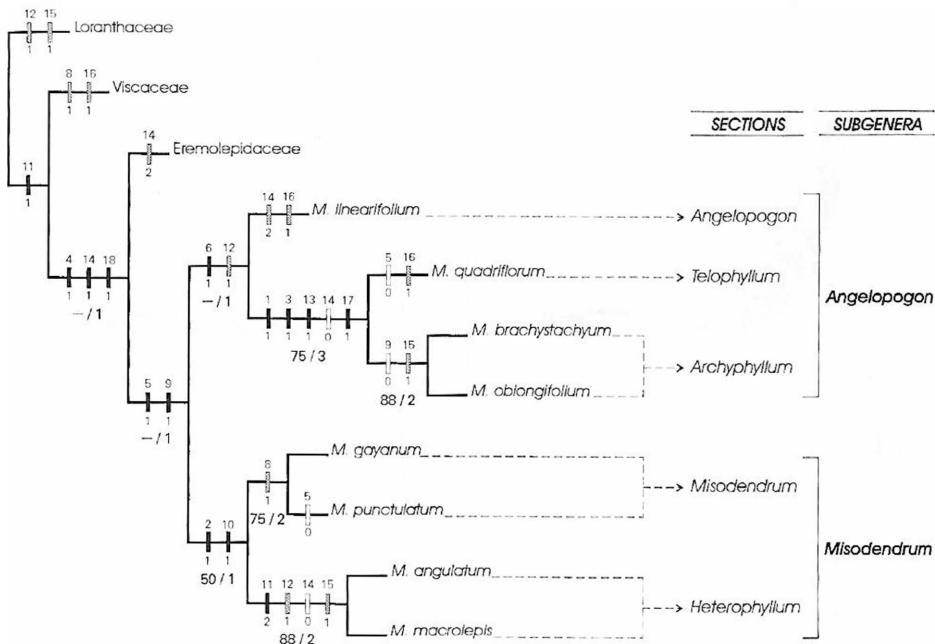


Fig. 11. Cladogram of *Misodendrum*. Character state changes are superimposed: solid black bars = synapomorphies; dotted bars = parallelisms; open bars = reversals

8 *Misodendrum linearifolium* DC., Prodr. 4: 12 (1830)

- = *Angelopogon linearifolium* (DC.) Poepp. ex Tiegh., Bull. Soc. Bot. France 43: 558 (1896)
- = *Misodendron linearifolium* DC. var. *contractum* Skottsb., Bot. Jahrb. Syst. 50: 390 (1913)
- = *Misodendron contractum* (Skottsb.) Orfila, Revista Fac. Agron. Univ. Nac. La Plata, ser. 2, 52(1-2) (1976)
- = *Misodendron densifolium* Orfila, Revista Fac. Agron. Univ. Nac. La Plata, ser. 2, 52(1-2): (1976)
- = *Misodendron reflexum* Orfila var. *reflexum* Orfila, Revista Fac. Agron. Univ. Nac. La Plata, ser. 2, 52(1-2): (1976)
- = *Misodendron reflexum* Orfila var. *brevisetaceum* Orfila, Revista Fac. Agron. Univ. Nac. La Plata, ser. 2, 52(1-2): (1976)

Plants pubescents. Stem cylindric, with a smooth or fissured-folded cortex. Leaves lineal, entire, sessile, ciliate. Floral buds over foliar buds; male flowers composed of compact spikes, each bracteole protecting 1 (2) flowers, stamens 3; basic female inflorescence composed of lax spikes, with 1(2) flowers in each bracteole, flowers alternate, sessile, stigma 3, ovary glabrous or pubescent. Aquene with straight bristles plumose up to the apex.

DISTRIBUTION. Widespread from Maule (Chile) to Tierra del Fuego (Argentina); fig. 10.

HOSTS PLANTS. *Nothofagus alpina*, *N. antarctica*, *N. dombeyi*, *N. obliqua*, and *N. pumilio*.

MATERIAL EXAMINED. ARGENTINA. Neuquén: *Spegazzini* 17565 (LP). «Aluminé», *Maldonado* 662 (LP). «Cañadón Seco», *Orfila* (LPAG). «colonia Bandurria, lago Lácar», *Gutiérrez* 257 & Zavarro (HAC); *Gutiérrez* 258 & Zavarro (HAC). «lago Hermoso», *Diem* 3167 (SI). «lago Meliquina», *Birabén & Birabén* 717 (LP). «parque nacional Lanín, lago Lolog», *Cabrera* 19741 (LP). «parque nacional Nahuel Huapi», *Diem* 799 (SI). «colonia Bayo», *Jones* 111 (LP). «colonia Cortinario, puerto Manzano», *Diem* 3064 (SI). «lago Traful», *Birabén & Birabén* 711 (LP). «valle del Pichío», *Boelcke* 13634 & al. (SI). «Villa La Angostura», *Fabris & Solbrig* 1027 (LP); *Gutiérrez* 178 & Zavarro (HAC). «Pino Hachado», *Burkart* 9697 (SI). «lago Aluminé», *Cabrera* 19115 & Crisci (LP). «Quetrihué», *Diem* 92 (LP). «San Martín de los Andes», *Bridarolli* 2075 (LP); *Dawson* 1290 (LP); *Spegazzini* 17561 (LP); *Diem* 3174 (SI). «colonia Bandurria, lago Lácar», *Gutiérrez* 260 & Zavarro (HAC). Río Negro: «parque nacional Nahuel Huapi, Bariloche, colonia Runge», *Covas* 6 (LP). «colonia Catedral», *Cabrera* 11498 pp. (LP). «colonia Otto», *Cabrera* 5863 (LP); *Neumeier* 330 (LP). «colonia Tronador», *Ruhilis* (LP); *Correa* (SI 26779); *Burkart* 26476 pp. & *Troncoso* (SI). «lago Mascardi», *Orfila* 540 (LPAG); *Orfila* 632 (LPAG); *Orfila* 635 (LPAG); *Orfila* 636 (LPAG); *Orfila* 639 (LPAG); *Gutiérrez* 108 & Zavarro (HAC); *Gutiérrez* 121 & Zavarro (HAC). Chubut: *Orfila* (LPAG). «Carrenleufú», *Illin* (LP). «Cordillera», *Bruneister* (LP). «laguna Blanca», *Spegazzini* 17562 (LP); *Koslowsky* 209 (SI). «Río Corcovado», *Illin* 99 (SI). Santa Cruz: «colonia Fitz Roy», *Dimitri* 10651 (LPAG). «lago Argentino», *Dimitri* 1078 (LPAG); *Dimitri* 10837 (LPAG); *Spegazzini* 17568 (LP); *Hicken & Hauman* 210 (SI). «lago Buenos Aires», *Greiner & Platen* 119 (SI). «lago San Martín», *Hogberg* 3 (SI). «Río Turbio», *Romero* 63 (LP). Tierra del Fuego: «estancia Viamonte», *Goodall* 546 (LP). «Lapataia», *Orfila* 597 (LPAG); *Orfila* 600 (LPAG); *Goodall* 2422 (SI). «Río Grande», *Spegazzini* 17569 (LP). «Ushuaia, estancia Harberton», *Goodall* 752 (LP). CHILE. Maule: «colonia del Roble», *Looser* 228 (SI). «Linares, Roblería, camino al Melano», *Ricardi* 2767 (LP). Bío-Bío: «Chillán», *Belfreund* (LP 33164, LP 33191). Los Lagos: «Valdivia, Puníre», *Hollermayer* 355 (SI). «Quinchilca», *Hollermayer* 239 (LP 53658, LP 53801). Aisén: «Los Mollines, Balmaceda», *Maldonado* 60 (LP). Magallanes: «laguna Sofía», *Pisano* 2813 (LPAG). «Punta Arenas», *Alhoff* (LP 21361); *Hicken* 136 (SI). «Miraflor», *Benove* 87 (SI). «Sección Lazo, colonia Toro», *Pisano* 4099 (LPAG). «seno Skyring, estancia María», *Raggi* 26 (SI). «Última Esperanza, puerto Prat», *Hicken* 134 (SI); *Hicken* 135 (SI).

CLADISTIC ANALYSIS OF *MISODENDRUM*

The analysis yielded one cladogram (fig. 11) with 30 steps, a consistency index of 0.63, and a retention index of 0.72. The random search of 10,000 of all possible trees produced a highly-skewed ($g_1 = -0.712$) frequency distribution of tree lengths, indicating considerable ($P < 0.01$) nonrandom structure in the data, HILLIS & HUELSENBECK (1992). In the cladogram, the following phylogenetic sequence results: (*Loranthaceae*, (*Viscaceae*, (*Eremolepidaceae*, ((*Misodendrum linearifolium*, (*M. quadriflorum*, (*M. brachystachyum*, *M. oblongifolia*)))), ((*M. gayanum*, *M. punctulatum*), (*M. angulatum*, *M. macrolepis*))))). Based on the cladogram, *Eremolepidaceae* are the sister group of *Misodendraceae*, supported by synapomorphies 4.1, 14.1, and 18.1.

Tree topology shows that there are two big monophyletic groups within *Misodendrum*, corresponding to the subgenera accepted by ROSSOW (1982, 1984). Subgenus *Misodendrum* is based on the warty cortex (2.1) and two stamens in the male flower (10.1). Two sections can be recognized within this subgenus: *Misodendrum punctulatum* and *M. gayanum* form section *Misodendrum*, based on scale-like bracts (8.1), and *Heterophyllum* (*M. macrolepis* and *M. angulatum*) is supported by the flower clusters in glomerules or umbelllets in each bracteole (11.2), lax internodes (12.1), pedicellated flowers (15.1), and many flowers in each bracteole (14.0).

Concerning subgenus *Angelopogon*, *M. linearifolium* corresponds with section *Angelopogon*, the sister group of the remaining species, which are supported by stems

swollen at base (1.1), waxy incrustations (3.1), bracteoles in the floral axis (13.1), two flowers per bracteole (14.0), and apex of bristles in pistillate flowers incurved or claviform (17.1). In this group the clade formed by *M. brachystachyum* and *M. oblongifolium* corresponds to section *Archiphyllum*, which is the sister group of section *Telophyllum* (*M. quadriflorum*).

Several characters have been attained in a parallel mode. Lax internodes in the inflorescence (12.1) are shared between *Angelopogon* and *Heterophyllum*, pedicellated flowers (15.1) are shared between *Archiphyllum* and *Heterophyllum* and opposite female flowers (16.1) are present in *Telophyllum* and *Angelopogon*. Three characters reverse to their plesiomorphic state, e. g., flower buds placed under foliar buds (5.0) in *M. quadriflorum* and *M. punctulatum*, male flowers numerous in each bracteole (9.0) in *Archiphyllum*, and 4-6 female flowers in each bracteole (14.0) in *Heterophyllum* and *Thelophyllum-Archiphyllum*.

The cladogram allows the re-examination of the taxonomic placement of *Misodendrum* (*Misodendraceae*). CANDOLLE (1830) included *Misodendrum* in *Loranthaceae* s. l. (i. e., including *Viscaceae* and *Eremolepidaceae*). Both AGARDH (1858) and HIERONYMUS (1889) gave separate family status to the genus, considered by the latter to be intermediate between *Santalaceae* and *Loranthaceae*. *Viscaceae* was recognized as a family distinct from *Loranthaceae* by BENTHAM in BENTHAM & HOOKER (1880), and *Eremolepidaceae* was validated as a family by KUIJT (1968). Our results show that all these families are part of the same phylogenetic lineage, where *Eremolepidaceae* is the sister group of *Misodendraceae*. Recent research using a traditional approach has distinguished two subgenera and five sections, ORFILA (1978), ROSSOW (1982), in *Misodendrum*. Our analysis confirms these findings through transformation of characters sequence using a phylogenetic analysis.

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TABLE I
TWO MOST RECENT CLASSIFICATIONS OF THE GENUS *MISODENDRUM*

Category	Orfila (1978)	Rossow (1982)
Genus	<i>Misodendrum</i> Banks ex DC.	<i>Misodendrum</i> Banks ex DC.
Subgenus	<i>Gymnophyton</i> Hooker	<i>Misodendrum</i> Banks ex DC.
Section	<i>Ephedranthus</i> Skottsb. <i>M. gayanum</i> Tiegh. <i>M. punctulatum</i> var. <i>punctulatum</i> DC. <i>M. punctulatum</i> var. <i>subumbellatum</i> DC. <i>M. recurvum</i> Tiegh.	<i>Misodendrum</i> Banks ex DC. <i>M. gayanum</i> Tiegh. <i>M. punctulatum</i> DC. s. l.
Section	<i>Heterophyllum</i> Skottsb. <i>M. angulatum</i> Phil. <i>M. macrolepis</i> Phil.	<i>Heterophyllum</i> Skottsb. <i>M. angulatum</i> Phil. <i>M. macrolepis</i> Phil.
Subgenus	<i>Eumyzodendron</i> Hooker	<i>Angelopogon</i> (Tiegh.) Rossow
Section	<i>Angelopogon</i> (Tiegh.) Skottsb. <i>M. linearifolium</i> DC. <i>M. contractum</i> (Skottsb.) Orfila <i>M. densifolium</i> Orfila <i>M. reflexum</i> var. <i>reflexum</i> Orfila <i>M. reflexum</i> var. <i>brevisetaceum</i> Orfila	<i>Angelopogon</i> (Tiegh.) Skottsb. <i>M. linearifolium</i> var. <i>linearifolium</i> DC. <i>M. linearifolium</i> var. <i>contractum</i> Skottsb.
Section	<i>Archiphyllum</i> (Tiegh.) Skottsb. <i>M. brachystachyum</i> DC. <i>M. oblongifolium</i> var. <i>oblongifolium</i> DC. <i>M. oblongifolium</i> var. <i>lilacinum</i> Orfila	<i>Archiphyllum</i> (Tiegh.) Skottsb. <i>M. brachystachyum</i> DC. <i>M. oblongifolium</i> DC., s. l.
Section	<i>Telophyllum</i> (Tiegh.) Skottsb. <i>M. quadriflorum</i> DC.	<i>Telophyllum</i> (Tiegh.) Skottsb. <i>M. quadriflorum</i> DC.

TABLE II
species of *Misodendrum* an their geographical distribution

<i>Misodendrum</i> species	Geographical distribution
<i>M. angulatum</i> Phil.	Argentina and Chile, from Los Lagos to Magallanes
<i>M. brachystachyum</i> DC.	Argentina and Chile, from Los Lagos to Tierra del Fuego
<i>M. gayanum</i> Tiegh.	Argentina and Chile, from Los Lagos to Río Negro
<i>M. linearifolium</i> DC.	Argentina and Chile, from Bío-Bío to Tierra del Fuego
<i>M. macrolepis</i> Phil.	Chile, restricted to Los Lagos
<i>M. oblongifolium</i> DC.	Argentina and Chile, from Bío-Bío to Chubut
<i>M. punctulatum</i> Banks ex DC.	Argentina and Chile, from Araucanía to Tierra del Fuego
<i>M. quadriflorum</i> DC.	Argentina and Chile, from Neuquén to Tierra del Fuego

TABLE III
data matrix and character list for the cladistic analysis of *Misodendrum*
0) plesiomorphic; 1, 2) apomorphic; P) polymorphic; -) not applicable or unknown

Terminal taxa	Characters																	
	P	0	0	0	0	P	P	0	-	0	0	1	0	-	1	0	-	0
<i>Loranthaceae</i>																		
<i>Viscaceae</i>	0	0	0	0	0	P	0	1	0	0	1	0	0	0	0	1	-	0
<i>Eremolepidaceae</i>	0	0	0	1	0	0	0	0	0	0	1	0	0	2	0	0	-	1
<i>M. angulatum</i>	0	1	0	1	1	0	0	0	1	1	2	1	0	0	1	0	0	1
<i>M. brachystachyum</i>	1	0	1	1	1	1	0	0	0	0	1	1	1	0	1	0	1	1
<i>M. gayanum</i>	0	1	0	1	1	0	0	1	1	1	1	0	0	1	0	0	0	1
<i>M. linearifolium</i>	0	0	0	1	1	1	P	0	1	0	1	1	0	2	0	1	0	1
<i>M. macrolepis</i>	0	1	0	1	1	0	0	0	1	1	2	1	0	0	1	0	-	1
<i>M. oblongifolium</i>	1	0	1	1	1	1	0	0	0	0	1	1	1	0	1	0	1	1
<i>M. punctulatum</i>	0	1	0	1	0	0	0	1	1	1	1	0	0	1	0	0	0	1
<i>M. quadriflorum</i>	1	0	1	1	0	1	0	0	1	0	1	1	1	0	0	1	1	1

Characters

- 1 Stem: (0) not swollen, (1) swollen
- 2 Cortex: (0) smooth or fissured-folded, (1) warty
- 3 Stem incrustations: (0) absent, (1) present
- 4 Leaves position: (0) opposite, (1) alternate
- 5 Position of floral buds in respect to foliar buds: (0) under, (1) over
- 6 Pubescence of flower shoots: (0) glabrate, (1) pubescent
- 7 Flowers: (0) unisexual, (1) hermafrodite
- 8 Bracts: (0) foliose, (1) scale-like
- 9 Number of staminate flowers/bracteole: (0) three or more, (1) one or two
- 10 Number of stamens: (0) three or more, (1) two
- 11 Type of basic inflorescence: (0) raceme, (1) spike, (2) spike of glomerules or umbellules
- 12 Inflorescence development: (0) compact, (1) lax
- 13 Position of bracteoles: (0) at base of flowers, (1) on the floral axis
- 14 Number of pistillate flowers/bracteole: (0) three or more, (1) two, (2) one
- 15 Pedicel of pistillate flowers: (0) absent, (1) present
- 16 Position of pistillate flowers on floral stem: (0) alternate, (1) opposite
- 17 Apex of bristles in pistillate flowers: (0) straight, (1) incurved or claviform
- 18 Stomata: (0) paracytic, (1) anomocytic