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Phenetic analyses of morphological traits in the *Malesherbia humilis* complex (Malesherbiaceae)

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Malesherbia (Malesherbiaceae) is a small, xerophytic group endemic to the Peruvian and Chilean deserts and adjacent Argentina. *Malesherbia humilis* var. *humilis*, *M. humilis* var. *propinqua*, *M. humilis* var. *parviflora*, *M. gabrielae*, *M. taltalina*, and *M. multiflora* form a morphologically cohesive group native to Chile and Argentina characterized by a profusion of small flowers and a short, bushy habit. The difficulty in distinguishing among these taxa suggests that the taxonomic delimitations may not be meaningful. A phenetic study was conducted to determine if this complex is best treated as a large, polymorphic species or as a series of very similar yet distinguishable taxa. Sixteen morphological characters were examined on 113 operational taxonomic units (OTUs); the data were analyzed using UPGMA, PCA, and discriminant analyses. Five clusters were identified by the analyses. These clusters are distinguishable by minor characters and are geographically cohesive. Because of the minor nature of the differences found and the unreliability of most differences noted in the descriptions of the taxa, these five clusters are recognized as varieties of *M. humilis*. A key to the varieties and short descriptions of each are presented.

KEYWORDS: Chile, *Malesherbia*, morphometrics, phenetics, species limits, varietal limits.

INTRODUCTION

Malesherbiaceae are a little-known group of xerophytic plants endemic to the Peruvian and Chilean deserts and adjacent Argentina. They are most closely related to Turneraceae, a largely neotropical family (Fay & al., 1997). Malesherbiaceae are distinguished from their closest relatives by the presence of an androgynophore (a stalk elevating the ovary above the floral tube base), a well-developed corona, and a floral tube bearing the perianth on its upper margin. In addition, most Malesherbiaceae have glandular hairs covering much of the plant body. The 27 species of the family's single genus, *Malesherbia*, colonize a wide variety of arid habitats, including the Mediterranean foothills of central Chile, the inter-Andean valleys of Peru, and the dry ravines of the northern Chilean Atacama Desert, a section of the driest coastal desert in the world (Trewartha, 1961). A diverse range of floral and vegetative morphologies has arisen in the family, perhaps in response to the patchy environment in which it inhabits.

One of the most distinctive groups of species in the family is the *Malesherbia humilis* complex. The taxa treated at the species level by Ricardi (1967) are *M. gabrielae* Ric., *M. humilis* Poepp., *M. multiflora* Ric., and *M. taltalina* Ric. These densely pubescent species are characterized by the production of numerous small flowers (floral tubes are 1.5–12 mm), bractless pedicels, leaves that are often very small and withered at anthesis,

and a very short (under 30 cm) bushy habit. This combination of features is unique in the family. The four taxa are difficult to distinguish because most features seem to intergrade from taxon to taxon. Moreover, most leaf traits are not useful characters for all specimens, because leaves are often missing or withered in flowering material.

Members of the *Malesherbia humilis* complex are found from Santiago, Chile (33°20'S) to Guatacondo (20°56'S) in the north of that country, although a few collections have been made in Province Neuquén, Argentina (37°15'S–37°30'S; Fig. 1). Specimens have been collected up to 2900 m, but the majority are from under 1000 m. These plants prefer rocky, arid soils characteristic of dry ravines, washes, and road cuts.

Although the climate of this entire range is dry, there is a gradient of increasing aridity from the south (Mediterranean) to the north (hyperarid). An anticyclone stationed over the Pacific Ocean off the coast of Chile heavily influences precipitation by blocking most of the moisture-laden polar air from moving north. The semi-arid zone (beginning about 30°S) that is the transition between the Mediterranean and true desert climates lies at the polar front's northern edge. The position of this front fluctuates with the seasonal migration of the anticyclone (Paskoff, 1973; Lauer & Frankenberg, 1984). In this transitional zone, occasional precipitation supports more permanent vegetation than found further to the north (Rundel & al., 1991; Gajardo, 1993). Semi-aridity

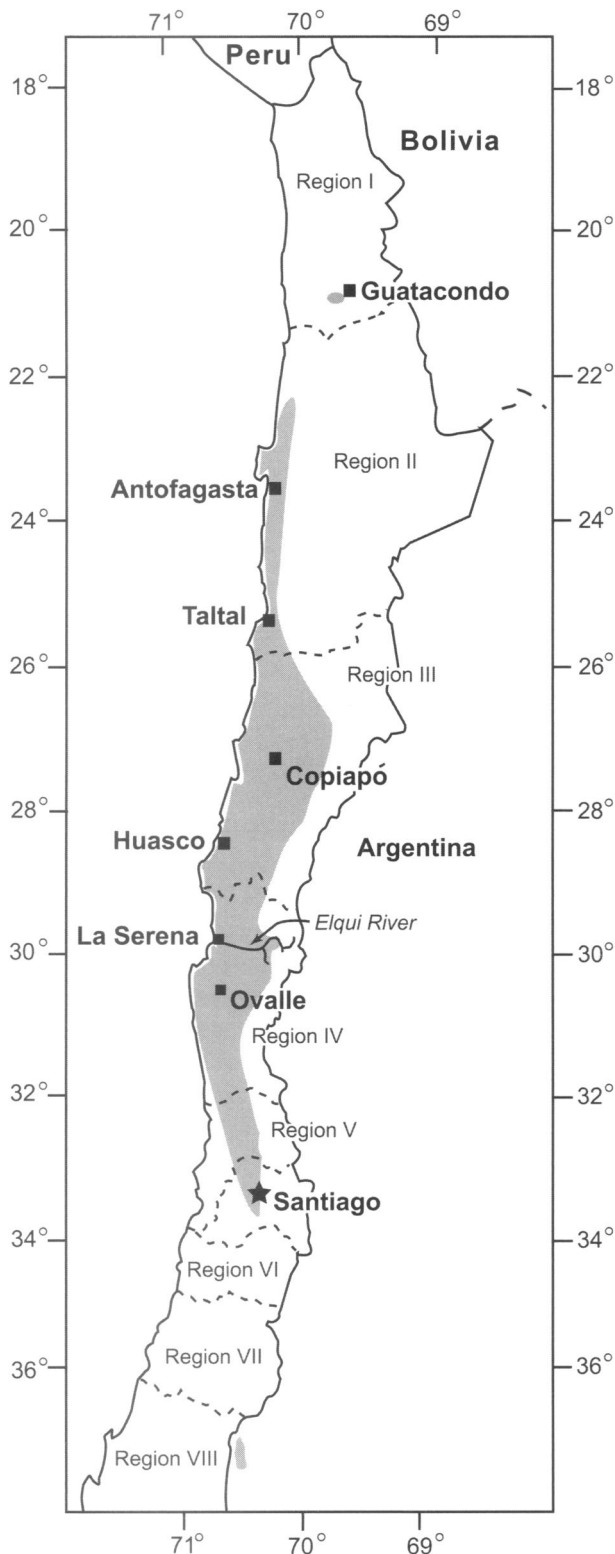


Fig. 1. Map of northern and central Chile and adjacent Argentina, Bolivia, and Peru. Political boundaries and the distribution of the *Malesherbia humilis* complex (shaded) are indicated.

ends and the true desert begins approximately at Huasco (28°30'S) in southern Region III (Chilean political divisions; Fig. 1; Börgel, 1973). The climate becomes extremely dry north of 27°S; most populations of the *M. humilis* complex are restricted to the coast by that point. Occasionally, *M. humilis* is found in dry ravines in the far north where moisture probably is available from mountain runoff or fossil water deposits.

Ricardi (1967), who last revised the family, was the first to treat the *Malesherbia humilis* complex in its entirety and to attempt to clarify the differences among taxa. He expanded the concept of the first species described in the group, *M. humilis*, to encompass two other species as varieties [*M. humilis* Poepp. var. *parviflora* (Phil.) Ric. and *M. humilis* Poepp. var. *propinqua* (Gay) Ric.]. Ricardi's three varieties of *M. humilis* are distributed over almost the entire range of the complex. This species is the only taxon in the complex with linear stipules. The type variety, found in the southern part of the range from Santiago to Huasco, has floral tubes 4.3–7.0 mm in length. *Malesherbia humilis* var. *propinqua*, in contrast, is endemic to the Elqui Valley (30°S) and the surrounding area in Region IV and is distinguished by its 8–11 mm long floral tube. *Malesherbia humilis* var. *parviflora*, having minute, sometimes obsolete, stipules and small floral tubes (2.5–3.5 mm), is found along the coast and in the pre-Andean foothills of Regions II and III; its distribution overlaps that of *M. humilis* var. *humilis* in the Huasco region.

The distribution of a second species, *Malesherbia multiflora*, largely overlaps that of *M. humilis* var. *parviflora*. Ricardi (1967) considered *M. multiflora* to be a pre-Andean species and *M. humilis* var. *parviflora* a coastal species. *Malesherbia multiflora* is distinguished from *M. humilis* var. *parviflora* by the presence of a mucron on the capsule and the absence of stipules.

The remaining two taxa are restricted in distribution. *Malesherbia taltalina*, endemic to the dry ravines around the coastal town of Taltal (25°26'S), is distinguished by its tiny flowers, which have orbicular petals that are much smaller than the sepals. The petals have a single glandular hair at the tip. This species lacks stipules, like *M. multiflora*, and has a dense, corymbiform inflorescence. The last species, *M. gabrielae*, is in many ways at the other extreme of the complex's morphological spectrum from *M. taltalina*. It is distributed in the Elqui Valley, like *M. humilis* var. *propinqua*. The flowers of this species, which is currently only known from the type, are the largest in the complex (floral tubes can be 12 mm long), and the stipules are bifid.

Although the descriptions of the taxa and the key in Ricardi's (1967) treatment should allow their separation based upon stipule and floral features, in practice this is often not the case. *Malesherbia humilis* var. *propinqua*

and *M. gabriellae* are almost indistinguishable, as are *M. multiflora* and *M. humilis* var. *parviflora*. *Malesherbia humilis* var. *humilis* grades into *M. humilis* var. *propinqua* at one extreme of its morphological variation and into *M. multiflora* and *M. humilis* var. *parviflora* at the other extreme. Because there seems to be a gradation of traits from *M. taltalina* through *M. multiflora* and into *M. humilis* var. *humilis*, which in turn appears to intergrade with *M. humilis* var. *propinqua* and *M. gabriellae*, the taxonomic status of these species and varieties is questionable.

A detailed analysis of the group is necessary to determine whether the *Malesherbia humilis* complex is best treated taxonomically as a large, polymorphic species or rather as a series of very similar yet distinguishable taxa. If more than one taxon can be recognized, it would be further necessary to determine which morphological characters should be utilized in the construction of a key to allow identification of individuals in the field and herbarium. Therefore, a phenetic study of morphological data was conducted to determine if Ricardi's (1967) revision accurately reflects the distribution of morphological characters in these plants.

MATERIALS AND METHODS

In total, 113 operational taxonomic units (OTUs) were examined for this study (Table 1). Multiple herbarium sheets from a single collection were grouped into a single OTU; 16 such OTUs were used. Of the 97 collections for which only one sheet was available, 69 consisted of more than one individual plant. One collection was split into two separate OTUs because initial examination suggested two separate collections may be mounted on three sheets labeled as one (*Johnston 4746*; F, US, GH). Each OTU was tentatively assigned to a taxon based on Ricardi's (1967) descriptions and key (Table 1). The character states of both quantitative and qualitative floral characters were recorded (Table 2); only qualitative vegetative characters were used, because sufficient leaf material for measurements was not available on many OTUs and because it was not possible in most cases to use comparable leaves. The characters were chosen based on differences among taxa noted by Ricardi (1967) and my observations of differences among OTUs. At least five separate measurements were taken (from different plants and herbarium sheets, when possible) to determine the averages of the quantitative characters for exterior floral characters. Three flowers from different plants, when available, were dissected to measure the androgynophore length. Stipules were considered to be present if even one was found on one of the plants comprising an OTU.

NTSYSpc version 2.0 (Rohlf, 1998) was used to analyze the resulting data matrix. The characters were standardized, then used to compute Manhattan distances, average taxonomic distances, and Euclidian distances among OTUs. Phenograms were constructed using the unweighted pair-group method with arithmetic averages (UPGMA). To test for consistency between the resulting phenogram and the original data, cophenetic correlation coefficients were calculated for each phenogram-data matrix pair. The phenogram with the highest cophenetic correlation coefficient is reported here. Large clusters were then isolated from the data set and analyzed separately to eliminate any influence OTUs outside the cluster may have on intracluster structuring (Whitkus & Packer, 1984).

A principal components analysis was also performed. The standardized data were used to compute a character-by-character correlation matrix, from which the eigenvectors were extracted. OTUs were plotted in the three-dimensional space defined by the first three eigenvectors.

Discriminant analyses were performed on the quantitative characters using SAS Release 6.12 (SAS Institute, Cary, North Carolina) to determine which characters, if any, are most useful in distinguishing among the clusters of OTUs found in cluster analysis. The PROC DISCRIM command (SAS, 1989) was employed in this analysis. The OTUs were assigned to a group for this procedure based on their position in the cluster analysis using average taxonomic distances.

RESULTS

Initial herbarium studies carried out prior to numerical analysis led to tentative identifications of the 113 OTUs in the study. It was most difficult to distinguish *Malesherbia multiflora* from *M. humilis* var. *parviflora*, *M. humilis* var. *propinqua* from *M. gabriellae*, and *M. humilis* var. *humilis* from *M. humilis* var. *propinqua*. Morphological variation, especially in flower sizes, was essentially continuous from *M. gabriellae*, with its relatively few, large flowers, through *M. humilis* var. *propinqua*, *M. humilis* var. *humilis*, *M. humilis* var. *parviflora*, *M. multiflora*, and *M. taltalina*, which has multitudes of extremely small flowers.

Average taxonomic distances yielded the phenogram with the least distortion ($r_{cs} = 0.87$). There are two large and two small clusters in this tree (Fig. 2). For convenience, the clusters will be referred to by the specific epithet or varietal name of the predominant taxon, as identified before the computer analysis, composing the cluster; these names will be in quotes to prevent confusion with the proper taxonomic name. One of the large clusters,

Table 1. Populations and specimens of Malesherbiaceae from Chile used in the analyses. Roman numbers refer to political regions (see. Fig. 1). Tentative identifications were made prior to analysis. G = *M. gabriellae*, H = *M. humilis* var. *humilis*, M = *M. multiflora*, Q = *M. humilis* var. *propinqua*, T = *M. humilis* var. *taltalina*, U = undetermined, V = *M. humilis* var. *parviflora*. Abbreviations for cluster membership: g = “*gabriellae*”, h = “*humilis*”, q = “*propinqua*”, t = “*taltalina*”, v = “*parviflora*”. Geographical abbreviations: Prov. = province, Qda. = quebrada (dry ravine).

Tentative identification	Cluster membership	Collection information, collector, and herbaria
G	g	Region IV, Prov. Elqui: Rivadavia, Sep 1980, <i>Montero 11686</i> (OS)
G	q	IV, Prov. Elqui: Qda. San Carlos, Nov 1978, <i>Puin s.n.</i> (ULS)
G	g	IV, Prov. Elqui: camino de Vicuña a Guanta, Oct 1964, <i>Ricardi, Marticorena & Matthei 1126</i> (CONC type)
Q/P	h	IV, Prov. Elqui: Paihuano, Oct 1937, <i>Gajardo s.n.</i> (CONC)
Q	g	IV, Prov. Elqui: Qda. Huanta, Nov 1991, <i>Arancio 91764</i> (ULS)
Q	q	IV, Prov. Elqui: Elqui Valley, cerca de Vicuña, Oct 1965, <i>Behn 1310</i> (CONC)
Q	q	IV, Prov. Elqui: Coquimbo-Cordillera de Paihuano, Dec 1942, <i>Gajardo s.n.</i> (CONC)
Q	q	Unknown, <i>Gay 345</i> (F)
Q	g	IV, Prov. Elqui: Cordillera de Guanta, Nov, <i>Gay s.n.</i> (GH)
Q	q	IV, Prov. Elqui: Cordillera de La Serena, Condoriaco, Nov 1967, <i>Jiles 5149</i> (OS)
Q	g	IV, Prov. Elqui: Estero de Guanta, Jan 1926, <i>Johnston 6235</i> (GH)
Q	g	V, Prov. Elqui: Hacienda Campana, Qda. de la Despensa, Oct 1940, <i>Looser 4287</i> (GH)
Q	q	IV, Prov. Elqui: Los Chiches, 3 km W of Vicuña along the road to La Serena, Oct 1939, <i>Wagenknecht 18447</i> (F, GH, MO, UC)
Q	q	IV, Prov. Elqui: road Vicuña to La Serena, ca. 5 km out of Vicuña, Nov 1938, <i>Worth & Morrison 16354</i> (GH, MO, UC)
Q/H	q	IV, Prov. Limarí: El Altar, Dec 1965, <i>Jiles 4748a</i> (OS)
H	h	IV, Prov. Limarí: Ovalle, Oct 1940, <i>Barros 5524</i> (US)
H	h	IV, Prov. Choapa: E of Illapel, Sep 1944, <i>Barros 3778</i> (GH)
H	h	IV, Prov. Elqui: Andacollo, Feb 1930, <i>Claude-Joseph 5420</i> (US)
H	h	Region Metropolitana: Santiago, Nov 1918, <i>Claude-Joseph 722</i> (US)
H	h	Unknown, <i>Philippi s.n.</i> (US)
H	h	IV, Prov. Choapa: Tilama, Feb 1930, <i>Fraga 1332</i> (GH)
H	h	Unknown, 1876, <i>Gay</i> or <i>Hennegart</i> (NY)
H	h	IV, Prov. Limarí: Hacienda Tamaya, Oct 1956, <i>Jiles 3050</i> (OS)
H	h	IV, Prov. Limarí: Cordillera de Ovalle, Río Palomo, Oct 1957, <i>Jiles 3267</i> (OS)
H	h	IV, Prov. Limarí: Cordillera de Ovalle, los Molles, Jan 1966, <i>Jiles 4771</i> (OS)
H	h	IV, Prov. Limarí: Cord. de Combarbala, las Lajas, Oct 1971, <i>Jiles 5675</i> (OS)
H	q	IV, Prov. Elqui: Vicuña, Cuesta del Churqui, Oct 1940, <i>Looser 4244</i> (GH)
H	h	IV, Prov. Elqui: Hacienda Campana, Qda. de la Despensa, Oct 1940, <i>Looser 4288</i> (GH)
H	h	Región Metropolitana: Qda. de Ramón, Oct 1948, <i>Looser 5555</i> (GH)
H	h	III, Prov. Huasco: Qda. El Morado, Oct 1971, <i>Marticorena, Rodriguez & Weldt 1776</i> (F)
H	h	III, Prov. Huasco: Chañaral de Aceituna, Oct 1971, <i>Marticorena, Rodriguez & Weldt 1830</i> (F)
H	h	IV, Prov. Elqui: Coquimbo, Sep 1934, <i>Montero 1839</i> (GH)
H	h	Región Metropolitana, <i>Philippi s.n.</i> (F)
H	h	Región V: between Puente de Las Vizcachas & Río Colorado, Dec, <i>Poeppig 134</i> (F, MO)
H	h	III, Prov. Huasco: Incahuasi, 12 km al S, Oct 1958, <i>Ricardi & Marticorena 4904/1289</i> (OS)
H	h	IV Prov. Choapa: Choapa, Oct 1914, <i>Rose & Rose 19216</i> (NY)
H	h	IV, Prov. Limarí: Fray Jorge, Aug 1917, <i>Skottsberg 772</i> (F, NY)
H	q	IV, Prov. Elqui: road to Condoriaco, 41.5 km NE of La Serena, Oct 1959, <i>Solbrig 3068</i> (GH)
H	h	IV, Prov. Elqui: Rte. 5 N of La Serena, ca. 1 km N of entrance to the El Tofo mine, Oct 1991, <i>Taylor, Bohlen & Marticorena 10672</i> (MO)
H	h	IV, Prov. Elqui: Cuesta El Almendro, 14 km on road Vicuña to Hurtado, Nov 1939, <i>Wagenknecht 18480</i> (F, GH, MO, UC)
H	h	IV, Prov. Elqui: Coquimbo, Nov 1923, <i>Werdermann 119</i> (F, GH, MO, UC)

Table 1 (continued).

Tentative identification	Cluster membership	Collection information, collector, and herbaria
H	h	IV, Prov. Elqui: Coquimbo, <i>unknown collector</i> (US 1360025)
M/H	h	IV, Prov. Limari: Fray Jorge, Oct 1991, <i>Billiet & Jadin 5289</i> (MO)
M/H	h	IV, Prov. Elqui: 30 km S of Totalillo, & 58 km S of La Serena, Nov 1987, <i>Dillon & Teillier 4981</i> (OS)
M/H	h	IV, Prov. Limari: Corral Quemado, Oct 1990, <i>Lammers, Baeza & Peñaillo 7587</i> (F)
M/H	h	III, Prov. Elqui: Guanaqueros, Sep 1975, <i>Zöllner 8270</i> (MO)
M/V	v	II, Prov. Antofagasta: Taltal, Sep 1940, <i>Barros 5538</i> (UC)
M/V	v	II, Prov. Antofagasta: Paposo, Nov 1991, <i>Billiet & Jadin 5496</i> (MO)
M/V	v	II, Prov. Antofagasta: Qda. Paposo, ca. 5–12 km E of Caleta Paposo, Sep 1988, <i>Dillon, Dillon & Poblete 5557</i> (F)
M/V	v	II, Prov. Antofagasta: Qda. Paposo, ca. 12 km E of Caleta Paposo, Dec 1987, <i>Dillon & Teillier 5122</i> (OS)
M/V	v	II, Prov. Antofagasta: Qda. Anchuñas, Nov 1995, <i>Gengler 106</i> (OS)
M/V	v	I, Prov. Iquique: Qda. Guatacondo Apr 1997, <i>Gengler 190</i> (OS)
M/V	v	II, Prov. Antofagasta: Qda. Ramón, al norte de Taltal, Dec 1988, <i>Hoffmann 212</i> (CONC)
M/V	v	II, Prov. Antofagasta: base of hills just SE of Qda. La Chimba, Oct 1925, <i>Johnston 3627</i> (US)
M/V	v	III, Prov. Copiapó: about 8 km E of Cerrillos, Nov 1925, <i>Johnston 4962</i> (GH)
M/V	v	II, Prov. Antofagasta: Taltal, Nov 1925, <i>Johnston 5096</i> (GH)
M/V	h	III, Prov. Huasco: Huasco, Cerro Colorado, Sep 1950, <i>Martcorena s.n.</i> (CONC)
M/V	v	IV, Prov. Elqui: Cuesta Pajonales, Jan 1973, <i>Martcorena, Matthei & Quezada 469</i> (OS)
M/V	v	II, Prov. Huasco: lomas lado sur, Sep 1978, <i>Montero 11020</i> (OS)
M/V	v	II, Prov. Antofagasta: Qda. La Chimba, Sep 1991, <i>Quezada & Ruiz 88</i> (CONC)
M/V	v	II, Prov. Antofagasta: Qda. Caleta del Cobre, Oct 1991, <i>Quezada & Ruiz 130</i> (CONC)
M/V	v	III, Prov. Copiapó: camino de Copiapó a Vallenar, km 70, Sep 1952, <i>Ricardi 2268</i> (OS)
M/V	v	III, Prov. Huasco: Agua Amarga, Oct 1952, <i>Ricardi 2316</i> (OS)
M/V	v	II, Prov. Antofagasta: Qda. Paposo, Mina Abundancia, La Posada, Sep 1953, <i>Ricardi 2633</i> (OS)
M/V	v	III, Prov. Huasco: Estancia Manflas, Nov 1956, <i>Ricardi & Martcorena 3740</i> (CONC)
		II, Prov. Antofagasta: between Taltal and Paposo, Oct 1991, <i>Taylor, Bohlen & Martcorena 10759</i> (MO)
M/V	v	II, Prov. Antofagasta: Taltal, Oct 1925, <i>Werdermann 778</i> (F, GH, MO, NY, UC, US)
M/V	v	II, Prov. Antofagasta: ca. 10 km E of Taltal, Qda. Taltal, Oct 1938, <i>Worth & Morrison 15797</i> (UC)
V	v	III, Prov. Huasco: Canto del Agua, camino a Carrizal Bajo, Oct 1965, <i>Garaventa 4737</i> (CONC)
V	v	II, Prov. Tocopilla: Tocopilla, Oct 1930, <i>Jaffuel 1058</i> (GH)
V	v	II, Prov. Antofagasta: Qda. Taltal, Nov 1925, <i>Johnston 5095</i> (GH)
V	v	Desert Atacama, Sep–Oct 1890, <i>Morong 1288</i> (MO, NY, US, GH, US)
V	v	III, Prov. Copiapó: camino entre Caldera y Chañaral, Caleta Obispito, Oct 1965, <i>Ricardi, Martcorena & Matthei 1313</i> (OS)
M	v	II, Prov. Antofagasta: Qda. del Gritón, W side of Cerro San Pedro, ca. 15 km SSW of Taltal, Oct 1988, <i>Dillon & Dillon 5686</i> (OS)
M	v	III, Prov. Huasco: 39 km S of Vallenar & 7 km N of Domeyko, Dec 1987, <i>Dillon & Teillier 5023</i> (OS)
M	v	II, Prov. Antofagasta: Miguel Diaz, directly N of Qda. Iscuña, Dec 1987, <i>Dillon & Teillier 5298</i> (F)
M	v	II, Prov. Antofagasta: Qda. de la Chimba, ca. 10 km NNE of Antofagasta, Dec 1987, <i>Dillon & Teillier 5324</i> (F)
M	v	III, Prov. Copiapó: cerros de Chanchoquin, Nov 1886, <i>Gigoux s.n.</i> (GH)
M	v	III, Prov. Copiapó: Potrerillos, Apr 1933, <i>Greninger 26</i> (GH)
M	v	III, Prov. Copiapó: Potrerillos, Oct 1925, <i>Johnston 3693</i> (F, GH)
M	v	III, Prov. Copiapó: Potrerillos, Oct 1925, <i>Johnston 4746</i> (F, GH, US)
M	v	III, Prov. Copiapó: hills back of El Barquito, Oct 1925, <i>Johnston 4759</i> (GH)
M	v	III, Prov. Copiapó: N of Copiapó, Nov 1925, <i>Johnston 5012</i> (GH)
M/H	h	IV, Prov. Elqui: La Rinconada, Coquimbo, Sep 1952, <i>Barros 10127</i> (CONC)
M	v	IV, Prov. Elqui: Cuesta de Pajonales, Jan 1973, <i>Martcorena, Mattei, & Quezada 466</i> (OS)
M	v	III, Prov. Copiapó: road to Tinogasta from Copiapó, ca. 55 kms E of Copiapó, Feb 1988, <i>Martcorena, Stuessy & Baeza 9813</i> (OS)

Table 1. (continued).

Tentative identification	Cluster membership	Collection information, collector, and herbaria
M	v	III, Prov. Chañaral: El Salvador, Feb 1988, <i>Martcorena, Stuessy & Baeza 9883</i> (OS)
M	v	III, Prov. Chañaral: 42.2 km W Diego de Almagro, Feb 1988, <i>Martcorena, Stuessy & Baeza 9892</i> (OS)
M	v	II, Prov. Antofagasta: Qda. Taltal, Jan 1939, <i>Morrison 17091</i> (GH, UC)
M	v	III, Prov. Copiapó: Copiapó, Oct 1991, <i>Muñoz, Teillier & Meza 2698</i> (SGO)
M	v	III, Prov. Copiapó: 1er km camino desde Copiapó a Inca de Oro, Oct 1991, <i>Muñoz, Teillier & Meza 2699</i> (MO, OS)
M	v	II, Prov. Antofagasta: bare rocky canyon, Apr 1925, <i>Pennell 13033</i> (F, GH, NY, US)
M	v	II, Prov. Antofagasta: parte superior Qda. camino Antofagasta-Calama, Feb 1968, <i>Ricardi 5503</i> (F)
M	v	III, Prov. Copiapó: Qda. al occidente de Las Bombas, Feb 1968, <i>Ricardi 5530</i> (F)
M	v	III, Prov. Huasco: Qda. Carrizal Bajo, Sep 1957, <i>Ricardi & Martcorena 4422/807</i> (OS)
M	v	III, Prov. Copiapó: camino al Salar de Maricunga, cerca de Puquios, Jan 1963, <i>Ricardi, Martcorena & Matthei 518</i> (OS)
M	v	III, Prov. Copiapó: camino al Salar de Maricunga, cerca de Puquios, Jan 1963, <i>Ricardi, Martcorena & Matthei 520</i> (OS)
M	v	III, Prov. Copiapó: camino entre Vallenar y Copiapó, Feb 1963, <i>Ricardi, Martcorena & Matthei 664</i> (OS)
M	v	III, Prov. Huasco: 30 km S of Vallenar, Oct 1965, <i>Ricardi, Martcorena & Matthei 1245</i> (OS)
M	v	III, Prov. Copiapó: 6 km al N de Paipote, Oct 1965, <i>Ricardi, Martcorena & Matthei 1461</i> (OS)
M	v	III, Prov. Copiapó: camino Internacional a Tinogasta, 2 km antes de Puquios, Feb 1966, <i>Ricardi, Martcorena & Matthei 1641</i> (OS)
M	v	III, Prov. Huasco: cerca de Estación Romero, Feb 1966, <i>Ricardi, Martcorena & Matthei 1689</i> (F, CONC type)
M	v	III, Prov. Huasco: 20 km north of Vallenar, Feb 1985, <i>Rosas 398</i> (OS)
M	v	II, Prov. Tocopilla: Tocopilla, Qda. Mamilla, Oct 1985, <i>Schlegel 7706</i> (CONC)
M	v	III, Prov. Copiapó: Rte 1 N of Caldera ca. 10 km, Oct 1991, <i>Taylor, von Bohlen & Martcorena 10699</i> (MO)
M	v	III, Prov. Huasco: 10 km E de Huasco, Oct 1987, <i>Teillier 932</i> (NY)
M	v	III, Prov. Copiapó: Caldera, Oct 1924, <i>Werdermann 1523</i> (NY)
M	v	III, Prov. Huasco: 60 km E of Vallenar, road to San Felix, Oct 1938, <i>Worth & Morrison 16210</i> (UC, GH)
M	v	II, Prov. Antofagasta: near Paposos, Dec 1987, <i>Zöllner 14760</i> (MO)
T	t	II, Prov. Antofagasta: Taltal, Qda. Anchuña, Sep 1953, <i>Ricardi 2530</i> (CONC type)
T	t	II, Prov. Antofagasta: hills S of Taltal, Feb 1939, <i>Beetle 26176</i> (GH, MO, UC)
U	h	IV, Prov. Elqui: Elqui Valley, Balala, Oct 1948, <i>Behn s.n.</i> (CONC)

cluster A (“*humilis*”), is composed largely of those OTUs identified as *Malesherbia humilis* var. *humilis* and a few others identified as *M. humilis* var. *propinqua* or whose identity was unclear. A subcluster B (“*propinqua*”) within this “*humilis*” cluster contains seven *M. humilis* var. *propinqua* OTUs, two *M. humilis* var. *humilis* OTUs, and one *M. gabriellae* OTU. In separate analysis of cluster A, subcluster B again appears; this separate analysis will not be further considered. “*Humilis*” will from this point forward refer to cluster A, with the exception of the “*propinqua*” OTUs.

The other large cluster, C (“*parviflora*”), contains those OTUs tentatively identified as *Malesherbia multiflora* and *M. humilis* var. *parviflora*, including the type specimen of *M. multiflora*. The small subclusters within

this larger cluster correspond neither to a taxon nor to a geographical region. Although many *M. multiflora* OTUs clustered together, others are mixed with OTUs which usually could not be assigned to either taxon with certainty. Separate cluster analysis of cluster C failed to show groupings corresponding to the two taxa as well.

Cluster D (“*gabriellae*”) contains only OTUs initially identified as *Malesherbia gabriellae*, including the type, or *M. humilis* var. *propinqua*. The final cluster, E (“*taltalina*”), contains only two OTUs, both identified as *M. taltalina*. One of these OTUs is the type for that species. No other OTUs were tentatively identified as *M. taltalina*.

In ordination, the first principal component accounts for 40.97% of the total variation with petal length, floral

Table 2. Characters and states used in the phenetic analyses of *Malesherbia*.

1.	Lower leaf (0 = leaves green, unwithered; 1 = leaves brown, withered)
2.	Pedicle length (mm)
3.	Leaf stipules (0 = absent; 1 = present)
4.	Bract stipules (0 = absent; 1 = present)
5.	Inflorescence (0 = loose panicle; 1 = corymbose panicle)
6.	Floral tube length (mm)
7.	Floral tube length / width ratio
8.	Floral tube shape when pressed (0 = wineglass-shaped; 1 = funnel-shaped)
9.	Sepal length (mm)
10.	Sepal veins (0 = not anastomose; 1 = anastomose)
11.	Adaxial face of sepals (0 = glabrous; 1 = pubescent with scattered hairs)
12.	Petal length (mm)
13.	Petal apex vestiture (0 = lacking a glandular hair at apex; 1 = having a glandular hair at apex)
14.	Androgynophore length (mm)
15.	Androgynophore vestiture (0 = glabrous; 1 = pilose)
16.	Capsule tip (0 = amucronate; 1 = mucronate)

tube shape, and sepal length having the highest loadings (Table 3). The second principal component explained 16.23% of the total variation. The presence or absence of anastomosing sepal veins, floral tube length, and androgynophore length had the highest loadings. Only 8.17% of the total variation was accounted for by the third principal component; sepal pubescence and petal apex vestiture were the only two characters with correlations greater than 0.5.

Ordination (Fig. 3) allows the recognition of two or possibly three groups corresponding closely to those in the cluster analysis. The cluster “*taltalina*” is differentiated from “*parviflora*” only by the third principal component. The “*parviflora*” + “*taltalina*” cluster is separated from the remaining OTUs, which fall into a loose group. The “*humilis*” OTUs lie between the “*parviflora*” + “*taltalina*” cluster and those OTUs assigned by cluster analysis to “*propinqua*” and “*gabrielae*”. “*Propinqua*” and “*gabrielae*” are only very weakly separated from each other. “*Propinqua*” and “*humilis*” are also difficult to separate.

Discriminant analyses were performed to determine if any of the characters used in this study define the clusters found in the cluster analysis. The five clusters from the cluster analysis, “*parviflora*”, “*humilis*”, “*propinqua*”, “*taltalina*”, and “*gabrielae*” were used to group the OTUs. Only two of the clusters had diagnostic characters. “*Taltalina*” could be accurately distinguished by the presence of an apical, glandular petal hair. “*Gabrielae*”

was distinguished by its pilose androgynophore. “*Propinqua*” + “*gabrielae*” could be identified by their large funnelform floral tubes, which were longer than 7 mm.

With the exception of the shape of the pressed floral tube, there was considerable overlap in the character states of “*parviflora*” and “*humilis*”. The shape of the floral tube did separate the two, although there was a single anomalous “*parviflora*” OTU with funnelform tubes like those of “*humilis*”.

DISCUSSION

The results of ordination and cluster analysis are

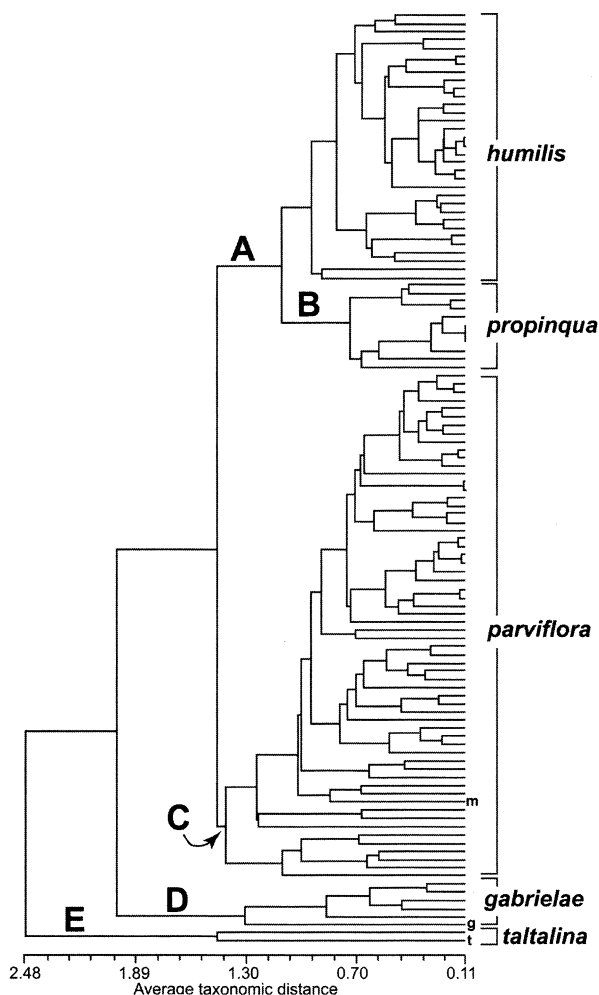


Fig. 2. UPGMA phenogram using average taxonomic distances. “*Humilis*” contains 33 OTUs, “*propinqua*” 10, “*parviflora*” 62, “*gabrielae*” 6, and “*taltalina*” 2. The capital letters mark clusters discussed in the text. Types are marked by lower-case letters: g = *M. gabrielae*, m = *M. multiflora*, and t = *M. taltalina*.

Table 3. Eigenvector coefficients for Principal Components Analysis of the *Malesherbia humilis* complex. Character loading values are for the first three Principal Component (PC) axes. The percent variation explained by each axis is also presented.

Character	PC 1 (40.97%)	PC 2 (16.23%)	PC 3 (8.17%)
Floral tube length	0.6985	0.6314	0.0849
Floral tube length/width	-0.6950	0.5114	0.0570
Sepal veins	0.3111	-0.6644	0.1791
Pedicel length	-0.1346	0.3704	0.3159
Leaf stipule	0.6938	-0.2949	0.1460
Bract stipule	0.8620	-0.2426	0.0152
Capsular mucron	-0.7632	0.3244	-0.2602
Floral tube shape	0.8824	-0.3466	-0.0190
Sepal length	0.8823	0.3649	0.0251
Sepal vestiture	-0.2138	-0.0344	0.7283
Petal length	0.8976	0.3537	-0.0396
Petal apex vestiture	-0.1977	-0.0765	0.6514
Androgynophore length	0.6233	0.6258	-0.0330
Androgynophore vestiture	0.5285	0.5118	0.1761
Inflorescence type	-0.5068	0.2246	0.2830
Lower leaf state	-0.5396	0.1307	-0.0735

largely consistent with Ricardi's (1967) concept of the morphological divisions in the *Malesherbia humilis* complex, although his concepts of some taxonomic boundaries require revision. Clusters roughly correspon-

ding to all four of his species were found. Ricardi's broad concept of *M. humilis*, however, is inconsistent with these results. *Malesherbia humilis* var. *parviflora* and *M. multiflora* are indistinguishable from each other and

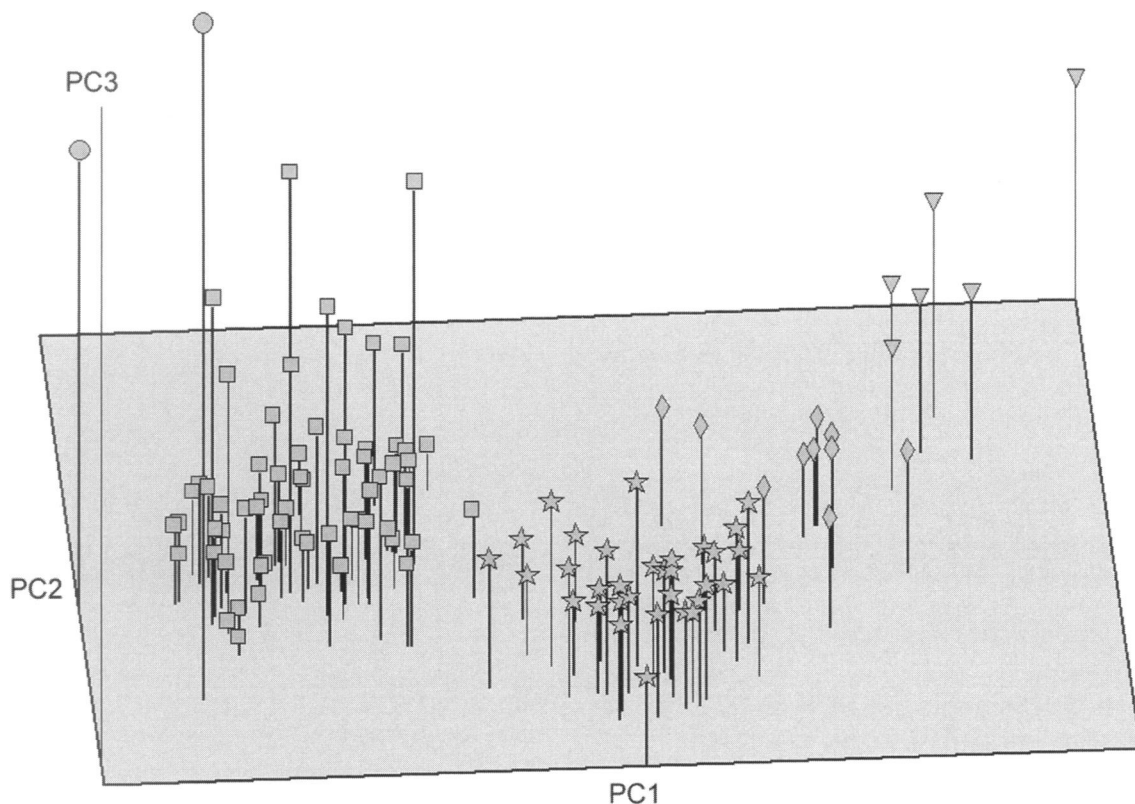


Fig. 3. Results of the principal components analysis. Triangle = "*gabriellae*", star = "*humilis*", square = "*parviflora*", diamond = "*propinqua*", circle = "*taltalina*".

together they are distinct from *M. humilis* var. *humilis*.

Ricardi (1967) based his distinction between *Malesherbia humilis* var. *parviflora* and *M. multiflora* largely upon *M. multiflora* lacking stipules and having a mucron on the capsule. According to Ricardi (1967), *M. humilis* var. *parviflora* has stipules and lacks the capsular mucron. In the preliminary herbarium studies, however, most stipulate “*parviflora*” OTUs were also found to have a mucron, and one OTU lacking stipules also lacked a capsular mucron. Moreover, OTUs with capsules lacking the mucron fail to cluster together in both the full cluster analysis and the separate analysis of the “*parviflora*” cluster. The presence or absence of an apical mucron is therefore an unreliable taxonomic character.

In the full cluster analysis (Fig. 2), there is also no cohesive pattern for the absence or presence of leaf stipules (as opposed to stipules found on the bracts) in “*parviflora*”. OTUs with leaf stipules are present in three subclusters also containing exstipulate OTUs, indicating that stipule presence is not as important as other characters that link stipulate OTUs to those lacking stipules. In separate analysis of the “*parviflora*” cluster, several subclusters of OTUs with leaf stipules form, but these subclusters again are not closely associated with each other and also usually contain exstipulate OTUs. Ordination fails to show a grouping containing all stipulate OTUs, although they tend to lie nearer to those OTUs in the “*humilis*” group (Fig. 3).

OTUs in the “*parviflora*” cluster—with or without stipules or a capsular mucron—tend to have floral tubes that do not flare open at the throat in a funnellform fashion (wineglass-shaped), withered lower leaves, corymbose panicles, no bract stipules, and a trend toward smaller floral parts than members of “*humilis*,” “*propinqua*,” or “*gabrielae*”.

In addition to sharing these morphological traits, *Malesherbia multiflora* and *M. humilis* var. *parviflora* also share geographic distributions. Ricardi (1967) described the distribution of *M. humilis* var. *parviflora* as coastal, with some populations approaching the interior, whereas *M. multiflora* was described as a native of the pre-Andes and upper reaches of the coastal desert. However, OTUs originally identified as *M. multiflora* (as well as those listed in Ricardi’s revision as *M. multiflora*) were often collected near the coast. Additionally, a number of OTUs of *M. humilis* var. *parviflora* are from the interior desert and higher elevations. Coastal OTUs may be stipulate or exstipulate, further evidence that the presence or absence of leaf stipules is not a taxonomically useful character in this cluster.

Their overlapping distributions and morphological similarity indicate that there is little evidence supporting the continued recognition of *Malesherbia multiflora* as

separate from *M. humilis* var. *parviflora*. *Malesherbia humilis* var. *parviflora* has nomenclatural priority, leaving *M. multiflora* as a synonym.

“*Taltalina*”, which is endemic to the ravines and hills around Taltal (25°26’S), is very similar to *Malesherbia humilis* var. *parviflora*. Its distribution falls within that of “*parviflora*,” which is also found in Taltal’s ravines. “*Taltalina*” forms its own cluster in the phenogram (Fig. 2), but it is only marginally distinct from “*parviflora*” in the ordination. According to Ricardi (1967), *M. taltalina* is distinguished by its obconical floral tube, orbicular and small petals with an apical glandular hair, violet flowers, and anastomosing sepal veins. “*Taltalina*” is not as clearly separated from “*parviflora*” as Ricardi suggests. Although “*taltalina*” does differ from “*parviflora*” by the presence of an apical glandular petal hair, the two groups have similar floral tube shapes. Violet flowers and anastomosing sepal veins are also found among members of “*parviflora*”. The type OTU of *M. taltalina* does have some flowers with orbicular petals, but other flowers have much narrower petals like those of the second OTU identified as “*taltalina*” and those of “*parviflora*”. In general, the petal length to sepal length ratio of “*taltalina*” is smaller than that of members of “*parviflora*”, although one “*parviflora*” OTU does have a smaller ratio than both “*taltalina*” OTUs. Because this tendency toward small petals and the presence of the apical glandular petal hair do permit recognition of the cluster, it should continue to be seen as a distinct taxon.

The second major group in the *Malesherbia humilis* complex is the “*humilis*” cluster (Figs. 2 & 3). Ordination indicates that “*humilis*” is the core of the entire complex. It is morphologically intermediate to “*parviflora*” and “*propinqua*,” which were both considered to be varieties of *M. humilis* in Ricardi’s (1967) work. “*Humilis*” is distinct from “*parviflora*” in ordination, but it is only weakly separated from “*propinqua*”.

Morphologically, “*parviflora*” is best distinguished from “*humilis*” by the shape of the flattened floral tube. The floral tubes of “*parviflora*” are, with the exception of one OTU, “wineglass-shaped” (i.e., the floral tube expands to accommodate the ovary after hugging the androgynophore, but does not flare wider than the ovary’s width at the throat). In “*humilis*”, on the other hand, the floral tubes are always funnellform (the throat of the floral tube flares wider than the width of the ovary). Although it was not available for the statistical analysis, examination of the type specimen of *Malesherbia humilis* var. *parviflora* at SGO showed that it, too, has the wineglass-shaped floral tube characteristic of “*parviflora*”. The single OTU clustering with “*parviflora*”, despite its funnellform floral tube was collected well north of the Huasco area (28°30’S), where the two clusters, as well as other elements of the northern

and southern coastal desert floras, overlap in distribution (Gajardo, 1993). The appearance of funnelform flowers in a “*parviflora*” OTU may be indicative of introgression or an ancestral polymorphism.

No other character used in this study separates “*humilis*” and “*parviflora*” as well as the floral tube shape. There are, however, some general trends. Members of “*parviflora*” tend to have smaller petals, sepals, and floral tubes, although there is extensive overlap with “*humilis*” in these features. When the floral tube length to width ratio is used in conjunction with locality data, the OTUs studied here can be separated. OTUs collected north of the coastal Huasco region or in the pre-Andean Huasco region belong to either “*parviflora*” or “*taltalina*”, whereas those collected south of that region are “*humilis*”, “*propinqua*”, or “*gabrielae*”. In the coastal Huasco region, all of the OTUs of “*parviflora*” used in this study have floral tube length to width ratios greater than 2.0, whereas those of “*humilis*” have ratios less than 1.6.

Further studies of “*humilis*” and “*parviflora*” should include more extensive field observations and sampling, especially where the two overlap in the region just southwest of Huasco. Available data are inadequate to address possible interbreeding, ecological differentiation, and population structure in this region. These data are critical to understand the relationship between these similar varieties. Although the relationship between the two taxa is not well understood, the morphological data do support the recognition of two taxa.

“*Parviflora*” and “*humilis*” are difficult to distinguish when dealing with small-proportioned specimens of the latter group. When individuals of “*humilis*” have larger flowers, they become difficult to distinguish from members of “*propinqua*”. Recognition of “*propinqua*” taxonomically was supported by cluster analysis, in which “*propinqua*” clustered with “*humilis*” at a high average taxonomic distance (approximately 1.06; Fig. 2). Ordination (Fig. 3) reaffirmed the affinities between the two clusters, but it also revealed the morphological similarity of “*propinqua*” and “*gabrielae*”, the two clusters with the largest flowers in the complex. The close relationship between “*gabrielae*” and “*propinqua*” may have been lost in the cluster analysis because this method of analysis can distort relationships among clusters (Sneath & Sokal, 1973).

“*Propinqua*” and “*gabrielae*” have floral tubes 7 mm long or more. In “*humilis*”, floral tubes are almost always less than 7 mm in length, although some individual plants may have a few flowers with floral tube lengths slightly exceeding 7 mm. These individuals, however, are few, and the vast majority of flowers on each plant have floral tubes under 7 mm long. Many of the OTUs assigned to “*propinqua*” or “*gabrielae*” also have bifid or

lobed leaf stipules. In contrast, all OTUs of “*humilis*” have linear, unlobed stipules.

“*Gabrielae*” is perfectly distinguished from “*propinqua*” by an unusual trait in the *Malesherbia humilis* complex, its pilose androgynophore. The presence of a diagnostic character and the distinctiveness of “*gabrielae*” in ordination and the cluster analysis support the recognition of that cluster taxonomically. “*Propinqua*” should also continue to be recognized because it is distinguishable from “*humilis*” by its longer floral tubes and often bifid stipules, and its glabrous androgynophore distinguishes it from “*gabrielae*”.

“*Gabrielae*”, “*propinqua*”, and “*humilis*” have more or less separate distributions. Although a few collections of “*humilis*” were made in the Elqui Valley (30°S), the majority were found closer to the coast and around the cities La Serena (29°54'S) and Ovalle, which have coastal and interior matorral steppe vegetation types, respectively (Gajardo, 1993). In contrast, “*gabrielae*” is endemic to the eastern Elqui Valley and the eastern tributaries of the Río Elqui, where the vegetation borders on shrubby pre-Andean steppe (Gajardo, 1993). Most “*propinqua*” OTUs were collected in the Elqui Valley, although a few were found 40–50 km to the north of the valley and to the south of the valley near Ovalle. It is associated with montane flowering desert and interior matorral steppe (Gajardo, 1993).

Within the Elqui Valley and its eastern tributaries, the locality data for “*propinqua*” and “*gabrielae*” indicate that the two have adjacent, yet separate, distributions. OTUs of “*gabrielae*” were all collected east of Diaguitas (65 km from the ocean), whereas those of “*propinqua*” were collected further to the west, south, or north. This distributional difference roughly corresponds to changes in vegetation type from the flowering desert of the hills to the shrubby pre-Andean steppe (Gajardo, 1993). “*Humilis*” has been collected in both eastern and southern areas of the valley.

Because the differences among the five clusters that are to be recognized taxonomically are minor, they are best treated as five varieties of a single species, *Malesherbia humilis*. Two new combinations are made. The varieties recognized are *M. humilis* Poepp. var. *gabrielae* (Ric.) Gengler (“*gabrielae*”), *M. humilis* Poepp. var. *humilis* (“*humilis*”), *M. humilis* Poepp. var. *parviflora* (Phil.) Ric. (“*parviflora*”), *M. humilis* Poepp. var. *propinqua* (Gay) Ric. (“*propinqua*”), and *M. humilis* Poepp. var. *taltalina* (Ric.) Gengler (“*taltalina*”).

■ BIOGEOGRAPHY OF MALESHERBIA HUMILIS COMPLEX

Hypotheses of the biogeography and evolution of the

Malesherbia humilis complex may be derived from the distributions of the five varieties and their morphological affinities. The combined distributions of *M. humilis* var. *humilis* and *M. humilis* var. *parviflora* cover almost the entire range of the complex. Judging from their broad distributions and their great morphological diversity, they are most likely the oldest varieties in the complex. These taxa co-occur only in southwestern Region III near Huasco, where the vegetation type and climate is in transition from semi-aridity to desert, suggesting that establishment of this climatic pattern may have split the distribution of the ancestor to *M. humilis* var. *humilis* and *M. humilis* var. *parviflora*. Alternatively, dispersal over this climatic transition zone with secondary contact between the resulting varieties may have created their largely allopatric distribution.

The other varieties are restricted in distribution, and they may be the results of recent range expansions to the north and into the pre-cordillera. In the north, *Malesherbia humilis* var. *taltalina* is probably derived from *M. humilis* var. *parviflora*, with which it is sympatric. The flora of Taltal is unusually rich due to the heavy ocean fogs which coat the steep slopes of the coastal mountains (Johnston, 1929; Rundel & al., 1991), and it is not surprising that a variety of *M. humilis* has evolved in that unusual habitat.

Malesherbia humilis var. *propinqua* is probably derived from the southern *M. humilis* var. *humilis*, judging from the morphological similarities between the two varieties. The morphological affinity between *M. humilis* var. *propinqua* and *M. humilis* var. *gabrielae* and their distinct but adjacent distributions further suggest that these varieties are phylogenetically closely related. The northern part of Region IV, which includes the Elqui Valley, is noted for its endemism (Ricardi, 1967), and the occurrence of three varieties of *M. humilis* in this region may reflect the overall diversity of the area. Although the flora is known to be diverse, little is known about community structure or distributions of plants within the area (Gajardo, 1993), except for the Doña Ana range in the east (Squeo & al., 1994). Such information would be very useful in understanding the evolutionary path of *M. humilis* in this part of its distribution.

It is impossible to determine from the data available why the taxa here recognized produce a continuum of morphologically intergrading OTUs (Fig. 3). If these taxa have only recently diverged, ancestral polymorphisms and incomplete reproductive barriers may explain the similarities among taxa. It is equally likely, however, that these taxa developed in isolation in response to different habitats and are now coming into secondary contact as their ranges expand. Another issue that needs to be resolved is how much of the variation seen within and among the taxa is due to phenotypic

plasticity. Hybridization and common garden experiments could be used as preliminary tools to explore these issues.

TAXONOMY

1. Floral tube funnellform when pressed flat, flaring from the base of the ovary to the throat. Distribution: 29°S–33°20'S 2
1. Floral tube wineglass-shaped when pressed flat, remaining narrow after flaring at the base of the ovary. Distribution: 29°S–21°S 4
2. Floral tube length generally less than 7 mm. Leaf stipules linear and lacking lobes 1. *M. humilis* var. *humilis*
2. Floral tube length greater than or equal to 7 mm. Leaf stipules often bifid or lobed, sometimes linear and/or unlobed 3
3. Androgynophore pilose over entire length 2. *M. humilis* var. *gabrielae*
3. Androgynophore glabrous, or pilose only at the base of the ovary 3. *M. humilis* var. *propinqua*
4. Petals lacking an apical glandular hair 4. *M. humilis* var. *parviflora*
4. Petals with a single apical glandular hair 5. *M. humilis* var. *taltalina*

1. *Malesherbia humilis* Poepp. var. *humilis*

This variety is distinguished from var. *parviflora* and var. *taltalina* by the shape of its floral tube, which is funnellform, flaring at the throat of the tube. In the Huasco region, where var. *humilis* and var. *parviflora* overlap and this character is sometimes not useful, the ratio of the floral tube length to width can be used to separate the two varieties. *Malesherbia humilis* var. *humilis* has a ratio less than 1.6. This variety has floral tubes less than 7 mm in length and has linear, unlobed stipules. The type variety has a wide distribution from Huasco (28°30'S) south to Santiago. Some collections have been made in the Elqui Valley, but the majority are from nearer the coast. The Argentinean populations are also of this variety.

2. *Malesherbia humilis* Poepp. var. *gabrielae* (Ricardi) Gengler, **comb. nov.** Basionym ≡ *Malesherbia gabrielae* Ricardi, Gayana Bot. 16: 120–123. 1967. – Type: Chile, Province Coquimbo. camino de Vicuña a Guanta. km 9, 27 Oct 1964. Ricardi, Marticorena & Matthei 1126 (Holotype: CONC [31879!]; isotype: CONC [31879!]).

This variety produces floral tubes greater than 7 mm in length, and its stipules are almost always bifid. It is distinguished from var. *propinqua* by its pilose androgynophore. It is endemic to the eastern Elqui Valley and

the Río Elqui's eastern tributaries (Region IV).

3. *Malesherbia humilis* Poepp. var. *propinqua* (Gay) Ricardi

This variety has flowers with longer floral tubes than var. *humilis* (greater than 7 mm), and its leaf stipules are usually lobed (although sometimes linear, unlobed stipules appear). It differs from var. *gabrielae* in that its androgynophore is not pilose along its entire length. The variety is distributed in Region IV in the western portion of the Elqui Valley, the region 40–50 km north of the valley, and the area surrounding Ovalle.

4. *Malesherbia humilis* Poepp. var. *parviflora* (Phil.) Ricardi, *Gayana, Bot.* 16: 117–119. 1967. ≡ *Malesherbia parviflora* Phil., *Anal. Univ. Chile.* 84: 977. 1893. – Type: Chile, Prov. Atacama, Chañarillo, Oct 1876, *P. Ortega X-1876* (Holotype: SGO [041120!]).

= *M. multiflora* Ricardi, *Gayana, Bot.* 16: 126. 1967. – Type: Chile, Region III, Prov. Huasco, cerca de Estacion Romero, Feb 1966, *Ricardi, Marticorena & Matthei 1689* (Holotype: CONC [31951!]; isotype: F!).

Members of this variety possess floral tubes that remain constricted to approximately the width of the ovary at the apex. The petals of this variety have no apical glandular hair, as does var. *taltalina*. The morphology of this taxon varies widely: some specimens are highly branched and bear hundreds of tiny flowers, whereas others have only a few branches bearing a few flowers. Stipules and an apical mucron on the capsule may or may not be present. In the Huasco region, var. *parviflora* is distinguished from var. *humilis* by a floral tube length to width ratio greater than 2.0.

This northern variety extends from southern Region III (Huasco) north to Guatacondo (20°56'S) and from the coast into the Andean foothills. In the north, the distribution is strictly coastal, except for the single OTU found in a dry ravine near Guatacondo.

5. *Malesherbia humilis* Poepp. var. *taltalina* (Ricardi) Gengler, **comb. nov.** ≡ *Malesherbia taltalina* Ricardi, *Gayana, Bot.* 16: 123–125. 1967. – Type: Chile, Prov. Antofagasta, Taltal, Quebrada Anchuña, flores violadas, 20 Sep 1953, *Ricardi 2530* (Holotype: CONC [14323!]; isotypes: CONC [14323!], CTES [221052!]).

This variety is distinguished by the glandular apical hair on each petal. The petals tend to be very small relative to the sepals, although this feature cannot be used to separate the variety from var. *parviflora* with great certainty. As does var. *parviflora*, var. *taltalina* produces many very small flowers with floral tubes that do not

flare open at their apices.

This variety is endemic to the lomas around Taltal in Region II. Although it has not been collected in the nearby lomas of Paposos, its distribution may well extend there.

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LITERATURE CITED

- Börgel, R.** 1973. The coastal desert of Chile. Pp. 111–114 in: Amiran, D. H. K. & Wilson, A. W. (eds.), *Coastal Deserts: Their Natural and Human Environments*. University of Arizona Press, Tucson.
- Fay, M. F., Swensen, S. M. & Chase, M. W.** 1997. Taxonomic affinities of *Medusagyne oppositifolia* (Medusagynaceae). *Kew Bull.* 52: 111–120.
- Gajardo, R.** 1993. *La Vegetación Natural de Chile: Clasificación y Distribución Geográfica*. Editorial Universitaria, Santiago, Chile.
- Johnston, I. M.** 1929. Papers on the flora of northern Chile. *Contr. Gray Herb.* 85: 1–171.
- Lauer, W. & Frankenberg, P.** 1984. Late Glacial glaciation and the development of climate in southern South America. Pp. 103–114 in: Vogel, J. C. (ed.), *Late Cainozoic Palaeoclimates of the Southern Hemisphere*. A. A. Balkema, Rotterdam.
- Paskoff, R.** 1973. The Plio-Quaternary climatic changes along the semiarid seaboard of Chile. Pp. 147–151 in: Amiran, D. H. K. & Wilson, A. W. (eds.), *Coastal Deserts: Their Natural and Human Environments*. University of Arizona Press, Tucson.
- Ricardi, M.** 1967. Revisión taxonómica de las *Malesherbiaceas*. *Gayana, Bot.* 16: 1–139.
- Rohlf, F. J.** 1998. *NTSYSpc version 2.0*. Exeter Software, Setauket, New York.
- Rundel, P. W., Dillon, M. O., Palma, B., Mooney, H. A., Gulmon, S. L. & Ehleringer, J. R.** 1991. The phytogeography and ecology of the coastal Atacama and Peruvian deserts. *Aliso* 13: 1–49.
- SAS.** 1989. *SAS/STAT user's guide, version 6*, ed. 4, vol. 1 & 2. SAS Institute Inc., Cary, North Carolina.
- Sneath, P. H. A. & Sokal, R. R.** 1973. *Numerical Taxonomy*.

W. H. Freeman and Company, San Francisco.

Squeo, F. A., Osorio, R. & Arancio, G. 1994. *Flora de los Andes de Coquimbo: Cordillera de Doña Ana*. Editorial Universitaria, Santiago, Chile.

Trewartha, G. T. 1961. *The Earth's Problem Climates*. University of Wisconsin Press, Madison.

Whitkus, R. & Packer, J. G. 1984. A contribution to the taxonomy of the *Carex macloviana* aggregate (Cyperaceae) in western Canada and Alaska. *Canad. J. Bot.* 62: 1592–1607.