# Systematics, ecology and evolution of *Heliotropium* sect. *Cochranea* (Heliotropiaceae) and the biogeography of the Atacama Desert

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# Contents

# List of Tables

# List of Figures

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# 1. General Introduction

## 1.1 Foreword

The motivation for carrying out this study on *Heliotropium* L. sect. *Cochranea* (Miers) Kuntze stems partially from the author's interest in both biogeography, the search for the patterns and causes of the distribution of species, and in the flora of the Atacama Desert, one of the most arid areas of the world. According to Cox and Moore (2000), two major branches of biogeography can be distinguished: ecological biogeography and evolutionary biogeography. The former deals with the ecological factors of the distribution of the species, while the latter focuses on the historical causes of the distribution of species, and hence has also been termed historical biogeography (e.g., Crisci et al., 2003).

Research on historical biogeography can be approached from at least two different perspectives: areas and lineages. The former is usually undertaken through the comparative study of local and regional biota from different places, either present or fossil, and the latter focuses on the comparative study of the distribution of groups of phylogenetically related organisms. In order to understand the distribution of species, both approaches are necessary and complementary, but rely upon different types of data and different methodologies.

Traditional studies of areas, initiated with the work of von Humboldt and Bonpland (1805), has evolved and diversified in several schools of thought, with increasing degrees of complexity in approaches and methodological tools, such as panbiogeography (Croizat, 1952; Craw et al., 1999), cladistic biogeography (Nelson and Platnick, 1981) and macroecology (Brown and Lomolino, 1998). Plant geography deals with areas using local floristic inventories as basic units of analysis. These compilations can be analysed and compared at different levels of the taxonomic hierarchy to formulate hypotheses about their relationships and origins. A central concept in the biogeographical study of areas is the 'floristic element', defined as a group of taxa sharing a common geographic area, ecology and history (Wulf, 1943). The composition of floristic elements of different floras can be compared; however, the proper identification of floristic elements is a challenging task. One approach to define floristic elements is the use of groups of related taxa (e.g., genera) with similar distribution patterns, so that several such groups can be said to belong to one floristic element (e.g., Frey and Lösch, 1998; Qian, 2001; Sklenář and Balslev, 2007). The evaluation of relatedness among taxa is a complex point, and historically has been approached by comparing membership of a taxon (e.g., species) in another taxon at a higher hierachial rank (e.g., genus). This is one aspect in which the biogeographical study of areas is strongly linked to the study of lineages.

Development of new tools and methods in the last four decades has enabled biogeographers to test hypotheses of relatedness, from which biogeographical patterns and processes can be inferred. A major advance was the foundation of phylogenetic systematics, traditionally associated with the work of Hennig (1950). From thence, numerous methodologies have been developed in order to infer phylogenies (e.g., Farris et al., 1970; Farris, 1973; Felsenstein, 1973a,b). The increasing availability of molecular data to systematists, especially in the last two decades, triggered an explosive development in phylogenetic reserach. The use of molecular data to infer phylogenies has become a standard in the toolbox of most botanist and zoologists. Recently, attention has turned to the use of phylogenies to test evolutionary hypotheses, beyond the identification of degrees of relatedness among taxa. These developments include, among others, the estimation of divergence times (Sanderson, 1997; Rambaut and Bromham, 1998; Thorne et al., 1998; Sanderson, 2002; Drummond et al., 2006) and the study of historical biogeography (e.g., Hovenkamp, 1997; Ronquist, 1997; Ree et al., 2005; Nylander et al., 2008; Ree and Smith, 2008).

The Atacama Desert of northern Chile (Fig. 1.1) is one of the most arid areas of the world (Walter and Breckle, 2004). The variety of vascular plants of this extremely dry area has attracted botanists since the nineteenth century. The first botanical observations in the Atacama Desert came from European collectors, such as Cuming (in 1828-29), Meyen (in 1831) and Gaudichaud (in 1832), but the Atacama Desert did not become botanically well-known until the works of Philippi (1860b), Reiche (1907b) and Johnston (1929c) were published. The flora of the Atacama Desert consists of about 550 vascular plant species (Dillon and Hoffmann, 1997). Most species are concentrated in the littoral zone, areas which are more humid than inland areas both in the form of rainfall and fog (Rundel et al., 1991; Muñoz Schick et al., 2001; Luebert and Pliscoff, 2006; Schulz, 2009). Most plant groups that inhabit the Atacama Desert are represented by a few species (Dillon, 2005a), but some apparently natural groups with higher species numbers have their centre of diversity in this area (e.g., *Copiapoa* N.L.Britton & J.N.Rose [Cactaceae], *Heliotropium* sect. *Cochranea* [Heliotropiaceae], *Nolana* L.f. [Solanaceae], *Oxalis* L. sect. *Carnosae* Reiche [Oxalidaceae], *Solanum* L. sect. *Regmandra* Ugent ex D'Arcy [Solanaceae]). These groups provide opportunities to understand the biogeographical origin and development of the Atacama Desert flora.

Several studies have contributed to the biogeography of the Atacama Desert with the publication of local and regional floras (e.g., Philippi, 1860b; Morong, 1891; Johnston, 1929c, 1932; Jaffuel, 1936; Armesto and Vidiella, 1993; Rundel et al., 1996; Dillon, 1997; Gutiérrez et al., 1998; Marticorena et al., 1998; Becerra and Faúndez, 2001; Muñoz Schick et al., 2001; Luebert et al., 2007; Pinto and Luebert, 2009), and some have addressed questions about its biogeography from the point of view of its flora (Ricardi, 1957; Rundel et al., 1991; Armesto and Vidiella, 1993; Richter, 1995; Dillon, 2005b; Pinto and Luebert, 2009). Recently, biogeographical questions have been approached through the examination of lineages in an explicit phylogenetic framework (Katinas and Crisci, 2000; Gengler-Nowak, 2002b; Luebert et al., 2009; Dillon et al., 2009; González and Pérez, 2010). The present work is a contribution to the understanding of the biogeography of the Atacama Desert through the study of one of its most diverse plant taxa, *Heliotropium* sect. *Cochranea*.

## 1.2 The Atacama Desert[a]

### 1.2.1 Boundaries

The extension of the Atacama Desert in terms of flora, vegetation, and climate has different boundaries, depending upon the concepts of the different authors who have studied the area. For instance, Rauh (1985) only included the inland areas devoid of vegetation of

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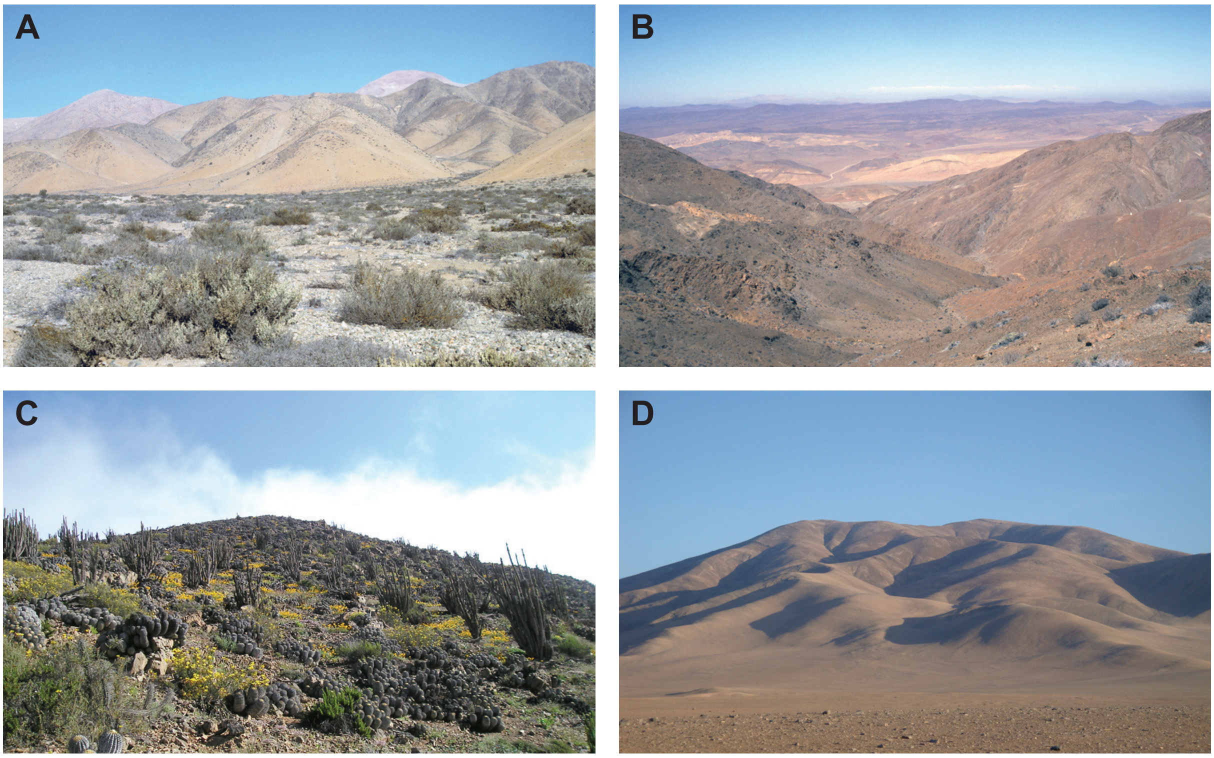

Figure 1.1: Vegetation and landscape of the Atacama Desert. A, Inland desert scrub dominated by *Atriplex deserticola* Phil. (Amaranthaceae), Llano Travesía, south of Copiapó, 27°34'S, 70°25'W, 19 Sept. 2003; B, Coastal desert scrub dominated by *Oxyphyllum ulicinum* Phil. (Asteraceae) on the eastern versant of the coastal Cordillera, Sierra Cifuncho, south of Taltal, 25°46'S, 70°34'W, 16 Sept 2004; C, Coastal desert scrub dominated by *Eulychnia iquiquensis* (K. Schum.) Britton & Rose and *Copiapoa* spec. (both Cactaceae), Quebrada Matancilla, north of Taltal, 25°5'S, 70°26'W, 8 Oct. 2005; D, Absolute inland desert, La Negra, east of Antofagasta, 23°48'S, 70°20'W, 22 Oct. 2009.

northern Chile. Walter and Breckle (2004) included the whole of northern Chile from 28°S northwards and from the sea level to the high Andes. Takhtajan (1986) included these areas in his Central Andean Province, which extends over central Peru and northern Chile, and also includes the high Andean mountains, similar to the circumscription adopted by Lailhacar (1986) and Katinas et al. (1999). Smith and Johnston (1945) restrict the Atacama Desert to the austral portion of what they designated Pacific Desert, which consists of the low-elevation zones ($<$ 2000–3000 m) of northern Chile from 30°S northwards. The latter notion was accepted by most authors (e.g., Udvardy, 1975; Rundel et al., 1991; Gajardo, 1994; Rivas-Martínez et al., 1999; Morrone, 2001) and is also adopted here.

The northern boundary of the Atacama Desert has been located at approximately 18°S latitude or the present border between Chile and Peru (Rundel et al., 1991; Galán De Mera et al., 1997; Dillon, 2005b; Pinto and Luebert, 2009). Apparently, the floristic transition between northern Chile and southern Peru is more abrupt along the coast than inland. A corridor promoting north-south floristic exchange along the western Andean foothills (2000–3000) - the highest elevations of the Atacama Desert - was proposed (Moreno et al., 1994), which is supported by recent floristic findings in southern Peru (Schwarzer et al., 2010).

At higher elevations in the Andes, the boundary of the Atacama Desert could be situated between 2000–3000 m, depending on latitude. This limit is the zone where the 'tolares', vegetation composed of a totally different high-Andean flora, begin to dominate (Villagrán et al., 1981; Arroyo et al., 1988; Rivas-Martínez and Tovar, 1993; Luebert and Gajardo, 2000, 2005). This transition coincides with the upper limit of what Gajardo (1994) terms the *Desierto Andino* (Andean Desert).

The southern boundary of the Atacama Desert is more difficult to define. Most of the authors set it at approximaely 30°S latitude (Rundel et al., 1991; Rivas-Martínez and Tovar, 1993; Gajardo, 1994; Morrone, 2001). However, it would be possible to extend it discontinuosly southwards, according to the physiognomy of the vegetation and dominant species, including what Gajardo (1994) designates *Matorral Estepario Costero* (coastal steppe scrubland) and *Matorral Estepario Interior* (inland steppe scrubland) (Luebert and Pliscoff, 2006). The scarcity of local floristic studies around the boundary zone (i.e., 29°–32°S latitude) makes a detailed assessment of the southern boundary difficult at this time.

According to the above mentioned considerations, the area of the Atacama Desert is depicted in Figure 1.2. It includes the plant formations of absolute desert, desert scrub, and desert dwarf scrub under the influence of hyperarid, arid, and semiarid ombroclimatic regimes (Luebert and Pliscoff, 2006). Detailed descriptions of the vegetation and bioclimates are available in di Castri and Hajek (1975), Lailhacar (1986), Rundel et al. (1991), Gajardo (1994), Amigo and Ramírez (1998), Luebert and Pliscoff (2006), Pliscoff and Luebert (2008).

### 1.2.2 Biogeographical Relationships

Several authors have proposed close phytogeographical relationships between the Atcama Desert and the Peruvian Desert (Johnston, 1929a; Ricardi, 1957; Rundel et al., 1991), or include both units in the same biogeographical province, called the Pacific Desert (Smith and Johnston, 1945; Udvardy, 1975; Rivas-Martínez and Tovar, 1993). This relationship seems evident if one considers the aridity along the coast of northern Chile and Peru, and the fact that numerous vascular plant genera are distributed in both units (e.g., *Heliotropium*, *Nolana*, *Palaua* Cav., see Rundel et al., 1991).

Other authors argued that in spite of the biogeographical relationships between the Atacama and Peruvian Deserts, they constitute separate units, or are related to each other at higher hierarchical levels. For example, Rundel et al. (1991) indicate the existence of a phytogeographical barrier at the latitude of Arica (∼18°30'S), which is supported by the works of Galán De Mera et al. (1997), Dillon (2005b) and Pinto and Luebert (2009). Morrone (2001) considers the Peruvian Desert as a unit separated from the Atacama Desert, and unites them only at the level of the Paramo-Puna sub-region from the Andean region, where Central Chile, Southern Chile and Patagonia are also included.

Some botanists have also proposed biogeographical relationships of the Atacama Desert with the Argentine Chaco (Rundel et al., 1991; Rivas-Martínez and Tovar, 1993), based on the fact that a number of genera (e.g., *Bulnesia* Gay, *Flourensia* DC., *Larrea* Cav., *Leptoglossis* Benth.) are disjunctly distributed on both sides of the Andes. Based primarily on the distribution of Arthropods, Morrone (2004, 2006) includes the Atacama Desert in the so-called South American Transition Zone. It also contains all remaining provinces of the Paramo-Puna sub-region of Morrone (2001) (i.e., North Andean Paramo, Peruvian Desert, Puna and Prepuna, the latter referred here as Mediterranean Andes, fide Gajardo (1994), Rivas-Martínez et al. (1999)), and the Monte province (Chaco sub-region). The Transition Zone is characterized by a mixture of biogeographical elements (Morrone,

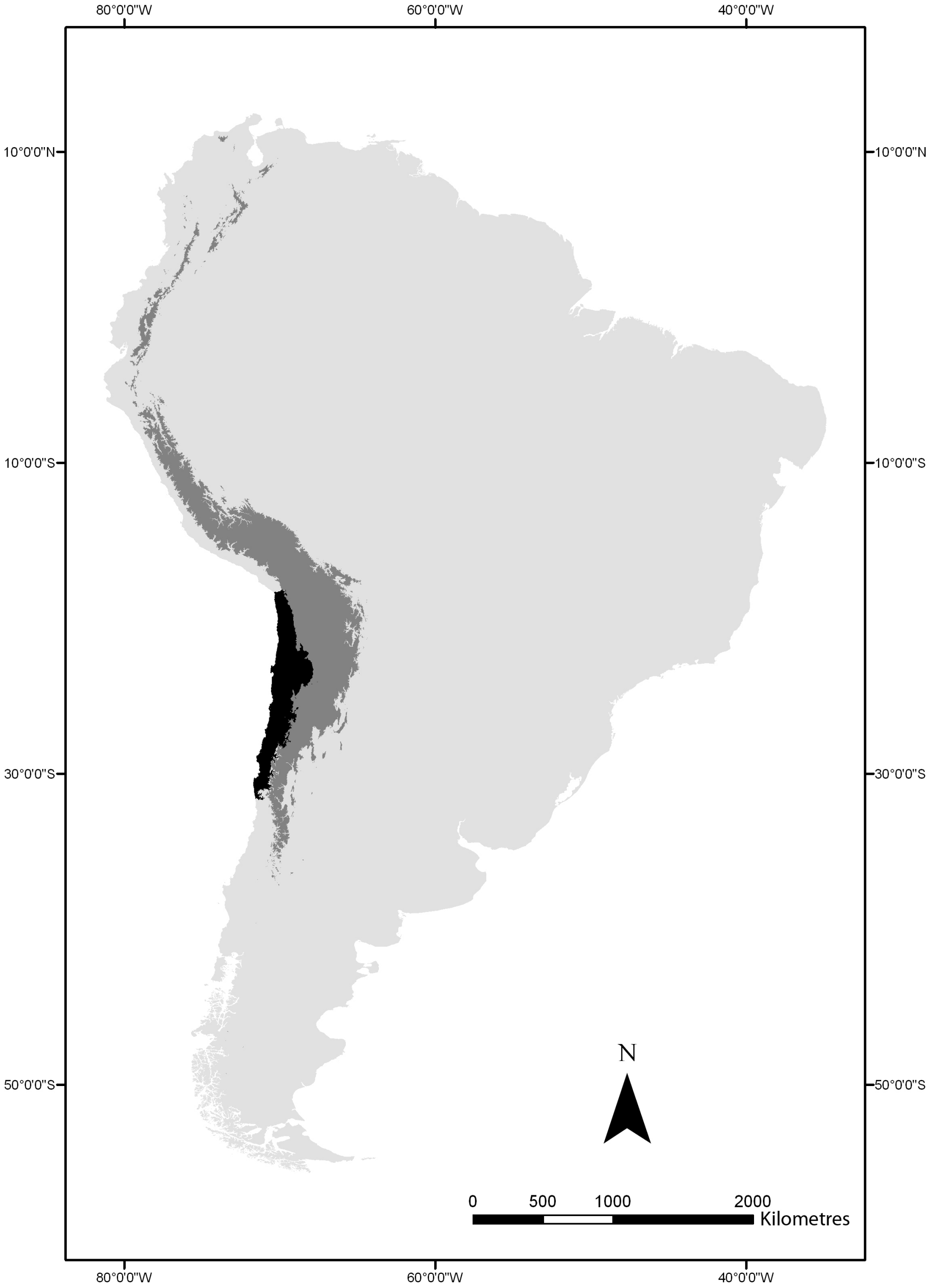

Figure 1.2: Location of the Atacama Desert (black area) in South America. The dark grey area indicates zones higher than 3000 m, showing the major extension of the Andes.

2004). In agreement with this, the analysis of Katinas et al. (1999) discuss the mixed character of the Puna province (where these authors include the Atacama Desert), on the basis of a panbiogeographical analysis of plants and animals.

Unfortunately, most of the works mentioned above do not make explicit use of phylogenetic studies. The use of phylogenetic studies in biogeography is not a new idea, and was proposed from the beginnings of the discipline, being explicit in the work of Hennig (1950). Phylogenetic studies can be useful to evaluate kinship relationships among taxa whose distribution is analysed in biogeographical studies.

### 1.2.3 Origin of Aridity

Aridity in the Atacama Desert is the result of subtropical atmospheric circulation, reinforced by the uplift of the Andes and the establishment of the Humboldt Current (Hartley, 2003; Garreaud et al., 2009). Permanent high-pressure cells and hot dry subsiding air result in a cloud-free region with high solar insolation and characteristic of atmospheric circulation in subtropical western South America. This factor exerts the major control on desert formation, and the Atacama region is likely to have been subject to its effect throughout the Cenozoic (Hartley, 2003; Hartley et al., 2005).

An intensification of the influence of the Humboldt Current on aridity seems to be related to the closing of the Central American seaway 3.5 Ma, and is correlated with an expansion of coastal upwelling in the Southeast Pacific and the abrupt cooling of surface water temperatures along the coast of Ecuador (Ibaraki, 1997). This is also associated with a global cooling trend during the Neogene (Zachos et al., 2001).

The uplift of the Andes has been instrumental in producing a rain shadow effect preventing humid air from the east from reaching the western versant (Houston and Hartley, 2003; Rech et al., 2010), and thus contributing to the aridity of the Atacama Desert. Several authors (e.g. Gregory-Wodzicki, 2000; Garzione et al., 2008) have suggested that the majority of the Andean uplift occurred in the late Miocene.

Progressive aridity in the Atacama Desert since the Pliocene has been documented (Arroyo et al., 1988; Hartley, 2003; Hartley and Chong, 2002), but with fluctuations likely associated with glacial cycles and variation in the latitudinal position of the Southern Westerlies (see Lamy et al., 1998; Betancourt et al., 2000; Holmgren et al., 2001a; Haselton et al., 2002; Maldonado and Villagrán, 2002; Núñez et al., 2002; Latorre et al., 2002, 2003; Núñez and Grosjean, 2003; Stuut and Lamy, 2004). El Niño and El Niño-like events (Garreaud and Battisti, 1999; Garreaud et al., 2009) seem to be at least partially responsible for current interannual and interdecadal variability of precipitation observed in the area.

## 1.3 *Heliotropium* sect. *Cochranea*

### 1.3.1 Systematic Placement and Taxonomy

Heliotropiaceae is one of the families of the order Boraginales, which is a member of the lamiid clade (Angiosperm Phylogeny Group, 2009). Besides Heliotropiaceae, Boraginales is composed of the families Boraginaceae s.str., Codonaceae, Cordiaceae, Ehretiaceae, Hoplestigmataceae, Hydrophyllaceae, Lennoaceae and Wellstediaceae (Ferguson, 1999; Gottschling et al., 2001; Stevens, 2001 onwards; Moore and Jansen, 2006; Angiosperm Phylogeny Group, 2009; Weigend and Hilger, in press). Angiosperm Phylogeny Group (2009) does not recognise the order Boraginales, and considers the family Boraginacae s.l. (i.e., composed of the above mentioned families at the subfamily level) as unplaced within the lamiid clade. Recognition of the order Boraginales has gained acceptance in the recent systematic literature (e.g., Mansion et al., 2009; Weigend et al., 2009, 2010; Moore et al., 2010; Weeks et al., in press).

*Heliotropium* is the most diverse genus of Heliotropiaceae. It is also a morphologically variable genus with woody (trees, lianas, shrubs) and herbaceous species distributed in temperate to tropical regions. *Heliotropium* was formally segregated into 19 sections and about 300 species (Förther, 1998). Recent molecular phylogenetic studies (Diane et al., 2002; Hilger and Diane, 2003) suggest that *Heliotropium* is paraphyletic with respect to *Tournefortia* L. sect. *Tournefortia*, and that *Heliotropium* sect. *Orthostachys* R.Br. is more closely related to *Tournefortia* sect. *Cyphocyema* I.M.Johnst. than to the remainder of *Heliotropium* and was thus moved to the segregate genus, *Euploca* Nutt. Four genera can therefore be recognised in Heliotropiaceae: *Euploca* (∼100 species, incl. *Heliotropium* sect. *Orthostachys*), *Heliotropium* (∼300 species, incl. *Tournefortia* sect. *Tournefortia*), *Ixorhea* Fenzl (monotypic), and *Myriopus* Small (12 species, ≡ *Tournefortia* sect. *Cyphocyema*).

According to Johnston (1928b), Förther (1998) and the current infrageneric classification of the genus (Hilger and Diane, 2003), South American species of *Heliotropium* fall into 9 sections: *Coeloma* (DC.) I.M.Johnst., *Schobera* (Scop.) I.M.Johnst., *Hypsogenia* I.M.Johnst., *Platygyne* Benth., *Plagiomeris* I.M.Johnst., *Tiaridium* (Lehm.) Griseb., *Heliotrophytum* G.Don., *Heliothamnus* I.M.Johnst. and *Cochranea*. *Heliotropium* sect. *Cochranea* (Figs. 1.3 and 1.4) is easily diagnosed and putatively monophyletic group (Hilger and Diane, 2003). Nineteen species and one variety are currently recognised in *Cochranea* (Johnston, 1928b, 1937; Förther, 1998):

1. *Heliotropium chenopodiaceum* (A.DC.) Clos var. *chenopodiaceum*
   *Heliotropium chenopodiaceum* (A.DC.) Clos var. *ericoideum* (Miers) Reiche
2. *Heliotropium eremogenum* I.M.Johnst.
3. *Heliotropium filifolium* (Miers) I.M.Johnst.
4. *Heliotropium floridum* (A.DC.) Clos
5. *Heliotropium glutinosum* Phil.
6. *Heliotropium huascoense* I.M.Johnst.
7. *Heliotropium inconspicuum* Reiche
8. *Heliotropium jaffuelii* I.M.Johnst.
9. *Heliotropium krauseanum* Fedde
10. *Heliotropium linariifolium* Phil.
11. *Heliotropium longistylum* Phil.
12. *Heliotropium megalanthum* I.M.Johnst.
13. *Heliotropium myosotifolium* (A.DC.) Reiche
14. *Heliotropium philippianum* I.M.Johnst.
15. *Heliotropium pycnophyllum* Phil.
16. *Heliotropium sclerocarpum* Phil.
17. *Heliotropium sinuatum* (Miers) I.M.Johnst.
18. *Heliotropium stenophyllum* Hook. & Arn.
19. *Heliotropium taltalense* (Phil.) I.M.Johnst.

Section *Cochranea* is discussed in the taxonomic works of Miers (1868), Philippi (1895), Reiche (1907a, 1910), Johnston (1928b, 1937) and Förther (1998). It should be noted that Förther (1998) did not assign sectional placement to *Heliotropium eremogenum* and *H. jaffuelli*, and that these species have never been included in a taxonomic treatment. Neither modern systematic treatment for the plant group nor any recent and reliable taxonomic revision exists.

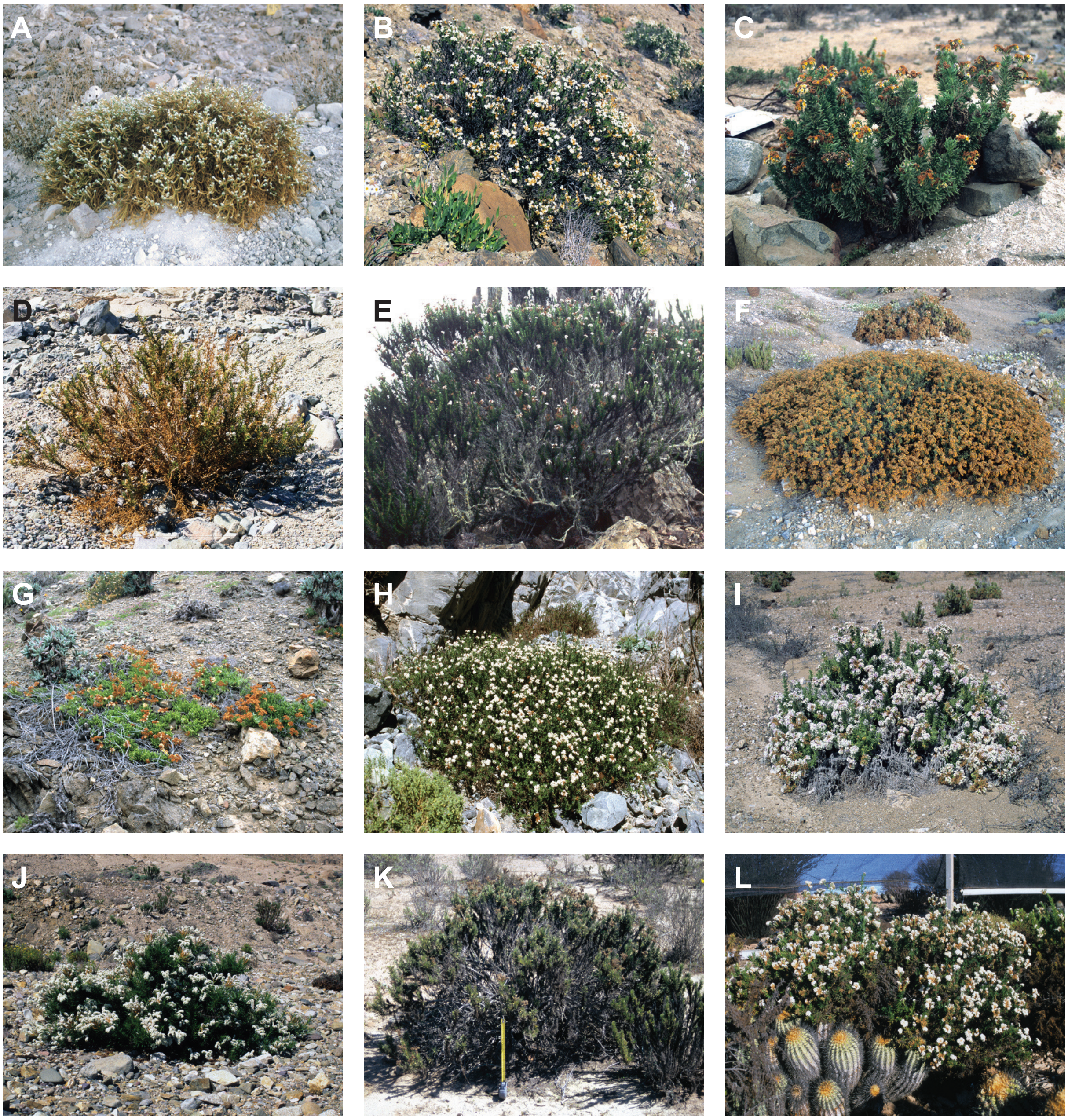

Figure 1.3: Examples of species of *Heliotropium* sect. *Cochranea* in their natural habitats. A, *Heliotropium chenopodiaceum* (Road to Nantoco, south of Copiapó, 27°36'S, 70°27'W, 19 Sept. 2003); B, *H. filifolium* (Totoral, south of Caldera, 27°53'S, 70°58'W, 13 Sept. 2004); C, *H. floridum* (Punta Lobos, north of Huasco, 28°17'S, 71°10'W, 14 Sept. 2003); D, *H. glutinosum* (Quebrada Potrerillos, east of Diego de Almagro, 26°24'S, 69°32'W, 20 Jan. 2004); E, *H. inconspicuum* (Pan de Azúcar National Park, north of Chañaral, 26°6'S, 70°38'W, 14 Oct. 2005); F, *H. linariifolium* (Breas, east of Taltal, 25°30'S, 70°24'W, 10 Oct. 2005); G, *H. megalanthum* (Carrizal Bajo, north of Huasco, 28°6'S, 71°6'W, 26 Sept. 2004); H, *H. philippianum* (Aguada Panulcito, north of Taltal, 24°48'S, 70°31'W, 19 Sept. 2004); I, *H. pycnophyllum* (Breas, east of Taltal, 25°30'S, 70°24'W, 10 Oct. 2005); J, *H. sinuatum* (Totoral, south of Caldera, 27°53'S, 70°58'W, 13 Sept. 2004); K, *H. stenophyllum* (El Tofo, north of Coquimbo, 29°27'S, 71°12'W, 17 Sept. 2005); L, *H. taltalense* (Cerro Perales, east of Taltal, 25°25'S, 70°25'W, 17 Sept. 2004).

Figure 1.4: Variation in flower display of *Heliotropium* sect. *Cochranea.* A, *Heliotropium chenopodiaceum* (Puquios, north of Copiapó, 27°9'S, 69°53'W, 19 Sept. 2003); B, *H. filifolium* (Totoral, south of Caldera, 27°53'S, 70°58'W, 13 Sept. 2004); C, *H. floridum* (Villa Alegre, south of Chañaral, 26°31'S, 70°41'W, 14 Sept. 2003); D, *H. glutinosum* (Quebrada Potrerillos, east of Diego de Almagro, 26°24'S, 69°32'W, 20 Jan. 2004); E, *H. linariifolium* (Road to Cifuncho, south of Taltal, 25°32'S, 70°26'W, 24 Oct. 2009); F, *H. longistylum*, (Road to Caleta Pajonales, south of Caldera, 27°50'S, 71°0'W, 13 Sept. 2004) G, *H. megalanthum* (Carrizal Bajo, north of Huasco, 28°6'S, 71°6'W, 26 Sept. 2004); H, *H. myosotifolium* (Canto de Agua – Totoral, north of Huasco, 28°4'S, 70°44'W, 13 Sept. 2004), I, *H. philippianum* (Miguel Díaz, north of Taltal, 24°33'S, 70°32'W, 5 Oct. 2005); J, *H. pycnophyllum* (Sierra Esmeralda, south of Taltal, 25°53'S, 70°39'W, 13 Oct. 2005); K, *H. stenophyllum* (Caleta El Toro, south of Coquimbo, 30°44'S, 71°41'W, 17 Sept. 2005); L, *H. taltalense* (Cerro Perales, east of Taltal, 25°25'S, 70°25'W, 17 Sept. 2004).

### 1.3.2 Distribution, Ecology and Evolution

*Heliotropium* sect. *Cochranea* is endemic to north and central Chile (Johnston, 1928b, 1932, 1937; Marticorena and Quezada, 1985; Förther, 1998; Luebert and Pinto, 2004), with the exception of a single species (*H. krauseanum*) ranging into coastal Peru (Brako and Zarucchi, 1993; Weigend et al., 2003) (Fig. 1.5).

*Heliotropium* sect. *Cochranea* is an ecologically diversified group, with numerous narrowly endemic species that occupy habitats as different as coastal seashores, Andean foothills, and lomas formations. Section *Cochranea* spans a geographic range of more than 2000 km (Fig. 1.5).

*Heliotropium* sect. *Cochranea* species are important components of the vegetation of the arid environments of northern and central Chile and southern Peru (e.g., Johnston, 1929c; Ricardi, 1957; Ferreyra, 1961, 1983; Mooney and Schlegel, 1966; Gajardo, 1978, 1994; Weisser and Rundel, 1980; Etienne et al., 1982; Oltremari et al., 1987a,b; Grau, 1995; Rundel et al., 1996; Dillon and Hoffmann, 1997; Olivares and Squeo, 1999; Arakaki and Cano, 2003). *Heliotropium* sect. *Cochranea* is mostly restricted to arid and semiarid habitats with extensions into the lomas formations and the Mediterranean habitats of central Chile. It is the only truly deserticolous species group in New World *Heliotropium* and shows some striking derivations in leaf morphology, which appear to be linked to this habitat. However, environmental conditions have not been studied and nothing is known about the climatic factors that control the distribution of the species of *Heliotropium* sect. *Cochranea*. Preliminary anatomical and morphological data (Diane et al., 2003; Brokamp, 2006) indicate that leaf anatomy and morphology of some species in section *Cochranea* are widely divergent, suggesting a potential adaptive radiation in the arid coastal region of western South America.

Adaptive radiations have long been thought to be one of the most important causes of species diversity (Schluter, 2000). Three major elements characterize adaptive radiations (Schluter, 2000; Glor, 2010): (i) common ancestry, (ii) adaptation (phenotype-environmental correlation and trait utility) and (iii) extraordinary diversification. Adaptive radiations can therefore be diagnosed using phylogenetic analyses (Glor, 2010). Assessing common ancestry is one of the most common applications of phylogenetic analyses. Adaptation can be evaluated via comparative analysis (Harvey and Pagel, 1991). Extraordinary diversification can be assessed with methods to estimate the timing of diversification via sister-group comparison of phenotypic disparity (e.g., Collar et al., 2005) or tests for bursts of diversification (e.g., Harvey et al., 1994; Pybus and Harvey, 2000).

Understanding the origin and evolution of a group also requires a previous hypothesis of relationships within the group and with other related groups. Phylogeny is a suitable and long accepted framework to assess relationships. In formulating and testing biogeographical hypotheses of lineages, phylogenetic relationships should be considered (Ball, 1975; Nelson and Platnick, 1981). Testing the monophyly of a group and its phylogenetic relationships is now understood as an integral component of historical biogeography (see Baldwin and Wagner, 2010; Lengyel et al., 2010; Mao et al., 2010; Thiv et al., 2010; for recent examples in plants). Monophyly and phylogenetic relationships cannot be assessed if the group under study is considered in isolation. Possible closely related taxa must therefore be incorporated in the analyses. Phylogenetic hypotheses of Diane et al. (2002) and Hilger and Diane (2003), consider section *Cochranea* as the sister group of the rest of sections of New World *Heliotropium* (incl. *Tournefortia* sect. *Tournefortia*), except section *Heliothamnus*. The closely related sections are distributed in eastern South America or in the Central Andes (Johnston, 1928b; Förther, 1998). The geographic distribution

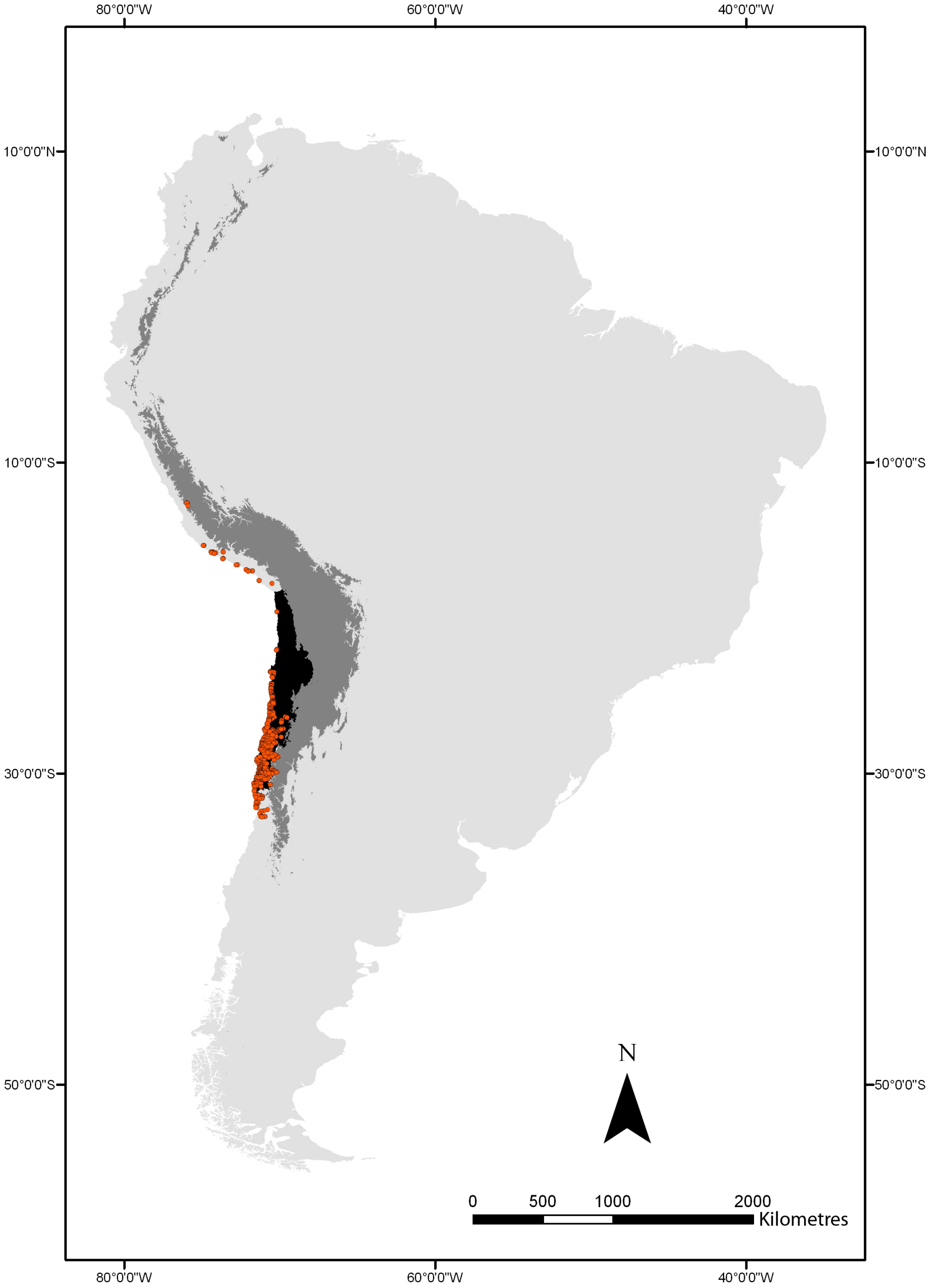

Figure 1.5: Distribution of *Heliotropium* sect. *Cochranea* (orange points) in the Atacama Desert (black area), based on herbarium specimens from CONC, SGO and ULS and records obtained from the literature (Johnston, 1928b; Weigend et al., 2003). The dark grey area indicates zones higher than 3000 m, showing the major extension of the Andes. The area of Atacama not occupied by *Heliotropium* sect. *Cochranea* corresponds to the extension of the absolute desert, where almost no plants can be found. Compare Fig. 1.2.

of these groups in relation to the current Andean Cordillera and the arid environments of the Atacama Desert suggests that the vicariant events generated by the Andean uplift and the development of hyperaridity of the Atacama are the major factors responsible for the origin of *Heliotropium* sect. *Cochranea*. However, sampling of section *Cochranea* and other New World *Heliotropium* in Diane et al. (2002) and Hilger and Diane (2003) was incomplete and some aspects of the internal phylogeny remain unresolved.

Purpose of this work is to contribute to the knowledge of the systematics and ecology of *Heliotropium* sect. *Cochranea* that are presently limiting the understanding of its origin and evolutionary diversification. A working hypothesis for the origin and evolution of *Heliotropium* sect. *Cochranea* can be formulated on the basis of the background presented above.

## 1.4 Hypotheses

*Heliotropium* sect. *Cochranea* originated and diversified in response to the development of the Atacama Desert. The species of *Heliotropium* sect. *Cochranea* may have experienced a recent adaptive radiation related to increasing aridity in the Atacama Desert, as a consequence of the Andean uplift during the Miocene, and subsequent late Tertiary and Quaternary formation of hyperarid environments. If so, (i) *Heliotropium* sect. *Cochranea* should be monophyletic, (ii) divergence time estimates should coincide with the major past geoclimatical events related to the development of aridity in the Atacama Desert, (iii) morphological diversity should be associated with the arid conditions under which *Cochranea* is found, and (iv) moisture must be a limiting factor for the distribution of species.

## 1.5 Goals

### 1.5.1 Research Questions

According to the hypotheses presented above, the following questions regarding *Heliotropium* sect. *Cochranea* have arisen, and are going to be dealt with in this work:

1. Which species comprise *Heliotropium* sect. *Cochranea*?
2. Is *Heliotropium* sect. *Cochranea* monophyletic?
3. Which major clades can be sensibly identified within *Heliotropium* sect. *Cochranea*?
4. To which other *Heliotropium* species-groups is *Heliotropium* sect. *Cochranea* related?
5. What are the ages of diversification of the major clades of *Heliotropium* sect. *Cochranea* and of the related species-groups?
6. Is morphological diversity in *Heliotropium* sect. *Cochranea* related to its habitat?
7. What are the limiting climatic factors determining the distribution of the species in *Heliotropium* sect. *Cochranea*?

### 1.5.2 Specific Objectives

1. Assess the monophyly of *Heliotropium* sect. *Cochranea*.

2. Infer the phylogenetic relationships among species of *Heliotropium* sect. *Cochranea*.

3. Infer phylogenetic relationships between *Heliotropium* sect. *Cochranea* and other *Heliotropium* groups.

4. Assess morphological diversity within *Heliotropium* sect. *Cochranea* and related groups and relate it with climatic conditions.

5. Estimate divergence time and biogeographical relationships of the major lineages of *Heliotropium* sect. *Cochranea* and related groups in *Heliotropium*.

6. Model the distribution of the species of *Heliotropium* sect. *Cochranea* and infer the climatic variables that exert a major control on their distribution.

7. Provide a taxonomic revision of *Heliotropium* sect. *Cochranea*, derived from a synthesis of all information currently available.

In order to achieve these objectives, several methods have been employed, including modern approaches to phylogenetic systematics (objectives 1-3) as well as traditional alpha taxonomy (objective 7) and morphological analyses (objective 3). Phylogeny-based divergence time estimations and event-based biogeographical analyses have been carried out in order to tackle objective 5. Ecological niche modelling has also been employed in an attempt at identifying climatic variables that control the distribution of the species of *Heliotropium* sect. *Cochranea* (objective 6).

## 1.6 Overview of the Dissertation

This dissertation is a cumulative work of manuscripts, either published, accepted, submitted or in preparation to be submitted. Therefore, Chapters 2 to 7 are structured as journal articles, each including a separate Materials and Methods' section. Bibliographic references cited through all chapters are listed together after Chapter 9.

**Chapter 2**[b] is a preliminary phylogenetic study of *Heliotropium* sect. *Cochranea*. Its main purpose is to assess the monophyly of section *Cochranea* (objective 1), to identify its major lineages and likely interspecific relationships (objective 2), and to provide a first estimate of its divergence time (objective 5) in direct relationship with the major hypothesis of this study. Phylogenetic analyses, based on four molecular markers (*ndhF*, *trnL-trnF*, *rps*16 and ITS) using maximum parsimony, maximum likelihood and Bayesian methods, were conducted in order to test monophyly and to assess phylogenetic relationships. A fossil-calibrated maximum likelihood *ndhF* phylogeny of the order Boraginales and the penalized likelihood method were used in order to estimate divergence times of the major lineages of *Heliotropium* sect. *Cochranea*. *Cochranea* was shown to be monophyletic, and originated during the middle to late Miocene, with a major diversification event during the early Pliocene.

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[b] Luebert, F. and Wen, J. 2008. Phylogenetic analysis and evolutionary diversification of *Heliotropium* sect. *Cochranea* (Heliotropiaceae) in the Atacama Desert. *Systematic Botany* 33(2): 390-402.

Phylogenetic relationships between section *Cochranea* and other *Heliotropium* species-groups (objective 3) are assessed in **Chapter 3**[c]. A broader sampling of *Heliotropium*, with emphasis on Neotropical species, based on previous studies in Heliotropiaceae (especially Hilger and Diane, 2003) was designed in order to infer relationships. Maximum parsimony, maximum likelihood and Bayesian methods were applied, and five molecular markers (*trnL-trnF*, *rps*16, *psbA-trnH*, *trnS-trnG* and ITS) were employed. Three major Neotropical clades of *Heliotropium* were identified, one of them being *Heliotropium* sect. *Cochranea*. For these clades, morphological diversity based on vegetative characters of habit and leaf was compared both among clades and among species growing in arid and humid environments of the Neotropics (objective 4). *Heliotropium* sect. *Cochranea* has high leaf morphological diversity, comparable to its sister group, which is species-richer. Morphological diversity tends to be greater in arid than in humid environments, especially in leaf morphology. This difference is likely due to the contribution of section *Cochranea* to the overall leaf morphological diversity of the Neotropical *Heliotropium* species from arid habitats.

In **Chapter 4**[d] divergence time and biogeographical relationships of the major clades of South American *Heliotropium* (objective 5) are studied using a phylogeny of Heliotropiaceae based on three plastid markers (*trnL-trnF*, *rps*16 and *trnS-trnG*). Representatives of the families Ehretiaceae and Cordiaceae from the order Boraginales are included to make fossil calibration of several nodes possible. A Bayesian uncorrelated lognormal relaxed clock approach is applied to estimate divergence times, while parsimony and maximum likelihood approaches are combined in order to infer ancestral areas of distribution of clades of the phylogeny. The chapter is focused on the role of the Andean uplift and the formation of arid environments in South America on the diversification of *Heliotropium* lineages. At least five independent Andean and extra-Andean diversification events were detected to have taken place in the late Miocene and early Pliocene, coinciding with the hypothesis of recent and rapid Andean uplift and subsequent development of aridity in South America.

Species distribution modelling based on climatic factors (objective 6) is undertaken in **Chapter 5**[e]. Several modelling techniques were employed using six different sets of climatic variables, and final models for each species were built via ensemble forecasting. Variable importance and climatic niche differentiation among species were assessed, and climate change effects on extinction risk were evaluated, as well as the possible effect of the set of climatic variables on model output. Winter precipitation and winter minimum temperatures were the most important variables for most species of *Heliotropium* sect. *Cochranea*. Summer maximum temperature was also important for several species. This results are consistent with the expectation that the distribution of the species of section *Cochranea* is mostly controlled by seasonal variation of precipitation and, secondarily, of extreme temperatures. The climatic niches of species of *Heliotropium* sect. *Cochranea* are

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[c] Luebert, F., Brokamp, G., Wen, J., Weigend, M and Hilger, H.H. Phylogenetic relationships and morphological diversity in Neotropical *Heliotropium* (Heliotropiaceae). *Taxon* (conditionally accepted, 07.09.2010).

[d] Luebert, F., Hilger, H.H. and Weigend, M. in prep. Diversification in the Andes: Age and origins of South American *Heliotropium* lineages (Heliotropiaceae, Boraginales). to be submitted to *Molecular Phylogenetics and Evolution*.

[e] Pliscoff, P., Luebert, F.. Hilger, H.H. and Guisan, A. in prep. Climatic control on distribution, niche differentiation, extinction risk, climate change effects and uncertainties associated with variable selection in *Heliotropium* sect. *Cochranea* a group of rare species from the Atacama Desert. to be submitted to *Journal of Biogeography*.

slightly differentiated from one another. The set of climatic variables has strong effects on species distribution models and on the evaluation of extinction risk and climate change effects on species distribution.

**Chapter 6**[f] is a taxonomic revision of *Heliotropium* sect. *Cochranea* (objective 7). Seventeen species are recognised and one new subspecies is described. Two species previously recognised, *Heliotropium huascoense* and *H. sclerocarpum*, are placed under the synonymy of *H. stenophyllum* and *H. chenopodiaceum*, respectively. All protologes and typifications were carefully revised, and one lectotype and one neotype are proposed. Two species (*Heliotropium eremogenum* and *H. jaffuelii*) are formally placed in section *Cochranea* for the first time. Distribution maps and original illustrations are provided. This revision is seen as a synthesis of the present state of the knowledge on section *Cochranea*.

Chapters 7 and 8 go beyond *Heliotropium* section *Cochranea*. **Chapter 7**[g] is considered as the first step in the systematic study of other Neotropical groups of *Heliotropium*. In this chapter, the name *Heliotropium arborescens* L. (the type species of *Heliotropium* sect. *Heliothamnus*) is epitypified. Allowing for taxonomic clarity and nomenclatural stability for this species, complex species delimitation and relationships in *Heliotropium* sect. *Heliothamnus* can be tackled.

**Chapter 8**[h] is a review of phylogenetic studies that include members of the Atacama Desert and their geographical distribution. The purpose is to identify floristic elements of the Atacama Desert flora on the basis of phylogenetic relationships and geographical distribution of lineages related to Atacama Desert taxa. Four floristic elements are identified (Neotropical, Central Chilean, Trans-Andean and Antitropical) and discussed in the context of possible geographical origins of the Atacama Desert flora.

In conclusions (**Chapter 9**), major aspects of the systematics, ecology and evolution of *Heliotropium* sect. *Cochranea*, discussed in previous chapters, are summarized. Some unstudied aspects of the systematics, ecology and evolution of *Heliotropium* sect. *Cochranea* and related groups and next steps of research are identified.

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[f] Luebert, F. in prep. Revision of *Heliotropium* sect. *Cochranea* (Heliotropiaceae). to be submitted to *Kew Bulletin*.

[g] Luebert, F., Weigend, M. and Hilger, H.H. 2010. Epitypification of *Heliotropium arborescens* L. (Heliotropiaceae). *Taxon* 59(4): 1263-1266.

[h] Luebert, F. 2010. Hacia una fitogeografía histórica del Desierto de Atacama. Revista de Geografía Norte Grande (invited contribution, submitted).

# 2. Phylogenetic Analysis and Evolutionary Diversification of *Heliotropium* sect. *Cochranea* (Heliotropiaceae) in the Atacama Desert[a]

## Abstract

*Heliotropium* sect. *Cochranea* (Heliotropiaceae) consists of 19 species endemic to the coastal Atacama Desert of Chile and Peru. This section has one of the most restricted geographic distributions and is the largest among the South American sections of *Heliotropium*. We performed a phylogenetic analysis of a total of 92 species using nuclear ribosomal ITS and chloroplast *ndhF*, *rps*16, and *trnL-trnF* sequences, and estimated the divergence times of major lineages of the group. Our results suggest that *Heliotropium* sect. *Cochranea* is monophyletic. There are two main well-supported lineages within the section: one is *H. pycnophyllum*, which is sister to rest of the species in the section. Within this second lineage, *H. filifolium*, *H. glutinosum*, *H. krauseanum*, and a large polytomous group composed of 15 species form a tetratomy. The age estimates using the penalized likelihood method suggests a minimum age of 14.0 ± 2.0 Ma for section *Cochranea*, and 4.6 ± 0.9 Ma for the large polytomous group within it. *Heliotropium* sect. *Cochranea* may have originated in the Miocene during the major uplift of the Andes, and then radiated in the Pliocene in the Atacama Desert.

## 2.1 Introduction

*Heliotropium* L. sect. *Cochranea* (Miers) Kuntze, composed of 19 shrubby species (Johnston, 1928b, 1937; Förther, 1998), is endemic to the coastal desert of north-central Chile and southern Peru (Johnston, 1928b; Weigend et al., 2003; Fig. 2.1). Recent phylogenetic studies of the family Heliotropiaceae (Diane et al., 2002; Hilger and Diane, 2003) suggest that section *Cochranea* is monophyletic, but the taxon sampling was limited. Monophyly of the section thus needs to be tested with an expanded sampling scheme, which represents its taxonomic and morphological diversity. One of the aims of this paper is to assess the monophyly of *Heliotropium* sect. *Cochranea* with additional molecular evidence and a sampling scheme covering nearly all species.

The family Heliotropiaceae (≡ Boraginaceae subfam. Heliotropoideae) has been largely recognised based on the morphology of its style-stigma complex. The stigma of Heliotropiaceae is elongated in a conical sterile head, with a basal, discoid, and laterally receptive area. The stigmatic head can vary in size, shape and the presence of different surface structures, as well as in its relative length with the style. Several classifications have been

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[a] Published as: Luebert, F. and Wen, J. 2008. Phylogenetic analysis and evolutionary diversification of *Heliotropium* sect. *Cochranea* (Heliotropiaceae) in the Atacama Desert. *Systematic Botany* 33(2): 390-402.

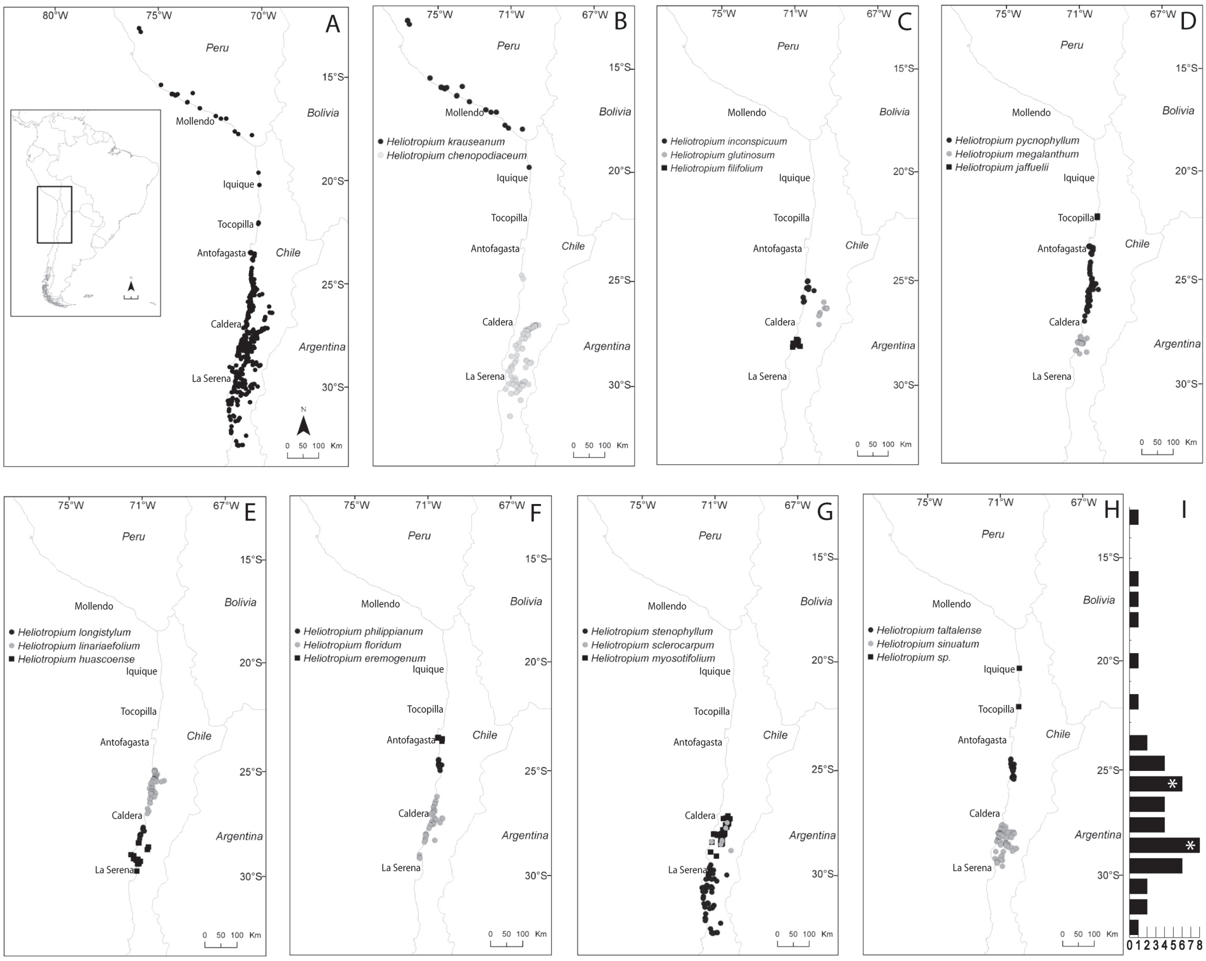

Figure 2.1: Maps of the geographic distribution of the species of *Heliotropium* sect. *Cochranea* in western South America. Collection points are based on specimens from CONC, SGO, EIF, US, and F. A, Total distribution of *Heliotropium* sect. *Cochranea*. B-H, Distribution of individual species of *Heliotropium* sect. *Cochranea*. I, Latitudinal variation of the number of species of *Heliotropium* sect. *Cochranea*; asterisks indicate the two centers of diversity of the group.

proposed at the generic level (e.g., Gürke, 1893; di Fulvio, 1978; Förther, 1998; Hilger and Diane, 2003). Förther (1998) recognised eight genera in Heliotropiaceae: *Heliotropium*, *Tournefortia* L., *Argusia* Boehm., *Ixorhea* Fenzl, *Nogalia* Verdc., *Ceballosia* G.Kunkel ex H.Förther, *Hilgeria* H.Förther, and *Schleidenia* Endl. Phylogenetic analyses (Diane et al., 2002; Hilger and Diane, 2003) suggested that *Tournefortia* and *Heliotropium*, in their traditional circumscriptions, are each polyphyletic. These authors segregated *Heliotropium* sect. *Orthostachys* R.Br., *Hilgeria*, and *Schleidenia*, and placed them in the genus *Euploca* Nutt. They also transferred *Tournefortia* sect. *Cyphocyema* I.M.Johnst. to the genus *Myriopus* Small. The remaining species of *Heliotropium* were still paraphyletic in relation to *Argusia*, *Ceballosia*, *Nogalia*, and *Tournefortia* sect. *Tournefortia*. Thus, Craven (2005) transferred the type species of *Tournefortia* (*T. hirsutissima* L.) to *Heliotropium*, along with the Malesian and Australian species of the genus. With these recent realignments, Heliotropiaceae would be composed of four monophyletic genera: *Heliotropium*, *Euploca*, *Myriopus*, and the monotipic *Ixorhea*. *Tournerfortia* has never been comprehensively revised and several combinations need to be made to transfer all *Tournefortia* to *Heliotropium*, whereas the systematic position of *Ixorhea* is still unclear within the Boraginales (Hilger and Diane, 2003). In this broad circumscription of *Heliotropium*, two sister clades can be recognised (Hilger and Diane, 2003): *Heliotropium* sect. *Heliothamnus* I.M.Johnst., and the rest of the species of *Heliotropium* (*Heliotropium*I and II sensuHilger and Diane (2003), including here the representatives of *Argusia*, *Ceballosia*, and *Tournefortia* sect. *Tournefortia*).

Johnston (1928b) based his infrageneric classification of the South American *Heliotropium* largely on the morphology of the ovary and the fruit, the stigmatic disk, the corolla tube, and the life form. Following Johnston's treatment, Förther (1998) recognised 19 sections in *Heliotropium.* Section *Cochranea* is characterized by its biovulate and uncleft carpels with two fertile cells and two seeds at maturity, corolla glabrous on the adaxial surface, and an erect shrubby habit (Johnston, 1928b; Förther, 1998) and has been previously recognised at either the sectional (Post and Kuntze, 1904; Reiche, 1907a; Johnston, 1928b; Förther, 1998) or the generic level (Miers, 1868; Gürke, 1893; Philippi, 1895). The previous assignments of the species currently considered in section *Cochranea* is summarized in Table 2.1.

Arid environments represent an ideal setting for studying evolutionary radiations, and aridity has long been proposed as promoting rapid evolution in plants (Stebbins, 1952; Axelrod, 1967; Solbrig, 1976; Gengler-Nowak, 2002b; Moore and Jansen, 2006). In arid zones slight changes in moisture create local ecological differentiation in space and time and consequently isolate populations. The population structure there is usually of small separated subunits with occasional genetic interchanges, which promote both isolation and recombination among the subunits (Stebbins, 1952).

The Atacama Desert is one of the most arid land areas in the world. Its annual mean rainfall is less than 1 mm across extensive areas (Almeyda, 1950; Luebert and Pliscoff, 2006), where plants can only be found in the wettest spots. Vegetation is also largely distributed and better developed along the wetter sectors of the coastal range (Rundel et al., 1991; Luebert and Pliscoff, 2006).

*Heliotropium* sect. *Cochranea* is a well-suited model to study plant diversification in the Atacama Desert. It is one of the most diverse plant groups of the Pacific Desert of South America (Dillon, 2005a) and also the largest section of South American *Heliotropium* (Johnston, 1928b; Förther, 1998; Hilger and Diane, 2003). *Heliotropium* sect. *Cochranea* is one of the most geographically restricted groups among the sections of *Heliotropium* in South America (see Johnston, 1928b). All species are restricted to the western side of the Andes (Fig. 2.1A). Most of the species have a restricted geographical distribution (Fig. 2.1). *Heliotropium krauseanum* Fedde and *Heliotropium chenopodiaceum* (A.DC.) Clos are the only species in section *Cochranea* whose geographical ranges have more than five degrees of latitudinal extension (Fig. 2.1B). Some species have isolated geographic ranges (*H. glutinosum* Phil., *H. jaffuelii* I.M.Johnst., *H. krauseanum*), but most of them have their distribution areas overlap with each other and are concentrated in two zones of maximum diversity (Fig. 2.1I), with no species common to both. In such areas where the geographic ranges overlap, the species are usually locally differenciated in space, in terms of altitudinal ranges or substrate, but some areas of sympatry of up to four species of the section can be found. The other groups of South American *Heliotropium* are distributed in Mesoamerica, Tropical Andes, wet Puna, Mediterranean and Patagonian Andes, eastern Patagonia, and tropical and subtropical eastern South America (Johnston, 1928b; Förther, 1998). The only species of *Heliotropium* that overlaps in distribution with section *Cochranea* is *Heliotropium curassavicum* L. This species is normally found on saline soils, where species of section *Cochranea* do not grow.

Table 2.1: Previous assignments of the species currently included in *Heliotropium* sect. *Cochranea*

| de Candolle (1845) | Clos in Gay (1849) | Miers (1868) | Reiche (1907a) | Johnston (1928b) | Förther (1998) |
|---|---|---|---|---|---|
| ***Heliophytum*** **(Cham.) DC. sect.** ***Heliophytum*** | ***Heliotropium*** **L.** | ***Cochranea*** **Miers** | ***Heliotropium*** **sect.** ***Cochranea*** | ***Heliotropium*** **sect.** ***Cochranea*** | ***Heliotropium*** **sect.** ***Cochranea*** |
| *H. chenopodiaceum* A.DC. | *H. chenopodiaceum* (A.DC.) Clos. | *C. chenopodiacea* (A.DC.) Miers | *H. chenopodiaceum* | *H. chenopodiaceum* | *H. chenopodiaceum* |
| - | - | *C. ericoidea* Miers | *H. chenopodiaceum* (A.DC.) Clos var. *ericoideum* (Miers) Reiche | *H. chenopodiaceum* var. *ericoideum* | *H. chenopodiaceum* var. *ericoideum* |
| *H. floridum* A.DC. | *H. floridum* (A.DC.) Clos | *C. florida* (A.DC.) Miers | *H. floridum* | *H. floridum* | *H. floridum* |
| - | - | - | *H. glutinosum* Phil. | *H. glutinosum* | *H. glutinosum* |
| - | - | - | - | *H. huascoense* I.M.Johnst. | *H. huascoense* |
| - | - | - | *H. inconspicuum* Reiche | *H. inconspicuum* | *H. inconspicuum* |
| - | - | - | - | *H. krauseanum* Fedde | *H. krauseanum* |
| - | - | - | *H. linariifolium* Phil. | *H. linariifolium* | *H. linariifolium* |
| - | - | - |  | *H. philippianum* | *H. philippianum* |
| - | - | - | *H. longistylum* Phil. | *H. longistylum* | *H. longistylum* |
| - | - | - | *H. crassifolium* Phil. | *H. megalanthum* I.M.Johnst. | *H. megalanthum* |
| - | - | - | *H. corymbosum* (Miers) Reiche |  |  |
| *H. stenophyllum* (Hook. & Arn.) A.DC. var. *myosotifolium* A.DC. | *H. stenophyllum* var. *myosotifolium* (A.DC.) Clos | *C. myosotifolia* (A.DC.) Miers | *H. myosotifolium* (A.DC.) Reiche | *H. myosotifolium* | *H. myosotifolium* |
| - | - | *C. hebecula* Miers |  |  |  |
| - | - | *C. hispidula* Miers | *H. hispidulum* (Miers) Reiche |  |  |
| - | - | - | *H. chenopodiaceum* (A.DC.) Clos var. *filifolium* (Miers) Reiche |  |  |
| - | - | - | *H. pycnophyllum* Phil. | *H. pycnophyllum* | *H. pycnophyllum* |
| - | - | - | *H. chenopodiaceum* (A.DC.) Clos var. *sclerocarpum* (Phil.) Reiche | *H. sclerocarpum* Phil. | *H. sclerocarpum* |
| *H. floridum* A.DC. var. *bridgesii* A.DC. | *H. floridum* (A.DC.) Clos var. *bridgesii* (A.DC.) Clos | - | *H. rugosum* Phil. | *H. sinuatum* (Miers.) I.M.Johnst | *H. sinuatum* |
| - | - | *C. sinuata* Miers |  |  |  |
| - | - | *C. conferta* var. *auriculata* Miers. |  | *H. taltalense* (Phil.) I.M.Johnst. | *H. taltalense* |
| *H. stenophyllum* (Hook. & Arn.) A.DC. | *H. stenophyllum* Hook. & Arn. | *C. stenophylla* (Hook. & Arn.) Miers | *H. stenophyllum* Hook. & Arn. | *H. stenophyllum* | *H. stenophyllum* |
| *H. stenophyllum* (Hook. & Arn.) A.DC. var. *rosmarinifolium* DC. | *H. stenophyllum* var. *rosmarinifolium* (DC.) Clos | *C. conferta* Miers | *H. stenophyllum* var. *rosmarinifolium* DC. |  |  |
|  |  |  | ***Heliotropium*** **sect.** ***Heliophytum*** |  |  |
| - | - | *C. filifolia* Miers | *H. kingi* Phil. | *H. filifolium* (Miers) I.M.Johnst. | *H. filifolium* |
|  |  |  |  |  | **Without sectional placement** |
| - | - | - | - | - | *H. eremogenum* I.M.Johnst |
| - | - | - | - | - | *H. jaffuelii* I.M.Johnst. |

The uplift of the Andes and the subsequent development of aridity in the Atacama Desert may have then played an important role in the origin and diversification of *Heliotropium* sect. *Cochranea*. The rise of the Andes has been proposed to be one of the important vicariant events in the recent evolutionary history of the South American biota (Schulte et al., 2000; Flores and Roig-Juñent, 2001; Roig-Juñent et al., 2006). It has been associated with rapid plant diversification episodes during the Cenozoic of the Neotropics (Vuilleumier, 1971; Simpson, 1975; Gentry, 1982; Richardson et al., 2001; Hughes and Eastwood, 2006; Jaramillo et al., 2006). The Andean uplift is also linked to the development of aridity in subtropical South America (Hartley, 2003; Houston and Hartley, 2003; Lamb and Davis, 2003; Clarke, 2006).

The aridity of the Atacama Desert is largely the consequence of the atmospheric circulation patterns over the subtropical eastern Pacific, reinforced by the presence of the Humboldt Current and the rain shadow effect of the Andes (Hartley and Chong, 2002; Hartley, 2003; Houston and Hartley, 2003; Hartley et al., 2005; Clarke, 2006). The Andean chain produces a rain-shadow effect preventing humid air from the east to reach the western side of the Andes (Houston and Hartley, 2003). An elevation of 2000-3000 m is apparently required to generate this effect (Alpers and Brimhall, 1988; Hartley, 2003) and it was only by the late Miocene that this region reached this elevation (Gregory-Wodzicki, 2000). An intensification of the influence of the Humboldt Current on aridity seems to be deeply related to the closing of the Central American seaway around 3.5 Ma, which is strongly correlated with an expansion of coastal upwelling in the southeast Pacific, the abrupt cooling of surface water temperatures along the coast of Ecuador (Ibaraki, 1997) and a global cooling trend (Zachos et al., 2001). The formation of hyperarid environments in the Atacama Desert would then have taken place since the Pliocene (see Hartley et al., 2005; and references therein).

In a phylogenetic context, Katinas and Crisci (2000) studied the plant genus *Polyachyrus* Lag. (Asteraceae) from the Atacama Desert and adjacent zones. They proposed a Pleistocene diversification of *Polyachyrus* in the Atacama Desert. Gengler-Nowak (2002b) suggests an early Pliocene origin for the plant family Malesherbiaceae and a subsequent diversification in the Atacama Desert as a consequence of the development of aridity.

We herein examined the phylogenetic diversification of *Heliotropium* section *Cochranea*. We tested the working hypothesis that section *Cochranea* experienced a radiation in the Atacama Desert as a consequence of the isolation of western South America after the Andes became an effective vicariant barrier and the climate finally turned to hyperaridity. To this end, the timing of the origin of section *Cochranea* and its main lineages was estimated in the phylogenetic context with fossil calibration and by means of the penalized likelihood (PL) method (Sanderson, 2002).

## 2.2 Materials and Methods

### 2.2.1 Plant Material and Outgroup Selection

Eighteen of the 19 recognised species and an additional undescribed species from *Heliotropium* sect. *Cochranea* (ingroup) plus 14 outgroup samples were sequenced for the nuclear ribosomal ITS, and the chloroplast *ndhF* gene, the *rps*16 intron, and the *trnL-trnF* region. The only species of section *Cochranea* not represented in this analysis is *Heliotropium jaffuelii*, a narrow endemic of the coastal hills of Tocopilla, Chile (22°03'S, 70°10'W; Fig. 2.1D). This species is only known from the type specimen and one other collection. A total of 207 sequences were deposited in GenBank. We also obtained 108 GenBank accessions representing 68 species of the Boraginales and related groups (Appendix A). The outgroup taxa were selected based on published studies on the phylogeny of Heliotropiaceae (Diane et al., 2002; Hilger and Diane, 2003), and representatives of related groups of Boraginales (Ferguson, 1999; Gottschling and Hilger, 2001; Gottschling et al., 2001, 2005; Moore and Jansen, 2006), Solanales and Gentianales (Bremer et al., 2002). Information on the names, voucher specimens and the GenBank accessions for the selected taxa used in the analyses are shown in Appendix A. Nomenclature of the species of Heliotropiaceae follows Förther (1998), Hilger and Diane (2003) and Craven (2005).

### 2.2.2 DNA Extraction, Amplification, and Sequencing

The DNAs from all samples of silica-gel-dried leaves were extracted with a modified CTAB method (Doyle and Doyle, 1987). For a few samples, we used the DNeasy QIAGEN extraction kit following the manufacturer's instructions. PCR amplifications were performed in a Peltier PTC-255 thermal cycler (MJ Research Inc., Watertown, Massachusetts) in 20 $\mu$l volume containing 1 U of Taq Polymerase, 2.5 mM $MgCl_2$,125 $\mu$m of each dNTP, 0.5 $\mu$M of each primer and about 25 ng of template DNA. Amplification primers and cycling conditions followed Moore and Jansen (2006) for *rps*16, *ndhF* and ITS. Primers 'c' and 'f' were used for the amplification of the *trnL-trnF* region (Taberlet et al., 1991) and the thermal cycling conditions were the same as that for *rps*16. PCR products were purified with the PEG precipitation (Rosenthal et al., 1993) and cycle sequencing was performed with BigDye Terminator v3.1 (Applied Biosystems, Foster City, California) following the manufacturer's instructions. Each sample was sequenced at least once in the forward and reverse directions. The resulting sequences were assembled using Sequencher 4.1.10 (Gene Codes Corporation, Ann Arbor, Michigan), and then aligned automatically using the software Qalign 2.0 (Sammeth et al., 2003) followed by manual adjustments using Se-Al 2.0a11 (Rambaut, 1996). Sequences were deposited in GenBank (Appendix A).

### 2.2.3 Phylogenetic Analysis

Our phylogenetic analysis was conducted with the maximum parsimony (MP, Farris et al., 1970) method, using PAUP* 4.0 (Swofford, 2003) and as a Bayesian analysis (BA, Mau et al., 1999) using MrBayes v. 3.1 (Ronquist and Huelsenbeck, 2003; Ronquist et al., 2005). The MP analysis was performed as a heuristic search for ITS and chloroplast DNA (cpDNA) data sets separately, setting MaxTrees to 10,000, random taxon-addition replicates to 100, tree bisection-reconnection branch swapping, multitrees in effect, collapsing branches of zero-length, characters as equally weighted and treating gaps as missing data. Branch support of the maximally parsimonious trees (MPTs) was performed by bootstrap (BS) analysis, using a heuristic search with 1000 replicates and the same settings as used in the MP search. Nucleotide substitution models were determined with Modeltest v.3.06 (Posada and Crandall, 1998) prior to the Bayesian inference. BA was carried out under the selected model, with a sampling frequency every 1000 generations and adding generations until the value of the standard deviation of split frequencies falls below 0.01. We tested the congruence of the ITS and the cpDNA data sets using the Incongruence Length Difference (ILD) test (Farris et al., 1994), as implemented in PAUP* 4.0. When the ILD test rejected the incongruence of the data sets, we proceeded to perform an analysis of the combined data set, with the same settings as mentioned above.

We employed two sampling strategies in our analyses. We first sampled broadly of 40 ingroup and 46 outgroup samples with only two markers (ITS1 and *trnL* intron) primarily to assess the monophyly of *Heliotropium* sect. *Cochranea*. The ITS1 and the t*rnL* intron were the only available markers in GenBank for such a broad sampling. This data matrix had 1.16% cells scored as missing data. Our second analysis included four markers (ITS, *ndhF*, *rps16*, *trnL-trnF*) with the sampling of 37 ingroup and 16 outgroup samples (12 samples of Heliotropiaceae and representatives of four closely related families in the Boraginales: Boraginaceae, Cordiaceae, Ehretiaceae, and Hydrophyllaceae). The second data matrix had 1.46% cells scored as missing data.

A matrix with 38 outgroup samples of Boraginales, Solanales, Gentianales, and 37 ingroup samples of the *ndhF* gene, similar to that of Moore and Jansen (2006), was designed for purposes of age estimates (Appendix A). The *ndhF* data matrix had 0.31% cells scored as missing data. Maximum likelihood analysis (ML Felsenstein, 1981) was conducted for the *ndhF* data matrix in order to obtain a tree topology for estimating divergence times. Modeltest v.3.06 (Posada and Crandall, 1998) was used prior to the ML analysis to determine the best-fit nucleotide substitution model for the dataset. The ML analysis was performed in PAUP* 4.0 with the heuristic search, under the selected substitution model and setting random taxon-addition replicates to 10, tree bisection-reconnection branch swapping, multitrees in effect and collapsing branches of zero-length. We rooted the trees using sequences of representatives of closely related orders of the Boraginales (Bremer et al., 2002), including *Nicotiana tabacum* (Solanaceae) from Solanales, *Gentiana procera* (Gentianaceae), *Logania vaginalis* (Loganiaceae) and *Luculia gratissima* (Rubiaceae) from Gentianales as outgroups (Appendix A).

The data matrices for the phylogenetic analysis were deposited in Tree-BASE (study number S1853).

### 2.2.4 Estimating Divergence Times

We used the *ndhF* ML topology for estimating divergence times. The *ndhF* gene is suitable for estimating divergence times in Heliotropiaceae because (1) its alignment is straightforward without ambiguities, and (2) there are several previously published sequences across Boraginales and related groups (e.g., Ferguson, 1999; Bremer et al., 2002; Moore and Jansen, 2006). We did not use the ITS sequences because our ITS sequences are very divergent from those of many outgroup species of Boraginales, which would not allow us to use a broad phylogenetic framework to estimate the divergence times of the nodes of interest with several fossils.

Three nodes of the *ndhF* ML tree (see below) were constrained with fossil data to estimate minimum ages for *Heliotropium* sect. *Cochranea* and lineages within the section:

1. Fossils of *Ehretia* P.Browne (Ehretiaceae) were reported from the lower Eocene (Ypresian, ca. 50 Ma) of the London Clay in England (Chandler, 1961, 1962, 1964; Collinson, 1983). Mai and Walther (1991) reported fossils of *Ehretia* from the upper Oligocene (ca. 24 Ma) of Saxony in Germany. Based on this fossil evidence, we constrained the node of *Eheretia*, *Bourreria* P.Browne, and *Tiquilia* Pers. to a minimum age of 50 Ma, because the node for the available *ndhF* sequences for *Ehretia* (*E. ovalifolia* and *E. anacua*) belong to the *Ehretia* II clade (Gottschling and Hilger, 2001) that occupies a more derived position than all of the fossils of that genus (Gottschling et al., 2002).

2. Fossil leaves of *Cordia* L. (Cordiaceae) have been reported by Chelebajeva (1984) for the lower Eocene (ca. 50 Ma) of Kamchatka in eastern Russia. Brea and Zucol (2006) have reported fossil woods of *Cordia* for the upper Paleocene (ca. 55 Ma) of Chubut, Argentina. We constrained the node of (*Cordia decandra* and *Cordia nodosa*) to a minimum age of 50 Ma, because they belong to the Sebestena and Collococcus clades, respectively (Gottschling et al., 2005), and the crown node of those clades includes both the Myxa clade to which the fossils of *Cordia* from Kamchatka have been assigned (Gottschling et al., 2004), and the Sebestena clade to which the fossils from Argentina can be referred (Gottschling et al., 2005; Brea and Zucol, 2006).
3. Fossil pollen of *Tournefortia* (Heliotropiaceae) were recorded by Graham and Jarzen (1969) for the San Sebastián formation of the lower Oligocene (ca. 30 Ma) of Puerto Rico. According to Gottschling et al. (2004), the fossil of *Tournefortia* belongs to the *Tournefortia* subclade of Hilger and Diane (2003). Thus we constrained the stem node of *Tournefortia* sect. *Tournefortia* to a minimum age of 30 Ma, ensuring that the *Tournefortia* subclade was included. It is worthy to note that the fossil pollen of *Tournefortia* were found only in one sample, where it was rare and there are no other fossil records for this genus (Graham and Jarzen, 1969).

We set the root age of the crown node of *Vahlia* Thunb. (Vahliaceae) and *Borago* L. (Boraginaceae) to 104 Ma (exact age) as estimated by Bremer et al. (2004). Because the molecular clock hypothesis was rejected for the *ndhF* data set (likelihood ratio test = 1375,7, df = 72, $p \ll 0.001$, see also Moore and Jansen, 2006), a smoothing method using the penalized likelihood analysis was conducted in r8s v.1.71 (Sanderson, 2003, 2006). The following options were used: TN algorithm with a cross validation, setting the smoothing parameter to 100 and checkGradient command active. All zero-length branches were collapsed. The result of the cross validation analysis minimizes the error (Sanderson, 2002) with a smoothing value of 180, with which we reanalysed the dataset. We carried out a sensibility analysis to compare the results obtained by removing one of the fossil-based calibration points from the analysis and keeping at least two calibration points. Confidence intervals of the estimated ages were obtained via bootstraping the original data matrix as recommended by Sanderson (2006).

## 2.3 Results

### 2.3.1 Phylogenetic Analysis

A total of 10,000 MPTs (Max-Trees) were recovered in each analysis. This is a good representation of the different tree shapes, because the strict consensus tree will not change with additonal MPTs, since the rearrangements of taxa occur only within one clade of *Heliotropium* sect. *Cochranea*.

The ILD test indicated that the homogeneity of the partitions of nuclear ITS and cpDNA cannot be rejected with a probability lower than 5% ($P = 0.059$).

#### Analysis with a Broad Outgroup Sampling and Two Molecular Markers

Our combined ITS1 and chloroplast *trnL* intron data set contained 288 aligned positions for the ITS1 region and 529 for the *trnL* intron. The ITS1 data had 174 variable sites, of which 132 were parsimony informative. The *trnL* intron data had 45 parsimony informative sites from a total of 73 variable sites. The total length of the ITS1 MPTs was

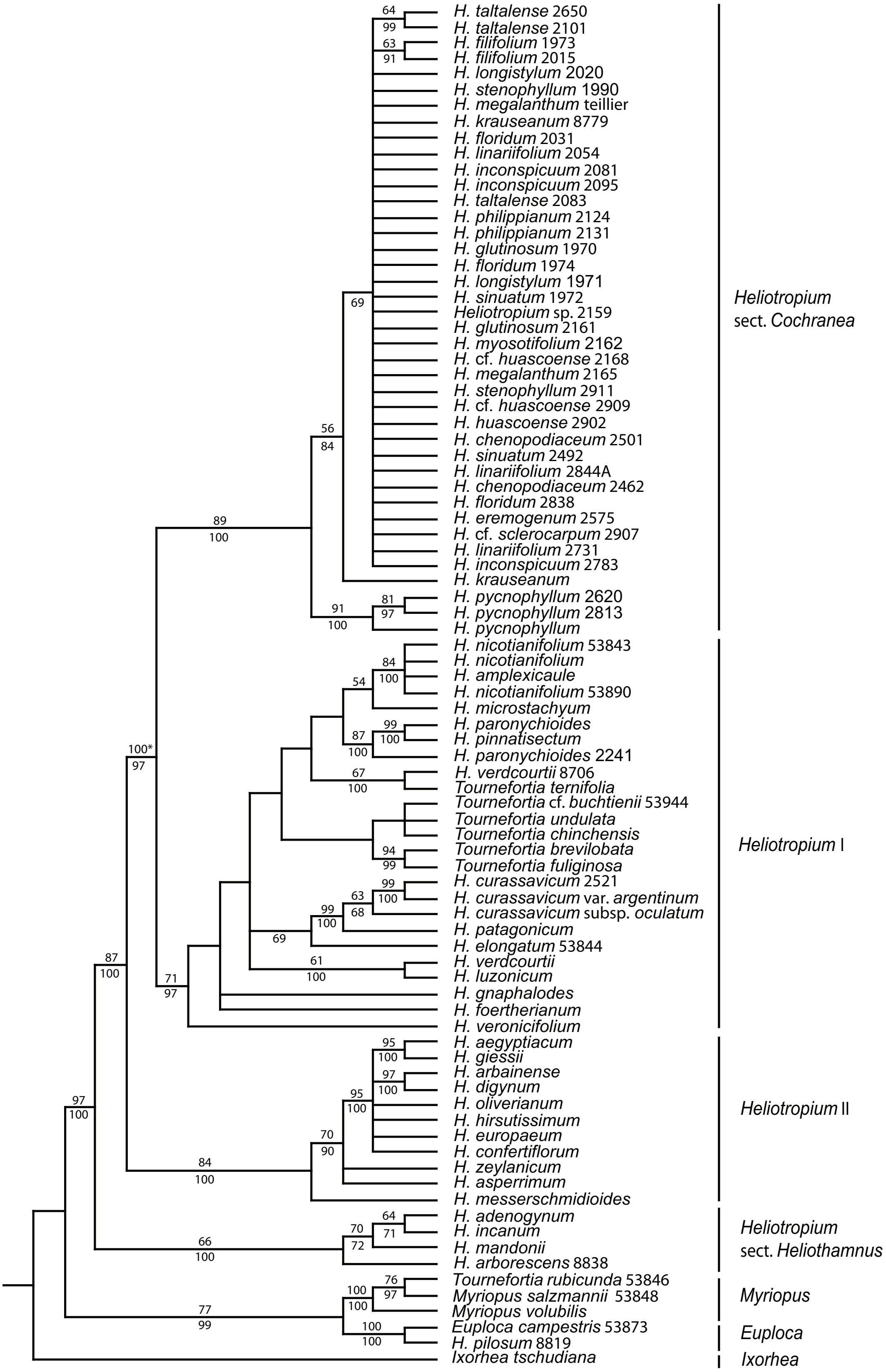

Figure 2.2: Strict consensus tree from the parsimony analysis of constrained ITS1 and *trnL* intron, with bootstrap support > 50% indicated above branches and Bayesian posterior probabilities > 50% below. The asterisk indicates the constrained node.

693 steps, with a consistency index (CI) of 0.51 and a retention index (RI) of 0.74. The MPTs of the *trnL* intron sequences had a total length of 93 steps, a CI of 0.84, and a RI of 0.94. The *trnL* tree was less resolved than the ITS1 tree. The combined analysis of the ITS1 and the *trnL* intron sequences produced MPTs with a total length of 755 steps, and a CI of 0.54 and a RI of 0.76. This analysis supports the monophyly of *Heliotropium* sect. *Cochranea*. Within the section, two well-supported lineages can be recognised: one is the *Heliotropium pycnophyllum*, which is sister to the rest of the species in the section (Fig. 2.2). No other well-supported relationships among species of *Heliotropium* sect. *Cochranea* are suggested by this analysis.

The BA and MP trees of the combined data set produced different topologies regarding the relationships among the clades *Heliotropium* sect. *Cochranea*, *Heliotropium* I and *Heliotropium* II. In the MP topology, *Heliotropium* sect. *Cochranea* is sister to a clade of all representatives of both the *Heliotropium* I and the *Heliotropium* II clades. In the Bayesian topology, *Heliotropium* II is the sister clade of both section *Cochranea* and *Heliotropium* I. Constraining the monophyly of *Heliotropium* I and section *Cochranea* to get the Bayesian topology, the MP analysis resulted in MPTs trees one step longer than the unconstrained topology. We present this last constrained tree in Fig. 2.2, but the unconstrained topology of the MP analysis was deposited in TreeBASE as well. Support for the *Heliotropium* I clade is poor. The *Heliotropium* II clade have moderate to high branch support in both parsimony bootstrap and Bayesian analyses in the constrained topology (Fig. 2.2), but not in the unconstrained one. These topologies (Fig. 2.2) also suggest that *Heliotropium* sect. *Heliothamnus* is sister to the rest of *Heliotropium*.

#### Analysis of *Heliotropium* sect. *Cochranea* with Four Molecular Markers

The ITS and cpDNA data set with only 16 outgroup samples consisted of 756 aligned basepairs for ITS (ITS1, 5.8S, and ITS2) and 4,051 basepairs for the three cpDNA markers (2017 basepairs for *ndhF*, 928 basepairs for *rps*16, and 1106 basepairs for *trnL-trnF*). The ITS data had 227 parsimony informative sites from a total of 369 variable sites. The cpDNA data had 891 variable sites, of which 370 were parsimony informative. The analysis of ITS yielded MPTs with a total length of 920, a CI of 0.66 and a RI of 0.64. The MPTs from the cpDNA data had 1205 steps in length, a CI of 0.85 and a RI of 0.86. The MPTs of the combined analysis had 2151 steps, and a CI and a RI of 0.76 and 0.76, respectively. Figure 3 shows the results of the MP phylogenetic analysis with the combined ITS and cpDNA (*ndhF*, *rps*16, *trnL-trnF*) data set. The strict consensus trees from the combined ITS+cpDNA analysis (Fig. 2.3) and the cpDNA analysis alone were identical. No conflicts were observed between topologies yielded by BA and MP analysis.

Monophyly of *Heliotropium* sect. *Cochranea* and the sister position of *Heliotropium pycnophyllum* to the other species of section *Cochranea* is supported by this analysis (Fig. 2.3). This analysis also suggests that *Heliotropium krauseanum*, *H. glutinosum*, *H. filifolium*, and the rest of the species of section *Cochranea* (excluding the above mentioned *H. pycnophyllum*) form a polytomy (Fig. 2.3). Furthermore this topology supports that *Heliotropium* sect. *Heliothamnus* is sister to the rest of *Heliotropium* (Fig. 2.3).

### 2.3.2 Age Estimates

The nucleotide substitution model for the *ndhF* matrix, as estimated using Modeltest, was GTR+I+Γ. The ML tree obtained under that model is shown in Fig. 2.4. The relationships

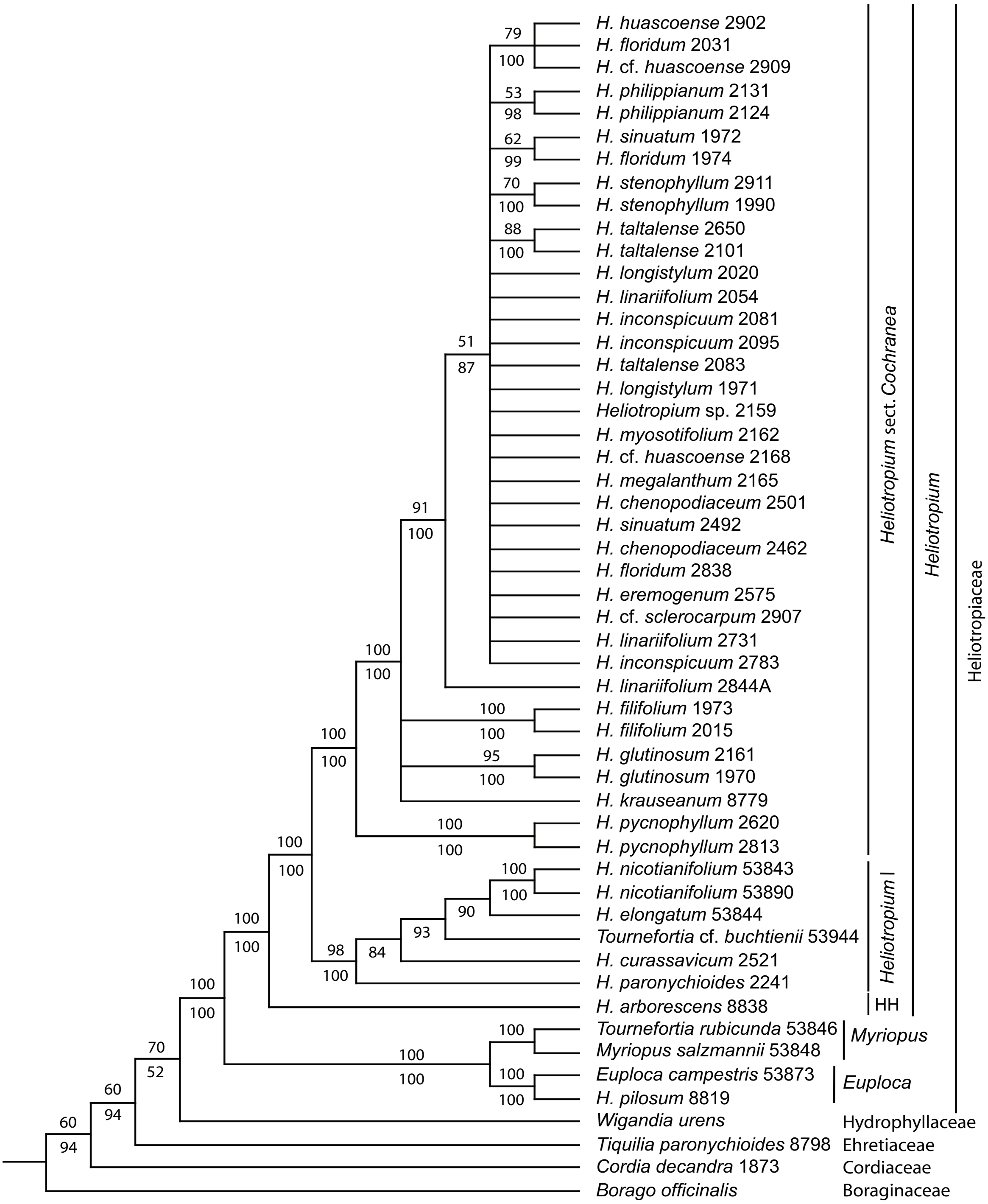

Figure 2.3: Strict consensus tree from the parsimony analysis of the combined analysis of ITS and cpDNA (*ndhF*+*rps*16+*trnL*-*trnF*), with bootstrap support > 50% indicated above branches and Bayesian posterior probabilities > 50% below. HH = *Heliotropium* sect. *Heliothamnus*.

within *Heliotropium* sect. *Cochranea* revealed in the ML *ndhF* tree are the same as those in the strict consensus tree obtained for the combined ITS+cpDNA analysis (Fig. 2.3).

The minimum ages of divergence times estimated for the nodes of *Heliotropium* sect. *Cochranea* with the three fossil-based constraints are shown in Fig. 2.4. The minimum age for the section was 14.0 ± 2.0 Ma (the middle Miocene) and the minimum age for the large polytomous group within the section was 4.6 ± 0.9 Ma (the early Pliocene). The sensibility

Table 2.2: Age estimates (mean±SD) for the main nodes of Heliotropiaceae, as a result of removing different fossil-based constrains during the analysis. Values in millions of years. Uppercase letters between parentheses in first column indicate nodes in Fig. 2.4

| Crown node | Constraints with three fossils | *Cordia* constraint removed | *Ehretia* constraint removed | *Tournefortia* constraint removed |
|---|---|---|---|---|
| (A) Heliotropiaceae | 55.5±5.8 | 51.8±6.1 | 55.5±5.8 | 52.3±6.3 |
| (B) *Euploca* + *Myriopus* | 35.8±10.2 | 33.5±10.5 | 35.8±10.2 | 33.5±10.5 |
| (C) *Heliotropium* | 37.9±2.0 | 36.9±1.8 | 37.9±2.0 | 29.6±3.0 |
| (IV) *Heliotropium* I + *Heliotropium* sect. *Cochranea* | 30.0 | 30.0 | 30.0 | 20.3±2.2 |
| (D) *Heliotropium* sect. *Cochranea* | 14.0±2.0 | 13.5±2.0 | 14.0±2.0 | 11.4±1.6 |
| (E) *Heliotropium krauseanum* + *H. filifolium* + *H. glutinosum* + Polytomous group | 7.4±1.0 | 7.0±1.0 | 7.4±1.0 | 6.5±0.9 |
| (F) Polytomous group | 4.6±0.9 | 4.4±0.9 | 4.6 ±0.9 | 4.1±0.8 |

analysis shows that there are no major changes in the estimates of divergence times by removing the fossil-based constraints at the *Ehretia* or the *Cordia* nodes. However, when we removed the constraint at the *Tournefortia* sect. *Tournefortia* node, the age for sect. *Cochranea* changed to 11.4 ± 1.6 Ma whereas the age for the polytomous group changed to 4.1 ± 0.8 Ma. The estimates for the nodes indicated in Fig. 2.4 under the different constraints are shown in Table 2.2.

## 2.4 Discussion

### 2.4.1 Systematic Implications of the Phylogenetic Analysis

Our results are in agreement with some of the relationships suggested by Diane et al. (2002) and Hilger and Diane (2003). These include the position of *Euploca* (represented in our analyses by *E. campestris* and *Heliotropium pilosum*) in relation to the rest of Heliotropiaceae and its close relationship with *Myriopus*, the polyphyly of *Tournefortia* s.l., and the subsequent paraphyly of *Heliotropium* in relation to *Tournefortia* sect. *Tournefortia*. The position of *Heliotropium* sect. *Heliothamnus* (represented in our data by *H. arborescens*) as a sister group of section *Cochranea*, *Heliotropium* I and II, is supported by our analysis (Fig. 2.3).

Our analyses support the monophyly of *Heliotropium* sect. *Cochranea* and its sister relationship with the *Heliotropium* I clade. Unfortunately, our ITS + cpDNA data set did not include any representatives of the *Heliotropium* II clade. The phylogentic relationships among the species and sections of *Heliotropium* I and II remain unclear, given the relatively low branch support for the main clades in the ITS1 + *trnL* intron analysis (Hilger and Diane, 2003; Fig. 2.2).

Hilger and Diane (2003) showed that *Heliotropium pycnophyllum* was sister to a clade consisting of the rest of the species of section *Cochranea* (cf. Hilger and Diane, 2003: 34–35). This placement is, however, different from the views previously proposed by Reiche (1907a) and Johnston (1928b, 1929a), largely based on the morphology of the style-stigma complex. Based on similarities of the relative lengths of the style and the stigmatic head, Reiche (1907a) and Johnston (1928b, 1929a) suggested that *H. pycnophyllum* was closely related to *H. linariifolium* (often sympatric with *H. pycnophyllum*), and to the other species of the section with conspicuous vegetative pubescence and with

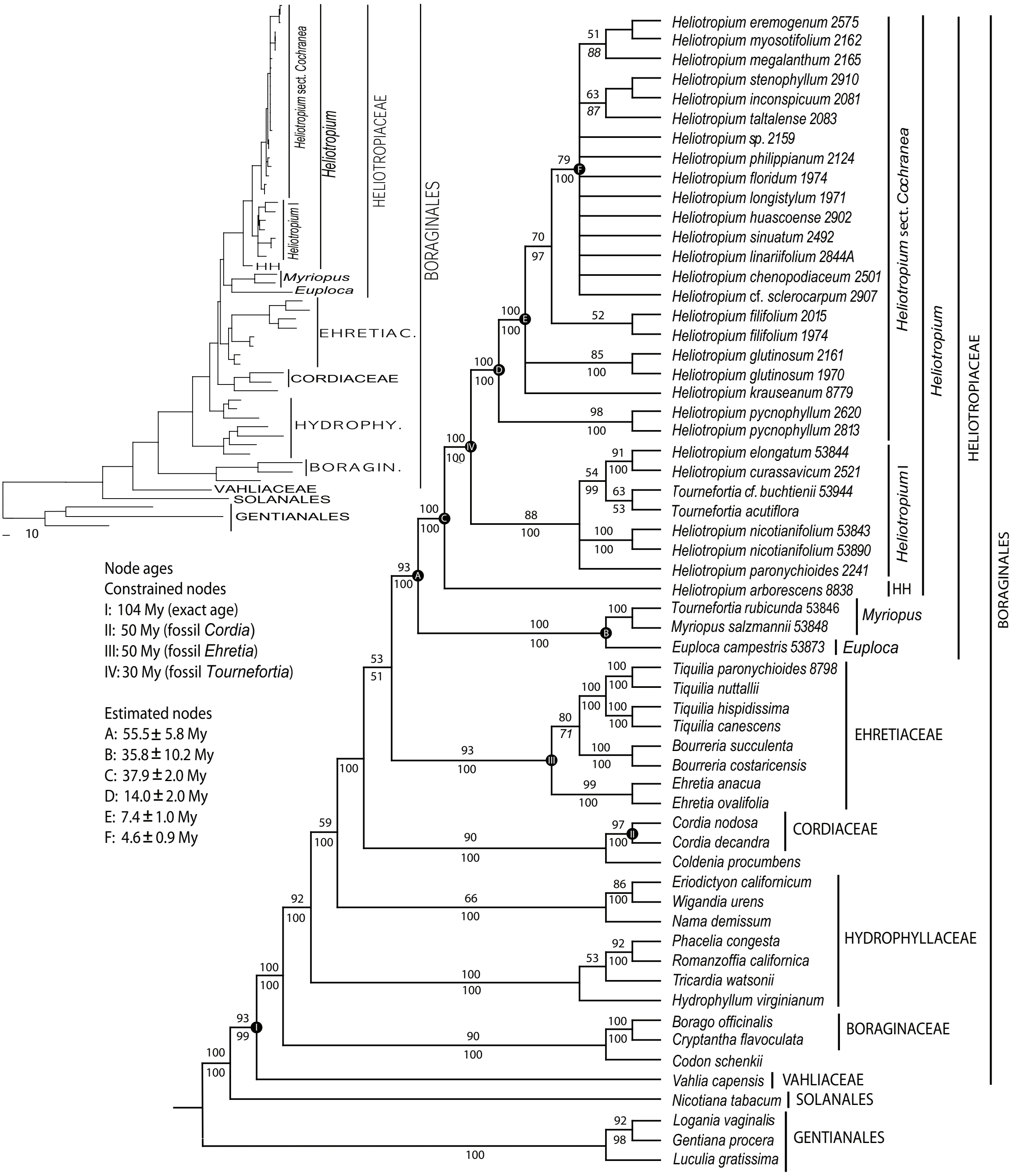

Figure 2.4: Cladogram and phylogram resulting from maximum likelihood analysis of the *ndhF* matrix with parsimony bootstrap support values > 50% indicated above branches and Bayesian posterior probabilities > 50% below. Nodes marked I-IV were constrained as indicated in the text, and nodes marked A-F were estimated as indicated here (three fossil-based constraints) and in Table 2.2. HH = *Heliotropium* sect. *Heliothamnus*.

styles longer than the stigmatic head (*H. floridum*, *H. philippianum*, and *H. eremogenum*). *Heliotropium pycnophyllum* can be distinguished from other species of the section by its folded, subterete and densely pubescent leaves (Reiche, 1907a; Johnston, 1928b). The position of *Heliotropium pycnophyllum* as a sister clade of the rest of the species of section *Cochranea* is also supported by our analysis with a broad sampling of the section. The other well-supported lineage in *Heliotropium* sect. *Cochranea* in our analyses is a tetratomous clade (bootstrap support = 100, Bayesian posterior probability = 100) consisting of *H. krausenaum*, *H. glutinosum*, *H. filifolium* and a large polytomous group of 15 species (Fig. 2.3). The large polytomous group is supported with a bootstrap value of 91% and a Bayesian posterior probability of 1 (Fig. 2.3). But to clarify the relationships among the taxa within the clade, more detailed studies are needed using sequences of fast-evolving nuclear markers or through molecular studies at the population level in combination with morphological analyses.

Johnston (1928b) suggested a close relationship among *Heliotropium sinuatum*, *H. taltalense*, and *H. krauseanum*, because they are all characterized by sinuate leaf-margin and rugose leaf surfaces. He even proposed that *H. krasueanum* could be only a septentrional variation of *H. taltalense* (Johnston, 1928b). Reiche (1907a) reunited *H. sinuatum* and *H. taltalense* under the same species (*H. rugosum* Phil. 1960 nom. illeg. non *H. rugosum* Mart. & Gal. 1844; Table 2.1). These relationships are not sustained by the phylogenetic analysis presented here, which imply *H. krauseanum* as a separate lineage in section *Cochranea* (Figs. 2.3, 2.4), and has *H. taltalense* more closely related to *H. sinuatum* (both fall in the large polytomous group, Fig. 2.3). *Heliotropium glutinosum* was suggested to be related to *H. stenophyllum*, distributed mainly south of La Serena, Chile (Fig. 2.1G), on the basis of the similarity in the morphology of their style-stigma complex (Johnston, 1928b). *Heliotropium filifolium*, another species that can be differentiated in the phylogenetic analysis, is the only species in section *Cochranea* with a sessile stigmatic head, a character commonly present in the sister group of section *Cochranea* (Johnston, 1928b; Gangui, 1955; Förther, 1998). This character led Reiche (1907a) to place *H. filifolium* (treated as *H. kingi* Phil.) in a separate section (Table 2.1). Our results showed that *H. filifolium* is nested within section *Cochranea*.

*Heliotropium eremogenum* was described by Johnston (1937), after his revision of *Heliotropium* in 1928. He suggested that it was closely related to *H. philippianum* of the section *Cochranea*. However, Förther (1998) did not assign this species to a section. Our results confirm the inclusion of *Heliotropium eremogenum* in section *Cochranea*. Our data also support the inclusion of an undescribed species (*Heliotropium* sp. Nr. 2159; Appendix A; Figs. 2.2–2.4) in section *Cochranea*. This species was collected at localities near Iquique and Tocopilla (Fig. 2.1H; Johnston, 1929b: 155; Johnston, 1932: 7; Johnston, 1937: 20), but the fragmentary condition of the material has made it difficult to either describe it as a new taxon or include it in one of the currently recognised species.

## 2.4.2 Age Estimates

### Origin of *Heliotropium* sect. *Cochranea*

The minimum age of *Heliotropium* sect. *Cochranea* was estimated as 14.0 ± 2.0 Ma (during the middle Miocene). The estimate of the middle Miocene origin coincides with a global warming peak, followed by a gradual cooling (Alpers and Brimhall, 1988; Zachos et al., 2001) and when the uplift rate of the Andes became higher (Gregory-Wodzicki, 2000). The uplift of the Andes may have promoted vicariant speciation, isolating section *Cochranea* to the western side, and other lineages of the South American *Heliotropium* (e.g. sections *Coeloma* and *Heliotrophytum*) to the eastern side of the Andes. Roig-Juñent et al. (2006) suggested similar timing and vicariant event for the biogeographical diversification of the arthropods on the arid lands of South America. However, a better resolved phylogeny at the infrageneric level is still needed to reconstruct the biogeographical relationships among the South American sections of *Heliotropium*.

### Diversification of *Heliotropium* sect. *Cochranea* in the Atacama Desert

The cooling trend continued until the early Pliocene (Zachos et al., 2001). During this period, a first diversification event in *Heliotropium* sect. *Cochranea* has been estimated with a minimum age of 7.4 ± 1.0 Ma (late Miocene; Table 2.2) for the crown clade of a tetratomy composed of *H. krauseanum*, *H. filifolium* and *H. glutinosum* and the polytomous group, which are, as a whole, sister to *H. pycnophyllum*. *Heliotropium pycnophyllum* is an extreme xerophyte distributed in the most arid habitats between Antofagasta and Caldera (Fig. 2.1D) in one of the centres of diversity of section *Cochranea* (Fig. 2.1I; Johnston, 1929a,b). *Heliotropium krauseanum* is the only species of section *Cochranea* distributed in Peru (Johnston, 1928b;Fig. 2.1B), mainly in the lomas vegetation of southern Peru (Ferreyra, 1961; Weigend et al., 2003) and northern Chile (Luebert and Pinto, 2004), but has also been reported for the Andean scrub vegetation of central Peru (Weigend et al., 2003). *Heliotropium glutinosum* is also geographically isolated from the rest of the species of section *Cochranea* , being the species with the easternmost distribution, endemic to the creeks of the Andean foothills of the area of Potrerillos, Chile (Johnston, 1928b; Fig. 2.1C). *Heliotropium filifolium* is restricted to the coastal areas between Caldera and la Serena in Chile, with less than a degree of latitudinal distribution (Fig. 2.1C). These geographic ranges as a whole suggest that most of the present distribution of *Heliotropium* sect. *Cochranea* was already established in the late Miocene, which may have been splited through an early major vicariance causing this first diversification event. Geological and climatic events, such as mass landslides from the Andes to the coast (Ochsenius, 1999), the formation of the modern topography of the Coastal Cordillera of northern Chile (González et al., 2003) and the increasing aridity (Hartley, 2003), may have been responsible for the isolated ranges of the individual species.

Another warming phase occurred in the early Pliocene (Zachos et al., 2001), which is coinciding with the estimated minimum age (4.8 ± 0.9 Ma) of the major polytomous lineage of *Heliotropium* sect. *Cochranea* (Figs. 2.3 and 2.4). A Pliocene diversification in the Atacama Desert was previously suggested for other plant groups, such as *Malesherbia* sect. *Malesherbia* (Gengler-Nowak, 2002b, 2003) and *Polyachyrus* (Asteraceae; Katinas and Crisci, 2000). Moore and Jansen (2006) reported an early Pliocene diversification event in the genus *Tiquilia* (Ehretiaceae) as correlated with the expansion of arid habitats in North and South America.

We interprete the lack of phylogenetic resolution with four molecular markers (Fig. 2.3), and the short branch lengths observed among the species of the large polytomous clade (see Fig. 2.4) as evidence for a rapid evolutionary radiation of *Heliotropium* sect. *Cochranea* in the coastal Atacama Desert of South America. However, we cannot conclude that the large polytomous group, as shown in the strict consensus tree of Fig. 2.3, is a 'hard' polytomy (Maddison, 1989). Analysis of more rapidly evolving molecular markers may enhance the phylogenetic resolution within this group. Nonetheless, the short branch lengths and the failure of the present phylogentic analysis to resolve relationships (Fig. 2.3) in both nuclear ITS and cpDNA topologies, indicate the close relationships and possibly lack of molecular differentiation between these species. An evolutionary radiation of most species of *Heliotropium* sect. *Cochranea* in the coastal Atacama Desert of South America in the early Pliocene is consistent with our result, but likely does not explain all the morphological diversity of the group. Further diversification events in *Heliotropium* sect. *Cochranea* may have taken place between the early Pliocene and the present, but they are not resolved in our analysis.

Stebbins (1952) viewed evolution in arid zones as a history of contraction-isolation and expansion-recombination among populations in response to changes in local climatic conditions. Such a process could be conceived under the framework of metapopulation dynamics (Hanski, 1998). *Heliotropium* sect. *Cochranea* may have diversified in such a way in the Atacama Desert. Paleoclimatic data reported for the Quaternary indicate a general trend to moisture fluctuation at different temporal scales over the Atacama (e.g., Lamy et al., 1998; Ochsenius, 1999; Betancourt et al., 2000; Holmgren et al., 2001a; Maldonado and Villagrán, 2002; Latorre et al., 2002, 2003; Núñez et al., 2002; Grosjean et al., 2003; Núñez and Grosjean, 2003; Stuut and Lamy, 2004; Maldonado et al., 2005). Isolation episodes may be the reason for the morphological, ecological and geographical differentiation among the species of *Heliotropium* sect. *Cochranea* that is not explained by our molecular analysis. The cpDNA markers used in this study (*ndhF*, *rps*16 and *trnL-trnF*) may also be too conservative to produce consistent differentiations among the species. The nuclear ITS sequences can be subject to the homogenizing effects of recombination via concerted evolution (Zimmer et al., 1980) during periods of expansion of populations. Additional studies are still needed to test these hypotheses.

# 3. Phylogenetic Relationships and Morphological Diversity in Neotropical *Heliotropium* (Heliotropiaceae)[a]

## Abstract

To understand morphological diversification of taxa it is fundamental to establish a phylogenetic framework and to document morphological variation. Little is known about the vegetative morphological diversification in Neotropical plant clades in comparison with the better studied diversification of reproductive characters. Phylogenetic relationships of the Neotropical *Heliotropium* (Heliotropiaceae) are studied and the vegetative morphological diversity (leaf morphology and habit) is compared among the clades resolved and between groups of species inhabiting dry and humid areas. A representative sampling of Neotropical *Heliotropium* was analysed, using four plastid regions (*trnL-trnF*, *trnS-trnG*, *trnH-psbA*, *rps*16) and nuclear ribosomal Internal Transcribed Spacer (ITS), with parsimony, maximum likelihood and Bayesian methods. Morphological diversity was measured as the amount of morphospace occupied and as the variance of individual characters. Neotropical *Heliotropium* is composed of three well-supported clades: (1) *Heliotropium* sect. *Heliothamnus* from the tropical Andes; (2) *Heliotropium* sect. *Cochranea* from the Peruvian and the Atacama Deserts; and (3) the *Tournefortia* clade, comprising the remaining American sections of *Heliotropium* and the mainly Neotropical *Tournefortia* sect. *Tournefortia*. Phylogenetic discordance between the plastid and nuclear partitions was detected. Lineage sorting and hybridization might be responsible for the phylogenetic discordance. The *Tournefortia* clade shows the greatest morphological diversity, which tends to be greater in dry than in humid areas, but with no statistical support. *Heliotropium* sect. *Cochranea* is as diverse as the *Tournefortia* clade in leaf morphology and may have experienced an adaptive radiation in the Atacama Desert. *Heliotropium* sect. *Heliothamnus* has the lowest vegetative diversity of the three Neotropical clades. This study further confirms the need to re-evaluate the infrageneric delimitation in *Heliotropium*.

## 3.1 Introduction

Recent phylogenetic studies on Neotropical vascular plants have often focused on the diversification of reproductive characters. The evolution of pollination mechanisms and concomitant changes in floral morphology have received much attention, with rapid evolutionary diversification observed in numerous Neotropical plant groups (see Jaramillo and Manos, 2001; Ackermann and Weigend, 2006; Smith and Baum, 2006; Weigend and Gottschling, 2006; Perret et al., 2007; Jabaily and Sytsma, 2010). Conversely, few studies have addressed the considerable divergence in vegetative morphology, especially habit

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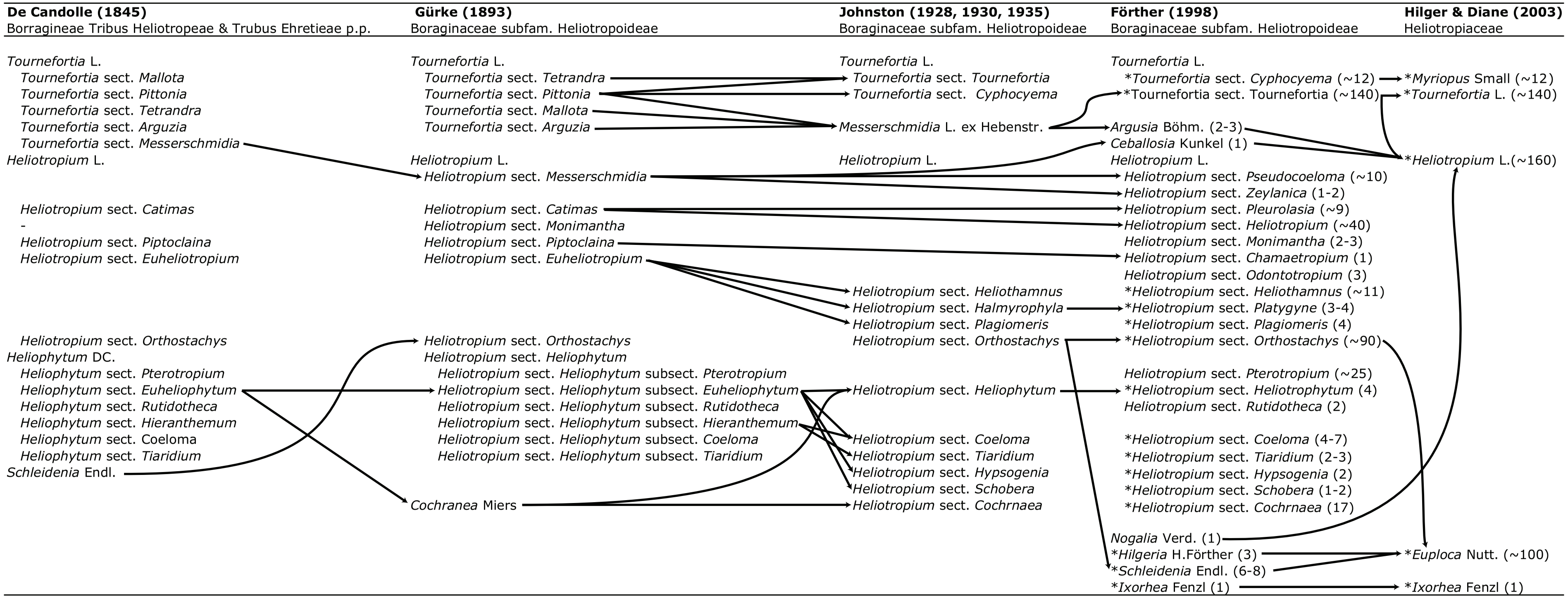
and leaf morphology (but see Struwe et al., 2009). This may be due to a variety of factors. For exmaple, habit is often largely conserved across genera, families, or even larger clades (Smith and Donoghue, 2008) and is often difficult to understand from inspection of herbarium specimens and is poorly documented in the literature. Also, in individual plant families with divergent vegetative morphology, the phylogenetic trees often do not have internal resolution, making it difficult to interpret the morphological diversification. This is for example the case in groups such as *Gentianella* (Gentianaceae, von Hagen and Kadereit, 2001) and *Lupinus* (Fabaceae, Hughes and Eastwood, 2006). In *Heliotropium* also, lack of phylogenetic resolution (Hilger and Diane, 2003) prevents the interpretation of vegetative morphological diversification (Diane et al., 2003).

Heliotropiaceae (≡ Boraginaceae subfam. Heliotropoideae) is a family of about 450 species, with a nearly worldwide distribution, mainly in the tropical and subtropical regions. It has one clear centre of diversity in the Neotropics, with the bulk of the species in *Tournefortia* L. and *Euploca* Nutt. (Förther, 1998; Gottschling et al., 2004). Due to the scarcity of informative reproductive characters, the systematics of the Heliotropiaceae has remained highly controversial. Table 3.1 summarizes the taxonomic history of the genus *Heliotropium* and its allies, and indicates the infrageneric units currently recognised in the Neotropics with their respective species numbers.

Neotropical representatives of *Heliotropium* in the current circumscription of the genus (Diane et al., 2002; Hilger and Diane, 2003) comprise only 50–60 species, but are widely variable in vegetative morphology. In contrast, their floral and fruit morphology is comparatively conserved. Habits of the two largest Neotropical subgroups are well known (Fig. 3.1). Members of both sect. *Heliothamnus* I.M.Johnst. (Andean, ca. 11 spp.) and sect. *Cochranea* (Miers) Kuntze (Atacama Desert, 17 spp.) are long-lived shrubs ca. 0.4–4 m tall. The remaining ca. 25 species are quite divergent in their vegetative morphology. These species include subshrubs (*H. amplexicaule* Vahl), small annuals (e.g., *H. paronychioides* A.DC.), leaf-succulent, halophytic, mat-forming perennials with massive tap-roots (*H. curassavicum* L.), tall indeterminate herbs from mesic habitats (*H. elongatum* (Lehm.) I.M.Johnst., and *H. indicum* L.), perennial herbs with root-tubers (*H. microstachyum* Ruiz & Pav.), or decumbent perennial herbs with extensively rooting, creeping shoots (*H. veronicifolium* Griseb.). Considerable variation among Neotropical *Heliotropium* has also been observed in leaf morphology and anatomy (Diane et al., 2003). Such vegetative diversity seems to be correlated with occurrence in dry climates (Diane et al., 2003). If so, vegetative diversity would tend to be greater in species groups growing in dry areas than in those associated with humid areas.

Molecular phylogenetic analyses (Diane et al., 2002; Hilger and Diane, 2003; Luebert and Wen, 2008; see Chapter 2), based on the nuclear ribosomal Internal Transcibed Spacer 1 (ITS1) and the plastid *trnL* intron, showed that the two largest genera of Heliotropiaceae, *Heliotropium* and *Tournefortia* as circumscribed by Förther (1998), are paraphyletic and polyphyletic, respectively. The Neotropical endemic sections *Cochranea* and *Heliothamnus* have been shown to be monophyletic. Tournefortia s.str. (≡ *Tournefortia* sect. *Tournefortia* ≡ *Tournefortia* sensu Förther (1998) excl. sect. *Cyphocyema* I.M.Johnst., the latter tranferred to *Myriopus* Small by Hilger and Diane (2003), see Table 3.1), with its drupaceous fruits, was shown to be deeply nested within the now more narrowly circumscribed dry-fruited genus *Heliotropium*, and in particular, was associated with the Neotropical species of that genus (*Heliotropium* I clade, Hilger and Diane, 2003). However, detailed phylogenetic relationships of Neotropical *Heliotropium* and *Tournefortia* s.str. have remained largely unresolved. The *Tournefortia–Heliotropium* clade (Hilger

Table 3.1: Systematics of Heliotropiaceae according to different authors. Note: In the two last columns, taxa with Neotropical representatives are indicated with an asterisk, and approximate number of species is given in parentheses.



| **De Candolle (1845)** | **Gürke (1893)** | **Johnston (1928, 1930, 1935)** | **Förther (1998)** | **Hilger & Diane (2003)** |
|---|---|---|---|---|
| Borragineae Tribus Heliotropeae & Trubus Ehretieae p.p. | Boraginaceae subfam. Heliotropoideae | Boraginaceae subfam. Heliotropoideae | Boraginaceae subfam. Heliotropoideae | Heliotropiaceae |
| *Tournefortia* L. | *Tournefortia* L. | *Tournefortia* L. | *Tournefortia* L. | |
| *Tournefortia* sect. *Mallota* | *Tournefortia* sect. *Tetrandra* | *Tournefortia* sect. *Tournefortia* | **Tournefortia* sect. *Cyphocyema* (~12) | **Myriopus* Small (~12) |
| *Tournefortia* sect. *Pittonia* | *Tournefortia* sect. *Pittonia* | *Tournefortia* sect. *Cyphocyema* | *Tournefortia sect. Tournefortia (~140) | **Tournefortia* L. (~140) |
| *Tournefortia* sect. *Tetrandra* | *Tournefortia* sect. *Mallota* | | | |
| *Tournefortia* sect. *Arguzia* | *Tournefortia* sect. *Arguzia* | *Messerschmidia* L. ex Hebenstr. | *Argusia* Böhm. (2-3) | |
| *Tournefortia* sect. *Messerschmidia* | | | *Ceballosia* Kunkel (1) | |
| *Heliotropium* L. | *Heliotropium* L. | *Heliotropium* L. | *Heliotropium* L. | **Heliotropium* L.(~160) |
| | *Heliotropium* sect. *Messerschmidia* | | *Heliotropium* sect. *Pseudocoeloma* (~10) | |
| | | | *Heliotropium* sect. *Zeylanica* (1-2) | |
| *Heliotropium* sect. *Catimas* | *Heliotropium* sect. *Catimas* | | *Heliotropium* sect. *Pleurolasia* (~9) | |
| - | *Heliotropium* sect. *Monimantha* | | *Heliotropium* sect. *Heliotropium* (~40) | |
| *Heliotropium* sect. *Piptoclaina* | *Heliotropium* sect. *Piptoclaina* | | *Heliotropium* sect. *Monimantha* (2-3) | |
| *Heliotropium* sect. *Euheliotropium* | *Heliotropium* sect. *Euheliotropium* | | *Heliotropium* sect. *Chamaetropium* (1) | |
| | | | *Heliotropium* sect. *Odontotropium* (3) | |
| | | *Heliotropium* sect. *Heliothamnus* | **Heliotropium* sect. *Heliothamnus* (~11) | |
| | | *Heliotropium* sect. *Halmyrophyla* | **Heliotropium* sect. *Platygyne* (3-4) | |
| | | *Heliotropium* sect. *Plagiomeris* | **Heliotropium* sect. *Plagiomeris* (4) | |
| *Heliotropium* sect. *Orthostachys* | *Heliotropium* sect. *Orthostachys* | *Heliotropium* sect. *Orthostachys* | **Heliotropium* sect. *Orthostachys* (~90) | |
| *Heliophytum* DC. | *Heliotropium* sect. *Heliophytum* | | | |
| *Heliophytum* sect. *Pterotropium* | *Heliotropium* sect. *Heliophytum* subsect. *Pterotropium* | | *Heliotropium* sect. *Pterotropium* (~25) | |
| *Heliophytum* sect. *Euheliophytum* | *Heliotropium* sect. *Heliophytum* subsect. *Euheliophytum* | *Heliotropium* sect. *Heliophytum* | **Heliotropium* sect. *Heliotrophytum* (4) | |
| *Heliophytum* sect. *Rutidotheca* | *Heliotropium* sect. *Heliophytum* subsect. *Rutidotheca* | | *Heliotropium* sect. *Rutidotheca* (2) | |
| *Heliophytum* sect. *Hieranthemum* | *Heliotropium* sect. *Heliophytum* subsect. *Hieranthemum* | | | |
| *Heliophytum* sect. Coeloma | *Heliotropium* sect. *Heliophytum* subsect. *Coeloma* | *Heliotropium* sect. *Coeloma* | **Heliotropium* sect. *Coeloma* (4-7) | |
| *Heliophytum* sect. *Tiaridium* | *Heliotropium* sect. *Heliophytum* subsect. *Tiaridium* | *Heliotropium* sect. *Tiaridium* | **Heliotropium* sect. *Tiaridium* (2-3) | |
| *Schleidenia* Endl. | | *Heliotropium* sect. *Hypsogenia* | **Heliotropium* sect. *Hypsogenia* (2) | |
| | | *Heliotropium* sect. *Schobera* | **Heliotropium* sect. *Schobera* (1-2) | |
| | *Cochranea* Miers | *Heliotropium* sect. *Cochrnaea* | **Heliotropium* sect. *Cochrnaea* (17) | |
| | | | *Nogalia* Verd. (1) | |
| | | | **Hilgeria* H.Förther (3) | **Euploca* Nutt. (~100) |
| | | | **Schleidenia* Endl. (6-8) | |
| | | | **Ixorhea* Fenzl (1) | **Ixorhea* Fenzl (1) |

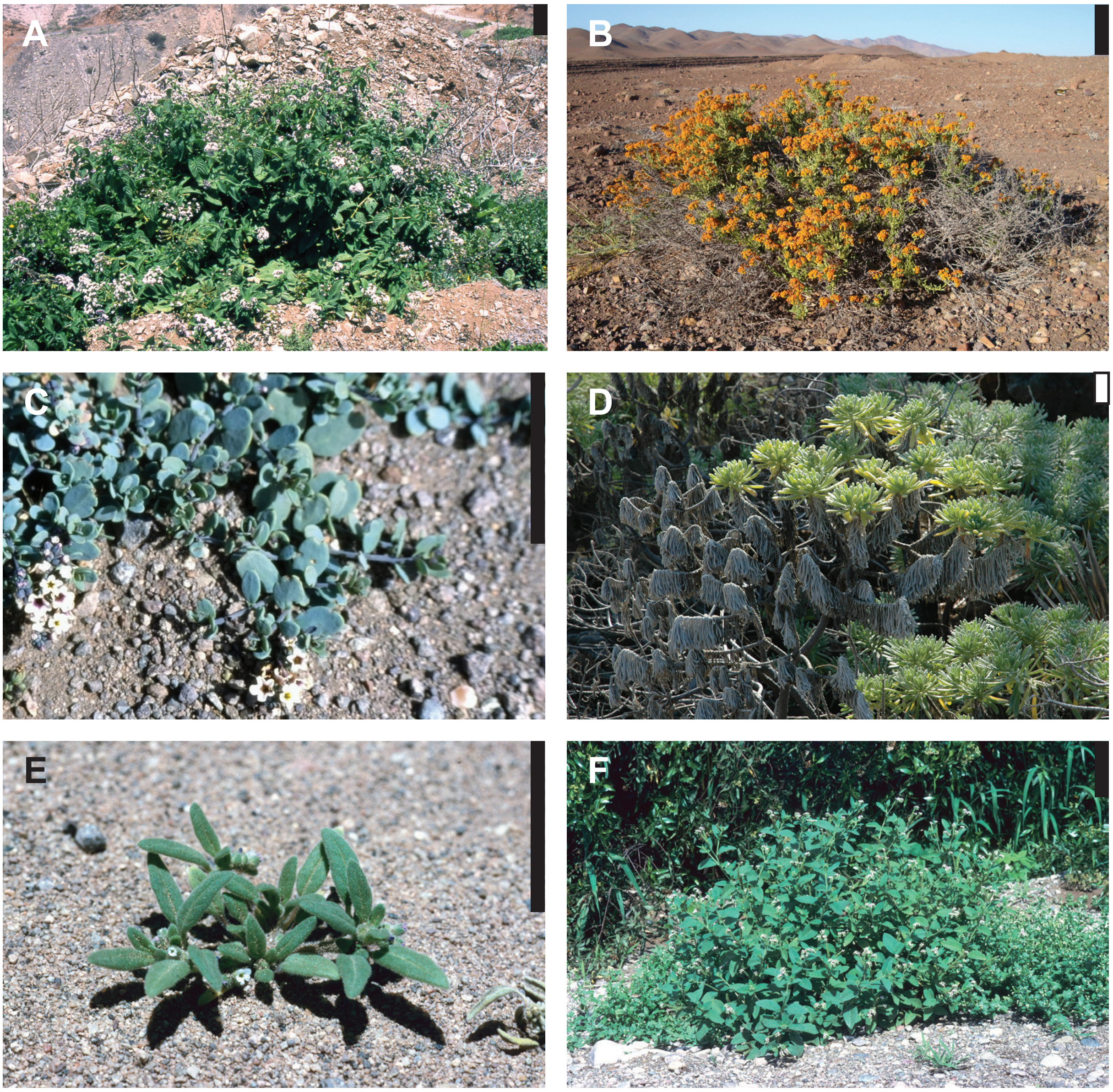


Figure 3.1: Habit of some Heliotropiaceae in their natural habitats. A, *Heliotropium arborescens* (sect. *Heliothamnus*, Photo M. Ackermann, Peru). B, *Heliotropium linariifolium* (sect. *Cochranea*, Photo F. Luebert, Chile). C, *Heliotropium. patagonicum* (sect. *Platygyne*, Photo M. Weigend, Argentina). D, *Tournefortia gnaphalodes* (Photo H.H. Hilger, Cuba). E, *Heliotropium paronychioides* (sect. *Plagiomeris*, Photo H.H. Hilger, Argentina). F, *Heliotropium nicotianifolium* (sect. *Heliotrophytum*, Photo H.H. Hilger, Argentina). Approximate scales bars (10 cm) are given in the top-right corner.

and Diane, 2003) now encompasses taxa with dry and drupaceous fruits, and annuals, halophytic and non-halophytic perennials, shrubs, woody lianas and small trees.

Morphological variation, or disparity (Foote, 1993, 1997), defined as the amount of morphospace occupied by a given taxon, has received increasing attention in several recent studies to assess the differences and likely explanations to the observation that disparity is unevenly distributed across clades (e.g., Collar et al., 2005, 2009; Sidlauskas, 2007; Adams et al., 2009). However, most studies of disparity have been carried out in animals. Furthermore, little is known about the possible effects of different ecological conditions on disparity. Two hypotheses are explicitly tested in this study: 1) that vegetative morphological diversity in Neotropical *Heliotropium* is unevenly distributed across the clades, and 2) that it may be associated with adaptations to dry habitats.

The present study therefore focuses on the following questions: (1) which clades can be resolved within the Neotropical *Heliotropium* and what is the relative branching order of these clades? (2) How are Neotropical *Heliotropium* related to Old World *Heliotropium* and to *Tournefortia* s.str.? (3) Are there differences in vegetative morphological disparity among clades of Neotropical *Heliotropium* or between groups of species inhabiting dry and humid environments? To address these questions, phylogenetic analyses using five molecular markers were carried out, with a dense sampling of New World sections of *Heliotropium*, and the habit and leaf morphology were investigated via extensive field work, cultivation, as well as laboratory and herbarium studies.

## 3.2 Materials and Methods

### 3.2.1 Plant Material and Outgroup Selection

Our taxon sampling for the molecular data included at least two representatives of each section currently recognised in Neotropical *Heliotropium* (sensu Förther, 1998 excl. section *Orthostachys* ≡ *Euploca*, sensu Hilger and Diane, 2003), eight species of *Tournefortia* sect. *Tournefortia* and six representatives of the Old World *Heliotropium* (*Heliotropium* II sensu Hilger and Diane, 2003). Our sampling also included the monospecific genus *Ceballosia* Kunkel ex H.Förther. We employed the plastid *rps*16 intron, *trnL-trnF* region, *trnH-psbA* and *trnS-trnG* intergenic spacers, and nuclear ribosomal ITS. Outgroup selection was based on Diane et al. (2002), Hilger and Diane (2003) and Luebert and Wen (2008; see Chapter 2), and comprised the genera *Euploca*, *Ixorhea* Fenzl and *Myriopus* from Heliotropiaceae, as well as one species from each of the following genera, *Tiquilia* Pers., *Cordia* L. and *Wigandia* Kunth, representing the closely allied families Ehretiaceae, Cordiaceae and Hydrophyllaceae, respectively (Ferguson, 1999; Gottschling et al., 2001; Moore and Jansen, 2006; Luebert and Wen, 2008). For *rps*16 and *trnL-trnF*, some already published sequences (Luebert and Wen, 2008) were included in the analysis (Appendix B.1). Three datasets were phylogenetically analysed: the plastid data (*rps*16, *trnL-trnF*, *trnH-psbA* and *trnS-trnG*), the ITS data, and the combined plastid and ITS data.

### 3.2.2 DNA Extraction, Amplification and Sequencing

DNA was extracted from samples of silica-gel-dried leaves or herbarium material with a modified CTAB method (Doyle and Doyle, 1987). The PCR amplifications were performed in a Trio-Thermoblock thermal cycler (Biometra, Göttingen, Germany) in a 25 $\mu$l volume containing 0.6 U of Taq Polymerase, 5.0 mM $MgCl_2$, 100 $\mu$M of each dNTP, 0.2 $\mu$M of each primer and about 50 ng of genomic DNA. Amplification primers and cycling conditions followed Moore and Jansen (2006) for *rps*16 and ITS. Primers ‘c’ and ‘f’ were used for the amplification of the *trnL-trnF* region (Taberlet et al., 1991) and the thermal cycling conditions were the same as that for *rps*16. Primers trnH$^{GUG}$ and psbA (Shaw et al., 2005) were used for amplifying the *trnH-psbA* intergenic spacer with 5 min initial denaturation at 95°C, 35 cycles of 95°C, 30 s; 48°C, 1 min; 72°C, 1 min, and a final elongation period of 4 min at 72°C. The amplification of the *trnS-trnG* intergenic spacer used primers trnS and trnG (Hamilton, 1999) with cycling conditions as for *trnH-psbA*, but with annealing temperature of 50°C instead of 48°C. PCR products were purified with the peqGold Cycle-

Pure Kit (PEQLAB Biotechnologie GmbH, Erlangen, Germany) or the QIAquick PCR Purification Kit (Qiagen GmbH, Hilden, Germany) following the manufacturer's instructions. Cycle sequencing was performed with BigDye Terminator v3.1 (Applied Biosystems, Foster City, California, USA). The resulting sequences were assembled using Chromas Pro v.1.33 (Technelysium Pty Ltd, Tewantin, QLD, Australia) and aligned using the software Mafft v.6.603 (Katoh et al., 2002) followed by manual adjustments using Se-Al 2.0a11 (Rambaut, 1996). Ambiguously aligned regions were removed from further analysis. The 215 new sequences were deposited in GenBank (Appendix B.1).

### 3.2.3 Phylogenetic Analysis

Phylogenetic analyses were carried out with maximum parsimony (MP, Farris et al., 1970), maximum likelihood (ML, Felsenstein, 1981) and Bayesian (BA, Mau et al., 1999) methods for the plastid and the ITS datasets separately. MP was performed with PAUP* 4.0. (Swofford, 2003); ML was run in Garli v.0.951 (Zwickl, 2006); and BA was conducted using MrBayes v.3.1 (Ronquist and Huelsenbeck, 2003). The MP analysis was done with the heuristic search, setting random taxon-addition replicates to 10, tree bisection-reconnection branch swapping, multitrees in effect, collapsing branches of zero-length, characters as equally weighted, gaps treated as missing data, and a maximum of 50,000 trees saved in each replicate. Branch support of the maximally parsimonious trees (MPTs) was assessed by bootstrap analysis, using a heuristic search with 1000 replicates and the same settings used in the MP search, but saving a maximum of 1000 trees in each random taxon-addition replicate. The nucleotide substitution model that best fits the data was determined with the AIC criterion using Modeltest v.3.7 (Posada and Crandall, 1998) prior to the ML and BA analyses. The ML analyses waere performed under the selected substitution model, with partitions linked in the plastid analysis, with random-starting parameters and using a random-starting tree. The run was terminated after 10,000 generations without an improvement of the topology under a 0.05 score improvement threshold. Branch support was calculated with 500 nonparametric bootstrap replicates using the same settings as described above. BA was carried out, under the selected model, with partitions linked in the plastid analysis, for $4\text{x}10^6$ generations with a sampling frequency every 1000 generations in two independent runs. After inspection of convergence in Tracer v.1.4 (available at `http://tree.bio.ed.ac.uk/software/tracer/`, accessed 24 April 2008), the $1\text{x}10^6$ first generations were discarded as burn-in.

To test incongruence between the plastid and the ITS datasets, the combined dataset with two data partitions was used and the Incongruence Length Difference (ILD) test (Farris et al., 1994) was performed in PAUP* 4.0. Incongruence was further explored in the parsimony context using the partitioned Bremer support (PBS; Baker and DeSalle, 1997) as implemented in TreeRot v.3. (Sorenson and Franzosa, 2007), using a heuristic search with 100 random addition replicates and saving maximum 500 trees in each replicate. As suggested by Lambkin et al. (2002), the average values, as well as the maximum and minimum values of the PBS were recorded. The PBS was calculated for the nodes of the MP strict consensus tree obtained from a MP combined analysis. To check for the consistency of the analysis, the decay index (Bremer, 1988) was also calculated for the clades recovered in MP strict consensus trees of the individual plastid and ITS partitions of the combined dataset using TreeRot v.3.

The MP and BA analyses were conducted on the computer cluster of the Freie Universität Berlin. All obtained trees were rooted with *Tiquilia*, *Cordia* and *Wigandia* as the outgroups (see Appendix B.1).

## 3.2.4 Vegetative Disparity of Clades

Seventeen vegetative morphological characters (leaf morphology and habit, Table 3.2) were coded for 61 species of Heliotropiaceae, 54 of which matched our molecular sampling. Data on habit, leaf size and leaf form were obtained from our field studies (FL, MW, HH) in Chile, Argentina, Peru, Ecuador and Colombia, herbarium work in A, AAU, B, BM, BSB, CONC, DR, EIF, F, G, GH, K, LL, M, MA, MO, NY, QCA, SGO, TEX, ULS, US, USM, and literature research (see Appendix B.2).

Table 3.2: Characters and character states used in the analysis of morphological diversity.

| | Character | Character states | Character type |
|---|---|---|---|
| | *Leaf morphology* | | |
| 1 | Leaf form | length:width ratio | continuous |
| 2 | Leaf size | $\log_{10}$-transformed of the area of an ellipse | continuous |
| 3 | Leaf venation | 0 = hyphodromous, 1 = brochidodromous | binary symmetric |
| 4 | Leaf anatomy | B = bifacial, S = subbifacial, I = isobilateral | nominal |
| 5 | Stomata distribution | 0 = hypostomatous, 1 = amphistomatous | binary symmetric |
| 6 | Multicellular glandular trichomes | 1 = present, 0 = absent | binary asymmetric |
| 7 | Unicellular simple hairs | 1 = present, 0 = absent | binary asymmetric |
| 8 | Unicellular two-armed hairs | 1 = present, 0 = absent | binary asymmetric |
| 9 | Trichome tip reduced | 1 = present, 0 = absent | binary asymmetric |
| 10 | Trichome cistolyth | 1 = present, 0 = absent | binary asymmetric |
| 11 | Crystal tubes in mesophyll | 1 = present, 0 = absent | binary asymmetric |
| 12 | Crystal druses in mesophyll | 1 = present, 0 = absent | binary asymmetric |
| | *Habit* | | |
| 13 | Habit | 0 = Woody, 1 = Herbaceous | binary symmetric |
| 14 | Longevity | 0 = perennial, 1 = Annual | binary symmetric |
| 15 | Axis orientation | E = erect, D = decumbent, S = Scandent | nominal |
| 16 | Root system | F = fibrous, T= tap-root, R = root tuber | nominal |
| 17 | Plant height | $\log_{10}$-transformed of total height (cm) | continuous |

Plant height, leaf length, and leaf width were assessed using the median values of ranges as given in the literature. Because only a few descriptions are available for *Heliotropium* sect. *Cochranea*, the values were obtained from measurements in the field (plant height) and on herbarium specimens (leaf length and width). Leaf size was estimated as the area of an ellipse. Leaf form was approximated using the length : width ratio (Martorell and Ezcurra, 2007). Plant height and leaf size were $\log_{10}$-transformed for all analyses, which is appropriate in this case because both characters span several orders of magnitude and log-ransformed values better represent proportional changes in size than absolute values (Kerkhoff and Enquist, 2009). Data on leaf anatomy and micromorphology were obtained from Light Microscopy (LM) and Scanning Electron Microscopy (SEM) from FAA-fixed material and from Diane et al. (2003) (see Appendix B.2). For LM, the tissue was dehydrated with formaldehyde-dimethyl-acetal (FDA) and embedded in paraplast via a graded ethanol-tertiary butanol series. After microtome sectioning, the samples were stained with safranin-astra blue. For SEM, the tissue was initially dehydrated in FDA and acetone, followed by critical point-drying with $CO_2$ (Pathan et al., 2008), and sputter-coated with gold. Terminology on micropmorphological and anatomical characters follows Diane et al. (2003).

To assess vegetative diversity a dissmiliarity matrix was built using the coefficient proposed by Gower (1971), which can handle mixtures of different kinds of data, as well as missing values (Gower and Legendre, 1986). This matrix was made Euclidean using the smallest positive constant (Cailliez, 1983). A Principal Coordinates Analysis (PCO) was conducted based on the Euclidean dissimilarity matrix, and the PCO space was considered as the morphospace of the vegetative traits of *Heliotropium* (Foote, 1999). Separate analyses were conducted for all characters (Table 3.2), leaf morphological characters (characters 1–12 of Table 3.2), and habit characters (characters 13–17 of Table 3.2). Species were mapped onto the first two axes of the PCO for visual inspection. To assess differences in morphological diversity among clades, pairwise differences in variance among clades was tested using the permutation test as proposed by Anderson (2006) with 999 permutations, that is a multivariate analogue of the Levene's test, which is robust to departures of normality (Anderson, 2006; Oksanen et al., 2010). This procedure is equivalent to compare disparity as defined in Foote (1993).

To assess whether high vegetative disparity is associated with dry habitats, we compared the morphological diversity, as described above, between two types of climates defined by aridity. The values of the aridity index (AI, Middleton and Thomas, 1992) were obtained in GIS from the map developed by Hoogeveen (2009), for the spatial median of each species. The spatial medians were calculated from georeferenced localities of the species from the revised herbarium specimens and from selected data accessed through the GBIF data portal (`http://data.gbif.org/`). For the purposes of the comparisons, the species were divided into two classes, dry ($AI<1$) and humid ($AI\geqslant1$), which correspond to negative and positive water balance, respectively. This comparison was performed for all Neotropical *Heliotropium* species, as well as for species within clades, insofar as the clades include both species inhabiting dry and humid areas.

Additional comparisons of disparity were conducted among Neotropical clades, but using single continuous variables, namely plant height, leaf form, and leaf size (characters 17, 1 and 2 of Table 3.2, respectively). The pairwise differences in variance of these variables were tested using Levene's test. The same procedure was employed to test differences in variances of these variables between the two classes of aridity described above. All statistical analyses were conducted in R v. 2.10.1 (R Development Core Team, 2009), using the packages ade4 (Dray et al., 2007), cluster (Maechler et al., 2005), and vegan (Oksanen et al., 2010).

## 3.3 Results

### 3.3.1 Phylogenetic Analysis of Plastid Data

Our plastid dataset (*rps*16, *trnL-trnF*, *trnS-trnG*, and *trnH-psbA*) contained 3414 aligned positions, of which 178 were excluded from the matrix due to ambiguous alignment, rendering an alignment of 3236 positions with 1149 variable and 520 parsimony-informative sites. The 500,000 MPTs from our MP analyses with the ambiguous regions removed had tree length of 1815 steps, a consistency index (CI) of 0.77 and a retention index (RI) of 0.77. The selected substitution model was GTR+Γ.

The results of the phylogenetic analyses are shown in Fig. 3.2. MP, ML and BA analyses revealed an identical topology with respect to the major clades. Monophyly of the family Heliotropiaceae was confirmed by our analysis. The position of *Ixorhea* was consistently recovered as sister to all other Heliotropiaceae, but with low support (57%

bootstrap support and <50% Bayesian posterior probability). The remaining taxa were segregated into two well-supported clades: *Euploca* and *Myriopus* forming one clade, and *Heliotropium* and *Tournefortia* s.str. constituting the other clade. *Tournefortia rubicunda* and *Heliotropium pilosm* are confirmed as members of *Myriopus* and *Euploca*, respectively.

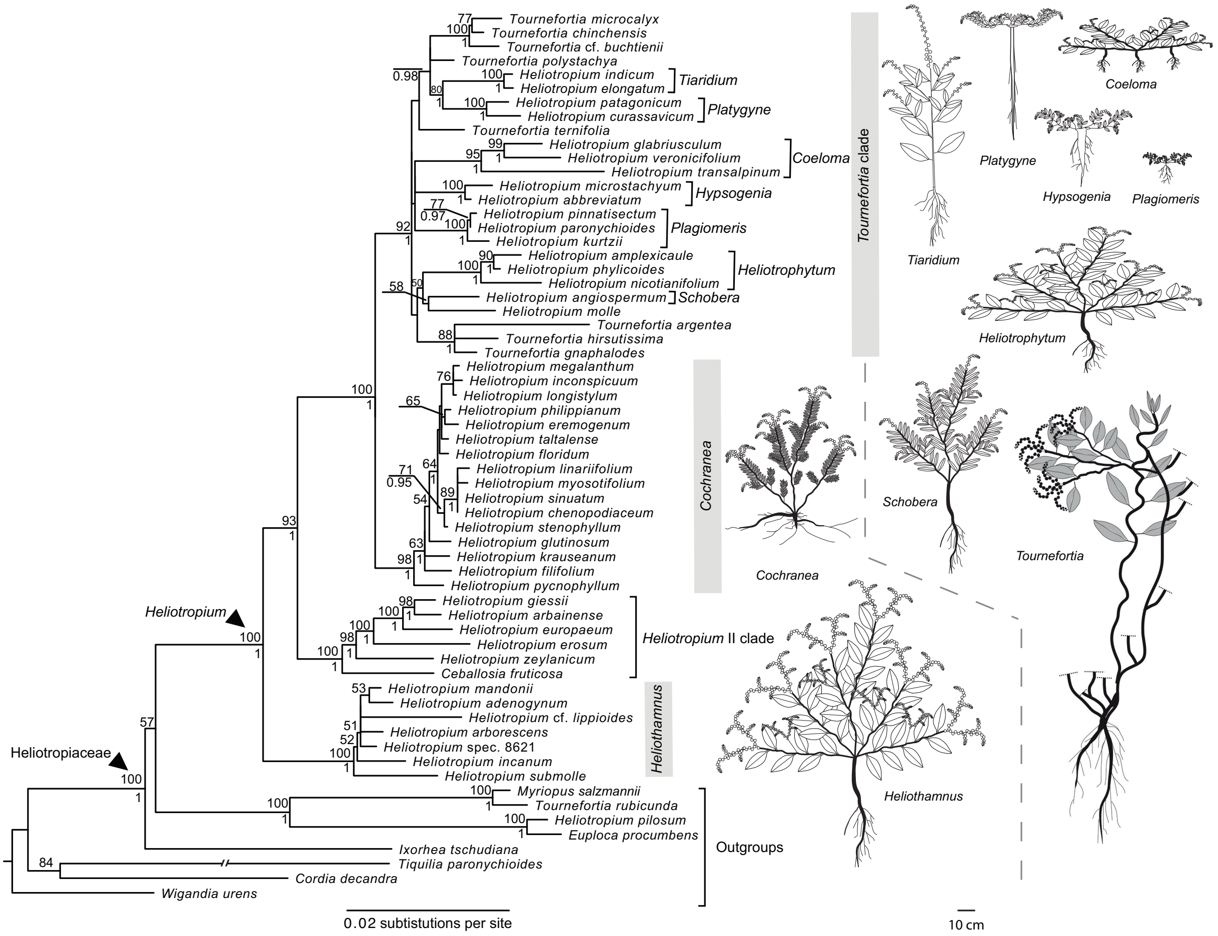


Figure 3.2: Maximum Likelihood phylogram of Heliotropiaceae based on plastid DNA (*trnL-trnF*, *trnS-trnG*, *trnH-psbA*, *rps*16). Major clades are indicated with Neotropical *Heliotropium* clades highlighted in grey. ML Bootstrap values >50% are indicated above branches and Bayesian posterior probabilities >0.9 below branches. Schematic representations of habit of some Neotropical *Heliotropium* are depicted, showing the variability among clades.

The major subclades of *Heliotropium* + *Tournefortia* were all well-supported. *Heliotropium* sect. *Heliothamnus* (*Heliothamnus*) is sister to the clade holding the rest of the species of the two genera. The latter includes the *Heliotropium* II subclade (Old World *Heliotropium* including *Ceballosia*), which is sister to *Heliotropium* sect. *Cochranea* (*Cochranea*) plus a well-supported subclade composed of all other sections of Neotropical *Heliotropium* and *Tournefortia* s.str. (*Tournefortia* clade). These four major clades (*Heliothamnus*, the *Heliotropium* II clade, *Cochranea*, and the *Tournefortia* clade) represent our *Heliotropium* s.l.

All three Neotropical clades including *Heliothamnus*, *Cochranea*, and the *Tournefortia* clade had poor internal resolution. *Cochranea* showed the same relationships as in Luebert and Wen (2008) with *Heliotropium pycnophyllum* Phil. sister to all other members of the section. Branching order of the *Heliotropium* sections in the *Tournefortia* clade was not fully resolved, neither the corresponding species of *Heliotropium* nor those of *Tournefortia* s.str. form a respective clade. However, the sections of *Heliotropium* were retrieved as well-supported monophyletic groups.

### 3.3.2 Phylogenetic Analysis of ITS

The ITS dataset contained 729 aligned positions, of which 403 were variable and 277 were parsimony-informative. The 60,000 MPTs had a tree length of 1348 steps, a CI of 0.62, and an RI of 0.66. The substitution model that best fitted the dataset was GTR+I+Γ. The Bayesian phylogeny of the ITS dataset is depicted in Fig. 3.3.

The relationships among taxa as resolved by the ITS analysis were similar to those from the plastid analyses. The monophyly of the three Neotropical clades (i.e., *Heliothamnus*, *Cochranea* and the *Tournefortia* clade) was well supported. Internal resolution was poor, though. The main difference with the plastid analysis data was the sister relationship of *Heliothamnus* and the *Heliotropium* II clade. This relationship, however, received low support (Fig. 3.3). The relationships within the *Tournefortia* clade also differ between the plastid and the ITS analyses, but the conflicting topologies had low support in ITS. Furthermore, neither *Heliotropium* nor *Tournefortia* s.str. is monophyletic. However, as in the plastid data, the monophyly of the sections of *Heliotropium* were well-supported (Fig. 3.3).

### 3.3.3 Incongruence between Plastid and Nuclear Partitions

The ILD test indicated that the plastid and ITS data partitions are incongruent ($P=0.019$). Plastid and ITS datasets were therfore not combied for ML and BA analyses, but we conducted a MP combined analysis in order to further explore incongruence via PBS. The combined dataset was composed of 3,965 aligned positions, of which 1552 were variable and 747 were parsimony-informative. The 150,000 MPTs had a tree length of 2760 steps, a CI of 0.69, and an RI of 0.71. The phylogenetic signal of the plastid dataset predominated the combined analysis (Fig. 3.4C), since both topologies were similar, at least concerning the major clades (Figs. 3.2 and 3.4). This is not suprising since the plastid data has the majority of parsimony informative sites. The PBS values (Fig. 3.4C; Appendix B.3) indicated that most of the incongruence resides in the internal nodes of the main clades, namely *Heliothamnus*, the *Heliotropium* II clade, *Cochranea*, and the *Tournefortia* clade, some of which were weakly supported in the separate as well as in the combined analyses (Figs. 3.2–3.4). The branching order and the monophyly of *Heliothamnus* and the *Heliotropium* II clade in the topology of the combined data, which are different from the ITS topology, appeared to be supported by the PBS of the ITS partition (Fig. 3.4), although there were instances in which they are not (see Appendix B.3).

### 3.3.4 Diversity of Vegetative Morphology

Leaf morphology and habit differed significantly among species and clades (see Appendices B.4 and B.5). The *Tournefortia* clade spaned the greatest range in habit (Figs. 3.1–3.2) as well as in leaf form (Fig. 3.3). Micromorphological and anatomical leaf characters were variable in the *Tournefortia* clade, with both types of stomata distribution, bifacial, subbifacial (Fig. 3.5A) and isobilateral (Fig. 3.5B) leaf anatomy, as well as presence of multicellular glandular trichomes (Fig. 3.5E), unicellular simple hairs (Fig. 3.5E), unicellular two-armed hairs, and trichomes with reduced tip and the presence of cystoliths

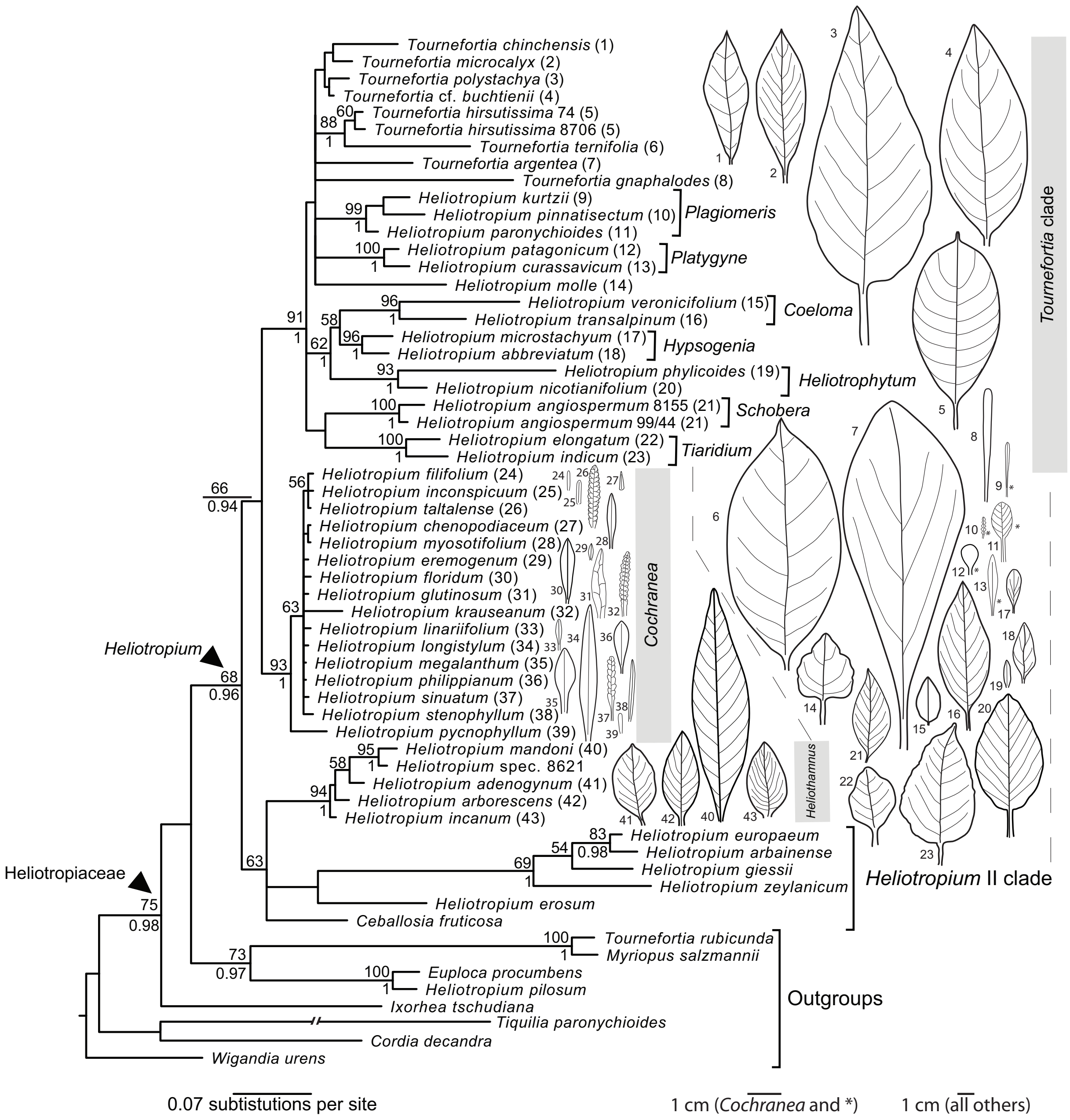


Figure 3.3: Bayesian phylogram of Heliotropiaceae based on ITS. Major clades are indicated with the Neotropical *Heliotropium* clades highlighted in grey. ML Bootstrap values >50% are indicated above branches and Bayesian posterior probabilities >0.9 below branches. Leaf outlines of the Neotropical *Heliotropium* species included in the phylogeny are depicted, showing the variability among clades, with the numbers on the left of each drawing corresponding to that in brackets after the species name in the phylogenetic tree. Note that the leaves of *Cochranea* and the species of the *Tournefortia* clade marked with an asterisk are depicted at a different, twice as large, scale than the others.

(Fig. 3.5A). In *Cochranea*, habit characters were relatively homogeneous, but leaf micromorphology and anatomy were variable, with both types of stomata distribution, bifacial, subbifacial (Fig. 3.5C) and isobilateral leaf anatomy, presence of multicellular glandular trichomes (Fig. 3.5C and F), as well as unicellular simple hairs (Fig. 3.5C, D and F) and cystoliths at the base of trichomes and in the mesophyll. In *Heliothamnus*, both leaf and

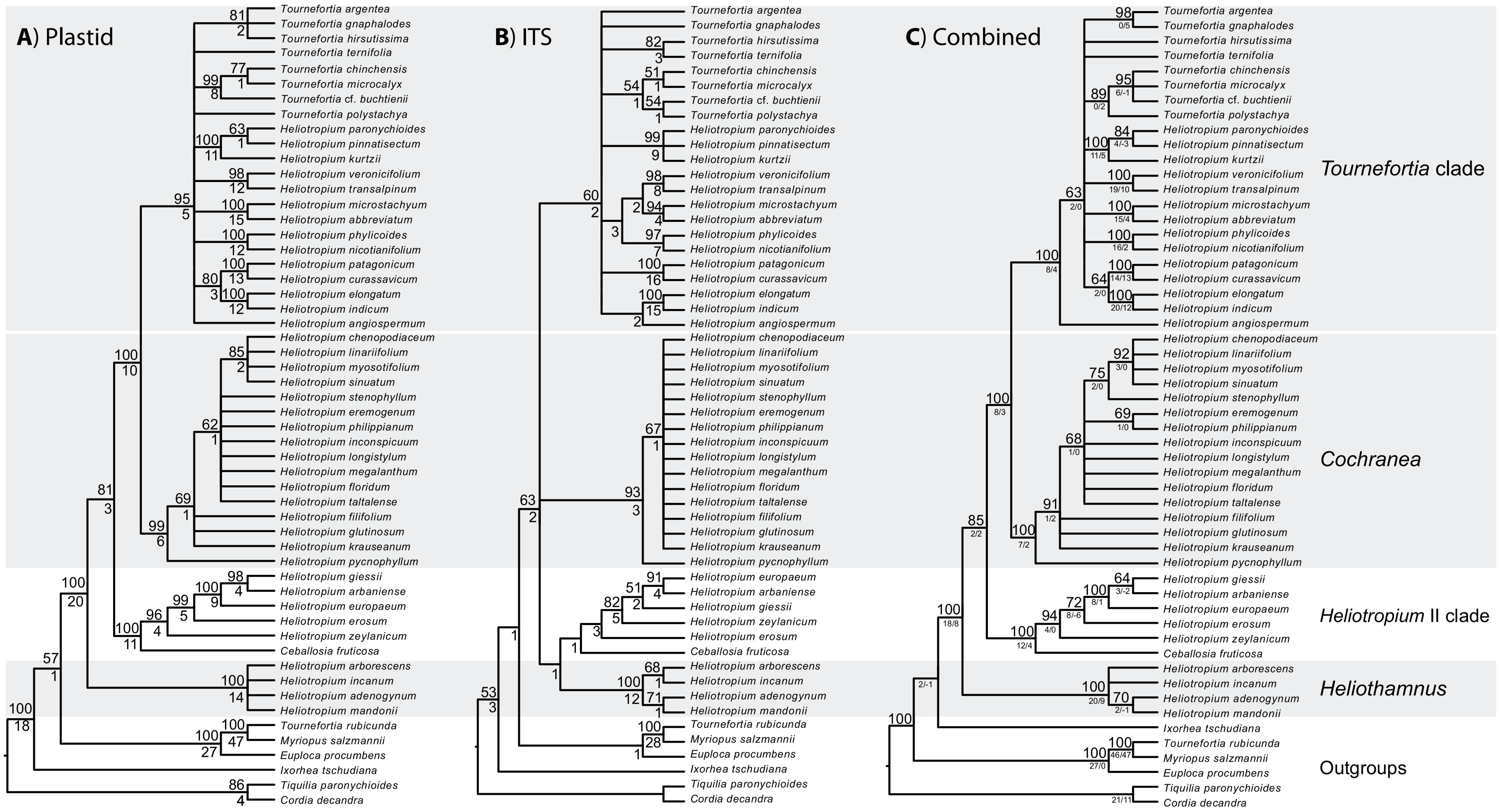


Figure 3.4: Maximum parsimony cladograms based on plastid DNA partition (A), ITS partition (B) and plastid and nuclear DNA partitions (C). Plastid and ITS trees were generated with the correponding partitions from the combined dataset to ensure they have the same taxon set. Only species without missing data are included in the trees. Major clades are indicated and Neotropical *Heliotropium* clades are highlighted in grey. Numbers above branches indicate parsimony bootstrap support >50% and numbers below branches are decay indexes (A–B) or plastid/ITS average partitioned Bremer support (C).

habit characters were relatively constant, with the sole exception the presence of crystal druses in the mesophyll (Appendix B.4).

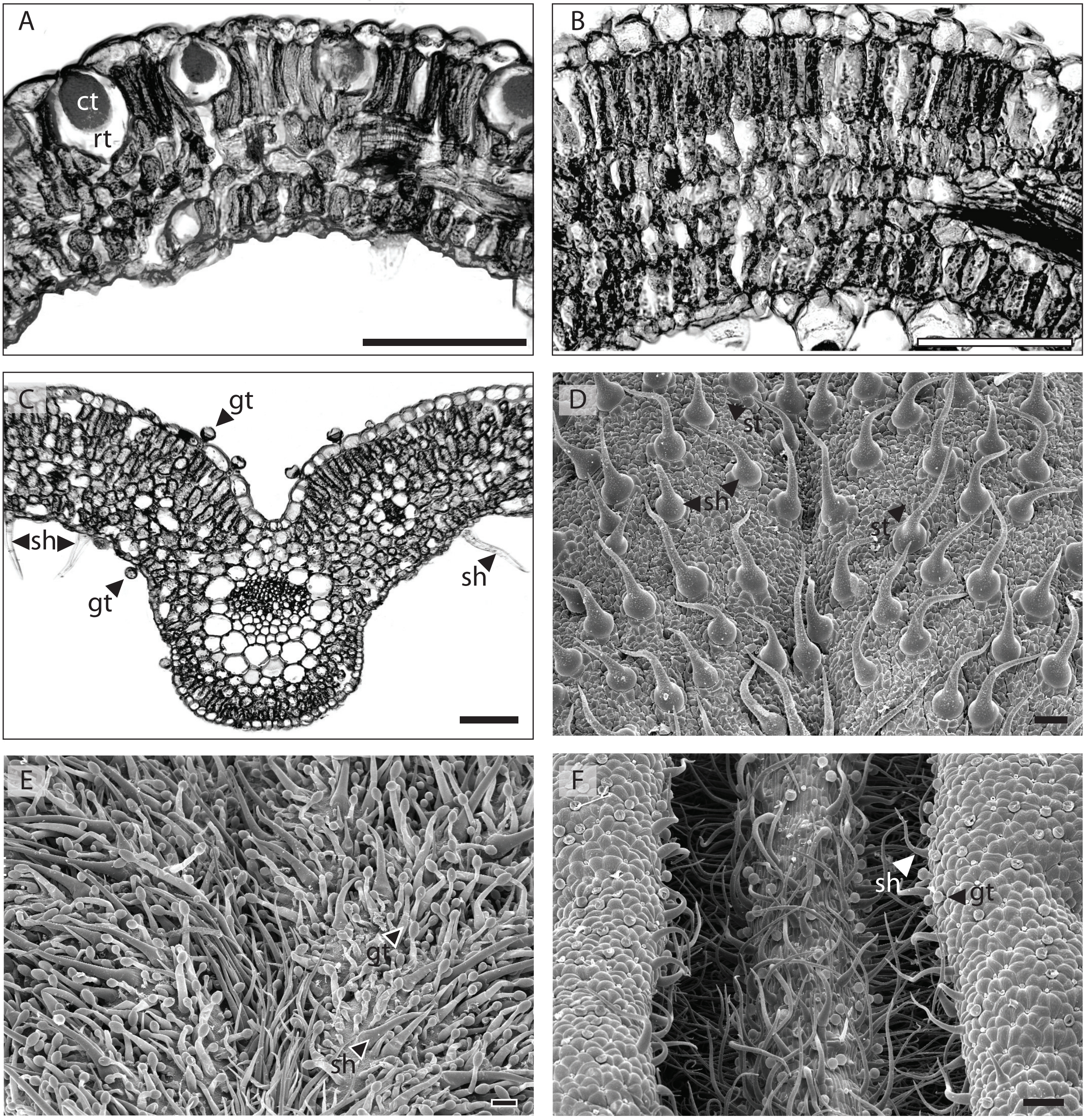


Figure 3.5: Examples of leaf anatomy and morphology in Neotropical *Heliotropium* (LM, A-C; SEM, D-F). A, *Heliotropium angiospermum* (sect. *Schobera*), transversal leaf section, subbifacial leaf anatomy with trichomes with reduced tip (rt) and cystolith (ct). B, *Heliotropium microstachyum* (sect. *Hypsogenia*), transversal leaf section, isobilateral leaf anatomy. C, *Heliotropium stenophyllum* (sect. *Cochranea*), transversal leaf section, subbifacial leaf anatomy, multicellular glandular trichomes (gt) and unicellular simple hairs (sh). D, *Heliotropium eremogenum* (sect. *Cochranea*), adaxial leaf surface with unicellular simple hairs (sh) and stomata (st). E, *Heliotropium nicotianifolium* (sect. *Heliotrophytum*), adaxial leaf surface with multicellular glandular trichomes (gt) and unicellular simple hairs (sh). F, *Heliotropium taltalense* (sect. *Cochranea*), abaxial leaf surface with multicellular glandular trichomes (gt) and unicellular simple hairs (sh). All scale bars = 100 $\mu$m. Source material and voucher specimens in Appendix B.2.

Table 3.3: Results of the permutation tests for the comparisons of morphological diversity among Neotropical *Heliotropium* clades (*Cochranea*, *Heliothamnus*, *Tournefortia* clade) and between classes of aridity (Dry, AI<1, Humid, AI⩾1), considering all three Neotropical *Heliotropium* clades ('all clades') and the *Tournefortia* clade alone. Values correspond to $P$ obtained from 999 permutations. **$P$<0.01, *$P$<0.05, NS: not significant

| Comparison | Total vegetative diversity | Leaf morphological diversity | Habit diversity |
|---|---|---|---|
| *Cochranea* - *Tournefortia* clade | 0.004** | 0.549 NS | 0.001** |
| *Cochranea* - *Heliothamnus* | 0.001** | 0.001** | 0.039* |
| *Heliothamnus* - *Tournefortia* clade | 0.001** | 0.001** | 0.009** |
| Dry-Humid (all clades) | 0.201 NS | 0.006** | 0.886 NS |
| Dry-Humid (*Tournefortia* clade) | 0.262 NS | 0.421 NS | 0.086 NS |

Results of the Principal Coordinates Analyses (eigenvalues for each PCO axis and coordinates of the species in the PCO axes are supplied in the Appendix B.6) indicated that both the *Tournefortia* clade and *Cochranea* occupy similar proportion of the morphospace in overall vegetative morphology (Fig. 3.6A) and leaf anatomy (Fig. 3.6B), but not in habit (Fig. 3.6C). *Heliothamnus* spaned a smaller proportion of morphospace in the three cases. The three clades appeared segregated in different regions of the morphospace in overall vegetative morphology (Fig. 3.6A) and leaf anatomy (Fig. 3.6B), but not in habit, where most species are clustered in a single, small region (on the right side of the graph in Fig. 3.6C). Overall vegetative disparity was greatest in the *Tournefortia* clade, followed by *Cochranea* and *Heliothamnus* (Fig. 3.6A and D). Pairwise permutation tests indicated that an overall vegetative disparity is significantly different among the three clades (Table 3.3). Leaf morphological diversity was similar between *Cochranea* and the *Tournefortia* clade (Fig. 3.6B and E) and was not significantly different according to the permutation test (Table 3.3); *Heliothamnus* had lower leaf morphological diversity, which is significantly different from *Cochranea* and the *Tournefortia* clade (Table 3.3). In habit, the *Tournefortia* clade showed the greatest diversity, followed by *Cochranea* and *Heliothamnus* (Fig. 3.6C and F), where the permutations tests showed significant differences in the three comparisons (Table 3.3).

Comparisons between aridity regimes based on the AI (data for individual species shown in Appendix B.7) considering the three Neotropical clades showed that overall vegetative disparity is greater in dry areas (AI<1, negative water balance), but not significantly (Fig. 3.7A, Table 3.3). A similar pattern was shown for leaf morphological diversity (Fig. 3.7C), but in this case the differences were significant (Table 3.3). Habit disparity was similar between humid and dry areas (Fig. 3.7E, Table 3.3).

Only the *Tournefortia* clade includes species whose spatial medians are located in both dry and humid habitats (in both *Cochranea* and *Heliothamnus* all species spatial medians are located in dry habitats; see Appendix B.7), so that comparisons within clades were conducted only in the *Tournefortia* clade. Patterns were similar to those found when considering all Neotropical clades (Fig. 3.7B,D,F, Table 3.3) except that greater diversity in habit was found in dry areas (Fig. 3.7F), but with differences not statistically significant; and differences in overall vegetative disparity and leaf morphological diversity between humid and dry areas were also not significant within the *Tournefortia* clade.

Comparisons of diversity of plant height, leaf form and leaf size among clades and between aridity regimes are depicted in Fig. 3.8. While median plant height did not vary considerably among clades (Fig. 3.8A), its variance was greater in the *Tournefortia* clade

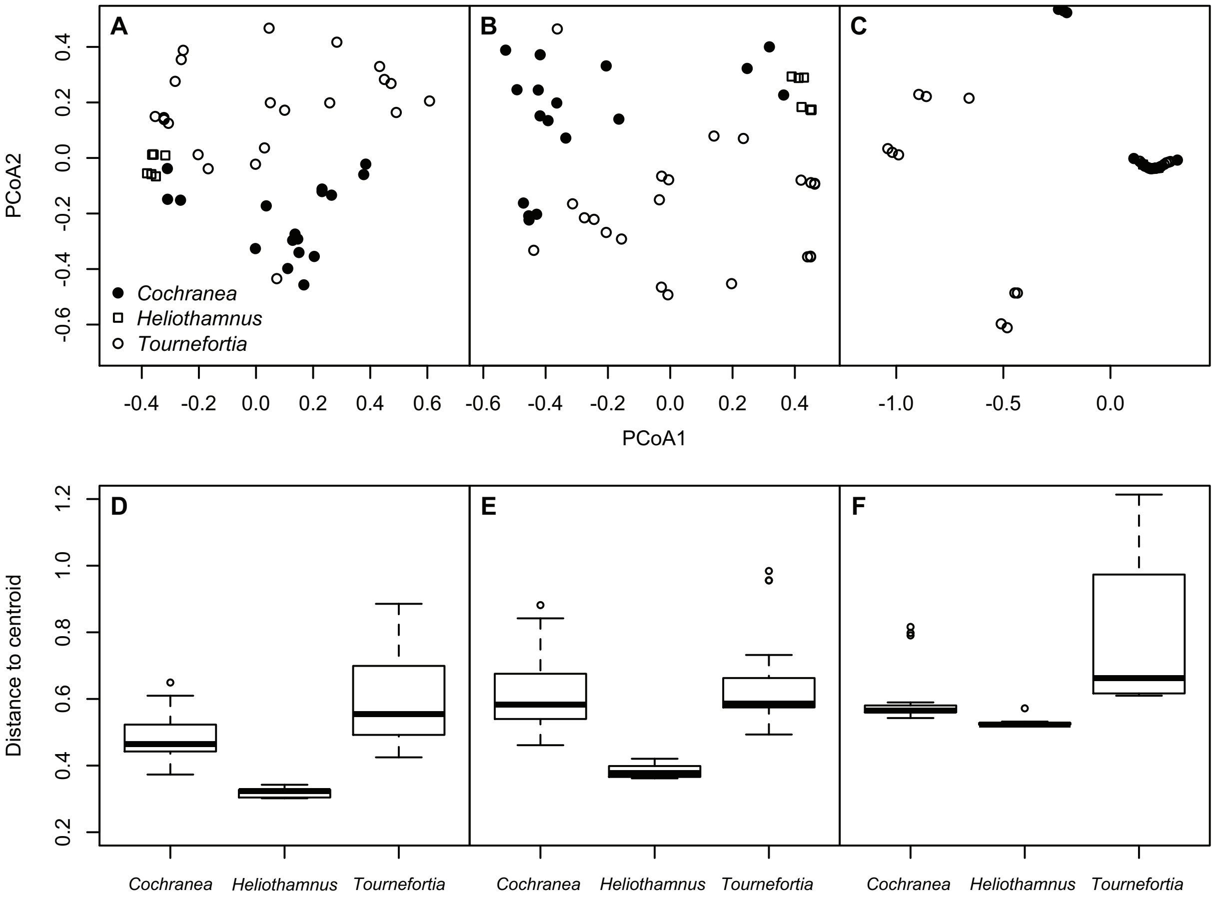


Figure 3.6: Morphological diversity of Neotropical *Heliotropium* clades. A–C, Distribution of clades in the first two axes of the PCO analyses: A, Total vegetative morphology. B, Leaf morphology. C, Habit. D–F, Box-and-whisker plots of the distance to the clade centroid in the PCO space (all axes included): D, Total vegetative morphology. E, Leaf morphology. F, Habit.

and was significantly greater than the variance in *Cochranea* and *Heliothamnus*, according to the Levene's test (Table 3.4). No significant differences in variance were recorded for habit between *Cochranea* and *Heliothamnus*. In leaf form *Cochranea* showed both the greatest values (i.e., leaves tend to be long and narrow) and variance (Fig. 3.8B). Its variability was, however, only significantly greater than that of *Heliothamnus*, while in the other two comparisons differences in variance were not statistically different. In leaf size the *Tournefortia* clade has both the greatest variance and values, but no differences in any of the three comparisons were revealed by the Levene's test. The comparisons between aridity regimes including all three clades of Neotropical *Heliotropium* (Fig. 3.8D-F) showed significant differences in variances only for leaf form and leaf size, where the variances were greater in dry areas (Fig. 3.8E-F, Table 3.4), while the difference in variance of plant height was not significant. When compared within the *Tournefortia* clade differences between aridity regimes (Fig. 3.8G-I) were significant only for leaf size, being greater in dry areas (Fig. 3.8I, Table 3.4).

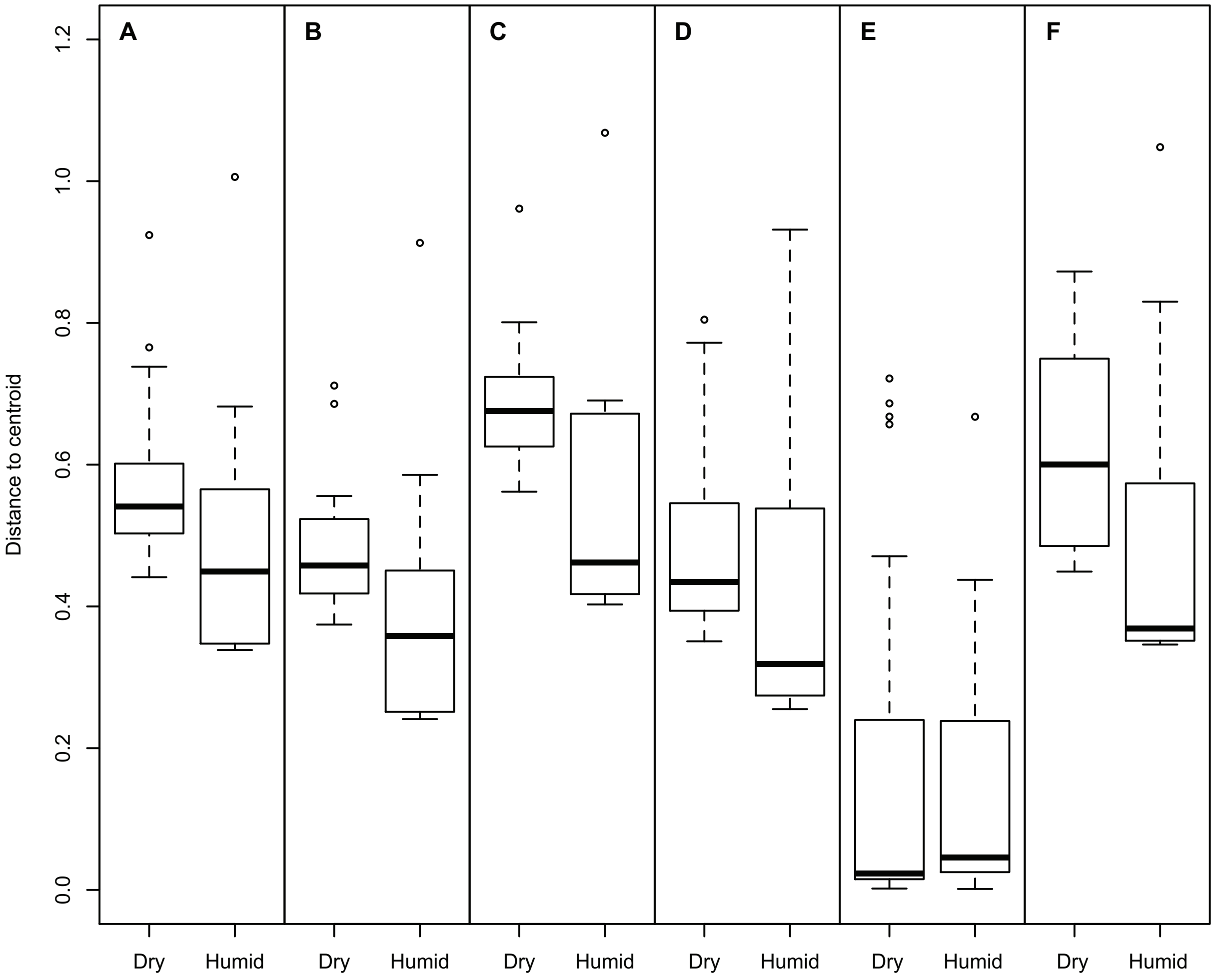


Figure 3.7: Box-and-whisker plots of the distance to the group centroid of the PCO space (all axes included), according to classes of aridity (Dry [AI<1] and Humid [AI⩾1]). A, Total vegetative morphology (all three Neotropical clades). B, Total vegetative morphology (*Tournefortia* clade). C, Leaf morphology (all three Neotropical clades). D, Leaf morphology (*Tournefortia* clade). E, Habit (all three Neotropical clades). F, Habit (*Tournefortia* clade).

## 3.4 Discussion

### 3.4.1 Systematics of Neotropical *Heliotropium*

The present analysis is the most critical test of relationships in Heliotropiaceae so far and is largely consistent with what has been shown in previous molecular phylogenetic studies (Diane et al., 2002; Hilger and Diane, 2003; Luebert and Wen, 2008; see Chapter 2). The genus *Ixorhea* is morphologically largely similar to *Heliotropium* (di Fulvio, 1978). *Ixorhea* possesses the key synapomorphy for Heliotropiaceae in Boraginales, which supports its inclusion in the family: the presence of a conical stigmatic head. However, its systematic position within the family is not clear. Setting aside *Ixorhea*, two main clades can be recognised within Heliotropiaceae. The first is composed of the genera *Myriopus* and *Euploca*, a relationship already suggested by Johnston (1930), based on morphological similarities, and by Hilger and Diane (2003), based on molecular data. The position of *Tournefortia rubicunda* and *Heliotropium pilosum* in *Myriopus* and *Euploca*, respectively, confirms

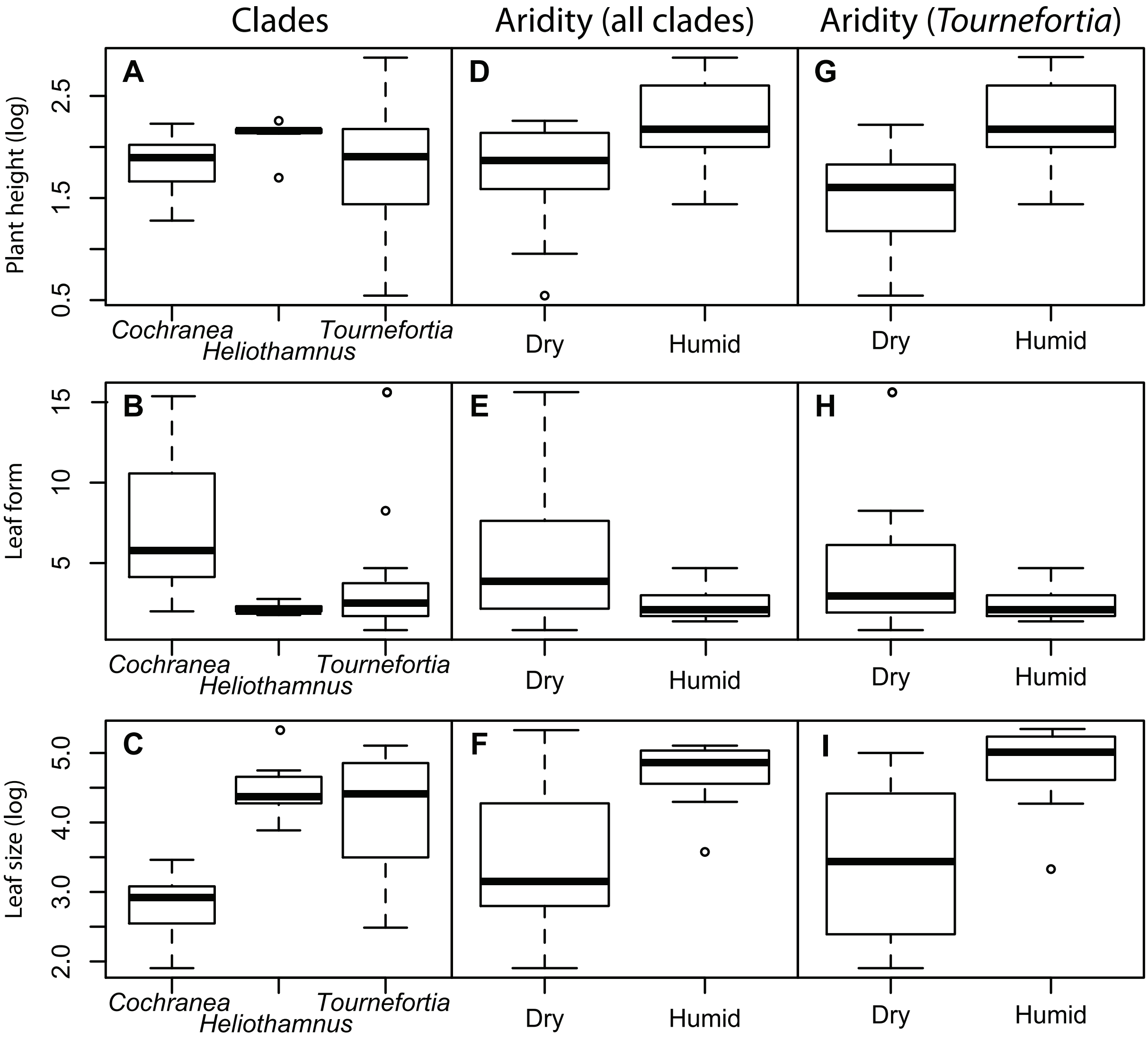


Figure 3.8: Box-and-whisker plots of the values of plant height, leaf form and leaf size compared among clades of Neotropical *Heliotropium* (A–C) and between classes of aridity (Dry [AI<1] and Humid [AI$\geqslant$1]) for all clades of Neotropical *Heliotropium* (D–F) and for the *Tournefortia* clade only (G–I).

the results of Luebert and Wen (2008; see Chapter 2), and is in agreement with expectations, beacuse they were previouly classified in *Tournefortia* sect. *Cyphocyema* (Johnston, 1930) and *Heliotropium* sect. *Orthostachys* (Johnston, 1928b), which constitute the core of *Myriopus* and *Euploca*, respectively (Hilger and Diane, 2003; see Section 3.1). The morphological and phylogenetic distinctiveness of these groups has already led some taxonomists to recognise *Myriopus* (e.g., Feuillet, 2008) and *Euploca* (e.g., Melo and Semir, 2006, 2009, 2010) as genera separate from *Tournefortia* and *Heliotropium*, respectively, but this taxonomic separation was rejected by Craven (2005), who considers the whole family Heliotropiaceae as composed of one large genus: *Heliotropium*.

The second clade is composed of what has been traditionally treated as the genus *Heliotropium* (excl. *Heliotropium* sect. *Orthostachys*, see above) including *Tournefortia* sect. *Tournefortia* and the Macaronesian monotypic genus *Ceballosia* (*C. fruticosa* ≡ *Heliotropium messerschmidioides* (L.f.) Kuntze). Four subclades can be recognised: the Old World *Heliotropium* II clade, the South American *Heliothamnus*, *Cochranea*, and

Table 3.4: Results of Levene's test for the comparisons of morphological variance of plant height, leaf form and leaf size among Neotropical *Heliotropium* clades (*Cochranea*, *Heliothamnus*, *Tournefortia* clade) and between classes of aridity (Dry, AI$<$1, Humid, AI$\geqslant$1), considering all three Neotropical *Heliotropium* clades ('all clades') and the *Tournefortia* clade alone. *$P<0.05$, NS: not significant

| | Plant height | | | Leaf form | | | Leaf size | | |
|---|---|---|---|---|---|---|---|---|---|
| Comparison | df | *F* | *P* | df | *F* | *P* | df | *F* | *P* |
| *Cochranea* - *Tournefortia*-clade | 1, 36 | 7.3662 | 0.01* | 1, 37 | 0.743 | 0.394 NS | 1, 37 | 4.094 | 0.051 NS |
| *Cochranea* - *Heliothamnus* | 1.22 | 2.9797 | 0.098 NS | 1, 22 | 6.8586 | 0.015* | 1, 22 | 0.1673 | 0.687 NS |
| *Heliothamnus* - *Tournefortia* clade | 1, 26 | 7.5625 | 0.01* | 1, 27 | 1.7742 | 0.194 NS | 1, 27 | 2.7311 | 0.11 NS |
| Dry-Humid (all clades) | 1,43 | 0.3227 | 0.573 NS | 1, 44 | 5.3302 | 0.025* | 1, 44 | 5.1494 | 0.028* |
| Dry-Humid (*Tournefortia* clade) | 1, 20 | 0.0049 | 0.945 NS | 1, 20 | 2.8849 | 0.105 NS | 1, 20 | 5.3338 | 0.032* |

the predominantly Neotropical *Tournefortia* clade. Old World *Heliotropium* is morphologically heterogeneous. Despite this morphological diversity, the clade has consistently been recovered as monophyletic (Hilger and Diane, 2003; Luebert and Wen, 2008). The *Tournefortia* clade is phylogenetically and morphologically the most puzzling clade and is taxonomically most challenging.

***Heliothamnus***. This is a group of ca. 11 species of shrubs and small trees, and the plants of these species are found usually in at least seasonally moist habitats. *Heliothamnus* has been recognised since Johnston (1928b) as a section of *Heliotropium* (see also Macbride, 1960; Förther, 1998). *Heliothamnus* is an important component of the Andean scrub at elevations between 1500 and 3500 m from Bolivia to Colombia (Johnston, 1928b; Förther, 1998). It shares some morphological characters with *Ixorhea*, *Myriopus* and *Euploca*, such as the presence of protracted, papillose connectives on the anthers and the fruits falling into four one-seeded nutlets. It differs from *Euploca* and *Myriopus* in having a straight embryo, which is characteristic for all other clades of *Heliotropium* and *Ixorhea*. Hilger (1992) pointed out that *Heliothamnus* deserves a higher than sectional rank in *Heliotropium*, because of its unique fruit, which distinct apical septa, a character absent in other species of *Heliotropium*. Species delimitation is very difficult to establish in *Heliothamnus*, and a recent revision is lacking (see Johnston, 1928b; Macbride, 1960). There are several widespread species complexes differing in habit and indumentum, but showing no clear-cut lines of division. Because of the difficult species delimitations, a critical revision of this group is needed.

***Cochranea***. This is another group of shrubby species, with ca. 17 taxa restricted to the Atacama Desert, extending over the Peruvian coastal desert with a single species. It has traditionally been considered as a natural group either at the generic (*Cochranea*, Miers, 1868; Gürke, 1893) or the sectional level in *Heliotropium* (Reiche, 1907a; Johnston, 1928b; Förther, 1998; see Table 3.1), and its phylogeny has already been explored in detail (Luebert and Wen, 2008; Chapter 2).

***Tournefortia* clade**. This is the most complex clade within Neotropical *Heliotropium*, because of its species richness (Table 3.1), great morphological variability (Figs. 3.6–3.8), and a wide geographical range, especially when compared to *Heliothamnus* and *Cochranea*. Most of the Neotropical sections recovered in this clade turn out to be monophyletic (*Tiaridium*, *Hypsogenia*, *Plagiomeris*, *Heliotrophytum*). *Heliotropium curassavicum* and *H. patagonicum* were traditionally placed in *Platygyne* and *Coeloma*, respectively (Johnston, 1928b; Förther, 1998). They are hypothesised to have a sister relationship, as first noted by Hilger and Diane (2003). Both species are glabrous, halophytic perennials with a unique combination of characters in the family. Their placement as sisters is thus not surprising given their morphological similarity. The North American *Heliotropium glabriusculum* is nested in a clade with other members of section *Coeloma* (Fig. 3.2) and closely allied to the South American *H. veronicifolium*. This was already suggested by Johnston (1964) based on similarities in fruit morphology and indumentum. Within the *Tournefortia* clade, resolution is poor and species of *Tournefortia* are seemingly related to species of *Heliotropium* in two different subclades in the plastid analysis (Fig. 3.2), but they fall a single subclade together with other New World-*Heliotropium* species in the ITS analysis, albeit with low support (Fig. 3.3).

### 3.4.2 Phylogenetic Incongruence

Our separate analyses and the ILD test suggested incongruence between the plastid and the ITS partitions. Such incongruence seems to reside mainly in the relative branching pattern of *Heliothamnus* and the *Heliotropium* II clade (Figs. 3.2, 3.3, 3.4A–B). However, branch support for these clades is moderate to low (63% Bootstrap support, < 50% Bayesian posterior probability) in the ITS analysis (Fig. 3.3). Partitioned Bremer support of the combined analysis (Fig. 3.4C) reveals that the incongruence may be due to differences of the internal relationships of *Cochranea* and the *Tournefortia* clade rather than to differences in the branching order of the major clades. The topology based on the the combined data set is similar to that based on the plastid data set. The major clades appear to be supported by both partitions, even those that are not resolved in the separate ITS analysis. This is a case of what has been termed as 'hidden support ' (Gatesy et al., 1999) of the ITS dataset. Nevertheless, maximum and minimum values of PBS (Appendix B.3) indicate that under some topological arrangements the ITS partition is incongruent with the basal branching pattern in *Heliotropium*, especially concerning the sister relationship of *Heliothamnus* and the *Heliotropium* II clade. Several scenarios can be invoked to explain phylogenetic incongruence between data partitions (Maddison, 1997; Slowinski and Page, 1999; Edwards, 2009). Long-branch attraction (Felsenstein, 1978) can be ruled out as a cause of incongruence since different methods (MP, ML, BA) render congruent results (Figs. 3.2–3.4; Huelsenbeck, 1997). To our knowledge, natural hybridization has not been documented in Heliotropiaceae, but polyploids, are common (di Fulvio, 1969; Frohlich, 1978; Luque, 1996), indicating potential occurrence of hybridization in the family. Low support for the sister relationship between *Heliothamnus* and the *Heliotropium* II clade in the ITS analysis and hidden support of the ITS dataset for the sister relationship between *Heliothamnus* and the remainder of *Heliotropium*, indicate that the exact phylogeny of *Heliotropium* still remains unresolved.

For the incongruence detected in *Cochranea*, lineage sorting (deep coalescence) may be a plausible explanation. While the plastid analysis resolves four grades in this group (Figs. 3.2 and 3.4A), the ITS topology resolves only the sister relationship between *Heliotropium pycnophyllum* and the rest of *Cochranea* (Figs. 3.3 and 3.4B). Luebert and Wen (2008) did not detect incongruence between plastid and ITS datasets in their analysis of *Cochranea* using a partially different set of plastid markers (*ndhF*, *rps*16, *trnL-trnF*). Nevertheless, they obtained identical relationships in *Cochranea* as shown here in the plastid and combined analyses. The PBS analysis (Fig. 3.4C) indicates that the ITS partition does not support the additional grades resolved by the plastid data partition. This can be due to the fact that the time to common ancestry may be longer in biparentally inherited alleles than in uniparentally inherited ones (Avise, 2004).

Incongruence within the *Tournefortia* clade may call for a more complex explanation. At this point, several possible scenarios should be considered. Incongruence in this clade may be due to reticulate evolution (i.e., hybridization-introgression), gene duplication, and/or lineage sorting. Hybridization may occur between species of the *Tournefortia* clade that have opverlapping distributions and inhabit similar habitats (e.g., in *Plagiomeris*, personal observation). With this in mind, hybridization might occur in the Caribbean and Central America, and especially in the Andes, the coastal range of northern South America, as well as in southeastern South America. Lineage sorting may also be involved, in part for the same reasons given above for *Cochranea*, since closely related species often have similar geographic ranges with overlapping distributions. Moreover, branch lenghts (Figs. 3.2– 3.3) indicate that rapid radiations may have taken palce in some of the major clades, which can also be a cause of lineage sorting (Knowles, 2009). Paralogous sampling in ITS may also cause the incongruence. We did not clone and generally did not sample more than one accession per species to assess this possibility. Concerted evolution in ITS may make this possibility difficult to detect, but it cannot be completely ruled out (Álvarez and Wendel, 2003).

### 3.4.3 Evolution of Vegetative Diversity

The distribution of vegetative diversity across clades of Neotropical *Heliotropium* largely confirms our expectations. Overall vegetative disparity (Fig. 3.6D), habit disparity (Fig. 3.6F) as well as disparity of plant height (Fig. 3.8A) are greater in the *Tournefortia* clade than in *Cochranea* and *Heliothamnus* (Tables 3.3–3.4). However, leaf morphological diversity (Figs. 3.6E and 3.8B–C) is not significantly greater in the *Tournefortia* clade than in *Cochranea* (Tables 3.3–3.4). We hypothesised that a greater morphological diversity in the *Tournefortia* clade may be the result of a diversification of habit associated with dry habitats. Although morphological diversity is in most cases greater in dry habitats (Figs. 3.7–3.8), this hypothesis is not confirmed by our results, because we did not find significant differences between dry and humid habitats within the *Tournefortia* clade in any comparison except leaf size (Table 3.4), whose disparity is greater in dry habitats (Fig.3.8I). Other explanations should be sought to better understand the higher morphological variation in the *Tournefortia* clade, as well as the high leaf morphological disparity present in *Cochranea*.

It has been suggested that morphological diversity of clades may depend on several factors, such as species diversity in the clade, species diversification rate, crown age and lineage turnover rate (Purvis, 2004; Ricklefs, 2004, 2006; Sidlauskas, 2007;but see Adams et al., 2009). Greater morphological diversity of the *Tournefortia* clade may be simply the result of its greater absolute species number (Table 3.1). On the other hand, asymmetry in tree topology may reflect differences in diversification rates (Mooers and Heard, 1997). The asymmetry in species number of *Heliothamnus* with respect to the rest of *Heliotropium*, and of *Cochranea* with respect to the *Tournefortia* clade appears to be correlated with asymmetry in overall morphological and habit disparity. It may be that an ability to evolve diverse morphological novelties potentiates speciation events and the survival of numerous lineages. The crown age of *Cochranea* ($\sim$15 Ma; Luebert and Wen, 2008) is half as old as the minimum age assigned to the *Tournefortia* clade based on fossil evidence (Graham and Jarzen, 1969). No data are available to estimate the crown age of *Heliothamnus*. Furthermore, average node age of the clades may better predict the patterns of vegetative morphological diversity in *Heliotropium*, in agreement with the predictions of Ricklefs

(2006). Nevertheless, the likely earlier onset of the diversification of the *Tournefortia* clade may have played a role in enabling its constituent lineages to diversify and colonize a greater variety of habitats than the younger and comparatively species-poor and eco-geographically restricted *Cochranea* and *Heliothamnus*.

It appears that the difference in leaf morphological diversity between dry and humid habitats (Fig. 3.7C) is largely restricted to *Cochranea*, because no differences are seen within the *Tournefortia* clade (Fig. 3.7D) and leaf morphological disparity in *Heliothamnus* is very low (Fig. 3.6B and E). Indeed, leaf morphological disparity is not different between *Cochranea* and the *Tournefortia* clade (Tables 3.3–3.4), in spite of the former's younger age and lower species richness. Luebert and Wen (2008) dated the major diversification of *Cochranea* as coincident with the development of hyperaridity of the Atacama Desert (Chapter 2, see also Chapter 4). The development of hyperaridity in the Atacama Desert may have led to a rapid diversification in leaf morphology of *Cochranea*, and subsequently an adaptive radiation (Schluter, 2000) in the most arid area of the earth.

It may be argued that our study does not take into consideration the possible confounding effects of phylogeny in the comparisons. In fact, as the Levene's test does not account for phylogenetic relatedness (Hutcheon and Garland, 2004; Collar et al., 2005; Sidlauskas, 2007), degrees of freedom may be inflated as the assumption of independence of the data is violated (Felsenstein, 1985), thus leading to type I error. With the consideration of this possibility, we tested the fit of the values of all axes of the PCO, as well as the three continuous characters to the Brownian motion model (Felsenstein, 1985) using our plastid-ML phylogeny and the AICc criterion of the R package Geiger (Harmon et al., 2008) and found that a more complex model (such as the Ornstein-Uhlenbeck model; Felsenstein, 1988) would better fit all our data (not shown). If our estimates of within-clade disparity can be seen as not confounded by phylogenetic effects, comparisons such as the Levene's test would then be appropriate to test differences in morphological diversity (Collar et al., 2005). Other approaches (e.g., Garland, 1992; Wagner, 1997; O'Meara et al., 2006) may also be appropriate, but they require more internal phylogenetic resolution than what is attained in this study.

### 3.4.4 Taxonomic Consequences

Based on the present data, current generic limits of *Heliotropium* and *Tournefortia* cannot be retained and re-arrangements of current classifications are required to obtain named, monophyletic groupings. The seemingly most parsimonious way to obtain monophyletic groups is to transfer *Tournefortia* sect. *Tournefortia* to *Heliotropium* (*Heliotropium* s.l.), since *Heliotropium* has priority over *Tournefortia* as Craven (2005) synonimized the latter under the former. This solution was previously suggested by Hilger and Diane (2003) and Craven (2005). The main argument for this, as presented by Craven (2005), is to maximize nomenclatural stability, since it is unlikely to overturn the placement of *Tournefortia* sect. *Tournefortia* in *Heliotropium*. However, making the new combinations for *Tournefortia* itself is a very problematic process. There has never been a comprehensive revision of the genus and its taxonomy is in a state of complete chaos. There are likely over 100 species, but over 300 species names in *Tournefortia*. Species delimitations are also very complex with many type specimens useless for unambiguous identification of the corresponding taxon. Alternative taxonomic solutions for transferring taxa of *Tournefortia* into *Heliotropium* may thus be considered. Such an alternative may include transferring all species of *Heliotropium* in the *Tournefortia* clade to the genus *Tournefortia* (*Tournefortia* s.l.), resurrecting the genus *Cochranea*, segregating and elevating *Heliothamnus* to genus level, and restricting the name *Heliotropium* to the species of the Old World *Heliotropium* II clade. The alternative solutions would require only around 40–50 species-name changes, which may be executed more easily since *Heliotropium* taxonomy has been clarified by Förther (1998). Furthermore, this alternative also represents a conservative as well as a phylogenetically satisfactory solution. The alpha-taxonomic problems in *Tournefortia* would still require attention at some point, but would not interfere with the nomenclatural process at this stage. However, this solution has the same major shortcoming as a simple transfer of *Tournefortia* to *Heliotropium*. Both cases will create genera which may lack clear morphological characters to distinguish them from one another, since most of the morphological variation in vegetative and fruit characters in Heliotropiaceae lies within the *Tournefortia* clade. Thus, both the *Heliotropium* s.l.-solution and the *Tournefortia* s.l.-solution will yield morphologically heterogenous genera, with the latter solution creating three clearly defined, monophyletic genera (*Heliotropium* s.str., *Heliothamnus* and *Cochranea*).

Nevertheless, critical evaluation of fruit, flower and pollen morphology may yield previously overlooked morphological characters that can be used to circumscribe such a broadly defined *Tournefortia* s.l., but the available data from the literature so far are too scanty to allow for complete evaluation. We are undertaking a detailed investigation of these character complexes across the family to address this problem.

### 3.4.5 New Combinations

Two new combinations in *Myriopus* and *Euploca* are necessary based on our phylogenetic analysis and Luebert and Wen (2008; Chapter 2):

*Myriopus rubicunda* (Salzm. ex DC.) Luebert, comb. nov.
Basionym: *Tournefortia rubicunda* Salzm. ex DC., Prodr. (DC) 9: 526. 1845.

*Euploca pilosa* (Ruiz & Pav.) Luebert, comb. nov.
Basionym: *Heliotropium pilosum* Ruiz & Pav., Fl. Peruv. [Ruiz & Pavon] 2: 3, t. 110b. 1799.

# 4. Diversification in the Andes: Age and Origins of South American *Heliotropium* Lineages (Heliotropiaceae, Boraginales)[a]

## Abstract

The uplift of the Andes was a major factor for plant diversification in South America and had significant effects on the climatic patterns at the continental scale. It was crucial for the formation of the arid environments in south-eastern and western South America. However, the timing of the major stages of the Andean uplift and of the onset of aridity in western South America remain controversial. In this paper we examine the hypothesis that the Andean South American groups of *Heliotropium* originated and diversified in response to Andean orogeny during the late Miocene and a the subsequent development of aridity. To this end, we estimate divergence times and likely biogeographical origins of the major clades in the phylogeny of *Heliotropium*, using both Bayesian and likelihood methods. Divergence times of all Andean clades in *Heliotropium* are estimated to be of late Miocene or Pliocene ages. At least three independent Andean diversification events can be recognised within *Heliotropium*. Timing of the diversification in the Andean lineages *Heliotropium* sects. *Heliothamnus*, *Cochranea*, *Heliotrophytum*, *Hypsogenia*, *Plagiomeris*, *Platygyne* clearly correspond to a late Miocene uplift of the Andes and a Pliocene development of arid environments in South America.

## 4.1 Introduction

Andean orogeny had a powerful effect on biotic diversification (Richardson et al., 2001; Jaramillo et al., 2006). On the one hand, it created a barrier for east-west dispersal of organisms, isolating previously continuous populations (e.g., Schulte et al., 2000; Flores and Roig-Juñent, 2001; Pirie et al., 2006; Roig-Juñent et al., 2006). On the other hand, it generated novel environments at the high elevations and a caused marked habitat turnover, which constitute significant promoters of speciation (e.g., Vuilleumier, 1971; Simpson, 1975; Gentry, 1982; Luteyn, 2002; Weigend, 2002; von Hagen and Kadereit, 2003; Bell and Donoghue, 2005; Hughes and Eastwood, 2006; Moore and Donoghue, 2007; Scherson et al., 2008). It also formed a North-South corridor for the dispersial of organisms (e.g., Moreno et al., 1994; Gengler-Nowak, 2002b; Antonelli et al., 2009; Luebert et al., 2009; Pinto and Luebert, 2009). It greatly modified the climatic patterns of South America (e.g., Hartley, 2003; Blisniuk et al., 2005; Barrett et al., 2009; Garreaud, 2009; Garreaud et al., 2009, 2010; Sepulchre et al., 2009). Andean uplift was likely the single most important geological event shaping patterns of South American biodiversity in Neogene history.

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[a] Manuscript in preparation: Luebert, F., Hilger, H.H. and Weigend, M. Diversification in the Andes: Age and origins of South American *Heliotropium* lineages (Heliotropiaceae, Boraginales). to be submitted to *Molecular Phylogenetics and Evolution.*

Recent studies show that the majority of the Andean uplift occurred between ∼ 10 and 6 Ma (Gregory-Wodzicki, 2000; Graham et al., 2001; Eiler et al., 2006; Garzione and Hoke, 2006; Garzione et al., 2006, 2008; Ghosh et al., 2006; Bershaw et al., 2010). This view, termed the 'rapid uplift model', was challenged by Sempere et al. (2006), Hartley et al. (2007), Ehlers and Poulsen (2009) and others, who argue that a rapid late Miocene uplift of the Andes is at odds with geological evidence, and that available paleoaltimetric estimates should be corrected (but see Hoke et al., 2009), resulting in an earlier onset of orogeny and a more gradual uplift of the Andes (Ehlers and Poulsen, 2009). Mulch et al. (2010) pointed out that additional studies integrating evidence from a larger spatial and temporal sampling size are required to resolve whether the paleogeographic data indicate a rapid or rather a gradual uplift of the Andes toward the late Miocene. Regardless of the exact timing of the uplift, all authors concur in that the the Andes reached their present elevation around the Mio-Pliocene (∼ 6–4 Ma).

The Andes have profound effects on climatic patterns at a continental scale (Garreaud et al., 2009). A rain shadow effect has been postulated, preventing the easterlies (westerlies) reaching the west (east) side of the Andes, reinforcing aridity on the Peruvian-Chilean coast (Houston and Hartley, 2003; Rech et al., 2010) and in Patagonia (Blisniuk et al., 2005). However, modelling studies have shown that the aridity of the Peruvian-Chilean coast may be not be affected by a rain-shadow effect (Garreaud et al., 2010), but rather indirectly by the influence of the Andes on the eastern Pacific sea surface temperature (Sepulchre et al., 2009), which, together with the influence of the Southern Pacific High, plays a major role in generating the arid conditions observed in western South America (Hartley, 2003; Sepulchre et al., 2009; Garreaud et al., 2009, 2010). While the onset of aridity over southeastern South America is relatively well-supported to be of Miocene age (e.g., Latorre et al., 1997; Blisniuk et al., 2005; Barreda and Palazzesi, 2007), the onset of aridity in western South America remains controversial. Some authors have postulated that hyperaridity in western South America is as old as the Late Jurassic (Hartley et al., 2005) or even the Late Triassic (Clarke, 2006). Other authors have argued for more recent ages, such as the Oligocene (Hartley, 2003; Lamb and Davis, 2003; Dunai et al., 2005), Miocene (Alpers and Brimhall, 1988; Rech et al., 2006), Pliocene (Hartley and Chong, 2002; Hartley and Rice, 2005; Arancibia et al., 2006) or even Pleistocene (Reich et al., 2009). These differences of more than 100 Ma may be due to the different methods and lines of evidence employed by different authors, but also to a lack of common and precise definition of 'hyperaridity' (Garreaud et al., 2010). If, as suggested by Garreaud et al. (2010), aridity 'represents the degree to which a climate lacks effective, life-promoting moisture', then biological evidence should be considered as a key component of this discussion.

Fossil evidence encompassing the relevant periods across the western flank of the Andes is scarce. Estimation of divergence ages onto plant molecular phylogenies (Renner, 2005) has the potential to contribute to this debate and to provide feedback in reconstructing the history of the earth and its biota. In South America, this type of evidence has been used to estimate the paleoelevation of the Andes (in *Solanum* L. and its cyst-nematodes (genus *Globodera* (Skarbilovich 1959)); Picard et al., 2008). Dated molecular phylogenies have also provided useful insights into the biotic history of Andean South America (e.g., Gengler-Nowak, 2002b; Hughes and Eastwood, 2006; Luebert and Wen, 2008; Scherson et al., 2008; Soejima et al., 2008; Antonelli et al., 2009; Dillon et al., 2009; Marquínez et al., 2009; Heibl et al., in press). Most studies show that Andean lineages (e.g., *Astragalus* L., L., *Lupinus* L., *Paranephelius* Poepp. & Endl.) and lineages from the arid western slopes of the Andes (e.g., *Heliotropium*, *Malesherbia* Ruiz & Pav., *Nolana* L.f.) experienced relatively recent diversifications (i.e., Pliocene or later), while trans-Andean disjunct lineages (e.g., Cinchoneae, *Drimys* J.R.Forst. & G.Forst.) are older (Miocene or earlier). Processes such as the Andean uplift causing vicariance, generation of high-elevantion evironments and off-Andes climate change are invoked to explain these phenomena.

The genus *Heliotropium* (including *Tournefortia* L. sect. *Tournefortia*) is composed of four major lineages, three of which have their centres of diversity in South America (Luebert et al., in press; see Chapter 3). Almost all South American sections of *Heliotropium* are well-supported monophyletic groups (Fig. 4.1; Hilger and Diane, 2003; Luebert and Wen, 2008; Luebert et al., in press; Chapter 3). The examination of their geographical distribution (Fig. 4.2) suggests that their origin might be related to the Andean uplift and the formation of arid environments in South America, but these hypotheses remain to be tested.

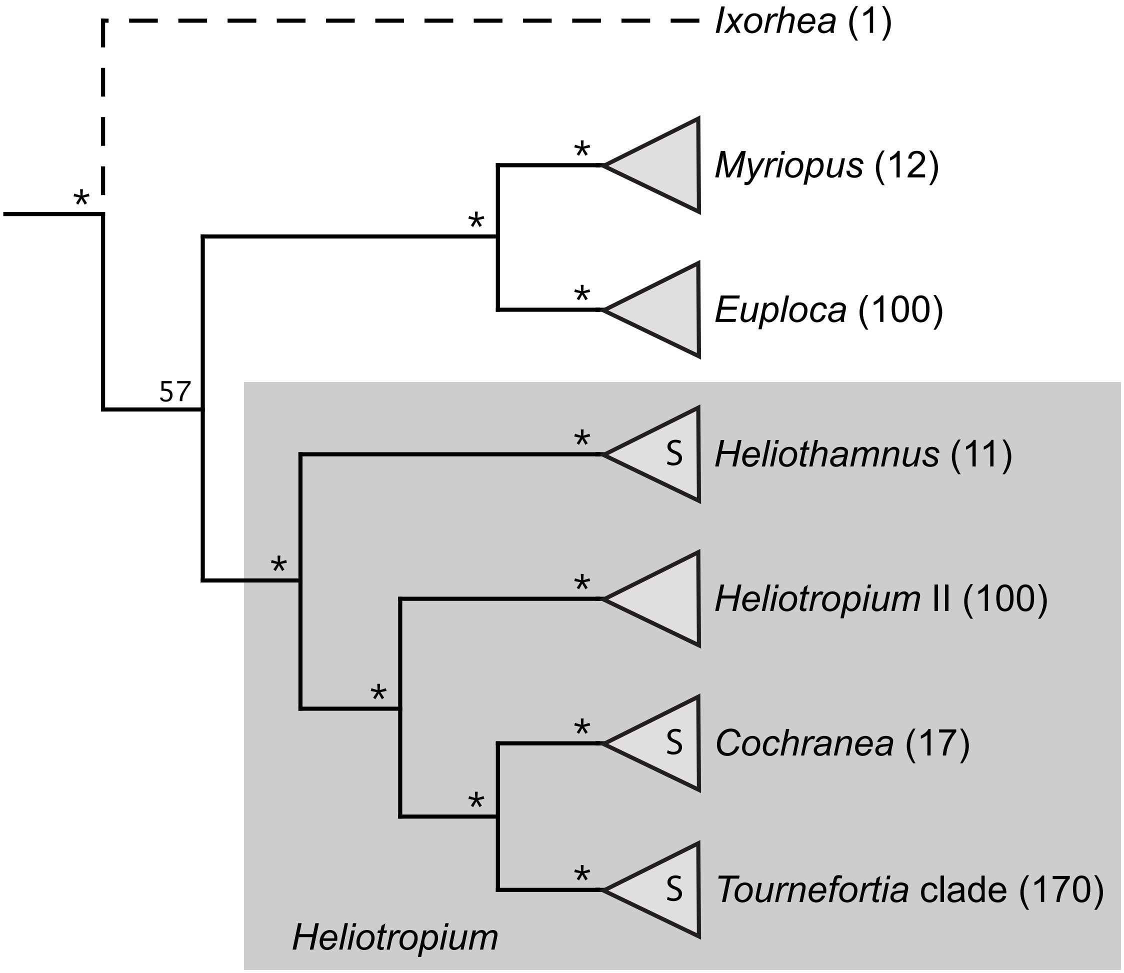

Figure 4.1: Phylogenetic relationships of major clades of Heliotropiaceae as currently resolved. The topology correspond to the analysis with four plastid markers (*rps*16, *trnL-trnF*, *trnS-trnG*, *trnH-psbA*) of Luebert et al. (in press; see Chapter 3). Asterisks indicate well-supported nodes with bootstrap values and Bayesian posterior probabilities. The dashed line indicates the unresolved position of *Ixorhea*. Approximate number of species are given in parentheses after the name of each clade. Major clades of *Heliotropium* are highlighthed and South American clades are marked with 'S'.

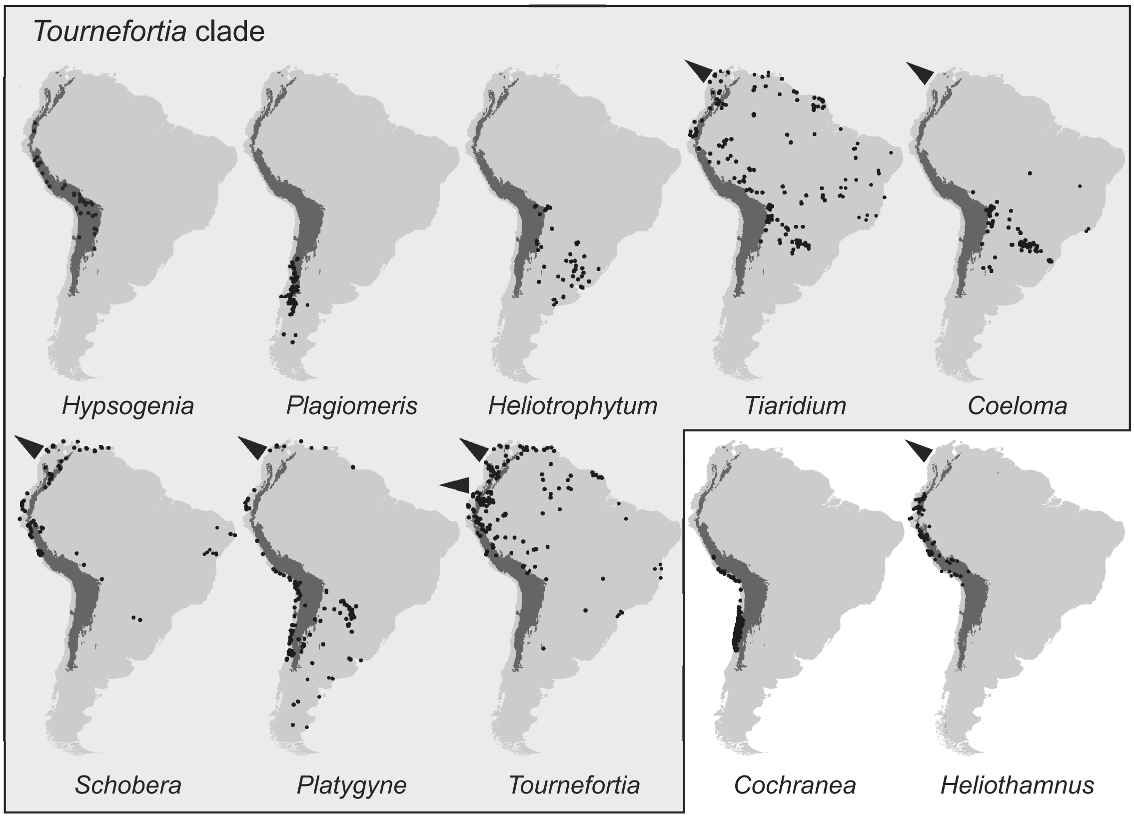

Figure 4.2: South American distribution of *Heliotropium* sections. The dark grey area indicates zones higher than 2000 m, showing the major extension of the Andes. Diagonal arrows indicate that the distribution of the group extends its distribution over Meosamerica and/or the Caibbean; a horizontal arrow in *Tournefortia* indicates that the distribution is also extended over the Indo-Pacific Region.

Three groups are essentially Andean: Sections *Hypsogenia* I.M.Johnst. and *Plagiomeris* I.M.Johnst. (both *Tournefortia* clade) are endemic to the Puna region and to the Mediterranean Andes and adjacent Patagonia, respectively, while section *Heliothamnus* I.M.Johnst. has its centre of diversity in the central and northern Andes, with a single species extending over Central America. Section *Cochranea* (Miers) Kuntze is endemic to the Peruvian and Atacama Deserts and is the only group in *Heliotropium* distributed only on the western flank of the Andes. It can therefore be regarded as Andean in a broad sense. The other sections are mostly extra-Andean. Sections *Heliotrophytum* G.Don and *Coeloma* (DC.) I.M.Johnst. (both *Tournefortia* clade) are distributed on the eastern side of the Andes and the latter extends over Mesoamerica. Sections *Platygyne* Benth., *Schobera* (Scop.) I.M.Johnst. and *Tiaridium* (Lehm.) Griseb. (all *Tournefortia* clade) are widely distributed in South America and range into Mesoamerica and the Caribbean. They rarely occur in the Andes, but are present on both Andean flanks. Today, they are usually found in human-disturbed areas and are sometimes considered weeds and their present distribution patterns may thus be of limited phytogeographical relevance. *Tournefortia* is widely distributed in the Neotropics (ca. 100–120 species), but is also in the Indo-Pacific Region with twelve species. It occurs on both sides of the Andes, including the Amazonian basin, as well as in the Andean region itself; it is also frequent in Mesoamerica and the Caribbean, but is absent from temperate regions and very rare in dry environments. It should be noted that the phylogenetic analyses (Diane et al., 2002; Hilger and Diane, 2003; Luebert and Wen, 2008; Luebert et al., in press; see Chapters 2 and 3) were unable to resolve *Tournefortia* as a monophyletic group within the *Tournefortia* clade, and all subclades recovered so far (including an Andean clade) are weakly supported. *Tiaridium* is the only section that occurs in the Amazonian basin, while the rest are restricted to arid, semiarid or even saline environments of the tropics and subtropics.

Most sections of South American *Heliotropium* are endemic or sub-endemic to zonally arid areas of eastern South America (sections *Coeloma*, *Heliotrophytum*, *Platygyne*), the Andes (sections *Hypsogenia*, *Plagiomeris*, *Heliothamnus*), or the Atacama and Peruvian Deserts (section *Cochranea*), and only sections *Tiaridium* and *Tournefortia* have centres of diversity in the humid tropics (Luebert et al., in press; Chapter 3). Luebert et al. (in press) showed that high vegetative morphological diversity in sect. *Cochranea* and the *Tournefortia* clade is associated with their distribution in arid environments of South America and that this high morphological diversity may therefore be an adaptive response to aridity.

It is unclear, however, whether the Andean or extra-Andean distributions of different clades are the result of separate independent origins, or rather of a single radiation caused by Andean uplift or the formation of arid environments. Based on the phylogenetic relationships so far resolved in *Heliotropium* and the distribution of its major lineages, we hypothesise that widespread groups (i.e., *Coeloma*, *Platygyne*, *Tiaridium*) should have relatively older diversifications than Andean-endemic or arid-adapted groups (i.e., *Cochranea*, *Plagiomeris*, *Heliothamnus*, *Heliotrophytum*, *Hypsogenia*), and that the different Andean groups originated and diversified independently. This, at least, appears obvious in the case of section *Heliothamnus*, which is sister to the remainder of *Heliotropium*, the latter distributed both in the New and the Old World (Fig. 4.1, see Chapter 3).

In previous studies Luebert and Wen (2008), using a relaxed clock method (penalized likelihood, Sanderson, 2002), estimated a Miocene origin of section *Cochranea* with a major diversification during the Pliocene, and regarded these dates as a consequence of the Andean uplift and the origin of hyperaridity in the Atacama Desert, respectively. The results of Luebert and Wen (2008) agree indeed with the rapid Andean uplift model and with the hypothesis of recent development of hyperaridity in western South America (see above). Gottschling et al. (2004) used a strict clock method to estimate ages across major nodes of Heliotropiaceae, while Moore and Jansen (2006) used the penalized likelihood approach to date nodes across Boraginales, with only two representatives of Heliotropiaceae. All these analyses render different results, probably because of differerences in sampling and methodology. None of them employed a dense sampling of *Heliotropium* and the methods applied are either strict clock or relaxed clocks with the expectation of autocorrelated rates along closely related branches (the case of the penalized likelihood method). The wide sampling of molecular data in *Heliotropium* from previous studies (Hilger and Diane, 2003; Luebert and Wen, 2008; Luebert et al., in press; Chapters 2 and 3), and the availability of methods for estimating divergence times with uncorrelated relaxed clock inference models (Drummond et al., 2006) provide an opportunity to re-examine divergence times in *Heliotropium*, and to contribute to the knowledge of the evolution of the poorly understood South American flora.

We therefore focus this paper on two aspects: (1) Divergence times of the major clades of *Heliotropium* and (2) their possible geographic area of origin. To this end we employed an uncorrelated relaxed clock approach to estimates the age of the nodes in the phylogeny of *Heliotropium*, and used these estimates to infer their probable geographical origins using a maximum likelihood method.

## 4.2 Materials and Methods

### 4.2.1 Plant Material and Taxon Selection

Plant material and data on distribution were obtained the revision of herbarium material at A, AAU, B, BM, BSB, CONC, DR, EIF, F, G, G-DC, GH, GOET, K, LL, M, MA, MSB, NY, QCA, SGO, TEX, ULS, US, USM (herbarium acronyms follow Holmgren and Holmgren, 1998 [continuously updated]), taxonomic literature (Johnston, 1928b, 1929a, 1930, 1932, 1935b,a, 1937, 1949, 1959; Gangui, 1955; Macbride, 1960; Pérez-Moreau, 1994; Gibson, 1970; Frohlich, 1981; Pérez-Moreau and Cabrera, 1983; Miller, 1988; Al-Shehbaz, 1991; Verdcourt, 1991; Barajas-Meneses et al., 2005; Melo and Semir, 2008; Melo et al., 2009; Melo and Semir, 2010), and selected data accessed through GBIF data portal (`http://data.gbif.org/`).

Sampling for the molecular data comprised at least two representatives of each section currently recognised in South American *Heliotropium* (sensu Luebert et al., in press; Chapter 3), and six representatives of Old World *Heliotropium* (*Heliotropium* II sensu Hilger and Diane, 2003; Luebert et al., in press; including *Ceballosia*, see Chapter 3), were isolated and sequenced. The chloroplast *rps*16 intron, *trnL-trnF* region and the *trnS-trnG* intergenic spacer were used. Outgroup selection was based on Diane et al. (2002), Hilger and Diane (2003), Luebert and Wen (2008) and Luebert et al. (in press; Chapter 3), and comprised the genera *Euploca* Nutt., *Ixorhea* Fenzl and *Myriopus* Small of Heliotropiaceae, as well as representatives of the closely allied (Boraginales) families Ehretiaceae, Cordiaceae, Hydrophyllaceae and Boraginaceae (Ferguson, 1999; Gottschling and Hilger, 2001; Moore and Jansen, 2006; Luebert and Wen, 2008), and *Nicotiana tabacum* L. from the order Solanales (Stevens, 2001 onwards; Bremer et al., 2002; Angiosperm Phylogeny Group, 2009). The former were selected, so that at least two nodes of Boraginales could be fossil-calibrated (see below), while the latter taxon was used for rooting the tree of Boraginales.

### 4.2.2 DNA Extraction, Amplification and Sequencing

Extraction of DNA from samples of silica-gel-dried leaves or herbarium material was performed with a modified CTAB method (Doyle and Doyle, 1987). PCR amplifications were performed in a Trio-Thermoblock thermal cycler (Biometra, Göttingen, Germany) in 25 $\mu$l volume containing 0.6 U of *Taq* Polymerase, 5.0 mM $MgCl_2$, 100 $\mu$M of each dNTP, 0.2 $\mu$M of each primer and about 50 ng of template DNA. Amplification primers and cycling conditions followed Moore and Jansen (2006) for *rps*16. Primers ‘c’ and ‘f’ were used for the amplification of the *trnL-trnF* region (Taberlet et al., 1991) and the thermal cycling conditions were the same as that for *rps*16. For the amplification of the *trnS-trnG* intergenic spacer, primers trnS and trnG (Hamilton, 1999) with cycling conditions set to 5 min initial denaturing at 95°C, 35 cycles 95°C, 30 s; 50°C, 1 min; 72°C, 1 min 30 s, and a final elongation period of 4 min at 72°C, were used. PCR products were purified with the peqGold Cycle-Pure Kit (PEQLAB Biotechnologie GmbH, Erlangen, Germany) or QIAquick PCR Purification Kit (Qiagen GmbH, Hilden, Germany) following the manufacturer’s instructions. Cycle sequencing was performed with BigDye Terminator v3.1 (Applied Biosystems, Foster City, California, USA) following the manufacturer’s instructions. Each sample was sequenced at least once in the forward and reverse directions. The resulting sequences were assembled using Chromas Pro v.1.33 (Technelysium Pty Ltd, Tewantin, QLD, Australia), and then aligned automatically using the software Mafft v.6.603 (Katoh et al., 2002) followed by manual adjustments using Se-Al 2.0a11 (Rambaut, 1996). Most sequences were already reported in Luebert and Wen (2008; Chapter 2), Weigend et al. (2009), Mansion et al. (2009) and Luebert et al. (in press; Chapter 3). GenBank accessions HQ286261–HQ286276 were produced specially for this study. A complete list of taxa with GenBank accession numbers is provided the Appendix C.1.

### 4.2.3 Phylogenetic Analysis and Divergence Time Estimation

Phylogenetic analyses were performed with Maximum likelihood (ML, Felsenstein, 1981) and Bayesian (BA, Mau et al., 1999) methods. Prior to the analyses the nucleotide substitution model that best fits the data was determined with the Akaike Information Criterion using Modeltest v.3.7 (Posada and Crandall, 1998). ML was run in Garli v 0.951 (Zwickl, 2006) under the selected substitution model for the whole three-marker dataset, with random-starting parameters and using a random-starting tree; the run was terminated after 10,000 generations without an improvement in the topology under a 0.05 score improvement threshold. ML analysis was used only for purposes of topological comparison with the BA analysis. It has been shown that ML method often outperforms other methods in recovering the true topology in phylogenetic inference (Wertheim et al., 2010). ML boostrap values were calculated in Garli with 500 replicates and the same settings described above.

BA was conducted in Beast v.1.5.4 (Drummond and Rambaut, 2007) with a partitioned dataset, setting a different substitution model for each three markers. Substitution rate was set to be estimated for the three partitions and a Speciation Yule Process with an initial random tree was set as tree prior. Two independent runs of $1\times10^6$ generations sampling every 1000 generations were performed. Convergence was checked in Tracer v.1.4 (available at `http://tree.bio.ed.ac.uk/software/tracer/`, accessed 24 April 2008) and the results were considered acceptable if the Effective Sample Size (ESS) was greater than 200 for all parameters (Drummond et al., 2007). Beast analysis was used to make divergence time estimations of the nodes of *Heliotropium* (Drummond et al., 2006). Since the strict clock was rejected in our combined dataset and also for each partition separately (LRT>700, $p<0.001$), all partitions were analysed under a uncorrelated lognormal relaxed clock model. The following calibration points were considered:

1. Age of the crown node of the order Boraginales estimated to 80.7±3.9 Ma, according to Moore and Jansen (2006), in agreement with Wikström et al. (2001). This is the only estimate available for this node. The analyses of Bremer et al. (2004) and Bremer (2009) include only one or no representative of Boraginales, respectively. Their time estimates are consistent with those of Moore and Jansen (2006) and Wikström et al. (2001), because they always render higher ages for the stem node of Boraginales (∼107 Ma, Boraginaceae s.l.+Vahliaceae; Bremer et al., 2004; Moore and Jansen, 2006; Bremer, 2009). This calibration was applied 'as is' to the crown node of Boraginales, i.e., a normal prior with mean 80.7 and SD 3.9 was prescribed.
2. Fossils fruits of *Ehretia* P.Browne (Ehretiaceae), reported from the Ypresian (early Eocene) of the London Clay (Chandler, 1961, 1962, 1964). According to Gottschling et al. (2002), these fruits take an intermediate phylogenetic position between the *Ehretia* I and *Ehretia* II clades of Gottschling and Hilger (2001). As our sampling includes representatives of both *Ehretia* I and II, the crown node of both clades was constrained to a minimum age of 50 Ma (compare Moore and Jansen, 2006; Luebert and Wen, 2008; Chapter 2). We used a lognormal prior with offset=50 Ma,

mean=2, and SD=1, which renders a median of 57.4 Ma with 5% and 95% quantiles of 51.4 and 88.3 Ma, respectively. Because the position of the members of the *Ehretia* III clade has been hypothesised to be also intermediate between *Ehretia* I and II (Gottschling and Hilger, 2004), lack of representatives of the former clade should not affect our calibration.

3. Fossil wood of *Cordioxylon* Awasthi has been reported from the Peñas Coloradas fomation of Puerto Visser, Chubut, Argentina (Brea and Zucol, 2006). These fossils show close affinity to *Cordia* L., especially *C. trichotoma* (Vell.) Steud. (Brea and Zucol, 2006), which belongs to the *Sebestena* clade of Gottschling et al. (2005). Upper Paleocene age for the Peñas Coloradas fomation has recently been confirmed (Iglesias et al., 2007; Raigemborn et al., 2009). Our sampling includes representatives of all three clades of the core Cordia (*Myxa*, *Collococcus* and *Sebestena* clades, Gottschling et al., 2005) and we therefore calibrated the crown node of *Cordia* to a minimum age of 55 Ma. We used a lognormal prior with offset=55 Ma, mean=2, and SD=1, which yields a median of 62.4 Ma with 5% and 95% quantiles of 56.4 and 93.3 Ma, respectively.
4. The age of the family Heliotropiaceae has been estimated in several papers, all reporting different results. Gottschling et al. (2004) applied a strict clock to an ITS phylogeny and obtained, as youngest estimate, an age of 122±13 Ma for the crown node of Heliotropiaceae; these authors sampled 12 species of Heliotropiaceae. On the other extreme Moore and Jansen (2006), with a sampling of two species and applying the penalized likelihood method (Sanderson, 2002) to a *ndhF* phylogeny, estimated an age of 24±4.9 Ma for the crown Heliotropiaceae. An intermediate estimation was provided by Luebert and Wen (2008; Chapter 2), with a sampling of 27 species and using the penalized likelihood method on an *ndhF* phylogeny similar to the approach of Moore and Jansen (2006), obtaining an age of 55.5±5.8 Ma. While the estimate of Gottschling et al. (2004) would push the crown node of Boraginales back into the Jurassic (older than the oldest angiosperm fossil), the estimate of Moore and Jansen (2006) is younger than the minimum age of Heliotropiaceae constrained by its oldest fossil (see below). We therefore use the calibration of Luebert and Wen (2008), to constrain the crown Heliotropiaceae using a normal prior with with mean 55.50 and SD 5.8.
5. Fossil pollen of *Tournefortia* was reported for the San Sebastián formation of the early Oligocene (∼35–30 Ma) of Puerto Rico, where it was rare (Graham and Jarzen, 1969). This finding has been confirmed in subsequent papers (Graham, 1996, 2003b; Alan Graham, personal communication). Luebert and Wen (2008; Chapter 2) constrained the stem node of *Tounefortia* sect. *Tounefortia* to a minimum age of 30 Ma, thus ensuring the inclusion of the '*Tournefortia* subclade' (Gottschling et al., 2004). As noted by Muller (1981), the pollen fossil of *Tournefortia* reported by Graham and Jarzen (1969) may correspond to the type III pollen of Nowicke and Skvarla (1974) reported for *Tournefortia bicolour* Sw., *T. coriacea* Vaupel, *T. cornifolia* Kunth, *T. cuspidata* Kunth and *T. hirsutissima* L. (Nowicke and Skvarla, 1974; Scheel et al., 1996), where the apertures seem to be obscured or hidden by characteristic large and numerous gemmae (Graham and Jarzen, 1969: Fig. 59; Nowicke and Skvarla, 1974: Fig. 7; Scheel et al., 1996: Fig. 5I-J). A more precise calibration is now possible due to our broader taxon sampling, which includes *T. hirsutissima*. Therefore, the crown node of the *Tournefortia* clade (see Luebert et al., in press; Chapter 3) was constrained to a minimum age of 30 Ma, setting a lognormal prior of 30 Ma, with

mean=2 and SD=1, which means a median of 37.4 Ma with 5% and 95% quantiles of 31.4 and 68.3 Ma, respectively.

Two analyses were carried out in Beast: (1) an analysis with all five age constraints mentioned above, and (2) an analysis with constraints 1 and 2 only. This allows for checking the sensitivity of the dataset and the analysis to the age constraints, both in terms of topology and branch lengths, keeping only the most reliable constraints in analysis (2). Trees with median heights are reported.

### 4.2.4 Biogeographical Analysis

We reconstructed the natural geographic distribution of all monophyletic groups on the basis of the data sources named above (Section 4.2.1). The following areas were considered, in correspondence with the proposal of Cox (2001) at worldwide Kingdoms and of Morrone (2001, 2002) for Neotropical Regions and Sub-regions:

A Andes (Andean Region, except central Patagonia, South American Kingdom)
B Eastern South America (Amazonian and Chaco Sub-regions + central Patagonia, South American Kingdom)
C Mesoamerica and the Caribbean (Caribbean Sub-Region, South American Kingdom)
D North America (North American part of the Holarctic Kingdom)
E Africa (African Kingdom)
F Eurasia (Eurasian part of the Holarctic Kingdom)
G Indo-Pacific (Indo-Pacific Kingdom)

Based on the ultrametric trees with node heights equivalent to age (in Ma) obtained from the Beast analysis, a Dispersal-Extinction-Cladogenesis (DEC) analysis (Ree et al., 2005; Ree and Smith, 2008) was conducted using the software Lagrange v.2.0.1 (available at `http://code.google.com/p/lagrange/`). Because our interest is chiefly on the biogeography of *Heliotropium*, only the Heliotropiaceae part of the phylogeny was considered. Branches with zero or nearly zero lengths that collapsed to polytomies were resolved as 0.0001 lengths using TreeEdit v.1.0a10 (Rambaut and Charleston, 2002). The Lagrange configurator interface (`http://www.reelab.net/lagrange/configurator/index`) was used to prepare the input file for Lagrange, where the maximum range size was constrained to the maximum number of areas occupied by extant taxa, which is equivalent to assume that dispersal abilities of the ancestors were as high as the dispersal abilities of extant taxa (Nylander et al., 2008). Three dispersal transition matrices were constructed for the periods 0-10 Ma, 11-30 Ma and 31-60 Ma (Appendix C.2). The constraints imposed by those matrices intended to reflect the variation in probabilities of interplate dispersal across the Boreotropical province and among Gondwanan plates throughout the Tertiary (Morley, 2003; Upchurch, 2008), and the higher likelihood of dispersal between Western and Eastern South America before the Andes reached its present elevation (see Section 4.1). This analysis was conducted on the computer cluster of the Freie Universität Berlin.

Because our sampling of *Euploca* and *Myriopus* is reduced (3 out of ∼112 species), the ancestral areas of the *Euploca* and *Myriopus* were previously estimated in a separate analysis using the phylogeny presented by Hilger and Diane (2003). As this phylogeny does not have branch lengths, Lagrange cannot be implemented. Instead, a Dispersal-Vicariance analysis (DIVA; Ronquist, 1997) was carried out. The program DIVA v.1.2

(Ronquist, 2001) was used with the default settings, except for holding the maximum possible reconstructions at a node (32,767) during the optimization and restricting the maximum number of areas (maxareas) to be retained in each reconstruction (Ronquist, 1996) to the maximum number of areas occupied by terminal nodes.

## 4.3 Results

### 4.3.1 Phylogenetic Analysis and Age Estimates

Our *rps*16 matrix had 1001 aligned positions, the *trnL-trnF* dataset had 1165 aligned sites, and the *trnS-trnG* matrix had 1181 aligned positions, giving a combined dataset (*rps*16 + *trnL-trnF* + *trnS-trnG*) with 3,347 aligned sites. The selected substitution model was GTR+Γ for all individual markers, as well as for the combined matrix.

Both ML and BA yielded similar topological results (Fig. 4.3). Regarding the Boraginales topology both analyses agree with (outgroup(Boraginaceae(Cordiaceae(Ehretiaceae(*Wigandia* Heliotropiaceae)))). With respect to the topology of Heliotropiaceae, ((*Euploca Myriopus*)(*Heliothamnus*(*Heliotropium*-II-clade(*Cochranea Tournefortia*-clade)))) was retrieved in both analyses. The main difference is the possition of the genus *Ixorhea*, sister to the remaining Heliotropiaceae in the ML analysis (not shown) and sister to (*Euploca* + *Myriopus*) in the BA analysis (Fig. 4.3), but with low branch support in both cases. Monophyly of Heliotropiaceae as well as all other major clades within the family are well supported in both analyses (Fig. 4.3).

Age estimates with both calibration schemes (five calibration points and two calibration points, see Section 4.2.3) rendered similar results (Table 4.1). As expected, calibrating less nodes reduces the age estimates for the nodes closer to the tips in Heliotropiaceae, although not significantly. All median ages estimated for the nodes fall in the range of the high posterior density (HPD) intervals. We concentrate on the presentation of the results around the five calibration points estimates, which render older ages, because divergence time estimates based on fossil calibrated nodes represent minimum ages.

Our analysis estimates the crown age of Heliotropiaceae to be of middle Paleocene to early Eocene. *Heliotropium* may have started its diversification during the early Eocene, although the lower bound of the 95% HPD interval in the two calibration points scheme pushes it into the late Oligocene. Crown *Heliothamnus* was estimated to be of late Miocene age (with 95% HPD between early Pliocene and middle Miocene). The *Heliotropium* II clade had an Oligocene crown age, with 95% HPD going into the early Miocene. The clade composed of *Cochranea* and the *Tournefortia* clade was estimated to be of late Miocene or Oligocene age (with 95% HPD reaching the early Miocene). The results of the analysis suggest a middle Miocene crown age for *Cochranea*, with a late Miocene to Pliocene diversification. Similar ages are suggested for most well-supported sections in the *Tournefortia* clade, except for crown *Coeloma* that was rather estimated to be of middle Miocene age. The *Tournefortia* clade, as a whole, was estimated to be of Oligocene age.

Table 4.1: Crown age estimates for the major nodes of Heliotropiaceae, as a result of the Beast analysis. Values are median ages given in millions of years. 95% highest posterior density intervals are given in parentheses. Estimates with five and two age calibration points are provided (see text). Clades as indicated in Fig. 4.3.

| Clade | Five-age constraints | Two-age constraints |
|---|---|---|
| Heliotropiaceae | 60.7 (53.2–68.1) | 56.9 (46.1–67.5) |
| *Myriopus* + *Euploca* | 37.9 (24.1–51.1) | 34.9 (22.9–48.0) |
| *Heliotropium* | 45.7 (39.1–52.7) | 36.5 (27.5–46.1) |
| *Heliothamnus* | 8.6 (3.9–14.5) | 7.0 (3.3–12.2) |
| *Heliotropium* II clade + *Cochranea* + *Tournefortia* clade | 41.1 (35.8–47.1) | 31.6 (23.8–40.1) |
| *Heliotropium* II clade | 30.3 (21.2–38.3) | 23.4 (16.2–31.1) |
| *Cochranea* + *Tournefortia* clade | 35.6 (32.1–40.2) | 24.8 (18.3–31.9) |
| *Cochranea* | 16.5 (9.2–27.6) | 13.2 (7.5–20.3) |
| *Cochranea* diversification | 7.4 (4.3–10.9) | 5.9 (3.5–8.7) |
| *Tournefortia* clade | 31.7 (30.2–34.2) | 20.6 (15.7–26.4) |
| *Heliotrophytum* | 8.5 (3.9–14.6) | 6.9 (3.2–11.0) |
| *Coeloma* | 15.6 (9.1–22.5) | 10.9 (6.5–15.9) |
| *Plagiomeris* | 5.6 (2.0–11.1) | 4.5 (1.7–8.5) |
| Andean *Tournefortia* | 11.9 (5.4–22.5) | 9.8 (4.4–16.5) |
| *Hypsogenia* | 6.8 (1.9–14.1) | 5.2 (1.9–10.4) |
| *Platygyne* | 7.8 (3.0–14.3) | 5.7 (2.2–9.9) |
| *Tiaridium* | 4.1 (0.5–10.4) | 3.1 (0.4–7. 9) |

### 4.3.2 Biogeographical Analysis

The DIVA analysis for *Euploca* and *Myriopus* (not shown) indicated that *Myriopus* originated in eastern South America (B), while *Euploca* originated in the Neotropics (ABC). We therefore ran the DEC analysis with the original distribution of the included species, because *Euploca procumbens* (Mill.) Diane & Hilger is widely distributed in the Neotropics, and the two species of *Myriopus* of our sampling are distributed in eastern South America.

The results of the DEC analysis are presented in Fig. 4.4. The DEC analysis suggests that Heliotropiaceae may have diversified in what is presently the Neotropics, North America, and Eurasia. A middle Eocene ($\sim 45$ Ma) dispersal into the present Andean region may have occurred along with the origin of the genus *Heliotropium* and the separation of *Heliothamnus* from the rest of *Heliotropium*. A separation of the *Heliotropium* II clade in Eurasia may have occurred towards the late Eocene ($\sim 40$ Ma), and a new separation into the Andean region is resolved towards the Eocene/Oligocene transition, along with the formation of *Cochranea* and the *Tournefortia* clade. The *Tournefortia* clade would have maintained a wide distribution in the Neotropics and Eurasia and would have dispersed from Eurasia into the Indo-Pacific region, with extinction in the former. Neotropical diversification of the *Tournefortia* clade would have occurred since the Oligocene/Miocene transition, with at least three different independent diversification events in the Andean region since the late Miocene.

## 4.4 Discussion

### 4.4.1 Intercontinental Biogeography of Heliotropiaceae

Our analysis suggests that Heliotropiaceae was already widespread in the New and Old Worlds at the time of its initial diversification during the Paleocene or earlier. This assumption is reasonable, taking into account that the related families Ehretiaceae and

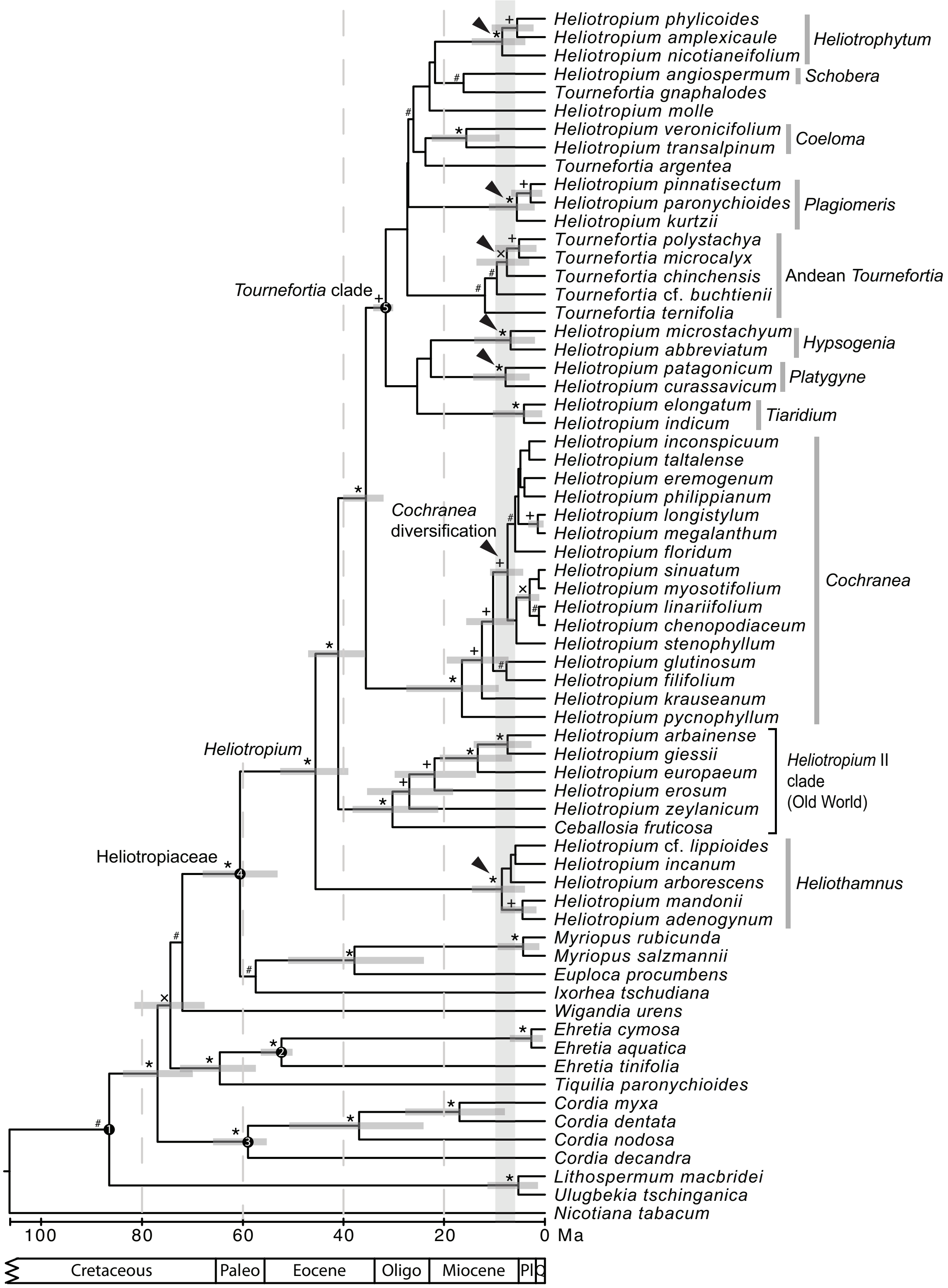

Figure 4.3: Bayesian maximum credibility chronogram (median ages) of Boraginales obatined from Beast analysis with five calibration points. Major clades are indicated. Nodes 1-5 are calibrated nodes: 1, Boraginales (80.7 Ma); 2, *Ehretia* (50 Ma); 3, *Cordia* (55 Ma); 4, Heliotropiaceae (55.5 Ma); 5, *Tournefortia* clade (30 Ma); see text for details. Bars around nodes are 95% highest posterior density intervals. Branch support is indicated as follows: $*$, ML Bootstrap Support (BS) and Bayesian Posterior Probability (PP) $\geqslant$ 95%; +, BS $\geqslant$ 70% and PP $\geqslant$ 95%; ×, BS $\geqslant$ 50% and PP $\geqslant$ 70%; #, BS < 50% and PP $\geqslant$ 50%. Arrows indicate nodes whose median age overlaps the rapid Andean uplift model, which is highlighted as a grey vertical bar between 10 and 6 Ma (see Section 4.1).

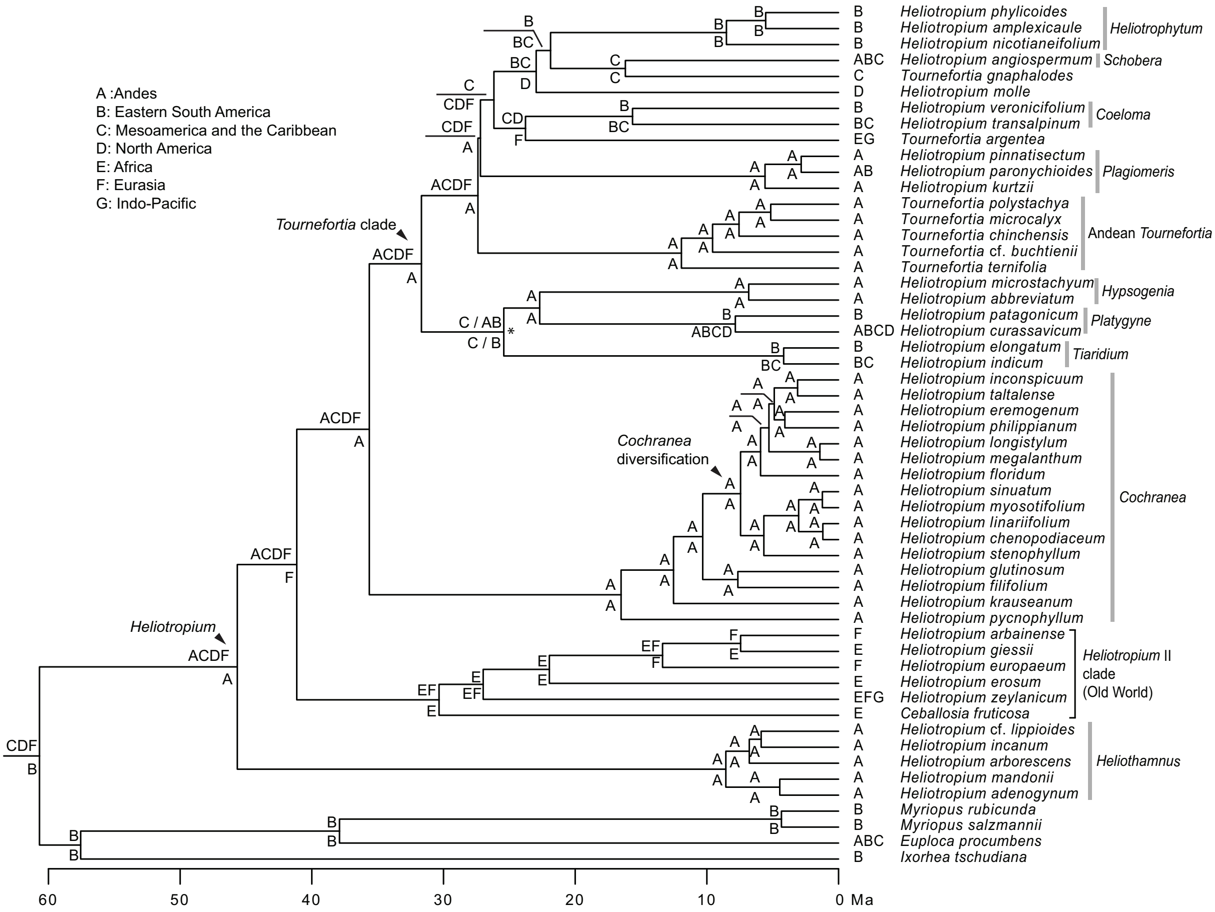

Figure 4.4: Maximum credibility chronogram of Heliotropiaceae (median heights) with maximum likelihood reconstruction of ancestral areas of the major clades obtained from the DEC analysis conducted in Lagrange. Major South American clades are indicated. Areas of terminal nodes are indicated to the left of taxon names as in the legend on the top left corner (see Section 4.2.4 for details). One node annotated with an asterisk indicates that two possible splits had the same likelihood.

Cordiaceae also have a pantropical distribution (Gottschling et al., 2004) and that the fossil record of Cordiaceae (Chelebajeva, 1984; Süss, 1987; Brea and Zucol, 2006) indicates that this family may have been already distributed in the Neotropics, Eurasia and Africa in the Paleogene. Heliotropiaceae may have been at least in part a component of the ‘Boreotropical flora’ (Wolfe, 1975), which was connected across the northern hemisphere before mid-Tertiary times (Tiffney, 1985), when it may have been replaced by temperate elements (Morley, 2003) as a consequence of the global cooling trend (Zachos et al., 2001).

*Euploca*, *Myriopus* and *Ixorhea* appear to have originated in the Neotropics during the Paleocene and *Euploca* may have dispersed from there into the arid tropics of Africa, Australia and the Indo-Pacific region. The Australian species of *Euploca* form a derived clade within the genus (Hilger and Diane, 2003) or two derived groups (Michael W. Frohlich, personal communication). This would suggest an early diversification from South America to Africa and SW Asia and a later colonization of Australia. Early Tertiary dispersal between South America and Africa may have been possible via interplate connections such as the Walvis Ridge/Rio Grande Rise and Sierra Leone Rise (Morley, 2003). Floristic exchanges between Africa and the Southeast of Asia and Australia via Madagascar, India and an island bridge formed at the NinetyEast Ridge may also have taken place during the early Tertiary (Morley, 2003; Morley and Dick, 2003; Carpenter et al., 2010; Renner, 2010). But to better understand the biogeographical history of *Euploca*, a denser sampling would be necessary in the phylogenetic analysis and it will therefore not be discussed further here.

The analysis suggests that Old World lineages of *Heliotropium* had two bouts of diversification. An initial diversification of the *Heliotropium* II clade in Eurasia is suggested to have taken place during the middle Eocene. The *Heliotropium* II clade would then have dispersed from Eurasia into the African continent in the late Eocene, when floristic interchanges took place between these two biogeographical regions (Cavagnetto and Anadón, 1996). The second diversification in the Old World may have occurred during the Oligocene with dispersal from Eurasia into the Indo Pacific region from an already widespread *Tournefortia* clade, giving rise to several narrowly endemic especies in the Indo Pacific region. Connections between SE Asia and the West Pacific Islands of the Indo Pacific Region have been postulated (Turner et al., 2001). Such connections have been suggested to be of Neogene age based on plate tectonics (Morley, 2003).

No intercontinental dispersal event is, however, necessary to account for the arrival of *Heliotropium* in South America, since all analysis concur in that the ancestor was distributed in South America at the time of its origin.

### 4.4.2 Andean Diversification of *Heliotropium*

The age estimates for the stem node of South American *Heliotropium* range from the early Paleocene to early Eocene (Table 4.1) with a median of 60.7 Ma (middle Paleocene), even if several constraint are removed from the Beast analysis. This estimate lies between the early Cretaceous estimate of Gottschling et al. (2004) and the early Miocene one of Moore and Jansen (2006). At least three independent Andean diversifications events were detected in the DEC analysis (Fig. 4.4), corresponding to the diversifications of *Heliothamnus*, *Cochranea* and the *Tournefortia* clade. At least one diversification event for each of them coincides with the Andean uplift as dated in the rapid uplift model (Fig. 4.3, see Section 4.1).

***Heliothamnus*** - *Heliothamnus*, as a lineage, had separated from the rest of *Heliotropium* as early as the middle Eocene (Fig. 4.3, Table 4.1). This separation took place in the same biogeographical area as the rest of *Heliotropium*, which was widespread in the Neotropics at that time (Fig. 4.4). Jaramillo (2002) and Jaramillo et al. (2006) reported a high Eocene plant diversity in the Neotropics, even higher than the present diversity, with a peak during the middle Eocene. This peak in plant diversity has been associated with a trend to a more humid climate during the middle Eocene, linked to the termination of the Eocene Thermal Maximum (Jaramillo, 2002); this author also indicates that high diversity of the middle Eocene flora in the Neotropics is correlated with a high rate of extinctions. Although Oligocene extinctions cannot be ruled out, two main external causes can be proposed to explain this late diversification. (1) During the Eocene-Oligocene transition, the global climate experienced a cooling, the ice sheet of Antarctica was forming and an ephemeral glaciation has been reported (Zachos et al., 2008; Liu et al., 2009). Plant lineages adapted to warm tropical environments may have experienced a reduction of their distribution areas due to local extinctions as a consequence of the climatic cooling (Jaramillo et al., 2006). This cold period was relatively stable during most of the Oligocene, but late Oligocene warming has been recorded (Zachos et al., 2001), which might have favoured a re-expansion of some pre-existing tropical lineages during the Miocene. (2) The age of diversification and the present Andean distribution of *Heliothamnus* (Fig. 4.2) suggest that its diversification may have been triggered by the uplift of the Andes, which would in turn be in agreement the rapid uplift model (see Section 4.1; Garzione et al., 2008; and references therein). The formation of the Andes may have promoted speciation in inner-Andean valleys and the Andean scrub, where most species of *Heliothamnus* currently grow, with most of the narrowly endemic taxa restricted to inner Andean valleys or valley systems. The alternative gradual Andean uplift model (Ehlers and Poulsen, 2009) would also agree with the dating of the origin of *Heliothamnus*, if it is assumed that the central Andes started their uplift during the Eocene, but it would not explain the Miocene diversification of *Heliothamnus*. The upper bound estimates of Ehlers and Poulsen (2009) for the early phases of the Andean orogeny would predict Andean paleoelevation increases greater than present elevation.

Other plant groups with similar distribution to *Heliothamnus*, such as the *Oxalis tuberosa* Molina alliance (Oxalidaceae; Emshwiller, 2002; Heibl et al., in press) and *Mosannona* Chatrou (Annonaceae; Pirie et al., 2006), have been estimated to have similar divergence ages. These estimates have been associated with the Andean uplift, an idea that has also been proposed to explain the diversification of the Andean cacti (Ritz et al., 2007). The centre of diversity of *Heliothamnus* is located in the central Andes, with a few species reaching the northern Andes and only one in Mesoamerica (Johnston, 1928b). On this basis, it is possible to propose an origin of *Heliothamnus* in the central Andes, and a later colonization of the northern Andes and Mesoamerica. As we could not include the Mesoamerican species (*Heliotropium rufipilum* (Benth.) I.M.Johnst.) in our sampling, this scenario is still speculative, but in agreement with a gradual north-to-south uplift of the Andes, as it has also been suggested to explain the distribution and diversification of other Andean taxa (see Picard et al., 2008; and references therein)

***Cochranea*** - Our results for dating *Cochranea* are largely consistent with what has been previously reported (Luebert and Wen, 2008; Chapter 2). These authors suggested that the middle Miocene crown age of *Cochranea* could be related to a vicariant Andean effect, but sister relationships were not clear. Our phylogenetic analysis clearly shows *Cochranea* as sister to the *Tournefortia* clade, which is mainly distributed along the central Andes and in eastern South America (Fig. 4.2). The biogeographic analysis presented here (Fig. 4.4) does not shed light on a vicariant scenario and rather suggests that during separation of *Cochranea* and the *Tournefortia* clade, both groups occupied the Andean region. Moreover, this separation is older than the main rise of the Andes. In spite of this, the onset of the diversification of *Cochranea* towards the middle Miocene (Table 4.1, Fig. 4.3) may be explained by the uplift of the Andes, which isolated *Cochranea* on their western flank, as is seen in its present distribution (Fig. 4.2). The onset of hyperaridity in the Atacama Desert from the late Miocene (Alpers and Brimhall, 1988; Dunai et al., 2005) and especially since Pliocene times (Hartley, 2003; Arancibia et al., 2006; Reich et al., 2009; see Section 4.1) could have acted as an additional barrier, filtering the dispersal of other *Heliotropium* species into the geographic range of *Cochranea*, and promoting speciation of *Cochranea* in the Atacama Desert.

***Tournefortia* clade** - The biogeography of the *Tournefortia* clade is complex. The fossil record of *Tournefortia* from the middle Oligocene of Puerto Rico (Graham and Jarzen, 1969) imposes a biogeographic constraint for the past distribution of the clade. This constraint indicates that a distribution in the Caribbean must have been reached early in the history of the *Tournefortia*-clade, and this is consistent with the biogeographical scenario reconstructed here (Fig. 4.4), in which Mesoamerica and the Caribbean were inhabited by *Heliotropium* since its origin during the Eocene (Fig. 4.3). Several authors have pointed out that South America and the Caribbean were connected during the middle and late Eocene (e.g., Graham, 2003a; Morley, 2003). It has also been suggested that a land connection between North-Western South America and the Greater Antilles during the Eocene/Oligocene transition served as dispersal route for birds (Iturralde-Vinent and MacPhee, 1999). Such a land connection, associated with a global fall in sea levels as a consequence of continental glaciations on Antarctica, may have also acted as dispersal route for early members of *Heliotropium*, which had later differentiated into the *Tournefortia* clade. This migration route has been suggested for other Caribbean plant groups with South American affinities (Graham, 2003b).

However, several members of the *Tournefortia* clade that are widely distributed in Mesoamerica, the Caribbean and tropical South America have a younger origin (sects. *Coeloma*, *Platygyne*, *Schobera*, *Tiaridium* Johnston, 1928b, 1930, 1935a; Figs. 4.2 and 4.3). For all of them, except sect. *Platygyne*, the DEC analysis suggests that South America was reached from the North (although the stem nodes of these clades are not well-supported). These distributions can be explained by the closing of the Panama Isthmus during the Pliocene (see Marshall et al., 1979; Morley, 2003; and references therein). Sections *Schobera* and *Tiaridium* are mainly distributed in eastern South America and in the Caribbean, and both reach the western side of the Andes; such a distribution in the west coast of South America may have been achieved after the uplift of the Andes through the Caribbean lowlands, as suggested by Haffer (1967), a hypothesis that is consistent with the biogeographic analyses presented here, but needs to be corroborated once the deeper nodes within the *Tournefortia* clade are better resolved.

Three well-supported groups within the *Tournefortia* clade are exclusively distributed in South America, corresponding to the sections *Heliotrophytum*, *Hypsogenia* and *Plagiomeris* (Fig. 4.2). *Heliotrophytum* inhabits the semiarid environments of eastern subtropical South America in N Argentina, SE Bolivia, S Paraguay, Uruguay and S Brazil, *Hypsogenia* is restricted to the high-Andean environments from NW Argentina to S Ecuador (wet Puna), while *Plagiomeris* is distributed along the Mediterranean and Patagonian Andes in Argentina and Chile. All theses sections show diversification times coincident with the major uplift of the Andes in the rapid uplift model (Fig. 4.3). The development of semiarid conditions in subtropical eastern South America after the major uplift of the Andes during the Miocene (e.g., Blisniuk et al., 2005), may have been responsible for the diversification of *Heliotrophytum* (and also for the South American Members of *Coeloma*). Such modifications of the climate have been suggested to be associated with the origin of arid-adapted floras in southern South America (Ezcurra, 2002; Gengler-Nowak, 2002b; Barreda and Palazzesi, 2007; Luebert and Wen, 2008; Heibl et al., in press). At the same time new environments may have become available for speciation into high-elevation habitats (e.g., Simpson, 1975), enabling the origin and diversification of *Hypsogenia* and *Plagiomeris*. Several age estimates for Andean plant taxa, such as *Astragalus* L. (Fabaceae Scherson et al., 2008), *Festuca* L. (Poaceae; Inda et al., 2008a; American II clade ), *Fuchsia* L. sect. *Hemsleyella* Munz (Onagraceae; Berry et al., 2004), *Lithospermum* L. (Boraginaceae Weigend et al., 2009), *Lupinus* L. (Fabaceae; Hughes and Eastwood, 2006), Paranepheliinae (Asteraceae; Soejima et al., 2008) have yielded similar diversification ages to those of *Hypsogenia* and *Plagiomeris*. These groups inhabit high-elevation environments, which likely became available for colonization when the Andes reached their present elevation.

The main control over the South American climatic patterns is exerted by the large-sacle circulation patterns (Hartley, 2003; Garreaud et al., 2009). The position and dynamic southeastern Pacific Subtropical Anticyclone, which is the primary responsible for the aridity of western South America is bounded to the north by the Inter Tropical Convergence Zone (ITCZ) and by the zonal eastward zonal flow to the south. Hartley (2003) suggested the existence of these circulation patterns throughout the Cenozoic. There is also evidence of the existence of the Humboldt System since the early Tertiary (Keller et al., 1997) and of non-significat shifts in the latitudinal position of South America during the Cenozoic (Hartley et al., 1992; Beck et al., 2000). If, in addition, the gradual Andean uplift model (Ehlers and Poulsen, 2009) is accepted, the divergence age estimates and biogeographical scenarios presented here for several Andean *Heliotropium* lineages, as well as those of many other Andean taxa would require a different explanation. In *Heliotropium*, Andean lineages (sections *Heliothamnus*, *Cochranea*, *Hypsogenia* and *Plagiomeris*) experienced diversification processes during the late Miocene or early Pliocene. Andean and extra-Andean lineages distributed in arid or semiarid environments of South America (sections *Heliotrophytum* and *Platygyne* in addition to *Cochranea* and *Plagiomeris*) also diversified during that period. The biological evidence accumulated to date on phylogeny-based age estimates and biogeography may be seen as evidence supporting the rapid uplift model and a late Tertiary development of aridity in western and eastern South America.

# 5. Climatic Control on Distribution, and Extinction Risk in *Heliotropium* sect. *Cochranea* (Heliotropiacae)[a]

## Abstract

Effects of the set of predictive variables on species distribution models have remained largely unstudied. Arid environments are among the most sensitive ecosystems to climate change effects, and can be useful to test model response to different sets of predictive variables. Here, potential distribution of 13 species of *Heliotropium* sect. *Cochranea*, a plant group with centre of diversity in the Atacama Desert, is modelled based on climatic variables. Eight modelling techniques were employed using six different sets of climatic variables, and final models for each species were built via ensemble forecasting. Variable importance and climatic niche differentiation among species were assessed, and climate change effects on extinction risk were evaluated, as well as the possible effect of the set of climatic variables on model output. Winter precipitation and winter minimum temperatures were the most important variables for most species of *Heliotropium* sect. *Cochranea*. Summer maximum temperature was also important for several species. This results are consistent with the expectation that the distribution of the species of *Heliotropium* sect. *Cochranea* is mostly controlled by seasonal variation of precipitation and, secondarily, of extreme temperature. The climatic niches of species of *Heliotropium* sect. *Cochranea* are slightly differentiated from one another. The set of climatic variables has strong effects on model output and on the evaluation of extinction risk and climate change effects on species distribution.

## 5.1 Introduction

Ecological theory predicts that climate controls the potential distribution and abundance of plant species at regional scale (Box, 1981; Woodward, 1987; Woodward and Williams, 1987; Breckle and Walter, 2002; Pearson and Dawson, 2003; Austin, 2007). Yet, simulating the response of plants to climatic influences can be complex, because different species exhibit different climatic tolerance, so that physiological responses to various climatic gradients vary among species and regions (Austin and Smith, 1989).

Climate variability at different spatio-temporal scales is a striking feature of arid environments (Whitford, 2002). Such fluctuations have potential effects on plant-species distribution, which may ultimately affect their extinction risk (IUCN, 2001). Arid ecosystems are also among the most sensitive ecosystems to climate change (Melillo et al., 1993; Lioubimtseva, 2004; Kefi et al., 2007). Identifying climatic factors that control the present

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distribution of species is therefore a key step in order to assess extinction risk, and to make predictions about potential effects of climate change on species distributions.

In desert environments, water availability can be considered as the most limiting factor controlling the abundance, co-occurrence and diversity of species (Noy-Meir, 1973, 1985; Ali et al., 2000; Enright et al., 2005). Variations in water supply, both spatially and temporally, may produce abrupt changes in the abundance and diversity of plant species (Holmgren et al., 2001b; Breckle and Walter, 2002; Meserve et al., 2003; Schwinning and Sala, 2004; Huang and Geiger, 2008; López et al., 2008; De La Maza et al., 2009). Desert plants are likely to respond differently to either rainfall events occurring in winter or in summer, thus seasonality should be an important factor of species distribution (Ogle and Reynolds, 2004). Precipitation may also be seen as a proxy of direct water availability for plants (Austin, 2007), and is related to several ecological and biogeochemical processes that affect plant species distribution (Schwinning and Sala, 2004; Jin et al., 2009; Patrick et al., 2009).

Minimum temperatures have been seen for a long time as an important climatic factor controlling plant distribution (Shreve, 1914; Turnage and Hinckley, 1938; Woodward, 1987). Since frost resistance is limited, absolute minimum temperatures impose a boundary to the expansion of species' range. In desert environments, incoming and outgoing solar radiation is generally high, so that daily fluctuations of temperature increase as precipitation decreases (Breckle and Walter, 2002). In coastal desert environments with influence of fog, such as the Pacific and the Namibia Deserts (Breckle and Walter, 2002), temperature fluctuations are regulated by both oceans and fog. Fog has the effect on decreasing both incoming and outgoing solar radiation in comparison with areas without influence of fog (Meserve et al., 2003). The latter factor may also have an effect on evapotranspiration (Fischer et al., 2009), enhancing the influence of rainfall pulses on plants. Thus, we hypothesise that seasonality of precipitation and temporal distribution of temperatures may play a combined role in defining environmental limits to species distribution in desert environments.

Species distribution models (SDMs, Guisan and Thuiller, 2005; Elith and Leathwick, 2009) can be used to identify relevant climatic factors or sets of climatic factors, influencing the distribution of species. Austin (2007) suggested that previous knowledge about the physiological response of plants to the environments, as well as the ecological theory (e.g., law of minimum), should be used in order to select variables for modelling their present distribution. Araújo and Guisan (2006) identified the selection of environmental predictors as one of the major SDM challenges, and recent studies (Dormann et al., 2008; Peterson and Nakazawa, 2008; Syphard and Franklin, 2009) showed that the selection of predictor variables (resulting in different sets) can actually affect the results and performance of SDMs. The set of variables to be used in practice, however, is limited both by the availability of information and the scale at which the phenomena are studied.

In modelling the present distribution of plant species at regional scale using climate data, it becomes apparent that yearly means can mask the effects of seasonality of temperature and precipitation, so that monthly variables or indexes, which capture the annual distribution of precipitation and temperature, should be considered as the primary sets, from which influential climatic variables can be selected. Recent studies showed that the use of monthly variables, rather than annual means or totals, improves the prediction of potential distribution of plant species (Laurent et al., 2004; Zimmermann et al., 2009). However, it is difficult to determine a priori which specific variables primarily influence the distribution of a species, even when there is a deep knowledge of its physiology. On the other hand, the inclusion of too many variables in a model may cause overfitting problems (Araújo and Guisan, 2006; Thuiller et al., 2008a), hence generating models too centred on occurrence data.

A parsimonious approach would be to select different subsets of variables with potential ecological meaning for the species under study, with low correlation among themselves and with each subset corresponding to a different hypothesis on how the environment controls the species distribution, and then to compare the performance of the models built with these different subsets and to assess the contribution of individual variables throughout all models. This could be done for instance in an information-theoretic multi-model framework, such as proposed by Burnham and Anderson (2002), which could be applied in linear regression modelling approach (Wisz and Guisan, 2009). Another problem is the way, in which climatic variables are treated before modelling, with several approaches being employed in the recent literature, such as the use of monthly values directly (e.g., Hijmans and Graham, 2006), climatic indexes (e.g., Broennimann et al., 2007) or orthogonal principal components (e.g., Loarie et al., 2008). The latter two correspond to combination of the initial monthly variables. Principal components analysis has the advantage of concentrating the variability of numerous variables into a reduced number of uncorrelated principal components, but often at the cost of losing predictive power, because the main components are not necessarily based on the most important variables for the modelled species (Muñoz and Felicísimo, 2004). Yet, the effects of pre-treatment of climatic variables on model performance have largely remained untested so far (Parra et al., 2004).

SDMs may also be considered as a useful tool to determine the extinction risk (Thuiller et al., 2005; Rödder et al., 2009). As a conservative approach to categorize extinction risk (Thuiller et al., 2005; but see Akçakaya et al., 2006), a model output can be equated to criterion of area of occupancy of IUCN (2001). However, several issues might complicate the application of SDMs to determine extinction risk. First, it is not clear whether or not variable selection has an effect in the final model output, hence influencing the extinction risk derived from the result of a given model (Syphard and Franklin, 2009). Second, a threshold has to be used in order to transform model output (generally given as some kind of probability of occurrence) into a binary presence/absence projection, on the basis of which areas are calculated (Barry and Elith, 2006). Third, species with restricted ranges usually have less information available than species with larger ranges, thus hampering the potential applicability of SDMs to these species (Guisan et al., 2006), which at the time are the most prone to be endangered (Lomba et al., 2010). Fourth, the scale at which the distribution is modelled can greatly affect the estimations of range size with SDMs (Seo et al., 2009). These issues related to the use of SDM have been insufficiently investigated so far.

Plant-species rarity seems to be common in arid environments (Stohlgren et al., 2005). This also appears to be the case for the Atacama Desert, which is arguably one of the most arid areas on earth (Walter and Breckle, 2004). Located in the west coast of South America, the Atacama houses around 550 species of vascular plants (Dillon and Hoffmann, 1997) and endemism can be up to 60% in some localities (Rundel et al., 1991). While several floristic studies throughout the Atacama Desert have been published, making it possible to asses spatial patterns of diversity in the area (e.g., Johnston, 1929c, 1932; Rundel and Mahu, 1976; Armesto and Vidiella, 1993; Richter, 1995; Rundel et al., 1996; Muñoz Schick et al., 2001; Luebert et al., 2007; Pinto and Luebert, 2009), it is still relatively little known about the climatic factors determining the distribution of plant species.

Table 5.1: Latitudinal and altitudinal range, total number of herbarium specimens, total unique occurrences and unique occurrences for each species of *Heliotropium* sect. *Cochranea*. Species marked with asterisks were not included in the analyses because of their low number of presence data. Spatial autocorrelation of the presence data (>1950) of each species as measured by Moran's I index is indicated in the last column.

| | | | Occurrences | | | |
|---|---|---|---|---|---|---|
| Species | Latitude S | Elevation (m) | Total | Unique | >1950 | Moran's I |
| *Heliotropium chenopodiaceum* (A.DC.) Clos | 26.2 – 31.5 | 200 – 2250 | 150 | 102 | 81 | 0.462 |
| **Heliotropium eremogenum* I.M.Johnst. | 23.4 – 23.7 | 100 – 1000 | 16 | 13 | 10 | |
| *Heliotropium filifolium* (Miers) I.M.Johnst. | 27.4 – 28.6 | 20 – 530 | 26 | 19 | 17 | 0.217 |
| *Heliotropium floridum* (A.DC.) Clos | 26.0 – 29.3 | 0 – 265 | 66 | 50 | 45 | 0.758 |
| **Heliotropium glutinosum* Phil. | 26.3 – 27.2 | 1195 – 2200 | 18 | 9 | 6 | |
| *Heliotropium inconspicuum* Reiche | 25.1 – 26.1 | 100 – 780 | 21 | 17 | 13 | 1.098 |
| **Heliotropium jaffuelii* I.M.Johnst. | 22.0 – 22.1 | N/A | 4 | 1 | 1 | |
| *Heliotropium krauseanum* Fedde | 12.6 – 19.6 | 0 – 1734 | 39 | 26 | 15 | 0.731 |
| *Heliotropium linariifolium* Phil. | 24.9 – 27.1 | 0 – 1300 | 104 | 68 | 55 | 0.595 |
| *Heliotropium longistylum* Phil. | 27.7 – 28.4 | 5 – 400 | 22 | 15 | 13 | 0.684 |
| *Heliotropium megalanthum* I.M.Johnst. | 27.8 – 28.6 | 0 – 620 | 40 | 26 | 24 | 0.427 |
| *Heliotropium myosotifolium* (A.DC.) Reiche | 27.1 – 29.2 | 170 – 900 | 56 | 40 | 30 | 0.675 |
| **Heliotropium philippianum* I.M.Johnst. | 24.4 – 25.1 | 20 – 1100 | 25 | 14 | 6 | |
| *Heliotropium pycnophyllum* Phil. | 23.5 – 27.1 | 0 – 930 | 141 | 92 | 74 | 0.824 |
| *Heliotropium sinuatum* (Miers) I.M.Johnst. | 27.7 – 29.7 | 0 – 1500 | 83 | 69 | 63 | 0.775 |
| *Heliotropium stenophyllum* Hook. & Arn. | 28.5 – 32.8 | 0 – 1200 | 204 | 104 | 79 | 0.351 |
| *Heliotropium taltalense* (Phil.) I.M.Johnst. | 24.4 – 25.5 | 50 – 1060 | 67 | 36 | 27 | 0.702 |
| Total | 12-6 – 32.8 | 0 – 2250 | 1082 | 701 | 559 | 0.638 |

A few attempts at modelling plant species distribution, including Atacama Desert plants, have been done in the past few years (Zizka et al., 2009; Nakazato et al., 2010); however, these studies have not specifically addressed the question of which climatic variables the best predict current distribution of species.

*Heliotropium* sect. *Cochranea* appears to be well suited for this purpose. Sixteen out of 17 species have a geographical range centred in the Atacama Desert (18°30'S – 31°30'S, 0 – 3,000 m; Table 5.1). Only one species has its centre of distribution in the Peruvian Desert (*H. krauseanum*), and one species extends its distribution over the Mediterranean woodland zone of central Chile (*H. stenophyllum*). Most species have narrow geographic ranges along the coast of a few kilometers wide (Johnston, 1928b; Luebert and Wen, 2008; see Chapters 2 and 6), being local endemics and geographically rare species. *Heliotropium* sect. *Cochranea* is one of the most diverse plant groups of the Atacama Desert (Luebert and Wen, 2008; see Chapter 2), and at the same time one of the best studied. Therefore, their full realized environmental niche can be captured, making current and future projections possible (Thuiller et al., 2004a).

*Heliotropium* sect. *Cochranea* is a monophyletic group, which has likely experienced a radiation in the Atacama Desert in the last 4 Ma (Luebert and Wen, 2008; see Chapters 2 and 4), likely resulting from gradual climatic niches differentiation. If this is the case, species should exhibit clear differences in their climatic niche and potential distribution. This can be assessed by using SDMs and variable selection approaches to evaluate the breadth and shape of climatic niches, shedding light on the evolutionary ecology of *Heliotropium* sect. *Cochranea*.

In this paper, using comprehensive data on *Heliotropium* sect. *Cochranea*, we focus more specifically on the following questions:

(1) What are the main climatic variables controlling the distribution of the species of *Heliotropium* sect. *Cochranea*?

(2) Do the species of *Heliotropium* sect. *Cochranea* exhibit different climatic niches?

(3) Are there differences in model performance and accuracy among different sets of climatic variables in arid environments?

(4) Are those differences affecting the estimations of extinction risk of rare species?

(5) How can climate change affect the extinction risk of rare species in arid environments?

(6) Are there differences in the estimation of climate change effects among different sets of climatic variables?

To address these questions, we propose a series of steps to generate different sets of climatic variables and compare the results of SDMs among those sets of variables, using different modelling techniques and two scenarios of climate change. We estimate the extinction risk of each species using different sets of variables, and evaluate the potential extinction risk under scenarios of climate change.

## 5.2 Materials and Methods

### 5.2.1 Study Area

The study was carried out in an area that includes the complete distribution of *Heliotropium* sect. *Cochranea* in the Peruvian and Atacama Deserts of South America. Most species are restricted to the Pacific coastal range, but few of them reach the foothills of the western slope of the Andes up to ca. 2,000 m. Therefore, the study area was circumscribed to the western side of the Andes of southern Peru and northern Chile between 10°S and 33°S from the coastline to 2,500 m of elevation (Fig. 5.1). Based on the revision of specimens at 22 herbaria, the literature and the fieldwork, we do not know any record of section *Cochranea* outside this area.

### 5.2.2 Climatic Data

Climatic surfaces were generated for this study using the software Anusplin v.4.36 (Hutchinson, 2006), which implements the methods described in Hutchinson (1995). We modelled monthly data of precipitation (P), mean temperature (T), mean maximum temperature (M) and mean minimum temperature (m), obtained from a total of 930 weather stations of Chile, Bolivia, Peru and Argentina, to generate climatic surfaces in an area larger than our specific study area, thus avoiding edge effects (Mesquita and Sousa, 2009). Interpolations were fitted with the second order-spline method using elevation as independent variable (Hutchinson, 2006). Although climatic surfaces are available for our study area from the widely used Worldclim (Hijmans et al., 2005), values obtained from weather stations from the study area and values extracted from Wordlclim differed substantially, especially for temperature (T, M, m) data. Such differences can be due to the scanty temperature data for the study area used in Worldclim project (Hijmans et al., 2005). The Global Historical Climate Network Dataset (GHCN, Peterson and Vose, 1997), used as primary source by Hijmans et al. (2005), does not contain extreme temperature data for our study area. Poor climatic documentation has negative effects on the performance of SDMs (Soria-Auza et al., 2010). Therefore, we built an expanded dataset that includes

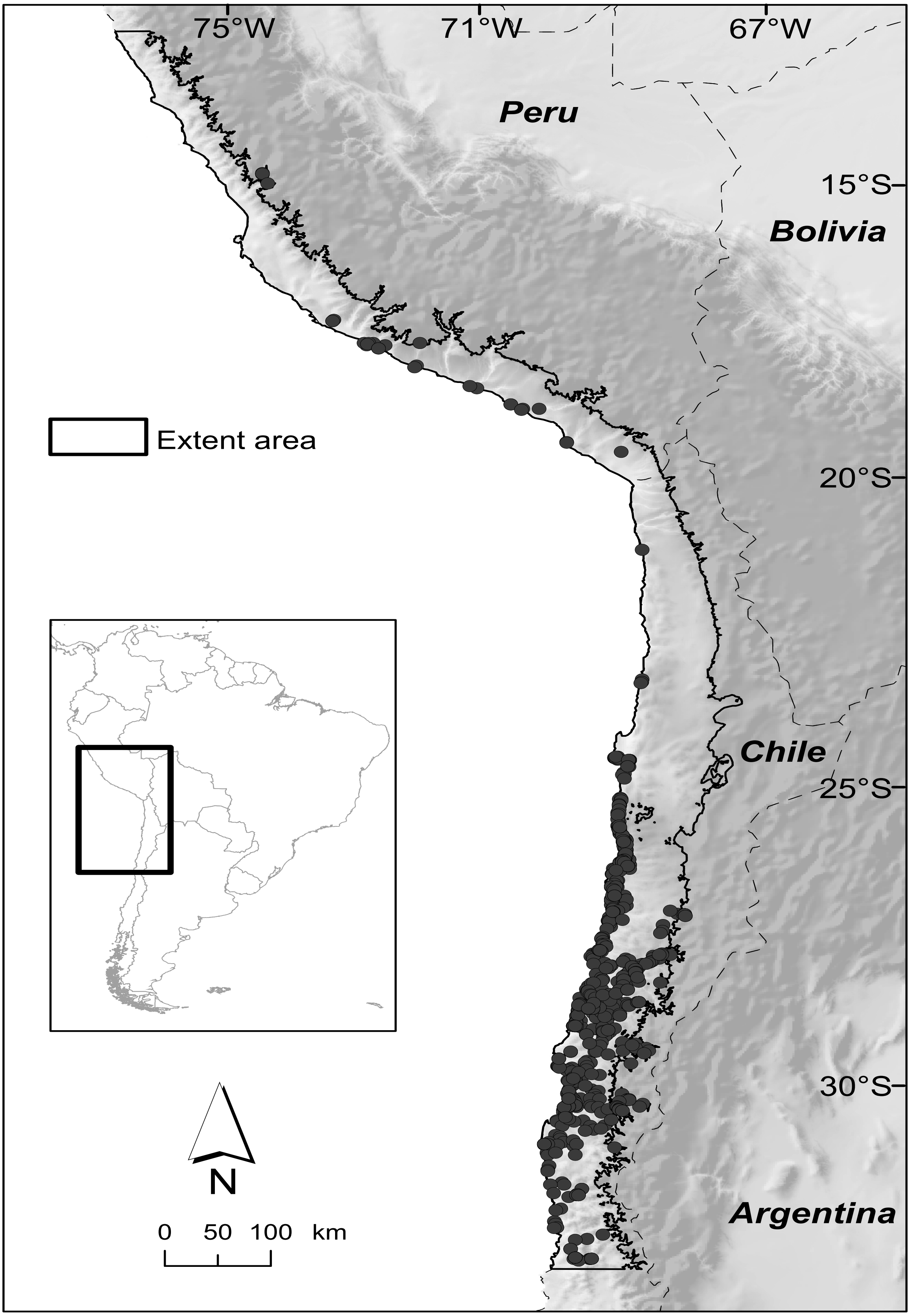

Figure 5.1: Study area indicating the distribution of *Heliotropium* sect. *Cochranea* (grey dots).

weather stations from specific Chilean sources. In addition to the Faoclim dataset (FAO, 2001), we used the stations reported by Hajek and di Castri (1975), Amigo and Ramírez (1998), Rivas-Martínez et al. (2003) and Luebert and Pliscoff (2006).

### 5.2.3 Presence Data

Herbarium samples of *Heliotropium* sect. *Cochranea*, including own collections, were critically revised and determined at the herbaria A, B, BM, BSB, CONC, DR, EIF, F, G, GH, K, M, MA, MSB, NY, SGO, ULS and US (acronyms according to the Index Herbariorum, Holmgren and Holmgren, 1998 [continuously updated]; available at `http://sciweb.nybg.org/science2/IndexHerbariorum.asp`). All specimens with ambiguous locality data were discarded from the analysis. A total of 1082 records, corresponding to 559 unique records from collections after 1950 (the timeframe of the weather station data used to generate the climatic surfaces), were included (Table 5.1). Only those species with more than 10 unique records (thirteen species, Table 5.1) were considered for analysis (Pearson et al., 2007).

### 5.2.4 Modelling Potential Distribution

BIOMOD v.1.1-5 (Thuiller et al., 2009) was used to generate SDMs. BIOMOD is a library of R (R Development Core Team, 2009) that implements ensemble forecasting, an approach that combines the results of several modelling techniques to arrive at a robust consensus solution (Araújo and New, 2007). This approach addresses some problems associated with uncertainty of single modelling techniques, especially when predicting impacts of climate change on species distribution (Araújo et al., 2005; Pearson et al., 2006; Buisson et al., 2010). Eight modelling techniques currently implemented in BIOMOD were used in our analysis: (1) artificial neural networks (ANN), (2) classification tree analysis (CTA), (3) generalized additive model (GAM), (4) generalized boosted model (GBM), (5) generalized linear model (GLM), (6) multivariate adaptive regression splines (MARS), (7) Random Forest (RF) and (8) Surface Range Envelops (SRE). Presence data set was randomly partitioned into 70% to calibrate every model (training data) and 30% to evaluate the model (test data). The modelling techniques implemented in BIOMOD need both presence and absence data. Since our data sets have only presence data, 10,000 pseudo-absences points were randomly selected from the extent, an approach that renders reasonable results (Wisz and Guisan, 2009).

Predictive power was evaluated with the Area under the relative operating characteristic curve (AUC) and the true skill statistic (TSS), except for SRE, for which AUC is not available. Ideally, training and test data should be statistically independent, because spatial autocorrelation can led to artificially high estimates of predictive power (Veloz, 2009). We, therefore, calculated Moran index (I) of spatial autocorrelation (Cliff and Ord, 1981) for each species and tested for correlation between AUC/TSS and I.

Consensus models were obtained using ensemble forecasting, excluding the results from techniques with low predictive power. Low predictive power was evaluated by comparison of TSS among models using the Wilcoxon rank test implemented in R (R Development Core Team, 2009).

### 5.2.5 Variable Importance and Sets of Climatic Variables

In order to assess the effect of different sets of climatic variables on modelling output, six sets of variables were assembled based on our climatic surfaces. Variable importance on species distribution was evaluated with RF as an integral part of the definition of sets of climatic variables Mr and Br (see below). The following sets were defined:

(1) Nineteen monthly values of Pi, Ti, Mi and mi (where i is the month number), where only the middle month from each season (DJF [summer], MAM [fall], JJA [winter], SON [spring]) was selected, provided that all correlations within the season were $>$ 0.9; when two (three) correlations among variables within the season were $<$0.9, one (two) more variables was (were) selected; hereafter ‘Mc’.

(2) One reduced subset of six monthly variables from Mc, resulted from a selection based on a variable contribution analysis in RF, using the greatest values of mean decrease accuracy (Thuiller et al., 2008b); hereafter ‘Mr’.

(3) The Bioclim set of 19 bioclimatic variables generated with the bioclim-aml (available at `http://www.worldclim.org/bioclim-aml`, accessed, 4 October 2010) hereafter ‘B’.

(4) A subset of 13 variables from B, resulted of the elimination of one of each pair of variables with correlations $>$0.9; hereafter ‘Bc’.

(5) One reduced subset of six variables from Bc, resulted from a selection based on a variable contribution analysis in RF, using the greatest values of mean decrease accuracy (Thuiller et al., 2008b); hereafter ‘Br’.

(6) The first six principal components resulted from a PCA of the 48 monthly variables within the extent; hereafter ‘PC’.

### 5.2.6 Comparing Sets of Climatic Variables

All eight modelling techniques were applied to each set of variables (6) and species (13) (total 624 partial models). In order to compare sets of variables, predictive power (AUC, TSS) was averaged across species and techniques, and compared using the Wilcoxon rank test. Final models of different sets of variables resulted from ensemble forecasting, were also compared using the Kappa ($\kappa$) statistic (Robertson et al., 2003). The latter is a measure of spatial agreement between models, which is not necessarily correlated with similarities in predictive power (Syphard and Franklin, 2009). The $\kappa$ statistic was calculated for binary (presence/absence) projections, obtained after the application of a probability threshold to the final models. The threshold was estimated optimizing the value of the TSS statistic (MaxSens+Spec criterion) available in the PresenceAbsence R library (Freeman and Moisen, 2008). For comparative purposes, a probability threshold of 0.5 was also used to generate binary models, but it was not used to calculate the $\kappa$ statistic.

### 5.2.7 Climate Change Scenarios

We used the HadCM3 (Hadley Centre Coupled Model, version 3) climate change model for the year 2050, with the SRES scenarios A2 and B2 (IPCC, 2007). The data were obtained from CIAT downscaled GCM data portal webpage (`http://gisweb.ciat.cgiar.`

`org/GCMPage/`, accessed 4 October 2010). Monthly data of precipitation, mean maximum temperature and mean minimum temperature were downloaded. Monthly mean temperature was calculated as the average of monthly mean minimum and maximum temperature surfaces. Since our current climatic surfaces were created in a different way (i.e., based on own meteorological station data interpolation), we obtained climate change scenarios for our study area following the procedure proposed by Buytaert et al. (2009), which consists in calculating anomalies for the future climate data (subtracting current to future values) and adding this differences to our own current climatic surfaces. These calculations were carried out using map algebra in ArcGis v.9.3 (ESRI, 2008). The same six sets of variables used for current climate (Mc, Mr, B, Bc, Br, PC) were created for each climate change scenario (HadCM3 A2 and HadCM3 B2). Climate change scenarios were used to re-project the models previously calibrated in BIOMOD, thus obtaining future projections of species distribution. Range shift under climate change scenarios were further compared among sets of climatic variables using the $\kappa$ statistic, calculated between present and future models, within species, climate change scenario and set of variables.

### 5.2.8 Extinction Risk

In order to assess extinction risk of each species, areas were calculated from the binary (presence/absence) projections of the final models (see above). Extinction risk was evaluated in two ways. First, we evaluated the extinction risk based on current distribution using the criteria of extent of occurrence (B1c) and area of occupancy (B2c) of IUCN (2001). The latter was proposed by Thuiller et al. (2005) as the criterion to be used with SDMs. We compared the results of these analyses across sets of climatic variables, and included, as reference, areas calculated using the minimum convex polygon (for extent of occurrence) and a buffer of 4 km2 of each locality (for area of occupancy), as recommended by IUCN (2001). In order to meet the criteria of the IUCN (2001), we assumed that area of occupancy experiences strong climatic inter-annual and inter-decadal fluctuations in rainfall (Garreaud and Battisti, 1999), which ultimately affects the expression of the populations in this extremely dry area. The area, using minimum convex polygon and 4 $km^2$ buffers, was also calculated for the four species not included in the modelling, for which the number of presence records is below recommended minimum values (e.g., Guisan et al., 2006; Pearson et al., 2007). Low number of presence records in these species is, at least partially, due to their natural rarity rather than to sampling effort, possibly because of being the most threatened species in *Heliotropium* sect. *Cochranea.*

Extinction risk was also assessed using the criterion A3(c) (IUCN, 2001), as suggested by Thuiller et al. (2005), using change in area of occupancy to the year 2050 as indicator of increase/decrease in population size. We compared the results of these analyses among sets of climatic variables, computing the number of changes in extinction risk between pairs of sets of variables.

## 5.3 Results

### 5.3.1 Variable Importance and Sets of Climatic Variables

Correlation matrices among monthly variables and among Bioclim indices are supplied in the Appendix D.1. After the comparison of the correlations, the following sets of variables were selected (see methods for details):

- Mc: P1, P3, P4, P5 P7, P9, P11, T1, T4, T7, T10, M1, M4, M7, M10, m1, m4, m7, m10
- Bc: BIO2, BIO3, BIO4, BIO5, BIO6, BIO7, BIO8, BIO9, BIO11, BIO14, BIO15, BIO18, BIO19

The RF analysis of variable importance yielded a different reduced set of climatic variables for each species (Table 5.2). In the Mr set, winter precipitation (P7) was selected for all species except *Heliotropium krauseanum*, and winter minimum temperature (m7) was selected for 10 out of 13 species. In the Br set, the precipitation of coldest quarter (BIO19) was selected for 10 species, while the maximum temperature of the warmest month (BIO5) for nine species.

Table 5.2: Variables selected from the analysis of variable importance conducted with Random Forest (RF). The sets of variables, Mr and Br, are different for each species and are subsets of Mc (monthly variables reduced after inspection of the correlation matrix) and Bc (Bioclim climatic indices reduced after inspection of the correlation matrix), respectively (see text for details). Numbers 1–6 correspond to the order of importance of the variables according to the RF results, being 1 the most important.

| | Mr | | | | | | Br | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | 1 | 2 | 3 | 4 | 5 | 6 | 1 | 2 | 3 | 4 | 5 | 6 |
| *Heliotropium chenopodiaceum* | P7 | M10 | m7 | M1 | M7 | M4 | BIO19 | BIO5 | BIO7 | BIO2 | BIO9 | BIO6 |
| *Heliotropium filifolium* | P7 | m7 | m1 | m10 | P3 | M1 | BIO11 | BIO3 | BIO9 | BIO8 | BIO19 | BIO15 |
| *Heliotropium floridum* | P7 | m1 | M4 | m4 | m10 | m7 | BIO4 | BIO3 | BIO5 | BIO15 | BIO9 | BIO7 |
| *Heliotropium inconspicuum* | P7 | m10 | M7 | M10 | T7 | m7 | BIO6 | BIO19 | BIO3 | BIO8 | BIO11 | BIO15 |
| *Heliotropium krauseanum* | M10 | M7 | P1 | P4 | P11 | m7 | BIO18 | BIO6 | BIO7 | BIO5 | BIO8 | BIO14 |
| *Heliotropium linariifolium* | P7 | m10 | M10 | M1 | m1 | M7 | BIO19 | BIO4 | BIO6 | BIO3 | BIO15 | BIO5 |
| *Heliotropium longistylum* | m1 | P7 | m10 | M4 | P3 | P5 | BIO3 | BIO2 | BIO9 | BIO7 | BIO5 | BIO8 |
| *Heliotropium megalanthum* | P7 | m1 | P5 | m7 | M10 | m4 | BIO11 | BIO3 | BIO9 | BIO19 | BIO15 | BIO8 |
| *Heliotropium myosotifolium* | P7 | M10 | m1 | m7 | M1 | T1 | BIO9 | BIO19 | BIO2 | BIO11 | BIO5 | BIO6 |
| *Heliotropium pycnophyllum* | m10 | M4 | T7 | M7 | P7 | M10 | BIO19 | BIO15 | BIO3 | BIO6 | BIO8 | BIO4 |
| *Heliotropium sinuatum* | P7 | m1 | m7 | M7 | P5 | M10 | BIO11 | BIO19 | BIO5 | BIO9 | BIO2 | BIO8 |
| *Heliotropium stenophyllum* | m7 | P7 | T1 | m4 | m1 | P3 | BIO19 | BIO6 | BIO9 | BIO2 | BIO5 | BIO7 |
| *Heliotropium taltalense* | T7 | m7 | P7 | M1 | m10 | M4 | BIO6 | BIO8 | BIO11 | BIO19 | BIO5 | BIO15 |

The six first principal components (eigenvectors and eigenvalues provided in the Appendix D.2) concentrated 97.2% of the total variance, and the 71.4% of the variance was held by the first two principal components. Comparisons of climatic envelopes of the most important variables (P7, m7, BIO19, BIO5, PC1 and PC2) reveal that breath, shape and distribution climatic niche vary across species (Fig. 2). Species with wider geographical distribution (*Heliotropium chenopodiaceum*, *H. krauseanum* and *H. stenophyllum*) tend to occupy larger proportion of the climatic envelope of the extent area. Species tend to be slightly differentiated in the precipitation gradient (axis X of Fig. 5.2A and B). The most humid extreme of the extent area in not occupied by any species in section *Cochranea*. *Heliotropium stenophyllum* tends to occupy more humid portion of the extent area than the rest of the species. Higher variation in breath and distribution of the species is observed along the temperature gradients (axis Y of Fig. 5.2A and B).

### 5.3.2 Species Distribution Models

In average GAM and GLM resulted the models with greatest predictive power (Fig. 5.3). ANN and SRE showed poor performance according to the TSS statistic, which was significantly different to all other techniques according to the Wilcoxon rank test (Table

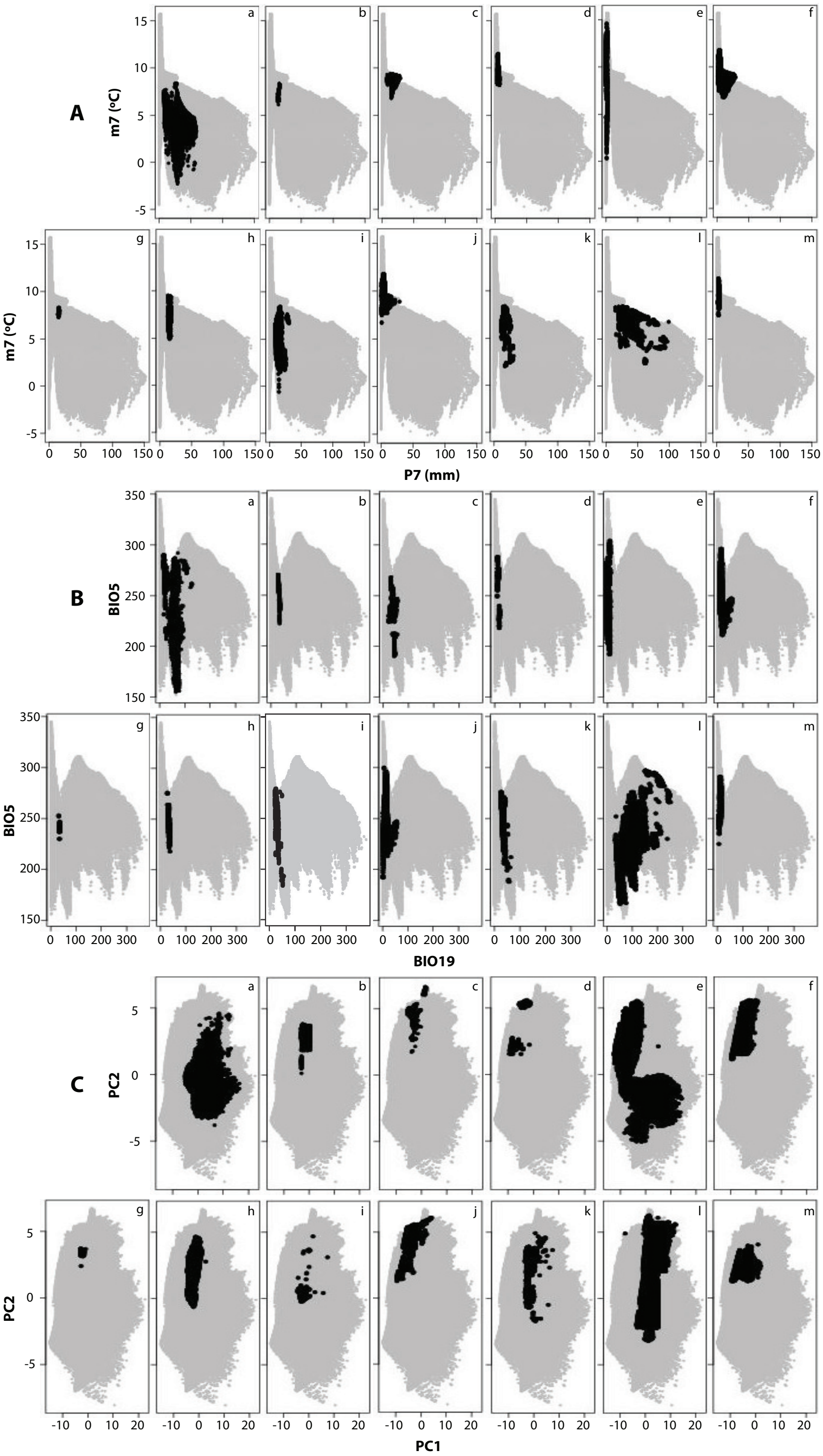

Figure 5.2: Comparison of climatic envelopes among modelled species. A, Climatic envelope of precipitation of July (P7) versus mean minimum temperature of July (m7), based on the final Mc binary model. B, Climatic envelope of precipitation of coldest quarter (BIO19) versus maximum temperature of warmest month (BIO5), based on the final B binary model. C, Climatic envelope of the two first principal components (PC1 versus PC2), based on the final PC binary model. Climatic envelope of the species according to binary final models (black) was plotted on the climatic envelope of the extent area (grey). Lower-case letters indicate species: a, *Heliotropium chenopodiaceum*; b, *H. filifolium*; c, *H. floridum*; d, *H. inconspicuum*; e, *H. krauseanum*; f, *H. linariifolium*; g, *H. longistylum*; h, *H. megalanthum*; i, *H. myosotifolium*; j, *H. pycnophyllum*; k, *H. sinuatum*; l, *H. stenophyllum*; m, *H. taltalense.*

3). The latter two techniques were therefore excluded from ensemble forecasting. For the remaining techniques, AUC was > 0.9 (excellent) on average, except in CTA, where it was > 0.8 (good), while TSS was usually > 0.8 (excellent) on average, except in MARS and RF, where it was > 0.7 (good).

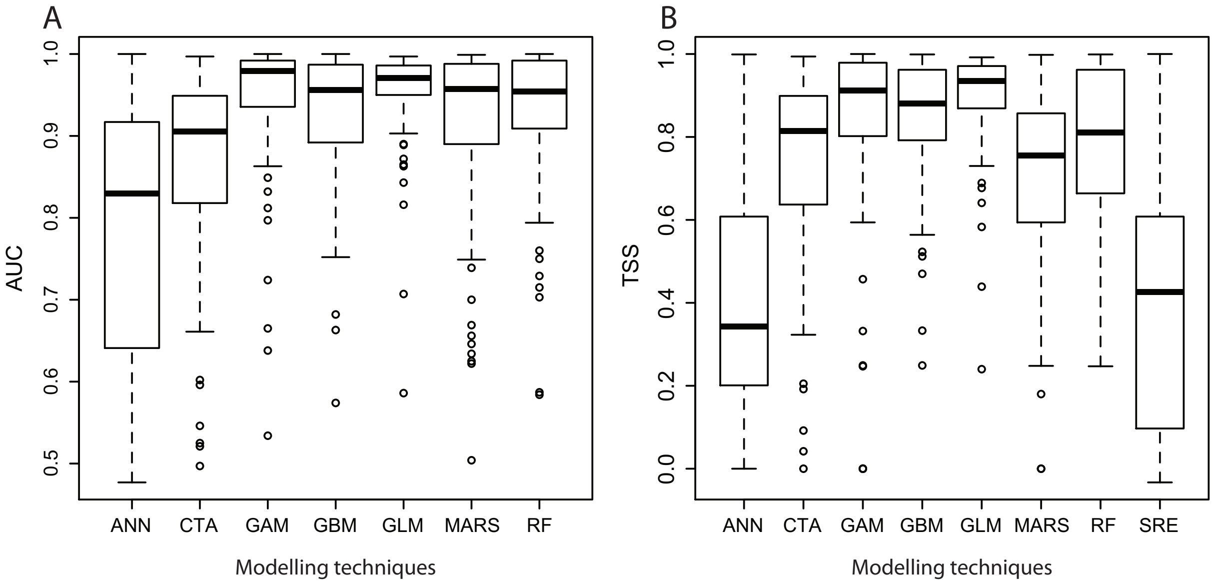

Figure 5.3: Box and whisker plots of the predictive performance of the different techniques used for SDMs. A, AUC; B, TSS. Values correspond to all species and variable sets.

All species have positive spatial autocorrelation (Table 5.1), and all are significant ($p \ll 0.0001$, data not shown), which means that presence data tend to cluster around certain points in the geographical space and are not randomly distributed. The Pearson's correlation coefficient calculated across species between mean TSS and Moran I (r = 0.0555) is not significantly different from zero (t = 0.1844, df = 11, $p$ = 0.857). In consequence, spatial autocorrelation (as measured by Moran's I) does not bear a linear relationship with predictive power (as measured by TSS). As the focus of this chapter is not on spatial autocorrelation, we will not analyse this aspect further.

### 5.3.3 Comparison Among Sets of Climatic Variables

#### Predictive Power

When compared predictive power among sets of climatic variables of single modelling techniques, no differences are apparent using TSS (Fig. 5.4). Results with AUC (not shown) follow the same pattern. Almost no significant differences in predictive power were detected among sets of climatic variables when compared across species and modelling techniques with the Wilcoxon rank test. The only trend in predictive power was towards a poorer performance of PC, which was significantly lower than Mr (W= 3597) and B (W= 3629), both with p<0.05.

#### Spatial pattern

When compared the spatial pattern of the projections among different sets of variables with the $\kappa$ statistic (Fig. 5.5), much more variation than in predictive power was observed. The variation in $\kappa$ values is depicted in Fig. 5.6 and ranges between <0.2 (very poor

Table 5.3: Wilconxon rank test (W) for the comparison of AUC (upper panel) and TSS (lower panel) among modelling techniques. Values under the headings 'AUC' and 'TSS' are the respective means. NS: not significant; * $p<0.05$; ** $p<0.01$, *** $p<0.001$.

| | | AUC | AUC | W | $p$ |
|---|---|---|---|---|---|
| ANN | CTA | 0.789 | 0.872 | 2186 | 0.00243 ** |
| ANN | GAM | 0.789 | 0.945 | 1016 | 0.00000 *** |
| ANN | GBM | 0.789 | 0.923 | 1431 | 0.00000 *** |
| ANN | GLM | 0.789 | 0.951 | 979 | 0.00000 *** |
| ANN | MARS | 0.789 | 0.912 | 1460 | 0.00000 *** |
| ANN | RF | 0.789 | 0.927 | 1354 | 0.00000 *** |
| CTA | GAM | 0.872 | 0.945 | 1306 | 0.00000 *** |
| CTA | GBM | 0.872 | 0.923 | 1959 | 0.00019 *** |
| CTA | GLM | 0.872 | 0.951 | 1291 | 0.00000 *** |
| CTA | MARS | 0.872 | 0.912 | 1950 | 0.00011 *** |
| CTA | RF | 0.872 | 0.927 | 1851 | 0.00002 *** |
| GAM | GBM | 0.945 | 0.923 | 3521 | 0.01963 * |
| GAM | GLM | 0.945 | 0.951 | 3305 | 0.16592 NS |
| GAM | MARS | 0.945 | 0.912 | 3563 | 0.02005 * |
| GAM | RF | 0.945 | 0.927 | 3361 | 0.11185 NS |
| GBM | GLM | 0.923 | 0.951 | 2543 | 0.10002 NS |
| GBM | MARS | 0.923 | 0.912 | 2978 | 0.93012 NS |
| GBM | RF | 0.923 | 0.927 | 2825 | 0.52521 NS |
| GLM | MARS | 0.951 | 0.912 | 3459 | 0.13979 NS |
| GLM | RF | 0.951 | 0.927 | 3258 | 0.44489 NS |
| MARS | RF | 0.912 | 0.927 | 2882 | 0.57179 NS |

| | | TSS | TSS | W | $p$ |
|---|---|---|---|---|---|
| ANN | CTA | 0.395 | 0.735 | 1061 | 0.00000 *** |
| ANN | GAM | 0.395 | 0.819 | 827.5 | 0.00000 *** |
| ANN | GBM | 0.395 | 0.841 | 589.5 | 0.00000 *** |
| ANN | GLM | 0.395 | 0.892 | 435 | 0.00000 *** |
| ANN | MARS | 0.395 | 0.693 | 1274 | 0.00000 *** |
| ANN | RF | 0.395 | 0.777 | 868.5 | 0.00000 *** |
| ANN | SRE | 0.395 | 0.379 | 3121 | 0.78066 NS |
| CTA | GAM | 0.735 | 0.819 | 1976 | 0.00016 *** |
| CTA | GBM | 0.735 | 0.841 | 2068.5 | 0.00056 *** |
| CTA | GLM | 0.735 | 0.892 | 1518 | 0.00000 *** |
| CTA | MARS | 0.735 | 0.693 | 3383 | 0.22746 NS |
| CTA | RF | 0.735 | 0.777 | 2719 | 0.25299 NS |
| CTA | SRE | 0.735 | 0.379 | 5189.5 | 0.00000 *** |
| GAM | GBM | 0.819 | 0.841 | 3244 | 0.47507 NS |
| GAM | GLM | 0.819 | 0.892 | 2824 | 0.44073 NS |
| GAM | MARS | 0.819 | 0.693 | 4240 | 0.00002 *** |
| GAM | RF | 0.819 | 0.777 | 3641.5 | 0.03373 * |
| GAM | SRE | 0.819 | 0.379 | 5465 | 0.00000 *** |
| GBM | GLM | 0.841 | 0.892 | 2493.5 | 0.05208 NS |
| GBM | MARS | 0.841 | 0.693 | 4201.5 | 0.00004 *** |
| GBM | RF | 0.841 | 0.777 | 3573.5 | 0.05981 NS |
| GBM | SRE | 0.841 | 0.379 | 5663 | 0.00000 *** |
| GLM | MARS | 0.892 | 0.693 | 4621.5 | 0.00000 *** |
| GLM | RF | 0.892 | 0.777 | 3963 | 0.0011 ** |
| GLM | SRE | 0.892 | 0.379 | 5855 | 0.00000 *** |
| MARS | RF | 0.693 | 0.777 | 2442.5 | 0.03374 * |
| MARS | SRE | 0.693 | 0.379 | 4941 | 0.00000 *** |
| RF | SRE | 0.777 | 0.379 | 5370.5 | 0.00000 *** |

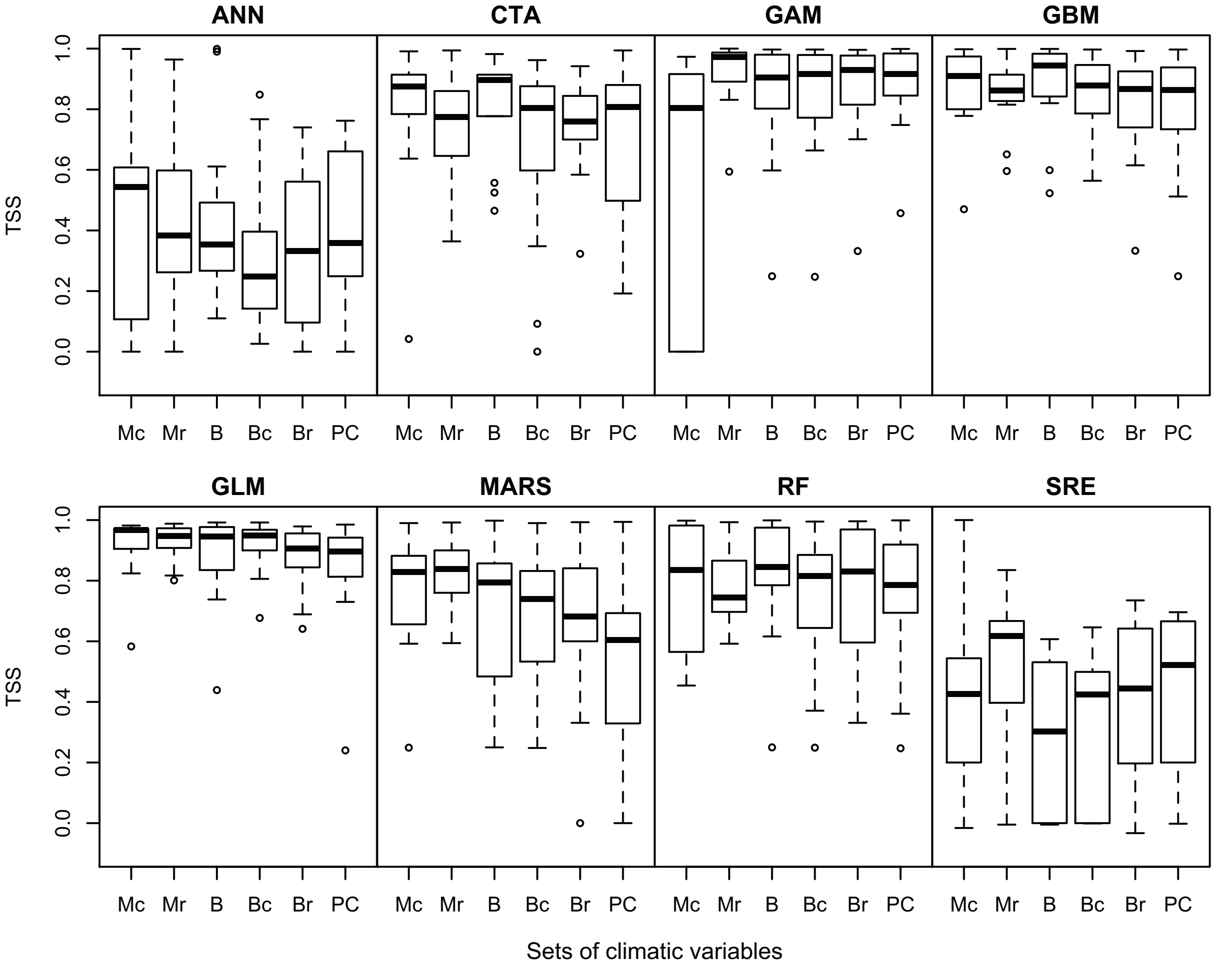

Figure 5.4: Box and whisker plots of the predictive performance (TSS) of the models with different sets of climatic variables across modelling techniques. Values of each technique and set of climatic variables correspond to the 13 species analysed.

agreement) and >0.8 (excellent agreement). In other words, in spite of the generally good and similar predictive power of the projections observed among sets of climatic variables, the spatial agreement of such projections varies considerably. However, no general trend is observed among the comparisons, which seem to be idiosyncratic.

### Climate Change Projections

For most comparisons no significant change in surface between the current models and the climate change scenarios was detected when averaged across species (present and future estimates of surface for each species under different thresholds, climate change scenarios and sets of climatic variables are presented in Appendix D.3). Only in three cases a significant trend to change in surface was detected. With the variables set B under the scenario A2 with a threshold of 0.5, the Wilcoxon rank test shows an increment in surface toward the future ($p<0.05$); with the variables set PC under the scenario A2 with both optimized and 0.5 thresholds, the Wilcoxon rank test shows a decrease in surface toward the future ($p<0.01$). However, when individual species are considered, some trends can be observed (Table 5.4). Three species (*H. filifolium*, *H. longistylum* and *H. megalanthum*) are predicted to reduce their surface under all sets of climatic variables, climate change scenarios and thresholds. Under the scenario A2, *H. floridum* also shows a decrease in

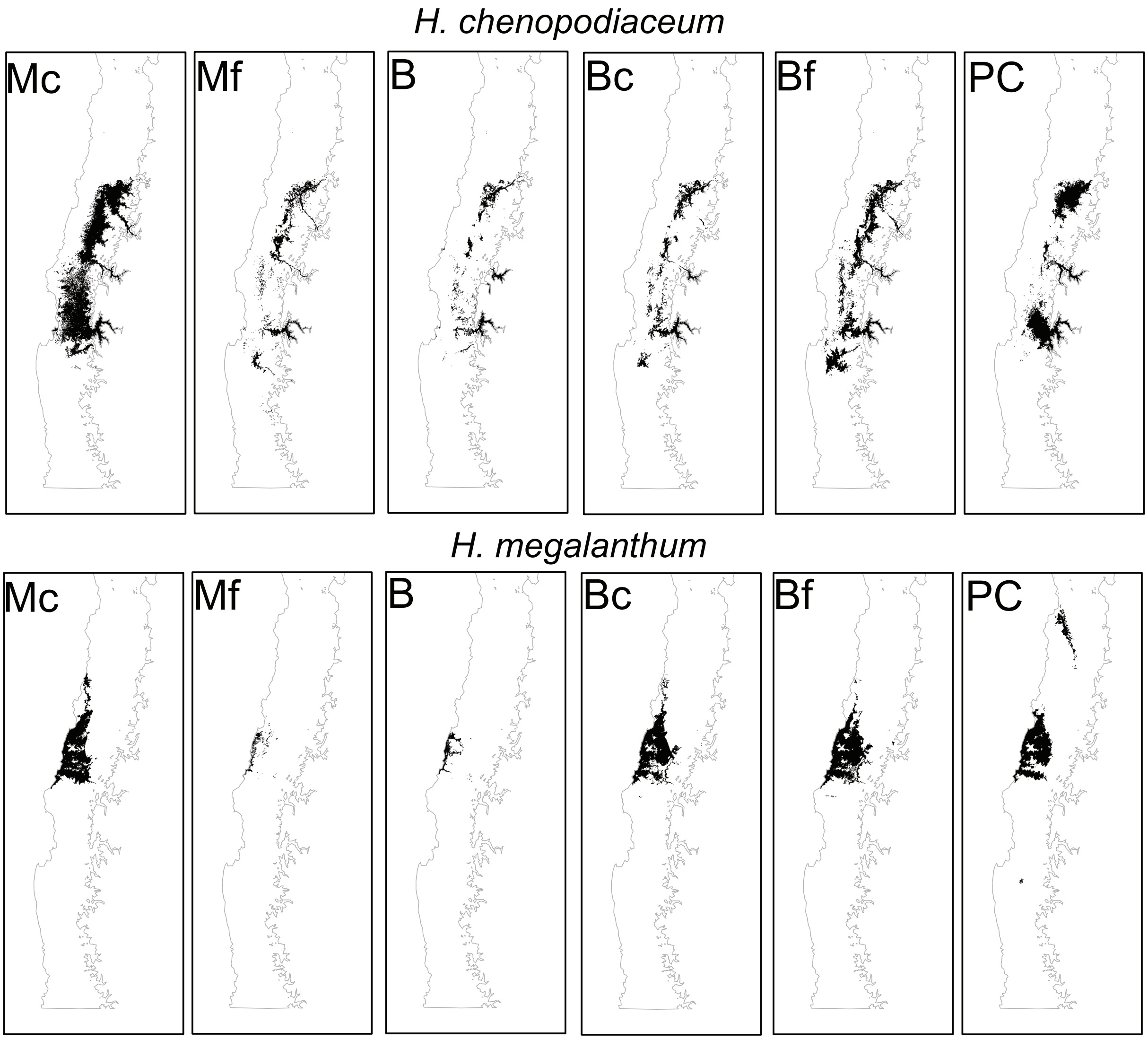

Figure 5.5: Final models of *Heliotropium chenopodiaceum* (upper panel) and *H. megalanthum* (lower panel) according to different sets of climatic variables.

surface for all sets of variables and thresholds, but not under the B2 scenario. Conversely, *H. myosotifolium* shows a decrease in surface under the B2 scenario for all sets of variables, but not under A2. Within climate change scenario and threshold, all other species vary among sets of climatic variables as to whether their surface would increase or decrease under climate change scenarios (Table 5.4).

The corresponding $\kappa$ statistics (i.e., for a given species and climate change scenario) are very low (mean 0.032, very poor) for all sets of climatic variables (Table 5.5); the maximum value (0.441, good) is reached by *H. stenophyllum* under scenario B2, set of climatic variable B. This result suggests that, under the climate change scenarios, the potential geographic ranges of the species will shift (Fig. 5.7), no matter whether the potential surface of the species increases of decreases across sets of climatic variables and climate change scenarios.

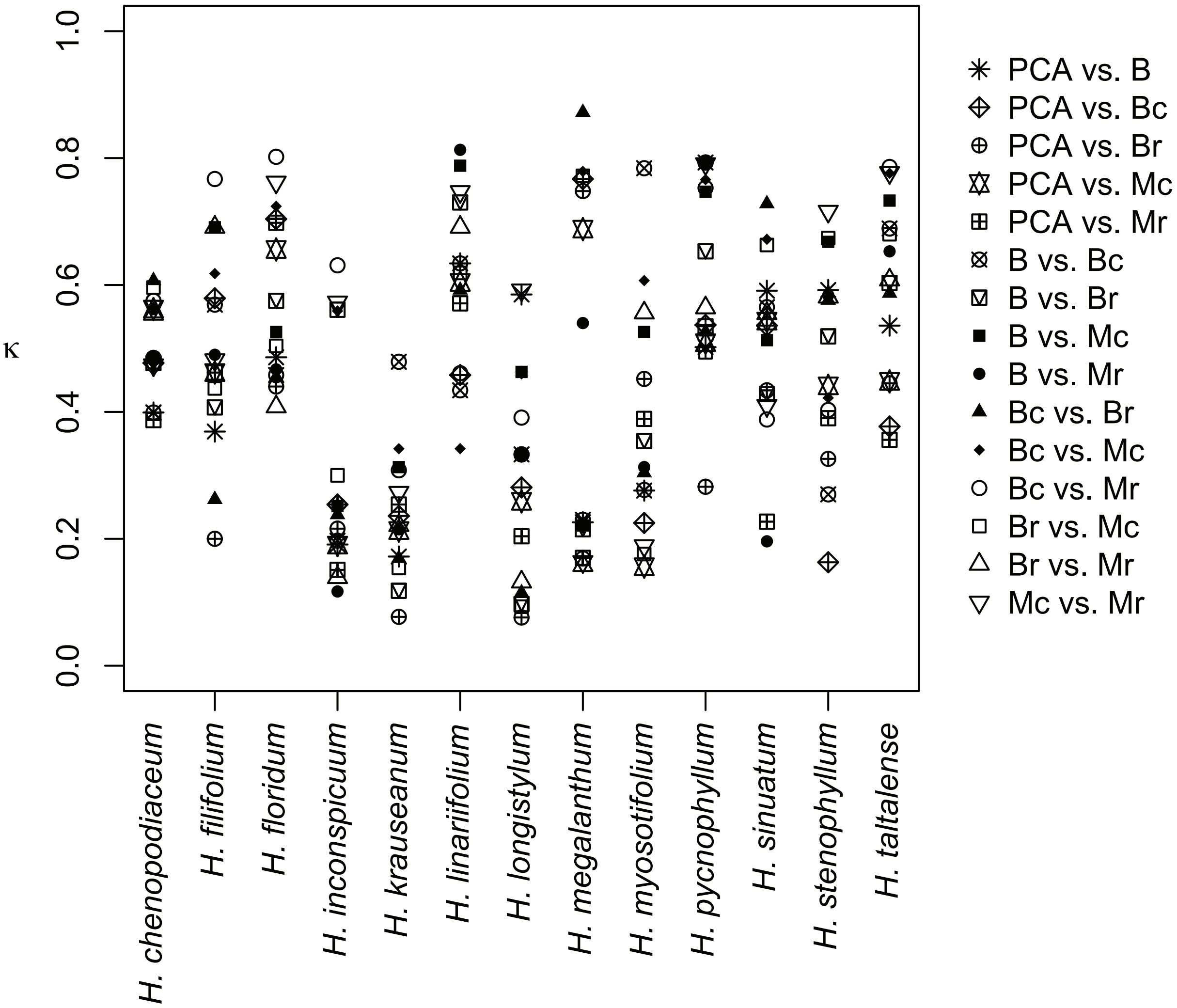

Figure 5.6: Kappa statistic for the comparison of present final models (optimized threshold) between pairs of sets climatic variables for each species.

### Extinction Risk

Present estimates of surface using SDMs lie, on average, between the estimates obtained with the minimum convex polygon (MCP) method and the 4 km$^2$ buffer around locality data points. Consequently, when the criterion of Extent of Occurrence (B1) is applied to the surfaces obtained with the SDMs, the results tend to inflate the criticality of the extinction risk in comparison with the surfaces obtained with MCP. Conversely, when the criterion of Area of Occupancy (B2) is employed, the SDMs tend to understate the criticality of the extinction risk in comparison with the surfaces obtained with the sum of 4 km$^2$ buffers around locality data points. When comparing the corresponding estimates of extinction risk (i.e., for a given species, threshold and climate change scenario) between pairs of sets of climatic variables, 30.8% of the comparisons render different conservations status under the criterion B1 and 34.9% under the criterion B2 (Table 5.6). Estimated extinction risk for each species, threshold, IUCN criterion and set of climatic variables are provided in the Appendix D.4.

Under the IUCN criterion A3, 52.4% of the corresponding comparisons (i.e., for a given species, climate change scenario and threshold) between pairs of sets of climatic variables produced different estimates of extinction risk (Table 5.6). Estimated extinction

Table 5.4: Change in surface of the 13 modelled species under climate change scenarios, thresholds and sets of climatic variables. Each of the four panels are the combination of threshold (OPTI and 0.5) and climate change scenarios (B2 and A2). '+' indicates an increase in surface while '–' a decrease. Increases are in bold to facilitate visual comparison.

| | OPTI / B2 | | | | | | OPTI / A2 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Mc | Mr | B | Bc | Br | PC | Mc | Mr | B | Bc | Br | PC |
| *Heliotropium chenopodiaceum* | + | + | + | + | + | – | + | + | + | + | + | – |
| *Heliotropium filifolium* | – | – | – | – | – | – | – | – | – | – | – | – |
| *Heliotropium floridum* | + | – | – | – | – | – | – | – | – | – | – | – |
| *Heliotropium inconspicuum* | + | + | + | + | – | – | + | + | + | – | – | – |
| *Heliotropium krauseanum* | – | – | + | + | + | – | + | – | + | + | + | – |
| *Heliotropium linariifolium* | + | + | + | + | + | – | + | + | + | – | + | – |
| *Heliotropium longistylum* | – | – | – | – | – | – | – | – | – | – | – | – |
| *Heliotropium megalanthum* | – | – | – | – | – | – | – | – | – | – | – | – |
| *Heliotropium myosotifolium* | – | – | – | – | – | – | – | – | – | + | – | – |
| *Heliotropium pycnophyllum* | + | – | – | + | – | – | + | + | – | – | – | – |
| *Heliotropium sinuatum* | – | + | – | – | – | – | – | – | – | – | – | – |
| *Heliotropium stenophyllum* | + | + | + | + | + | – | + | + | – | – | + | – |
| *Heliotropium taltalense* | + | – | – | – | – | – | + | + | – | – | – | – |

| | 0.5 / B2 | | | | | | 0.5 / A2 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Mc | Mr | B | Bc | Br | PC | Mc | Mr | B | Bc | Br | PC |
| *Heliotropium chenopodiaceum* | + | – | + | + | + | + | + | + | + | + | + | – |
| *Heliotropium filifolium* | – | – | – | – | – | – | – | – | – | – | – | – |
| *Heliotropium floridum* | + | – | – | – | – | – | – | – | – | – | – | – |
| *Heliotropium inconspicuum* | + | + | + | + | – | + | + | – | + | – | – | + |
| *Heliotropium krauseanum* | – | – | + | – | – | + | + | – | + | + | – | – |
| *Heliotropium linariifolium* | + | + | + | + | + | – | + | + | – | – | + | – |
| *Heliotropium longistylum* | – | – | – | – | – | – | – | – | – | – | – | – |
| *Heliotropium megalanthum* | – | – | – | – | – | – | – | – | – | – | – | – |
| *Heliotropium myosotifolium* | – | – | – | – | – | – | – | – | + | + | + | – |
| *Heliotropium pycnophyllum* | + | – | + | + | – | – | + | + | – | – | – | – |
| *Heliotropium sinuatum* | – | + | – | – | – | – | – | – | – | – | – | – |
| *Heliotropium stenophyllum* | + | + | + | + | + | – | + | + | – | – | + | – |
| *Heliotropium taltalense* | – | + | – | – | – | + | – | + | – | – | – | + |

risk for each species, threshold, climate change scenario and set of climatic variables are provided in the Appendix D.5. When single species are inspected (see Appendix D.5), some trends can be observed. For instance, *Heliotropium chenopodiaceum* is estimated as Least Concern (LC) with most sets of variables, thresholds and climate change scenarios, while *H. filifolium* is estimated as critically endangered (CR) in most scenarios.

## 5.4 Discussion

### 5.4.1 Climatic Control on Distribution and Climatic Niches

In agreement with theoretical expectations (see Section 5.1), the most important climatic variables for the distribution of the species of *Heliotropium* sect. *Cochranea* are precipitation and minimum temperatures (Table 5.2). In particular, winter precipitation (P7 and/or BIO19) appears to be among the first six most important variables for all species

Table 5.5: Kappa statistics for the comparisons between current potential distribution (optimized threshold) and climate change projections under scenarios A2 and B2 for different sets of climatic variables.

| | A2 | | | | | | B2 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Mc | Mf | B | Bc | Bf | PC | Mc | Mf | B | Bc | Bf | PC |
| *Heliotropium chenopodiaceum* | 0.213 | 0.022 | 0.103 | 0.182 | 0.194 | -0.003 | 0.28 | 0.071 | 0.226 | 0.232 | 0.319 | -0.029 |
| *Heliotropium filifolium* | 0 | -0.001 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.000 |
| *Heliotropium floridum* | -0.003 | -0.005 | 0 | -0.009 | 0.034 | 0 | 0.032 | 0.103 | 0 | -0.001 | 0.023 | -0.001 |
| *Heliotropium inconspicuum* | 0.016 | -0.007 | 0 | 0 | 0 | 0 | 0.025 | 0.012 | 0.004 | 0.036 | 0 | 0.000 |
| *Heliotropium krauseanum* | 0.082 | 0 | 0.04 | 0.055 | 0.11 | -0.007 | -0.006 | 0.001 | 0.025 | 0.022 | 0.089 | 0.062 |
| *Heliotropium linariifolium* | 0.115 | -0.025 | 0.151 | -0.003 | 0.046 | 0 | 0.248 | -0.026 | 0.321 | 0.003 | 0.216 | 0.000 |
| *Heliotropium longistylum* | 0 | 0 | 0 | 0 | 0.075 | 0 | 0 | 0 | 0 | 0 | 0.031 | 0.000 |
| *Heliotropium megalanthum* | -0.02 | 0 | 0 | -0.002 | -0.006 | -0.012 | -0.01 | 0 | 0 | -0.002 | 0.018 | -0.017 |
| *Heliotropium myosotifolium* | 0 | -0.003 | -0.005 | -0.015 | -0.002 | 0 | 0 | -0.002 | 0 | 0 | 0 | -0.001 |
| *Heliotropium pycnophyllum* | 0.065 | 0.021 | 0.022 | 0.003 | 0.043 | 0 | 0.112 | 0.219 | 0.19 | 0.008 | 0.104 | 0.000 |
| *Heliotropium sinuatum* | 0 | -0.035 | -0.001 | -0.001 | -0.009 | -0.001 | 0 | -0.009 | 0.001 | 0 | 0.02 | -0.005 |
| *Heliotropium stenophyllum* | 0.012 | -0.001 | 0 | 0 | 0.014 | -0.023 | 0.066 | 0.024 | 0.441 | 0.016 | 0.063 | -0.023 |
| *Heliotropium taltalense* | -0.003 | -0.002 | 0.002 | 0 | 0 | 0 | -0.001 | -0.001 | -0.001 | 0 | 0 | 0.000 |

Table 5.6: Number of comparisons (N), number of differences (C) and percentage of differences (%) between pairs of sets of climatic variables for the different IUCN criteria of extinction risk (B1, B2, A3). Number of comparisons under criterion A3 is lower when the set PC is compared because the current area of two species (*Heliotropium inconspicuum* and *H. taltalense*) was estimated to zero under the 0.5 threshold, which is therefore applied to two climate change scenarios, rendering four undeterminable estimates of area change under the IUCN criterion A3.

| | B1 | | | B2 | | | A3 | | |
|---|---|---|---|---|---|---|---|---|---|
| Comparison | N | C | % | N | C | % | N | C | % |
| Mc - Mr | 26 | 9 | 34.6 | 26 | 8 | 30.8 | 52 | 24 | 46.2 |
| Mc - B | 26 | 8 | 30.8 | 26 | 7 | 26.9 | 52 | 18 | 34.6 |
| Mc - Bc | 26 | 6 | 23.1 | 26 | 6 | 23.1 | 52 | 25 | 48.1 |
| Mc - Br | 26 | 9 | 34.6 | 26 | 11 | 42.3 | 52 | 29 | 55.8 |
| Mc - PC | 26 | 10 | 38.5 | 26 | 9 | 34.6 | 48 | 35 | 72.9 |
| Mr - B | 26 | 9 | 34.6 | 26 | 8 | 30.8 | 52 | 27 | 51.9 |
| Mr - Bc | 26 | 7 | 26.9 | 26 | 7 | 26.9 | 52 | 27 | 51.9 |
| Mr - Br | 26 | 6 | 23.1 | 26 | 12 | 46.2 | 52 | 29 | 55.8 |
| Mr - PC | 26 | 11 | 42.3 | 26 | 9 | 34.6 | 48 | 36 | 75.0 |
| B - Bc | 26 | 8 | 30.8 | 26 | 7 | 26.9 | 52 | 18 | 34.6 |
| B - Br | 26 | 9 | 34.6 | 26 | 10 | 38.5 | 52 | 27 | 51.9 |
| B - PC | 26 | 6 | 23.1 | 26 | 9 | 34.6 | 48 | 25 | 52.1 |
| Bc -Br | 26 | 5 | 19.2 | 26 | 13 | 50.0 | 52 | 23 | 44.2 |
| Bc - PC | 26 | 8 | 30.8 | 26 | 12 | 46.2 | 48 | 28 | 58.3 |
| Br - PC | 26 | 9 | 34.6 | 26 | 8 | 30.8 | 48 | 27 | 56.3 |
| Total | 390 | 120 | 30.8 | 390 | 136 | 34.9 | 760 | 398 | 52.4 |

except *Heliotropium krauseanum*. *H. krauseanum* is the only species in section *Cochranea* that has most of its distribution in tropical climate in northern Chile and south-central Peru (Weigend et al., 2003; Luebert and Pinto, 2004), while all other modelled species in this section do not or barely surpass the Tropic of Capricorn and have all or most of their geographic rage under the influence of Mediterranean climate (Luebert and Pliscoff, 2006). As Mediterranean climates are characterized by warm-dry summers and cold-wet winters (Rivas-Martínez, 2008), species' geographic ranges may be limited by the severity of the wet season in the arid extreme of the Mediterranean climate, which appears to be the case of the Mediterranean species of *Heliotropium* sect. *Cochranea*. Moreover, in years with high precipitation, associated with El Niño events, rainfall occurs mostly in winter (Houston, 2006c). Such events are associated with increments in primary productivity (Squeo et al., 2006), trigger phenological responses of shrubby plants in the Atacama

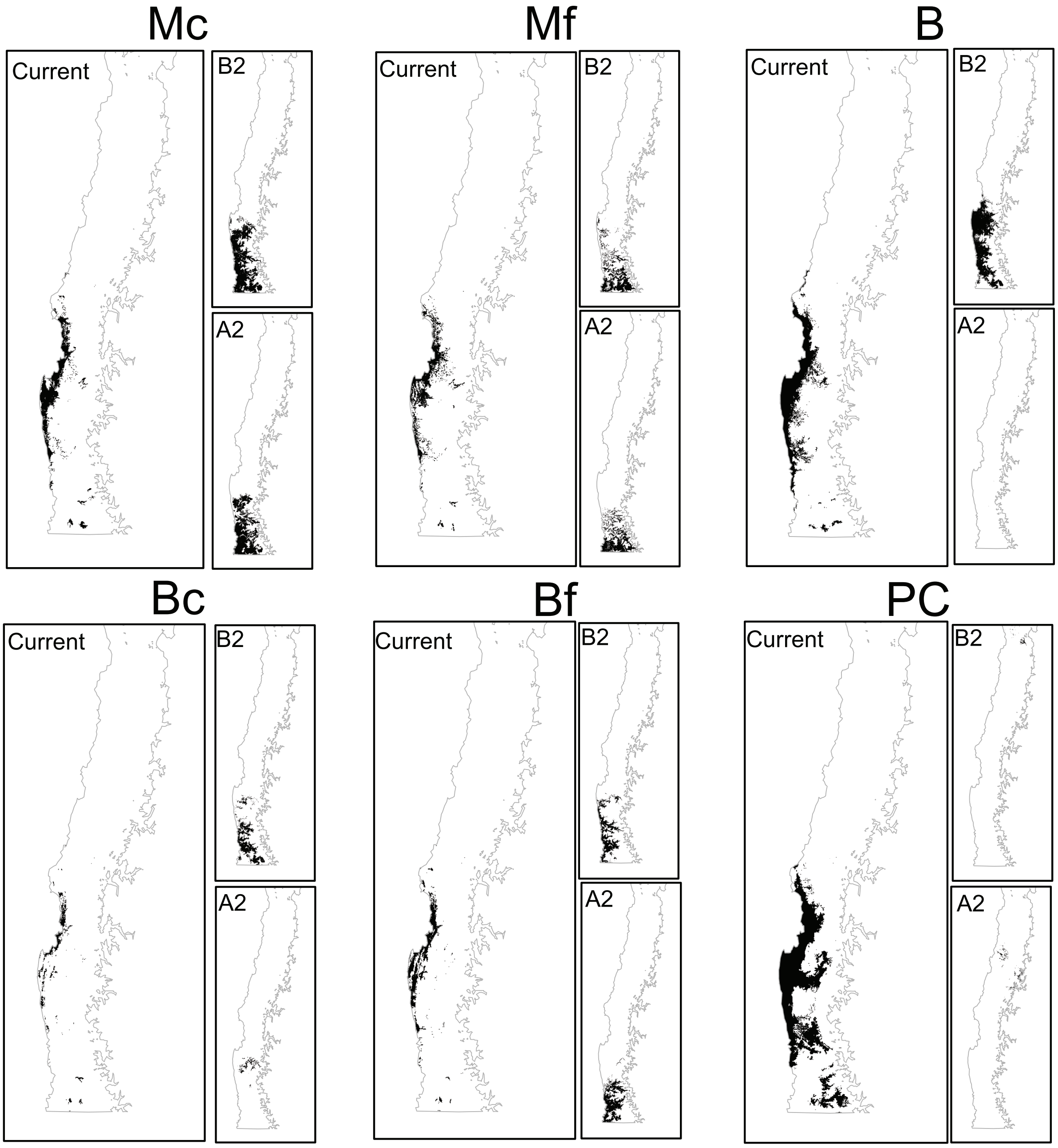

Figure 5.7: Comparison of present and climate change projections of *Heliotropium stenophyllum* according to different sets of climatic variables. Final binary models are depicted for the present models and for climate change scenarios A2 and B2.

Desert (Vidiella et al., 1999) and, therefore, may play an important role in shaping their distribution. Conversely, in tropical climates, where precipitation occurs mostly in summer, the distribution of *Heliotropium krauseanum*, which is also distributed in the most arid extremes of the tropics, may be limited by the severity of the wet season. In fact, late spring, summer and early fall precipitation (P11, P1, P4) appear to be important variables for the distribution of *H. krauseanum* (Table 5.2).

Minimum winter temperature (m7) was the second most important variable, being among the six most important variables for all species except *Heliotropium linariifolium*, *H. longistylum* and *H. pycnophyllum*, for which spring minimum temperature (m10) was one of the most important. As stated above (see Section 5.1) frost resistance may limit the distribution of species along the range of absolute minimum temperature, beyond a certain threshold, of which, species cannot survive (Woodward, 1987). Since minimum temperature tends to decrease lineally with altitude in the Atacama Desert (Houston, 2006a), this may explain the fact that most species of *Heliotropium* sect. *Cochranea* occupy low-elevation habitats (<1000 m, see Table 5.1).

Maximum summer temperature (BIO5) was also an important variable, being among the six most important for 9 out of 13 species (Table 5.2). As summer is the driest and warmest season in most of the Atacama Desert, evapotranspiration during this period might be very high (Houston, 2006a), and the water budget may be strongly limited. Therefore, maximum temperatures may shape species distribution by increasing evapotranspiration. Near the coast, where thermal amplitude is reduced and maximum temperatures are not extremely high, apparently constitutes ideal habitat for the species under study, most of which occupy coastal environment along the Atacama Desert. Moreover, the coastal range of the Atacama Desert is frequently covered by fog, which in turn can reduce incoming solar radiation and thereby evapotranspiration. Houston (2006a) also reports that evaporation decreases with elevation in the Atacama Desert, likely due to the effect of increased cloud cover. This may explain, for instance, why *Heliotropium krauseanum* inhabits the lomas formations of Peru, under the influence of fog, and also Andean higher-elevation environments without altitudinal continuity (Weigend et al., 2003).

Subtle differences in the combination of winter and summer drought tolerance, as well as frost resistance among the species of *Heliotropium* sect. *Cochranea* may be the result of climatic niche differentiation that made its diversification in the Atacama Desert possible. Comparisons of climatic envelopes (Fig. 5.2) suggest that this is the case of *Heliotropium* sect. *Cochranea*. In the Caprifolium clade of the genus *Lonicera* L. (Caprifoliaceae), a plant group from similar environments of the northern Hemisphere, Smith and Donoghue (2010) showed that niche differentiation driven by climatic change is an important process promoting divergence between phylogenetically closely related species.

### 5.4.2 Effects of the Sets of Variables on SDMs

Several sources of uncertainty in SDMs have been reported (e.g., Araújo et al., 2005; Barry and Elith, 2006; Pearson et al., 2006; Buisson et al., 2010). They include modelling techniques, model specification, presence/absence data, environmental data, choice of threshold to in convert probabilistic predictions to binary ones, and the climate change scenarios. In this paper, we provide evidence showing that the choice of the environmental dataset has potential effects on the outcomes of the SDMs in rare species, especially concerning the spatial arrangement of the predictions derived from the application of SDMs. These effects are transferred to the projections of the consequences of climate change on species distribution and extinction risk. Other studies have also explored the effect of the set of variables on the outcomes of SDMs and have found similar results. Peterson and Nakazawa (2008) compared the SDMs using six sets of climatic variables obtained from different sources and found differences in the predicted potential distribution of *Solenopsis invicta* (Hymenoptera: Formicidae). Syphard and Franklin (2009) showed that different types of environmental predictors (e.g., climate or soil) contribute differently to the performance and spatial patterns of SDMs of plants from southern California. These authors stress that, although predictive performance (e.g., AUC) may be high for different strategies of SDMs, spatial arrangement of the SDMs may vary considerably, pointing out that the only use of predictive performance as means of evaluation of SDMs may not always be appropriate. Our results are complimentary to these previous findings in two senses. First, results of SDMs may vary among sets of environmental predictors not only when they are of different character (e.g., climate and soil) or taken from different sources, but also when they are selected or processed from within the same set of original data. On the other hand, in spite of the fact that the generally high predictive performance achieved under different sets of variables, the spatial arrangement of the model may vary. This supports the statement of Syphard and Franklin (2009) that model evaluation should consider the spatial pattern of predictions. Our results also indicate that such an evaluation may be critical for conservation decisions, as those derived form extinction risk assessment based on SDMs.

### 5.4.3 Can We Assess Extinction Risk and Climate Change Effects in *Heliotropium* sect. *Cochranea*?

Akçakaya et al. (2006) pointed out several potential sources of uncertainty in evaluating extinction risk with SDMs using the IUCN (2001) criteria. These refer, for example, to assumptions related to temporal scale (i.e., arbitrary definition of generation times), spatial scale (i.e., including only part of the geographic range of the species or use of inappropriate spatial resolution) and abundance patterns (lineal relationship between range area and abundance) usually made in evaluation of extinction risk with the IUCN (2001) criteria using SDMs. These assumptions together with aspects poorly covered in SDMs, such as biotic interactions, landscape process and local population dynamics, yielded underestimations and overestimations in modelled distributions, which directly affect the application of IUCN criteria for the definition of extinction risk.

Table 5.7: Mode of extinction risk categories for the analysed species of *Heliotropium* sect. *Cochranea* under the IUCN (2001) criteria B1, B2 and A3. Mode was calculated over all estimates of extinction risk according to different sets of climatic variables, threshold and climate change scenario (for criterion A3). Extinction risk categories: CR, Critically endangered; EN, Endangered; VU: Vulnerable; LC, Least concern.

| | IUCN Categories | | |
|---|---|---|---|
| Species | B1 | B2 | A3 |
| *H. chenopodiaceum* | EN-VU | LC | LC |
| *H. filifolium* | EN | VU | CR |
| *H. floridum* | EN | LC | CR |
| *H. inconspicuum* | EN | VU | LC |
| *H. krauseanum* | EN | LC | LC |
| *H. linariifolium* | EN | LC | LC |
| *H. longistylum* | EN | EN | CR |
| *H. megalanthum* | VU | VU | CR |
| *H. myosotifolium* | VU | LC | CR-EN |
| *H. pycnophyllum* | EN | LC | LC |
| *H. sinuatum* | EN-VU | LC | CR |
| *H. stenophyllum* | VU | LC | LC |
| *H. taltalense* | EN | VU | CR |

Some of the problems mentioned by Akçakaya et al. (2006) are also present in our analyses. However, especially problems associated with spatial and temporal scale are minimized in our study (as all species of *Heliotropium* sect. *Cochranea* have similar generation times), spatial resolution was set to 1 km$^2$ (which is the resolution used in the IUCN (2001) criteria), and whole species geographic ranges were included.

Our assessment of extinction risk in *Heliotropium* sect. *Cochranea* varied, depending on climate change scenario, threshold and set of climatic variable. These introduce an additional element of uncertainty in the assessment of extinction risk. The problem can be seen as, whether it is possible to handle this uncertainty and evaluate extinction risk using the IUCN (2001) criteria, based on the SDMs generated here. Most problems suggested by Akçakaya et al. (2006) that are not overcome in our study affect estimation of extinction risk with the A3 criterion. Assuming a conservative approach, we extracted the least critically threatened estimated IUCN category for each species and considered them as the 'upper bound' of extinction risk. Under these perspective, all modelled species of *Heliotropium* sect. *Cochranea* should be classified as Least Concern (LC). However, IUCN (2001) recommends the so-called precautionary attitude, which consists in using rather lower bound in determining extinction risk. Under the latter approach and using the criterion A3(c), all modelled species would be categorized as Critically Endangered (CR). It seems evident that a different intermediate approach is necessary to handle this uncertainty. One possibility is to assign the extinction risk with the greatest mode among estimates. This approach would lead to the results shown in Table 5.7.

Applying the IUCN (2001) B2 criterion in such a way yields similar results to what would be obtained, if that criterion is applied to an area calculated with a 4 km$^2$ buffer (see Appendix D.4), which is one of the measures of Area of Occupancy recommended by IUCN (2001). Applying the B1 criterion would overestimate the extinction risk in comparison with the results based on minimum convex polygon estimates of Extent of Occurrence (Appendix D.4). Finally, the A3 criterion tends to generate extreme estimations of extinction risk, either Least Concern or Critically Endangered.

# 6. Revision of *Heliotropium* sect. *Cochranea* (Heliotropiaceae)[a]

## Abstract

A revision of the *Heliotropium* L. sect. *Cochranea* (Miers) Kuntze (Heliotropiaceae) is presented and a total of 17 species is recognised. Description, ecology, distribution, conservation status and phenology of all species are presented. One subspecies, *Heliotropium krauseanum* Fedde subsp. *jahuay* Luebert is described as new taxon. Two previously recognised species names, *Heliotropium sclerocarpum* Phil. and *H. huascoense* I.M.Johnst., are placed in the synonymy of *H. chenopodiaceum* (A.DC.) Clos and *H. stenophyllum* Hook. & Arn., respectively. One neotype and one lectotype are designated here.

## 6.1 Introduction

The family Heliotropiaceae is composed of four monophyletic genera, *Ixorhea* Fenzl, *Myriopus* Small, *Euploca* Nutt. and *Heliotropium* L. (Diane et al., in press; see Chapter 3). For detailed accounts of the family Heliotropiaceae and its classification see Hilger and Diane (2003), Diane et al. (in press) and Luebert et al. (in press; Chapter 3). Within *Heliotropium*, four major clades can be recognised from phylogenetic analyses (Chapter 3): (1) *Heliotropium* sect. *Heliothamnus* I.M.Johnst., composed of ca. 11 species with a centre of diversity in the Andes of Ecuador and Peru (Johnston, 1928b), which is sister to the remainder of *Heliotropium*; (2) Old World *Heliotropium*, including the genera *Ceballosia* G.Kunkel ex Förther, *Argusia* Boehm. and *Nogalia* Verdc., with about 100 species (Förther, 1998); (3) *Heliotropium* sects. *Coeloma* (DC.) I.M.Johnst., *Heliotrophytum* G.Don, *Hypsogenia* I.M.Johnst., *Plagiomeris* I.M.Johnst., *Platygyne* Benth., *Schobera* (Scop.) I.M.Johnst., *Tiaridium* (Lehm.) Griseb. and *Tournefortia* L. sect. *Tournefortia*, which is composed of ca. 160 species and is broadly distributed in America, from southern United States to Patagonia, and in the Indo-Pacific region with ca. 12 species (Johnston, 1928b, 1930, 1935b,a; Förther, 1998); (4) *Heliotropium* sect. *Cochranea* (Miers) Kuntze, with 17 species from the Peruvian and Atacama Deserts (Johnston, 1928b, 1937; Weigend et al., 2003; Luebert and Pinto, 2004; Luebert and Wen, 2008). A current species-level revision is pending for all groups in *Heliotropium*, some of which have never been taxonomically treated. Section *Cochranea*, subject of this work, has not been revised since Johnston (1928b).

The first quotation of the presence of a species today assigned to *Heliotropium* sect. *Cochranea* in the taxonomic literature comes from Molina (1810) in his description of *Meladendron chilense* Molina. No type specimen has been found for this species (Förther, 1998). Philippi (1864) suggested that this species corresponds to *Cordia decandra* Hook. & Arn., but most later authors (Reiche, 1907a, 1910; Johnston, 1928b; Gunckel, 1972;

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[a] Manuscript in preparation: Luebert, F. Revision of *Heliotropium* sect. *Cochranea* (Heliotropiaceae). to be submitted to *Kew Bulletin*.

Förther, 1998) placed it in the synonymy of *Heliotropium stenophyllum* Hook. & Arn. (non *H. chilense* Bertero 1829 = *H. curassavicum* L.). Hooker and Arnott (1830) described *Heliotropium stenophyllum*, the first name still in use within the section. Since then new currently recognised species today in *Heliotropium* sect. *Cochranea* have been described in the works of de Candolle (1845), Philippi (1860a, 1873, 1895), Miers (1868), Krause (1906), and Johnston (1928b, 1937). The most important revisionary works are those of de Candolle (1845), Clos in Gay (1849), Miers (1868), Reiche (1907a, 1910) and Johnston (1928b). De Candolle (1845) assigned all the members of the current *Heliotropium* sect. *Cochranea* hitherto described to the genus *Heliophytum* (Cham.) A.DC.; later Clos (in Gay, 1849) transferred all Chilean *Heliophytum* sensu de Candolle (1845) back to *Heliotropium*; Miers (1868) coined the generic name *Cochranea* Miers, which was later accepted by Bentham (1876), F. Philippi (1881), Gürke (1893) and Philippi (1895); the names under *Cochranea* were again reunited in the genus *Heliotropium* in the revisions of Reiche (1907a, 1910) and Johnston (1928b), who also placed numerous Miers's (1868) and Philippi's (1873, 1895) names in the synonymy and fixed several nomenclatural problems. The work of Johnston (1928b) is the most important revision of *Heliotropium* in South America and is still used today. Some additional contributions to the knowledge of *Heliotropium* sect. *Cochranea* have also been made by Philippi (1861, 1891), Fedde (1906), Johnston (1929c), Macbride (1960), Förther (1998), Weigend et al. (2003) and Luebert and Pinto (2004). Recently, molecular phylogenetic analyses (Luebert and Wen, 2008) have confirmed the monophyly of *Heliotropium* sect. *Cochranea*.

In spite of the efforts of these and other authors, there are not comprehensive and consistent descriptions of the species of *Heliotropium* sect. *Cochranea*, for Johnston (1928b) did neither provide them nor attempt to do it. No illustrations have been published yet. On the other hand, the knowledge, particularly regarding the distribution and systematic affinities of the species, accumulated since the last revision of Johnston (1928b), needs to be systematized. The purpose of this paper is to provide descriptions and illustrations of the species of *Heliotropium* sect. *Cochranea* and a key for their determination, actualizing the knowledge accumulated since the work of Johnston (1928b) and trying to fill the gaps left by him. The nomenclature of the species was fully revised and their distribution was updated.

## 6.2 Material and Methods

Field studies were conducted in Chile between 2002 and 2009, where 181 collections of *Heliotropium* sect. *Cochranea* from different populations were made. More than 1,600 specimens of the herbaria A, B, BM, BSB, CONC, EIF, F, G, G-DC, GH, K, M, MA, MSB, NY, P, SGO, ULS, US were critically revised, most of them at CONC and SGO. All cited specimens have been seen by the author, unless otherwise indicated. Measurements of width of structures are given for the widest portion (e.g, middle portion of the leaves, basal portion of the stigmatic head).

All typifications were carefully revised. Published and unpublished documents were examined in order to determine the source of type specimens and to interpret their identity. Since most of the names in *Heliotropium* sect. *Cochranea* were published by R.A. Philippii, particular attention was paid to the interpretation of those specimens with respect to collector, exact locality, date of collection and distribution across herbaria, taking into account the relevant literature associated to them, including the original descriptions (Philippi, 1860a, 1861, 1873, 1895), typifications (Johnston, 1928b; Förther, 1998) and the documentation about Philippi's specimens and collecting trips (Philippi, 1886; Johnston, 1929a; Muñoz, 1960; Muñoz Schick, 1973, 1991; Taylor, 1994). Förther (1998) lectotypified almost all Philippi's names with specimens of SGO, unfortunately without seeing the material, and, in some cases, without taking its quality, suitability or previous typifications into account. In this case, Johnston's (1928b) explicit indications of types from syntypes of Philippi's names are considered valid lectotypifications.

Several names were described on the basis of specimens collected by Thomas Bridges in Chile. The localities of this collector are often difficult to establish, because the labels do not include any specific information. Turrill (1920), Johnston (1928a) and other authors provided relevant data about Bridges' itineraries in Chile. Most important information is contained in the manuscript entitled 'A catalogue of plants found in the province of Coquimbo, Republick [sic] of Chile SL 27-32, Collected by Thomas Bridges 1841' consulted at the archives of the Natural History Museum in London. This catalogue contains approximate localities and collecting dates of all Bridges specimens used as types in *Heliotropium* sect. *Cochranea* (N°s. 1338-1343). Other Bridges specimens corresponding to these species but distributed without numbers seem to be duplicates of them (see Johnston 1928a, 1928b). I follow this information in the interpretation of Bridges material.

Conservation status is given according to IUCN (2001) categories. It was assessed with species distribution modelling for 13 species (see Chapter 5), and the criterion of area of occupancy (B2) was used. The remaining four species were evaluated according to the more critical IUCN category, estimated from the surface of a Minimum Convex Polygon (criterion of extent of occurrence, B1) and from a buffer of 4 km$^2$ assigned to each occurrence (criterion of area of occupancy, B2), as recommended by IUCN (2001).

## 6.3 Species Concept

The taxonomic units at the specific and infraspecific level are here considered as composed by populations, so that no taxon will be recognised as belonging to the same population of another taxon. The species concept applied here is in agreement with de Queiroz (2005, 2007). Morphologically differentiable and geographically segregated metapopulations are here recognised as different species. Given the young age of most species of *Heliotropium* sect. *Cochranea* (Luebert and Wen, 2008), it is possible that closely related species are potentially interfertile.

Sympatric and locally parapatric species are recognised if they can be differentiated in terms of general morphology, paying attention to flower characters that can be associated to different pollinators and may therefore favour reproductive isolation. In this sense, the relation of the length of the style and the stigmatic head and the relative position of the gynoecium in relation to the stamens can play a major role in the reproductive isolation of sympatric populations, as they could be associated to different pollinators. After the examination of numerous specimens, it became clear that the relative length of the style and the stigmatic head is relatively constant within populations and is associated with other vegetative characters, although it possibly exhibits single-locus Mendelian inheritance (Barrett et al., 2000). Morphologically similar and geographically parapatric metapopulations are also recognised as different taxonomic entities, provided that they can be delimited with vegetative morphology and are geographically and ecologically recognisable. In the Atacama Desert, where most species of *Heliotropium* sect. *Cochranea* occur, climate fluctuates, with high inter-annual rainfall variability (Luebert and Pliscoff, 2006: 45, and references therein). In the cases of both sympatry and parapatry, hybridization might take place during rainy years, when more flowering individuals emerge and the geographic range of the metapopulations is fully expressed, so that parapatric populations come into contact at the edges of their distribution ranges. Allopatric metapopulations might expand their geographic ranges and come into contact less frequently, likely allowing gene flow among species during such 'expansion' periods. The geographic ranges are contracted during dry periods, leading to isolation of metapopulations. This process, suggested for *Heliotropium* sect. *Cochranea* by Luebert and Wen (2008), causes, according to Stebbins (1952), species diversity and rapid temporal species turnover in arid environments.

## 6.4 Taxonomy

### 6.4.1 Nomenclature

**Heliotropium** L. sect. **Cochranea** (Miers) Kuntze, in Post and Kuntze (1904: 271); Reiche (1907a: 234); Reiche (1910: 192); Johnston (1928b: 25); Förther (1998: 72). Lectotype (Johnston 1928b: 25): *Cochranea conferta* Miers (= *Heliotropium stenophyllum* Hook & Arn.).

*Cochranea* Miers (1868: 124); Bentham (1876: 834); Philippi (1881: 253); Gürke (1893: 95); Philippi (1895: 338). Type as above.
*Meladendron* Molina (1810: 143). Type: *Meladendron chilense* Molina
*Heliophytum* (Cham.) DC. sect. *Heliophytum* (de Candolle, 1845: 552) *pro parte* excl. type (ser. *stigma elongatum, lineari-conicum, striatum, apice bilobum*).

The name *Cochranea* honours Thomas Cochrane (Förther, 1998), british officer who served in the war of the Chilean independence (see Miers, 1826). John Miers travelled in Chile between 1819 and 1825, initially attracted by Cochrane to develop the mining industry in this country (Marticorena, 1995).

### 6.4.2 Habit

All species of *Heliotropium* sect. *Cochranea* are shrubs, but exhibit considerable variation in size and axis orientation, from low decumbent- (e.g., *Heliotropium megalanthum*) to tall erect shrubs (*H. sinuatum*). Tall erect shrubs are usually resinous and apparently more tolerant to drought than low shrubs, maintaining their above-ground structures during dry years and flowering throughout. Low shrubs generally loss all above-ground structures during dry years, maintaining at most only some latent stem axes, without production of leaves and flowers, where the stems are dry but still able to regenerate above-ground structures during rainy years (Fig. 6.1); these species are not resinous and usually have pubescent foliage. These two general strategies can be expressed in different degrees, depending on species and on the duration (in years) of the dry period. Some species, for instance *Heliotropium chenopodiaceum*, a low but resinous shrub, is able to resist one year without rainfall, still producing leaves and flowers, but a second year of drought causes the loss of all above-ground tissues. Several years of continuous drought can cause the loss of above-ground structures of whole populations, even of tall shrubs. These personal field observations have, however, not yet quantified in formal studies.

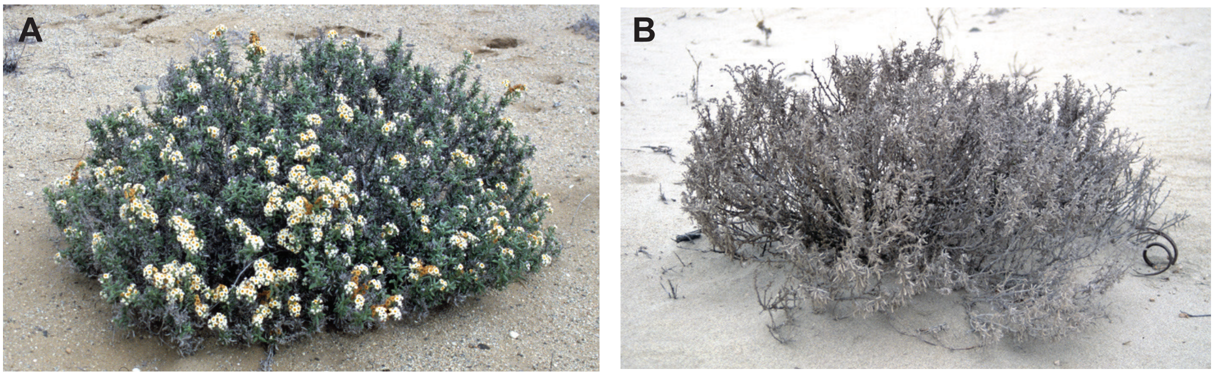

Figure 6.1: *Heliotropium floridum* after a rainy and a dry period. A, After a rainy season, Sept. 2004, between Totoral and Bahía Salada, south of Caldera, 27°49'S, 71°0'W; B, After two years of drought, Jan. 2004, Playa Ramadas, north of Caldera, 26°59'S, 70°48'W.

Only few species have been characterized in terms of root morphology. In *Heliotropium stenophyllum* a laterally extended root system has been reported (Squeo et al., 1999) as well as for *H. pycnophyllum*, where a short thick tap root branches into secondary roots, which extend laterally (Rundel et al., 1980). Field observations indicate that most species of *Heliotropium* sect. *Cochranea* have such laterally extended root systems.

### 6.4.3 Leaf Morphology and Anatomy

Leaves of *Heliotropium* sect. *Cochranea* are alternate, sessile and usually small, ranging from 0.2 to 6.5 cm and from 0.05 to 1.1 cm in width. Leaves can be solitary or grouped in fascicles of up to ca. 20 leaves. Shape varies from linear to elliptic or spathulate (Fig. 6.2). The margins are entire or sinuate and usually revolute, thereby leaves of some species are terete or sub-terete in transverse section. Lamina is generally smooth, but in some species can also be rugose (*Heliotropium glutinosum*, *H. sinuatum*, *H. taltalense*, *H. krauseanum*). Pubescence is variable in density and is present on both sides, but normally denser on the adaxial surface, being simple adpressed hairs in combination with stipitate or sessile glandular trichomes the most common (see Diane et al., 2003; Brokamp, 2006; Chapter 3).

### 6.4.4 Flower Morphology

The flowers of *Heliotropium* are disposed in terminal scorpiod monchasia (boragoids, Buys and Hilger, 2003). Flowers of section *Cochranea* conform to the general pattern found in *Heliotropium*. Calyx lobes are linear-lanceolate, totally free to partially fused. The corolla is infundibuliform, generally exceeding the calyx, mostly white with a yellow or orange throat, but it can also be completely orange as in *Heliotropium linariifolium*. In late anthetic flowers the corolla turns purplish or violet in several species (e.g., *H. pycnophyllum*). Corolla length ranges from 2 to 11 mm and the corolla limb can be 1.5 – 12.5 mm wide. The stamens are included, but in late anthetic flowers they can be exserted; the filaments arise from inside the corolla tube and the anthers are linear with cordate base, usually glabrous or with apical papillae. The ovary is cleft by a commisure dividing it into two biovulate carpids, without empty cells, each composed of parts of both carpels (syn-mericarpids, Hilger, 1992). A protuberant nectar disk at the base surrounds the ovary. The style can be elongated (mostly) or absent (*Heliotropium filifolium*, Figs. 6.3B and 6.6) and its relative length in relation to the stigmatic head varies among species,

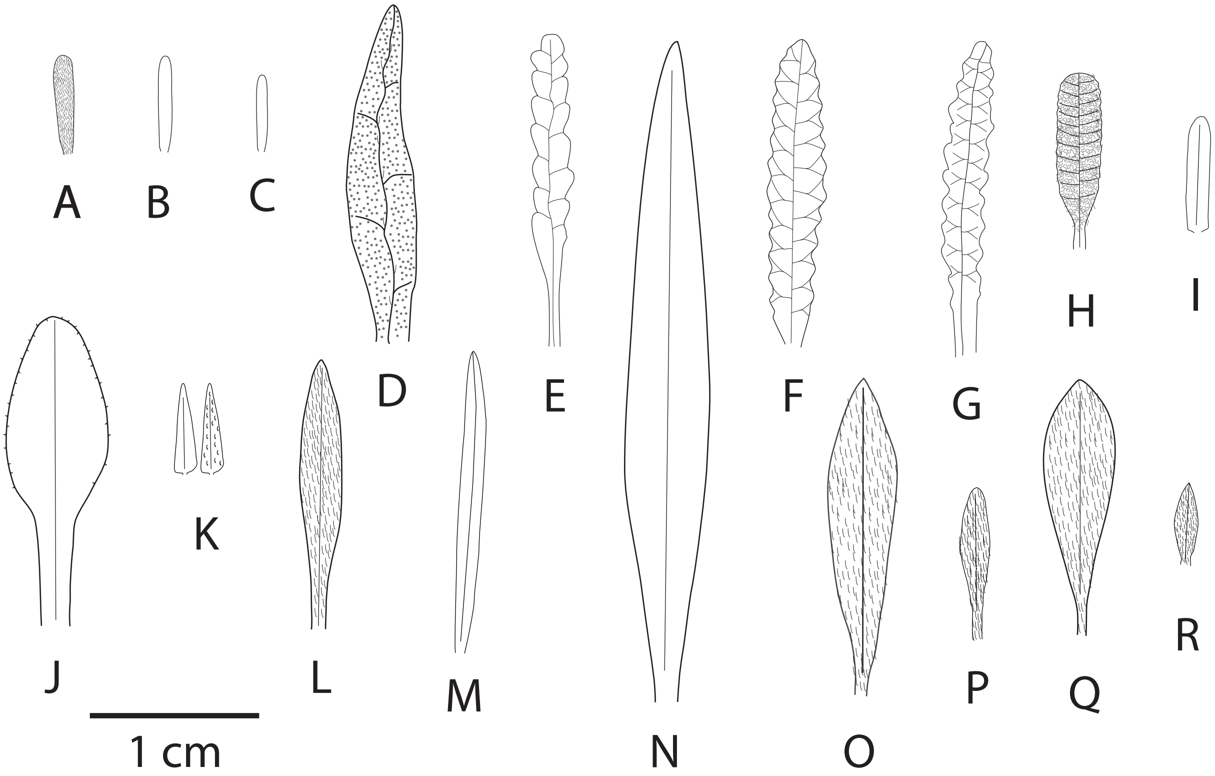

Figure 6.2: Leaf outline of all recognised taxa of *Heliotropium* sect. *Cochranea*. A, *H. pycnophyllum*, from *Luebert & Kritzner* 1850, BSB; B, *H. filifolium*, from *Luebert & Kritzner* 1818, BSB; C, *H. jaffuelii*, from *Jaffuel* 2524, G; D, *H. glutinosum*, from *Luebert & Torres* 1970, BSB; E, *H. sinuatum*, from *Luebert & Kritzner* 1809, BSB; F, *H. taltalense*, from *Dillon et al.* 5583, F; G, *H. krauseanum* subsp. *krauseanum*, from *Dostert & Cáceres* 1025, BSB; H, *H. krauseanum* subsp. *jahuay*, from *Ferreyra* 2511, F; I, *H. inconspicuum*, from *Teillier et al.* 2944, F; J, *H. megalanthum*, from *Philippi* s.n., SGO 54364; K, *H. chenopodiaceum*, from *Gay* s.n., K; L, *H. myosotifolium*, from *Bridges* 1338, G; M, *H. stenophyllum*, from *Dillon et al.* 5428, F; N, *H. longistylum*, from *Ackermann* 518, BSB; O, *H. floridum*, from *Philippi* s.n., SGO 54384; P, *H. linariifolium*, from *Teillier et al.* 2727, F; Q, *H. philippianum*, from *Johnston* 5233, GH; R, *H. eremogenum*, from *Jaffuel* 1120, GH.

being shorter in some species, approximately equal, or longer (Fig. 6.3). The gynoecium is usually glabrous, only in *Heliotropium pycnophyllum* the style and the stigmatic head are shortly pubescent (Fig. 6.3A and 6.4). The stigma is elongated into a conical structure (Fig. 6.3) with a basal receptive area, which is typical of Heliotropiaceae. The anthers can be located above the stigmatic head or, more commonly, the base of the anthers overlap the apical portion of the stigmatic head.

### 6.4.5 Fruit and Seed Morphology

Fruits are 4-seeded, usually fleshy, becoming ligneous at maturity, falling apart into two 2-seeded nutlets (each bicarpellate), while the calyx remains persistent on the dry inflorescence; only in *Heliotropium pycnophyllum* the calyx remains attached to the fruit, which does not divide into nutlets. Fruits are sub-spherical, glabrous, rugose, with a dark-brown to yellow exocarp. Diameter does not exceed 2 mm in most species. Testa smooth. Embryo straight.

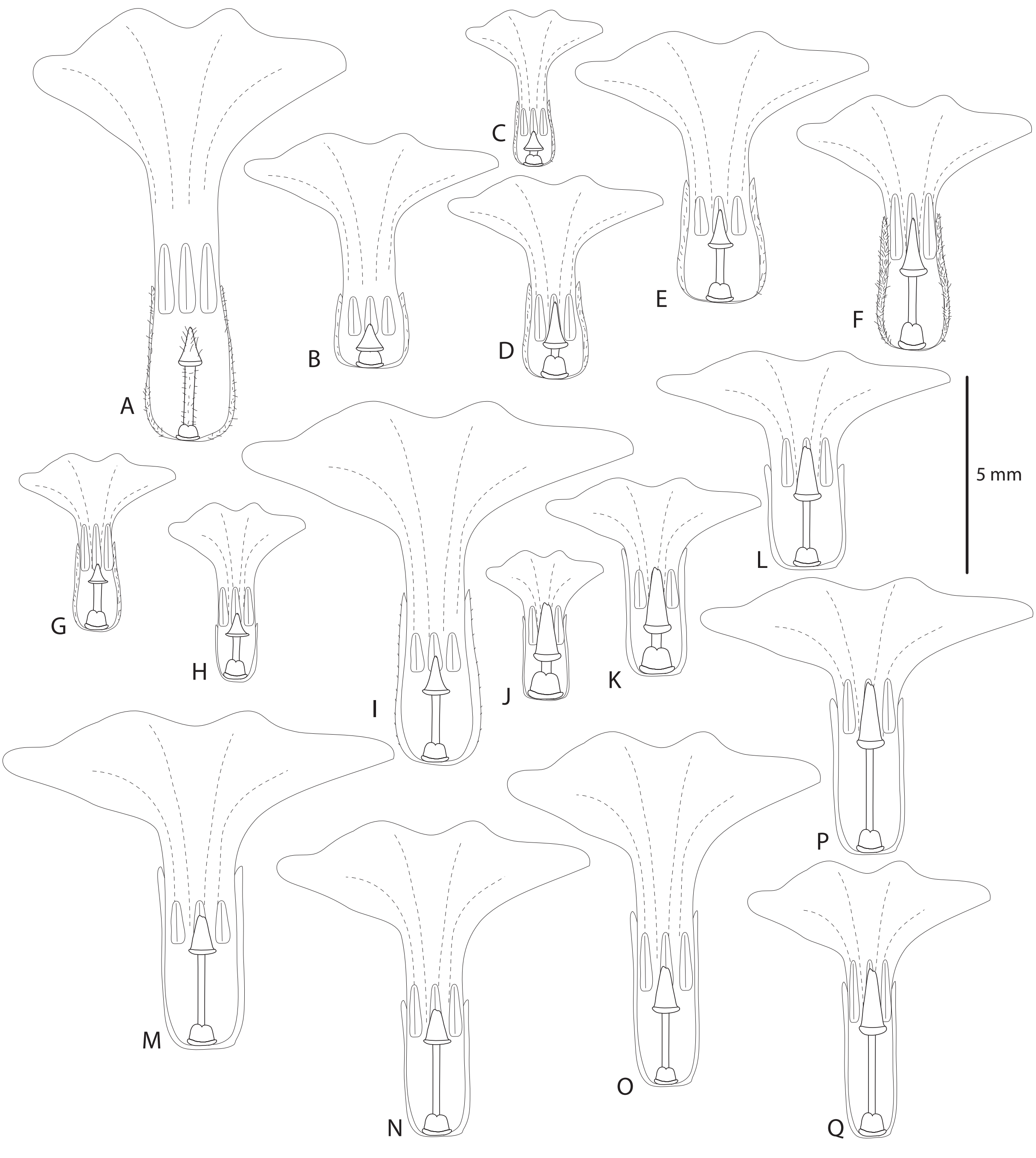

Figure 6.3: Schematic representation of floral morphology of *Heliotropium* sect. *Cochranea*. Inner view showing style-stigma complex and approximate position of anthers is depicted. A, *H. pycnophyllum*, based on *Luebert & Kritzner* 1850, BSB; B, *H. filifolium*, based on *Luebert & Kritzner* 1818 (BSB); C, *H. jaffuelii*, based on *Jaffuel* 2524, G; D, *H. glutinosum*, based on *Luebert & Torres* 1970, BSB; E, *H. sinuatum*, based on *Luebert & García* 2492/886, BSB; F, *H. taltalense*, based on *Luebert et al.* 2083, BSB; G, *H. krauseanum* subsp. *krauseanum*, based on *Dostert & Cáceres* 1025, BSB; H, *H. inconspicuum*, based on *Luebert & García* 2690/1084, BSB; I, *H. megalanthum*, based on *Luebert & Becker* 2165, BSB; J, *H. chenopodiaceum*, based on *Jiles* 3152, CONC; K, *H. myosotifolium*, based on *Luebert et al.* 2011, BSB; L, *H. stenophyllum*, based on *Luebert & Becker* 2910, BSB; M, *H. longistylum*, based on *Luebert et al.* 2020, BSB; N, *H. floridum*, based on *Schlegel* 3876, CONC; O, *H. linariifolium*, based on *Luebert et al.* 2055, BSB; P, *H. philippianum*, based on *Luebert et al.* 2124, BSB; Q, *H. eremogenum*, based on *Jaffuel* 1120, GH.

### 6.4.6 Pollen Morphology

Pollen of 11 species of *Heliotropium* sect. *Cochranea* were studied by Marticorena (1968). According to this author, all species are 3-colporate, 3- pseudocolpate, pseudocolpi non-anastomosed at the poles; colpus sides almost parallel or little convex; amb 6-lobate. This combination of characters is consistent with type I of Nowicke and Skvarla (1974). The descriptions of the pollen provided for each species are based on Marticorena (1968) and own SEM observations.

### 6.4.7 Distribution

*Heliotropium* sect *Cochranea* is restricted to the Peruvian and Atacama Deserts of northern Chile and Southern Peru (see Fig. 1.5, p. 1.5). Only one species occurs in Peru, *Heliotropium krauseanum*, from the Department of Lima (12°38'S, 75°58'W; Weigend et al., 2003) to the province of Iquique in northern Chile (19°37'S, 70°11'W; Luebert and Pinto, 2004) (Fig. 6.15, p. 6.15). The remainder of the group is distributed in the Atacama Desert of northern Chile, with the northernmost population around Iquique (20°22'S, 70°12'W), to central Chile in the surroundings of La Calera and Laillay (32°50'S, 71°09'W). Two major centres of diversity can be recognised (Luebert and Wen, 2008), the first located in the coastal range of Taltal and Paposo (24°-25°S latitude) in the region of Antofagasta, where six species can be found, and the region between Huasco and Caldera (27°-28°S latitude), with eight species. Most species are located in the coastal range or at the immediately adjacent inland areas and only two species, *Heliotropium chenopodiaceum* and *H. glutinosum*, occur on the foothills of the Andes. *Heliotropium krauseanum*, *H. sinuatum* and *H. stenophyllum* can also eventually reach the Andean foothills, but they are also present in the coast. The altitudinal range of *Heliotropium* sect. *Cochranea* extends from sea level to a maximum elevation of 2.200 m (*H. glutinosum*).

### 6.4.8 Ecology

The species of section *Cochranea* have their geographic range restricted to the arid and hyperarid zones of the Atacama and Peruvian Deserts, with *Heliotropium stenophyllum* as the only outlier reaching the sclerophyllous woodland zone of central Chile, where it is restricted to the driest slopes. *Heliotropium* is frequently a dominant component of the vegetation of which it takes part and several studies have documented their presence in specific vegetation types (see Gajardo, 1994; Luebert and Pliscoff, 2006; and references therein).

*Heliotropium* sect. *Cochranea* is one of the most diversified groups of plants of the Atacama Desert (Luebert and Wen, 2008). Its diversity probably indicates the success of this group to survive in extremely arid environments and this should be reflected in morphological and/or physiological adaptations to tolerate drought. Ehleringer et al. (1998) studied carbon isotope ratios of three species of *Heliotropium* sect. *Cochranea* (*H. linariifolium*, *H. pycnophyllum* and *H. taltalense*) from the coastal areas of Paposo (25°01'S, 70°28'W) and Pan de Azúcar (26°01'S, 70°35'W). All three species resulted to have $C_3$ photosynthetic pathway; Diane et al. (2003) also suggested $C_3$ photosynthetic pathway for *H. krauseanum* based on leaf anatomy. Constantly more positive-than-average values of leaf carbon isotope ratio (meaning low intercellular $CO_2$ concentration), with a variation consistent with local changes in aridity were also reported by Ehleringer et al. (1998). Whether these low levels of intercellular $CO_2$ concentration represent an adaptation to hyperarid conditions was unknown, but the authors suggested that tolerating water stress might be a dominant factor in the plant's life cycle of this region (Ehleringer et al., 1998). For *Heliotropium pycnophyllum*, Rundel et al. (1980) suggested that a main strategy of the species to tolerate aridity is to become dormant during the driest periods. Secretion of resin, small leaf size and dense pubescence in some species of *Heliotropium* sect. *Cochranea* may be interpreted as complementary adaptations to reduce water loss.

The flowers of *Heliotropium* sect. *Cochranea* are generally white with a yellow to orange spot in the centre of the throat. This spot may be an indication to insects as to where is the nectar located. Field observations indicate that the colour of the flowers changes over the flowering season. This change may be an indication to insects that the flower does not produce more nectar or pollen and that the stigma is no longer receptive. In *Heliotropium amplexicaule* Vahl (section *Heliotrophytum*), Weiss (1991) showed a significant decrease in flower visits after the colour change. The flowers of *Heliotropium* have a nectar disk at the base of the ovary and the typical Heliotropiaceae sterile conical development of the stigma; the receptive tissue is located at the base of the stigmatic head and the stamens are positioned surrounding the stigmatic head or above it, enclosing the flowers at the apex of the corolla tube and leaving limited space to the insects to reach the nectar disk. Such arrangement of the flower led Nowicke and Skvarla (1974) to suggest that most species of Heliotropiaceae may appear to be primarily self-pollinated, because it would make 'the stigma inaccessible to all but the smallest insect or insect part', with which Weigend et al. (2003) agree. However, the variation in the relative position of stamens and stigmatic head and in their relative and absolute length as well as flower display and the presence of a nectar ring a the basis of the ovary, which is observed among the species of *Heliotropium* sect. *Cochranea*, might be an indication of adaptation to insect pollination (Weigend et al., 2003). Pollination has not been systematically studied in *Heliotropium* sect. *Cochranea* and the evidence is anecdotic. *Chilicola deserticola* Toro & Moldenke, 1979 and *C. erithropoda* Toro & Moldenke, 1979 (Hymenoptera: Colletidae) have been observed visiting flowers of *Heliotropum stenophyllum* Hook. & Arn. (Moure and Urban, 2002)[b]. Toro et al. (1996) report observations of a species of the genus *Megachile* (Hymenoptera: Apoidea) visiting flowers of *Heliotropium linariifolium* Phil. Floral morphology and scent of some species indicate insect pollination (Knuth, 1899). Casual personal observations of flower visitors in *Heliotropium* sect. *Cochranea* include small Lepidoptera, Hymenoptera and Coleoptera. The role that these groups play in the pollination is however unknown. Darrault and Schlindwein (2005) studied the pollination of *Hancornia speciosa* Gomes (Apocynaceae), whose tubular flowers are characterized by a long style and a stigmatic head, above which the stamens enclose the flower, while the nectary is located at the basis of the flower, similar to what is found in *Heliotropium*. These authors suggested that the pollinators need to have a long proboscis to reach the receptive part of the stigmatic head, even if the are not able to collect nectar; insects with shorter proboscis would remove pollen, but would not cross pollinate flowers due to failure to reach the receptive stigmatic surface.

Differences in phenology may account for reproductive isolation among species living in sympatry, but there is not empirical evidence for that. Phenology has been recorded for two species of *Heliotropium* sect. *Cochranea*, *Heliotropium megalanthum* (Vidiella et al.,

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[b] It is probably not *Heliotropium stenophyllum*, because both insect species were collected around the town of Pueblo Hundido (now Diego de Almagro) in northern Chile (Toro and Moldenke, 1979) where this species does not occur. Instead, it is most probably *Heliotropium glutinosum* Phil., certainly inhabiting the surroundings of Diego de Almagro.

1999) and *H. stenophyllum* (Olivares and Squeo, 1999). In both species the peaks in flowering is reached at the beginning of the austral spring after winter rains.

Diaspore dispersal of *Heliotropium* sect. *Cochranea* is probably geochorous. No seed predators are known, no adaptations to wind-dispersal are present and the seeds seem to remain in the immediate vicinity of the mother plants (Rundel et al., 1980). The fruit morphology of *Heliotropium pycnophyllum*, with non-divided fruits and the calyx remaining attached to it at maturity, resembles that of *Heliotropium supinum* L. and *H. drepanophyllum* Baker. For these two species inflated calyces attached to the fruits, which are not divided, is interpreted as an adaptation to hydrochory, but this phenomenon has not been observed in *H. pycnophyllum*.

### 6.4.9 Phytochemistry

Several phytochemical studies have been conducted in *Heliotropium* sect. *Cochranea*. Chemical composition of the resinous exudates has been reported for 10 species, *Heliotropium chenopodiaceum* (Urzúa et al., 1998), *H. filifolium* (Torres et al., 1994), *H. glutinosum* (Modak et al., 2007), *H. longistylum* (Villarroel et al., 2001; erroneously reported as *H. huascoense*), *H. megalanthum* (Urzúa et al., 2000), *H. myosotifolium* (Modak et al., 2009b; as *H. sclerocarpum*), *H. pycnophyllum* (Wollenweber et al., 2002), *H. sinuatum* (Torres et al., 1996), *H. stenophyllum* (Villarroel et al., 1991; Wollenweber et al., 2002) and *H. taltalense* (Modak et al., 2009a). Most of the compounds present in the resinous exudates are flavonoids and aromatic geranyl derivatives and their presence appears to be directly related to the resin on the leaves and branches, thus the non-resinous species do not produce such compounds (R. Torres, personal communication). Apart from the apparent role of the resin itself in the control of water loss in response to aridity, these compounds have shown to have antioxidant (e.g., Modak et al., 2007), antiviral (Torres et al., 2002), antibacterial (e.g., Modak et al., 2004a), and/or antifungal (Mendoza et al., 2008) properties. These kinds of compounds have not been reported for other *Heliotropium* groups apart from section *Cochranea* and are therefore of potential systematic value within the genus.

Pyrrolizidine alkaloids have been also reported in *Heliotropium* sect. *Cochranea* (Reina et al., 1997, 1998). These kinds of compounds are ubiquitous in *Heliotropium* (e.g., Medina et al., 2009) and in the Boraginales (e.g., Alali et al., 2008).

### 6.4.10 Biogeography and Evolution

*Heliotropium* sect. *Cochranea* has been individualized as a monophyletic group within Heliotropiaceae (Fig. 2.2; Chapters 3 and 4). The sister group of *Heliotropium* sect. *Cochranea* is a large clade composed of seven sections of South American *Heliotropium* (sects. *Coeloma*, *Heliotrophytum*, *Hypsogenia*, *Plagiomeris*, *Platygyne*, *Tiaridium* and *Schobera*) and *Tournefortia* sect. *Tournefortia*. The latter clade has a mostly Neotropical distribution (Johnston, 1928b, 1930, 1935a; Förther, 1998) with ca. 12 representatives of *Tournefortia* in the Indo-Pacific region (Johnston, 1935b; Riedl, 1997; Craven, 2005). The biogeographical mechanisms by which these groups could have achieved such distribution have not been evaluated in detail yet. Age estimates performed by Gottschling et al. (2004) led these authors to suggest long-distance dispersal between America and the Indo-Pacific region during the Tertiary. *Heliotropium* sect. *Cochranea* may have originated *in situ* from a Neotropical ancestor. Luebert and Wen (2008; Chapter 2) estimated a middle Miocene age for the crown node of *Heliotropium* sect. *Cochranea*, with a major diversification event during the early Pliocene. These ages are in agreement with the proposed timing of increase in uplift rates of the Andes (Gregory-Wodzicki, 2000; Garzione et al., 2008), and the onset of hyperarid conditions in the Atacama Desert (Hartley, 2003), respectively. The uplift of the Andes may have reinforced arid conditions over Atacama (Hartley, 2003) and, at the same time, isolated *Cochranea* on the western versant of the Andes, as suggested by Luebert and Wen (2008; Chapter 2). The final turn to hyperarid conditions in Atacama may have triggered a rapid diversification process during the Pliocene (Luebert and Wen, 2008; Chapter 2). This scenario has also been suggested for the genera *Nolana* L.f. (89 species, Dillon et al., 2009), the most diverse group of the Atacama Desert (Dillon, 2005b), and *Oxalis* L. sect. *Carnosae* Reiche (12 species, Heibl et al., in press).

### 6.4.11 Key to the Species of *Heliotropium* sect. *Cochranea*

**1** Style and stigmatic head shortly hispid, calyx remains attached to the fruit during dispersal, fruit 4-seeded, not divided . . . . . **1. *H. pycnophyllum***
\- Style and stigmatic head glabrous, calyx persistent on the inflorescences, detached fruit dividing into two 2-seeded nutlets . . . . . **2**
**2** Leaves terete, stigmatic head sessile or sub-sessile . . . . . **3**
\- Leaves non-terete, margin folded, stigmatic head with distinct style . . . . . **4**
**3** Corolla limb more than 4 mm wide. Plants from Región de Atacama, Chile **2. *H. filifolium***
\- Corolla limb less than 4 mm wide. Plants from Tocopilla, Chile . . . . . **3. *H. jaffuelii***
**4 (2)** Leaves with sinuate margin and rugose on the adaxial surface . . . . . **5**
\- Leaves with entire margin, not rugose on the adaxial surface . . . . . **9**
**5** Secondary veins of the leaves simple, reaching margin, not forked . . . . . **6**
\- Secondary veins of the leaves forked . . . . . **8**
**6** Glands visible with naked eye on the leaves. Style shorter than the stigmatic head **4. *H. glutinosum***
\- Glands not visible with naked eye on the leaves. Style longer than or equaling stigmatic head . . . . . **7**
**7** Resinous plant with scarce simple hairs on the adaxial surface. Plant from the provinces of Huasco and Elqui, Chile . . . . . **5. *H. sinuatum***
\- Resinous plant densely pubescent on the adaxial surface. Plant from the department of Arequipa, Peru . . . . . **7a. *H. krauseanum*** subsp. ***jahuay***
**8 (2)** Calyx densely hirsute, corolla tube longer than 4.5 mm at anthesis, style as long as or shorter than the stigmatic head. Plant from the coast of the province of Antofagasta, Chile . . . . . **6. *H. taltalense***
\- Calyx sparsely hirsute, corolla tube not longer than 4.5 mm at anthesis, style longer than the stigmatic head. Plant from the coast and interior lomas of south-central Peru and northernmost Chile . . . . . **7. *H. krauseanum*** subsp. ***krauseanum***
**9 (4)** Style shorter than or equaling the stigmatic head . . . . . **10**
\- Style definitely longer than the stigmatic head . . . . . **15**
**10** Stems without evident strigose pubescence on the vegetative parts of the plant . . **11**
\- Stems with evident strigose pubescence on the vegetative parts . . . . . **13**
**11** The longest leaves longer than 15 mm . . . . . **12. *H. stenophyllum***
\- The longest leaves shorter than 15 mm . . . . . **12**

12 Leaves linear-oblong with conspicuous white bands on the abaxial surface. Style as long as the stigmatic head . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **8. *H. inconspicuum***
- Leaves linear-lanceolate without white bands on the abaxial surface. Style 3 or more times shorter than the stigmatic head . . . . . . . . . . . . . . . . . . . . . . . . **10. *H. chenopodiaceum***

13 (10) Leaves pubescent only on the margin . . . . . . . . . . . . . . . . **9. *H. megalanthum***
- Leaves pubescence spread on the whole blade . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **14**

14 Glutinous plants. Calyx lobes fused at least to the half of their length. Corolla usually less than 5 mm wide . . . . . . . . . . . . . . . . . . . . . . . . . . . **10. *H. chenopodiaceum***
- Non glutinous plants. Calyx lobes free. Corolla 5-7 mm wide . **11. *H. myosotifolium***

15 (9) Leaves glabrous . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **13. *H. longistylum***
- Leaves pubescent . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **16**

16 Leaves shorter than 6.5 mm. Plant from the area of Antofagasta (La Chimba-Cerro Moreno), Chile, or north thereof . . . . . . . . . . . . . . . . . . . . . . . . **17. *H. eremogenum***
- Leaves generally longer than 6.5 mm. Plants from south of Antofagasta . . . . . . . **17**

17 Decumbent shrubs, corolla orange . . . . . . . . . . . . . . . . . . . . . . . . **15. *H. linariifolium***
- Erect shrubs, corolla white . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **18**

18 Shrubs generally shorter than 0.6 m. Plants from Chañaral or south thereof **14. *H. floridum***
- Shrubs taller than 0.6 m. Plants from north of Taltal . . . . . . . **16. *H. philippianum***

### 6.4.12 Species Descriptions

**1. Heliotropium pycnophyllum** *Phil.* (Philippi, 1860a: 38); Reiche (1907a: 238); Reiche (1910: 196); Johnston (1928b: 35); Marticorena (1968: 45); Förther (1998: 215). Type: Chile, Región de Atacama, Prov. Chañaral, Cachinal de la Costa, Dec. 1853, *R.A. Philippi* s.n. (holotype SGO 54374 [photo F, GH, NY, US]).

*Heliotropium breanum* Phil. (Philippi, 1895: 357). Type: Chile, Región de Antofagsata, Prov. Antofagsata, Breas, 1888, *A. Larrañaga* s.n. (holotype SGO 54371 [photo F, GH, MSB, NY, US]; isotypes GH, SGO 54373, SGO 54369 [photo MSB]).

*Heliotropium brevifolium* Phil. (Philippi, 1895: 357), **nom. illegit.**, non Wall., in Roxburgh (1824: 2). Type: Chile, Región de Antofagsata, Prov. Antofagsata, Hueso Parado, Oct. 1887, *A. Borchers* s.n. (lectotype SGO 54372 [photo F, GH, MSB, NY, US], selected by Johnston (1928b: 35 – 36)).

*Cochranea pycnophylla* F.Phil. ex Reiche (1907a: 238). **nom. invalid.** (cited as a synonym).

*Low and globose erect shrub*, (0.2 –) 0.4 – 1.0 (– 1.5) m tall, profusely branched, with short branches, densely foliose to the apex. Stems and foliage densely covered by short, substrigose and incane pubescence, somewhat glutinous. *Leaves* alternate, solitary or grouped in fascicles of up to 16 leaves, sessile, succulent, linear, oblong-linear or oblong-ovate, 3.5 – 12 (– 16) × 0.7 – 3 (– 4.5) mm, sub-terete due to the strongly revolute margins; lamina pubescent, green to greyish-green, margin entire, base and apex obtuse, veins inconspicuous, pubescence short, incane, strigose. *Inflorescences* terminal, globose, dichotomically branched, to ca. 5 cm long. *Flowers* sessile, alternate, erect, aromatic. Calyx cylindric, pale green; calyx lobes linear, fused only at the base or rarely up to the middle, strigose on both sides, 2.5 – 6.5 × 0.5 – 1 mm, free portion 0.5 – 5 mm long, apex acute or rarely obtuse. Corolla infundibuliform, hispid outside, white with yellow throat, becoming pur-

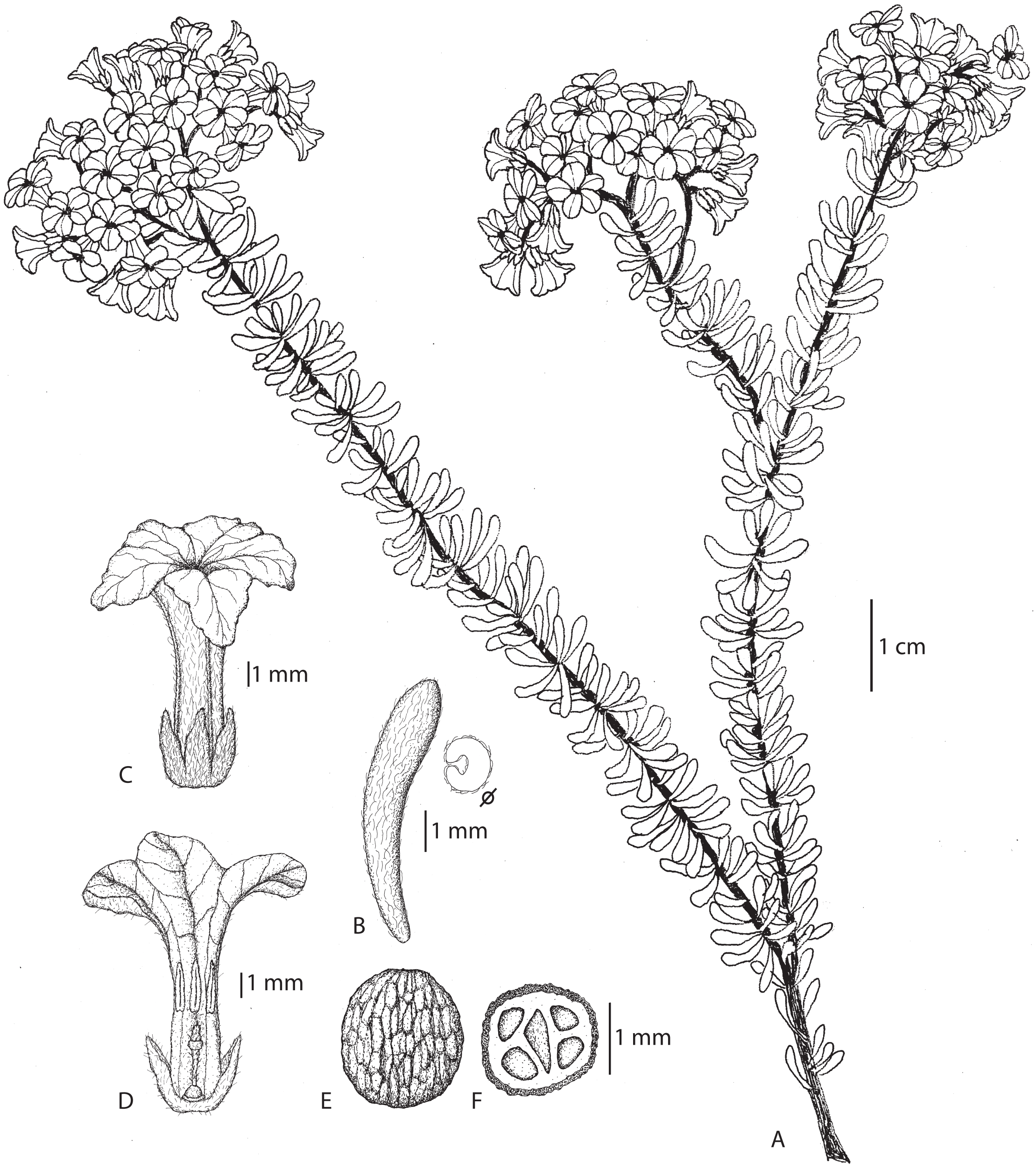

Figure 6.4: *Heliotropium pycnophyllum.* A, Flowering branch; B, Leaf; C, Flower - outer view; D, Flower - inner view; E, Fruit - dorsal view; F, Fruit - transversal view. (A-D from *Luebert & Kritzner* 1850, BSB; E-F from *Luebert et al.* 2128, BSB). Drawn by Anja Salchow.

plish or violet; limb horizontally spreading, 6 – 12 mm wide, lobes rounded; tube almost twice as long as the calyx, 6 – 10 (– 12.5) mm long. Stamens included; filaments adnate to petals; anthers oblong, glabrous, base cordate, apex obtuse, 2 – 2.5 mm long, generally located above the apex of the stigmatic head or shortly overlapping it. Ovary glabrous, ca. 0.5 mm diam., with a basal nectar ring. Style hispid, ca. 1.3 – 1.7 mm long, longer than the stigmatic head. Stigmatic head conic, 0.8 – 1.2 × 0.4 – 0.8 mm, column hispid. *Fruits* dry, spheric, rugose, glabrous, dark brown, 1.5 – 2.5 mm diam., 4-seeded, not falling apart at maturity, dispersed together with the calyx. Fig. 6.4.

*Pollen* prolate, 26 – 29.5 × 17 – 18.5 $\mu$m. Amb lobes not deep. Endoapertures ca. 5 $\mu$m diam., circular or somewhat lalongate and then contracted at the centre. Exine thickness

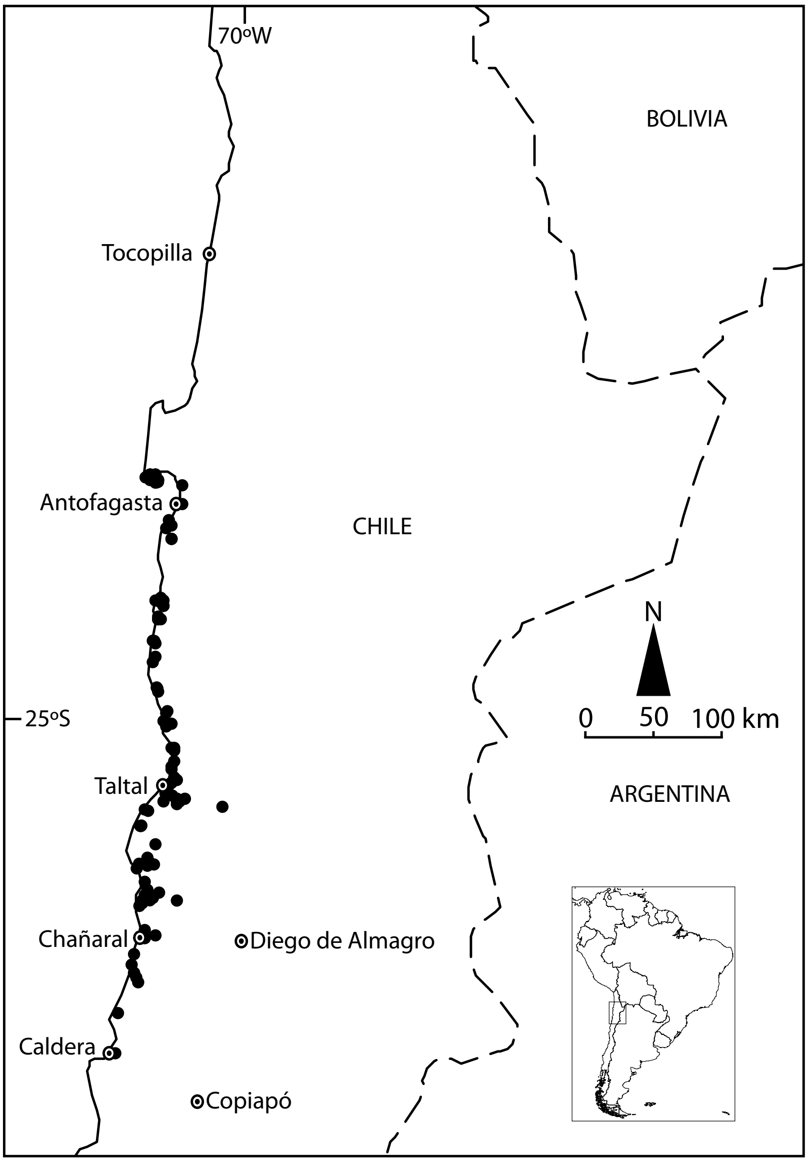

Figure 6.5: Distribution of *Heliotropium pycnophyllum*.

ca. 1.3 $\mu$m, without differences between apocolpia and mesocolpia (from *Ricardi* 3134 in Marticorena, 1968).

**DISTRIBUTION**. Coastal dry areas of the provinces of Chañaral (Región de Atacama) and Antofagasta (Región de Antofagasta) in Chile, 23°28' – 27°4' S (Fig. 6.5).
**SPECIMENS EXAMINED**. See Appendix E (p. 297).
**HABITAT**. A xerophyte, never found in the fog zone, but in low areas next to the coast, on sandy substrates, alluvial foothills, and gravelly hillsides or on the eastern plains of the coastal Cordillera (see Johnston, 1929a), between the sea level and 950 m. Locally dominant in the vegetation together with *Nolana villosa* (Phil.) I.M.Johnst. (Solanaceae), *Frankenia chilensis* C.Presl (Frankeniaceae), *Gypothmanium pinifolium* Phil. (Asteraceae), *Heliotropium linariifolium* (Heliotropiaceae) (Reiche, 1911). It has been reported for the coastal dunes, where the dominant species are *Nolana mollis* (Phil.) I.M.Johnst. (Solanaceae) and *Tetragonia maritima* Barnéoud (Aizoaceae) (Kohler, 1970).
**CONSERVATION STATUS**. Least concern (LC), criterion B2(c), see Chapter 5.

**FLOWERING TIME**. September to November.
**ETYMOLOGY**. The epithet *pycnophyllum* refers to its dense foliage.
**VERNACULAR NAME**. Palo negro (Spanish).
**USES**. Riedemann et al. (2006) suggest its potential use as ornamental.
**NOTES**. This is a very distinct species from the coastal Atacama Desert. In gross habit it resembles the other species of sect. *Cochranea* with conspicuous pubescence, but it differs from all other species of the section in its strongly revolute leaves and in its hispid style and stigmatic head, a combination of characters that is only present in the distantly related Old World species *Heliotropium supinum* L. and *H. drepanophyllum* Baker (Hilger, 1987; Verdcourt, 1988). In the phylogenetic analysis of Luebert and Wen (2008; Chapter 2) this species was resolved as sister to the remainder of the section.

Johnston (1928b: 36) pointed out the confusion in the original description of Philippi (1860b), subsequently accepted by Reiche (1907a, 1910), who indicated orange-coloured corollas for *Heliotropium pycnophyllum*. Intensive field observations, including all type localities, confirm that the corollas of this species are never orange, character only found in *Heliotropium linariifolium*. Förther (1998) mentions a possible isotype collection of *Heliotropium pycnophyllum* at B (destroyed, photo F neg. n° 17341: F, GH, NY, US); this specimen does not correspond to *H. pycnophyllum*, but to *H. linariifolium*, except for the fragment seen at the bottom-right corner of the photograph.

Muñoz (1960: 109) refers three syntype collections to *Heliotropium brevifolium* (SGO 54369, 54372, 54371) and none to *Heliotropium breanum*. The first is actually a lectoparatype of *H. brevifolium* and, at the same time, an isotype of *H. breanum*; the second is the lectotype of *H. brevifolium*; the third is the holotype of *H. breanum* (it is the only specimen in SGO holding the name in Philippi's handwriting).

**2. Heliotropium filifolium** (*Miers*) *I.M.Johnst.* (Johnston 1928b: 32); Förther (1998: 195). Type: Chile, Región de Atacama, 'Conception' [dry valleys and hills between Huasco and Copiapó], [Sept. 1841], *T. Bridges* 1343 (lectotype BM [fragm. + photo GH], selected by Johnston (1928b: 32); duplicates A, E not seen (digital photograph!), G, K [photo SGO 2263], P not seen [digital photograph!, fragm. F 515812, photo MSB], W not seen).

*Cochranea filifolia* Miers (1868: 131); Philippi (1881: 253); Philippi (1895: 346). Type as above.
*Heliotropium chenopodiaceum* (A.DC.) Clos var. *filifolium* (Miers) Reiche (1907a: 244); Reiche (1910: 202). Type as above.
*Cochranea kingi* Phil. (Philippi, 1895: 350). Type: Chile, Región de Atacama, Prov. Huasco, valle Carrizal, Sept. 1885, *s.col.* [*F. Philippi*?] (holotype SGO 54430 [fragm. GH, photo F, GH]; isotype B† [photo F neg. n° 17321: F, GH, NY], possible isotype K).
*Heliotropium kingi* (Phil.) Reiche (1907a: 238); Reiche (1910: 196). Type as for *C. kingi*.

*Erect shrubs*, 0.3 – 1 m tall, profusely branched, with short branches, densely foliose to the apex. Stems and foliage glabrous, or papillose-tomentose on the younger parts, glutinous. *Leaves* alternate, grouped in fascicles of up to 10 leaves, sessile, linear, 2 – 11 (– 13.5) × 0.5 – 1.5 mm, terete; lamina glabrous, with inconspicuous glandular trichomes, green, margin entire, base and apex obtuse, veins inconspicuous. *Inflorescences* terminal, elongate, dichotomically branched, to ca. 5 cm long. *Flowers* sessile, alternate, erect, aromatic. Calyx cylindric, pale green; calyx lobes oblong or obovate, fused only at the

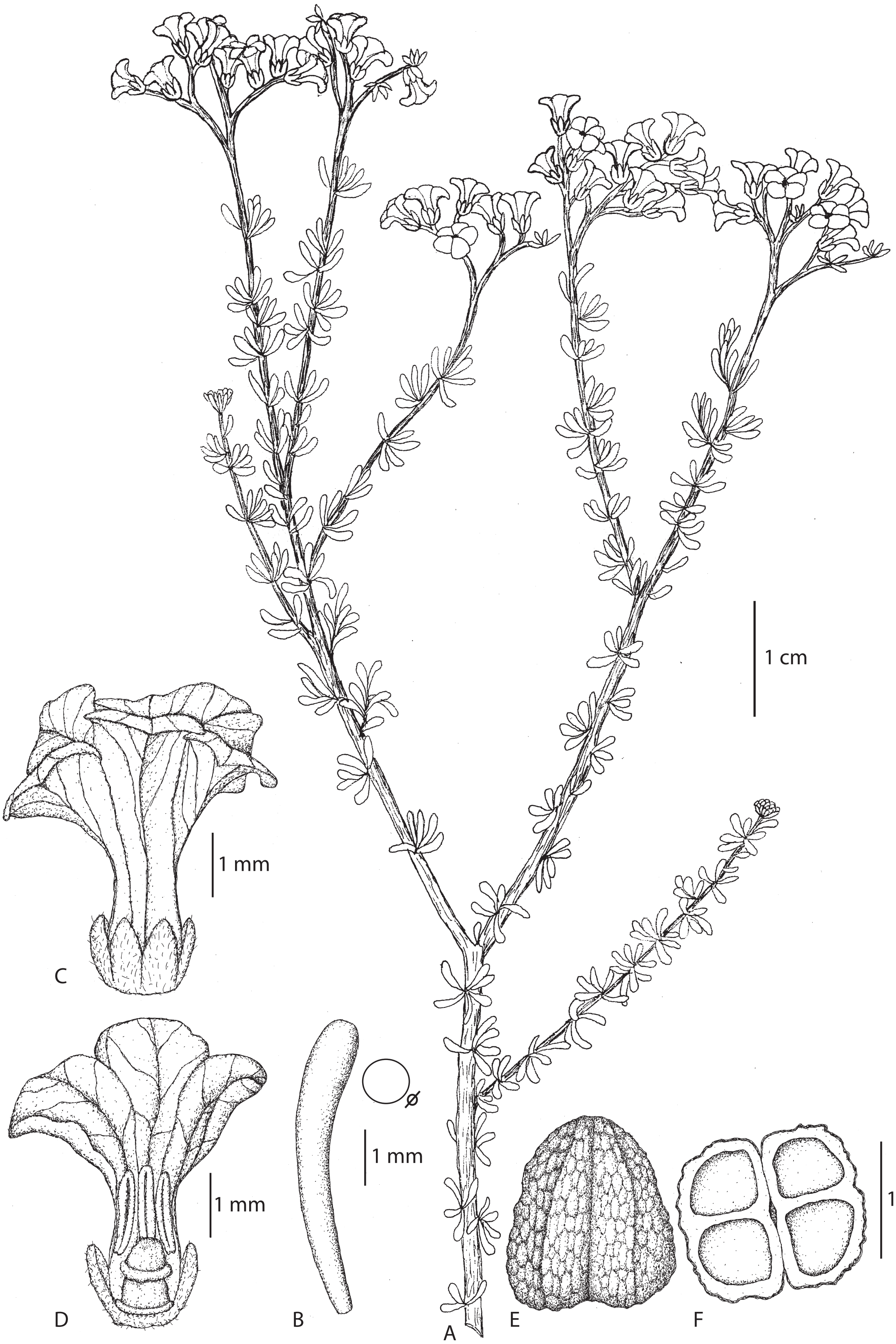

Figure 6.6: *Heliotropium filifolium.* A, Flowering branch; B, Leaf; C, Flower - outer view; D, Flower - inner view; E, Fruit - dorsal view; F, Fruit - transversal view. (All from *Luebert & Kritzner* 1818, BSB). Drawn by Anja Salchow.

base, sparsely strigose outside, glabrous within, 1 – 2.5 × 0.5 – 1.5 mm, free portion 1 – 2.5 mm long, apex obtuse. Corolla infundibuliform, hispid outside, white with yellow throat; limb horizontally spreading, 4 – 9 mm wide, lobes rounded; tube 2 – 3 times as long as the calyx, 2 – 6 mm long. Stamens included or exserted; filaments adnate to petals; anthers oblong, glabrous, base cordate, apex obtuse, 0.7 – 1.2 mm long, generally located above the apex of the stigmatic head or shortly overlapping it. Ovary glabrous, subglobose, ca. 0.7 mm diam., with a basal nectar ring. Style glabrous, 0 – 0.05 mm long, shorter than the stigmatic head. Stigmatic head conic, glabrous, 0.4 – 0.9 × 0.8 – 1 mm. *Fruits* dry, ellipsoid, rugose, glabrous, light brown, ca. 1.6 × 1.3 mm diam., falling apart at maturity into two 2-seeded nutlets, each ca. 1.6 × 0.8 mm diam. Fig. 6.6.

*Pollen* prolate, 22 – 26 × 13 – 15.5 $\mu$m. Endoapertures 3 – 3.5 $\mu$m diam., circular or slightly lalongate. Exine thickness ca. 1 $\mu$m. Colpiferous sides slightly convex (from *Ricardi* 2281 in Marticorena, 1968).

**DISTRIBUTION**. Coastal areas of the provinces of Huasco and Copiapó (Región de Atacama, Chile), 27°24' – 28° 36' S. It founds its northern limit in the surroundings of Totoral (Fig. 6.7).

**SPECIMENS EXAMINED**. See Appendix E (p. 299).

**HABITAT**. Coastal plains, slopes and ravines of the fog-free area, between 20 and 530 m. It also occurs some kilometers inland. Scarce, sometimes found in populations of several individuals, where is locally dominant. It forms part of a vegetation dominated by *Atriplex clivicola* I.M.Johnst. (Amaranthaceae), *Balbisia peduncularis* D.Don (Ledocarpaceae), *Eulychnia breviflora* Phil. (Cactaceae), *Nolana werdermannii* I.M.Johnst. (Solanaceae), *Oxalis virgosa* Molina (Oxalidaceae).

**CONSERVATION STATUS**. Vulnerable (VU), criterion B2(c), see Chapter 5.

**FLOWERING TIME**. September to November, or throughout the year at locally humid spots.

**ETYMOLOGY**. The epithet *filifolium* refers to its thread-like leaves.

**VERNACULAR NAME**. Palo negro (Spanish).

**USES**. Natural and the semi-sinthetic compounds of the resin of *Heliotropium filifolium* have shown antiviral propierties (Torres et al., 2002; Modak et al., 2004a, 2010) as well as inhibitory effects of the complement system (Larghi et al., 2009), with potential pharmacological applications. Riedemann et al. (2006) suggest its potential use as ornamental.

**NOTES**. Förther (1998: 229) erroneously quotes the material of *Bridges* 1343 at BM as the holotype, though Miers (1868: 131) had indicated two specimens (BM, K), one of which (BM) was later chosen by Johnston (1928b: 32) as the lectotype. The collection *Bridges* 1343 (G) was mentioned by de Candolle (1845: 553) among the syntypes of *Heliotropium chenopodiaceum*, but was distinguished by Miers (1868) as a different species. The collection was made by *Bridges* in 1841 (Johnston, 1928a) without H. Cuming, as indicated by Förther (1998: 229, '[& Cumming]' (sic)), because Cuming was not in Chile that year (Dance, 1980).

Reiche (1907a: 244, 1910: 202) applied this name (under *Heliotropium chenopodiaceum* var. *filifolium*) to a different species, namely *Heliotropium chenopodiaceum*, by referring *Cochranea sentis* Phil. under its synonymy (see discussion under *Heliotropium chenopodiaceum*). Since Reiche did not see the type specimen of *Cochranea filifolia* and recognised *Heliotropium kingi* as a different, valid, species, even in a different section, the taxonomic placement of this name in Reiche's treatment is understandable. The recognition of *Heliotropium chenopodiaceum* and *Heliotropium filifolium* as different species is clear on the

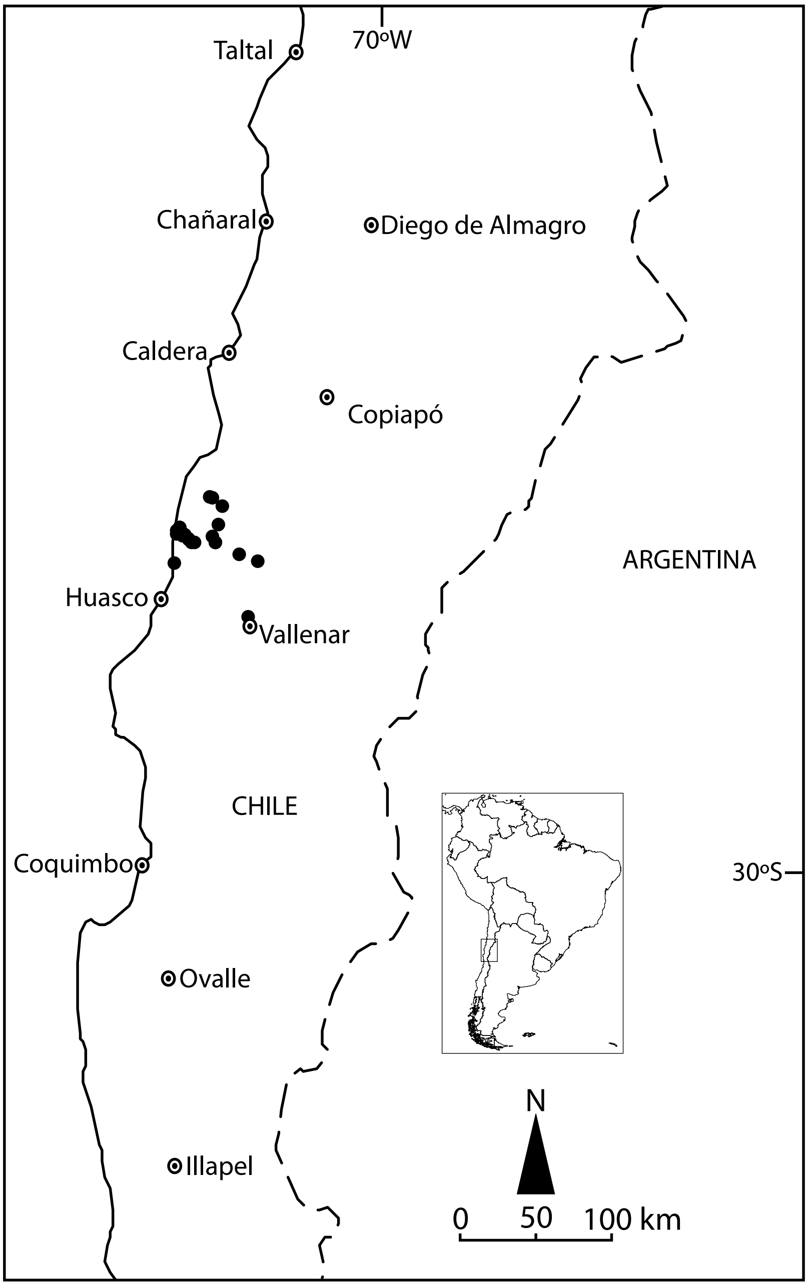

Figure 6.7: Distribution of *Heliotropium filifolium*.

basis of morphology, geographic distribution and phylogenetic position (Johnston, 1928b; Luebert and Wen, 2008), while the synonymy of *Cochranea kingi* under *Heliotropium filifolium* is evident and does not admit doubts (Johnston, 1928b). The type specimen of *Cochranea kingi* was likely collected either by F. Philippi or Juan King (see Philippi, 1886), but not by Thomas King (Johnston, 1928b; Förther, 1998), because he was not in Chile in 1885 (Desmond, 1994) when that material was collected, none of the type specimens has '*King*' as collector in the label, and the Chilean materials of Thomas King were described by Philippi (1873).

**3. Heliotropium jaffuelii** *I.M.Johnst.* (Johnston, 1937: 19); Förther (1998: 201). Type: Chile, Región de Antofagasta, Prov. Tocopilla, Tocopilla, Nov. 1931, *F. Jaffuel* 2524 (holotype GH; isotypes CONC, G).

*Erect shrubs*, laxly ramified. Stems and foliage glutinous, covered by inconspicuous short-strigose pubescence. *Leaves* alternate, solitary or grouped in fascicles of up to 8 leaves, sessile, linear, 4 – 10 × 0.5 – 1 mm, terete; leaf balde glabrous or inconspicuously pubescent, greyish-green, margin entire, base and apex obtuse, veins inconspicuous. *Inflorescences* terminal, dichotomically branched, 1 – 4 cm long. *Flowers* sessile or shortly pedicellate (pedicle $< 1$ mm), alternate, erect. Calyx globose to cylindric, pale green; calyx lobes linear-lanceolate, fused only at the base, pubescent outside, glabrous inside, 1.5 – 2 × 0.5 – 1 mm, free portion 0.8 – 1.5 mm long, apex acute. Corolla infundibuliform, inconspicuously pubescent outside; limb horizontally spreading 2.5 – 4 mm wide, lobes rounded, ca. 0.8 × 0.8 mm; tube more than twice as long as the calyx, 3 – 4 mm long. Stamens included or little exserted; filaments adnate to petals; anthers lanceolate, glabrous, 0.4 – 0.9 mm, base cordate, apex acute, overlapping the apex of the stigmatic head. Ovary glabrous, ca. 0.3 mm diam., with a basal nectar ring. Style glabrous, ca. 0.1 mm long, shorter than the stigmatic head. Stigmatic head conic, glabrous, ca. 0.3 – 1 × 0.5 – 0.6 mm. *Fruits* dry, ellipsoid, rugose, glabrous, light brown, ca. 2.4 × 1.6 mm diam., falling apart at maturity into two 2-seeded nutlets, each ca. 1.5 × 1.2 mm diam. Fig. 6.8.

*Pollen* prolate, 17.4 – 21.1 × 8.4 – 11.6 $\mu$m (from *Jaffuel* 2424, G).

**DISTRIBUTION**. Endemic to the coastal areas north of Tocopilla (22°S), Región de Antofagasta, Chile, 22°6' – 22°2'S (Fig. 6.9).
**SPECIMENS EXAMINED**. See Appendix E (p. 300).
**HABITAT**. Coastal hills on gravelly slopes at the fog zone (Jaffuel, 1936). The vegetation is a desert scrub dominated by *Eulychnia iquiquensis* (K.Schum.) Britton & Rose and *Ephedra breana* Phil. (Luebert and Pliscoff, 2006; Luebert et al., 2007).
**CONSERVATION STATUS**. Critically endangered (CR), according to the criterion of area of occupancy (B2(c), IUCN, 2001). This species is known from one locality, and has been collected only twice.
**ETYMOLOGY**. The name was dedicated to Felix Jaffuel, collector of the type specimen.
**NOTES**. Only known from the type specimen and one additional gathering, both collected in the surroundings of Tocopilla, Chile. Attempts at collecting the plant at the type locality failed. It is likely a very rare and local endemic. Due to its geographical distribution, leaf and floral morphology, this species is readily distinguished from the other members of section *Cochranea*.

**4. Heliotropium glutinosum** *Phil.* (Philippi, 1860a: 38); Reiche (1907a: 242); Reiche (1910: 200); Johnston (1928b: 33); Förther (1998: 197). Type: Chile, Región de Atacama, Prov. Chañaral, Agua Dulce in Deserto Atacama, 26°16' [sic] lat. S, 6300 p.s.m. [1920 m], 21 Feb. 1854, *R.A. Philippi* s.n. (holotype SGO 54387 [fragm. GH, photo F, GH, MSB, NY, US]; isotype B† [photo F neg. n° 17323: F, GH, MSB, NY, US]).

*Cochranea glutinosa* (Phil.) Phil. (Philippi, 1895: 349). Type as above.

*Erect shrubs*, 0.2 – 0.8 (– 1.3) m tall, profusely branched, densely foliose to the apex, but losing most leaves during dry years. Stems and foliage glutinous. *Leaves* alternate,

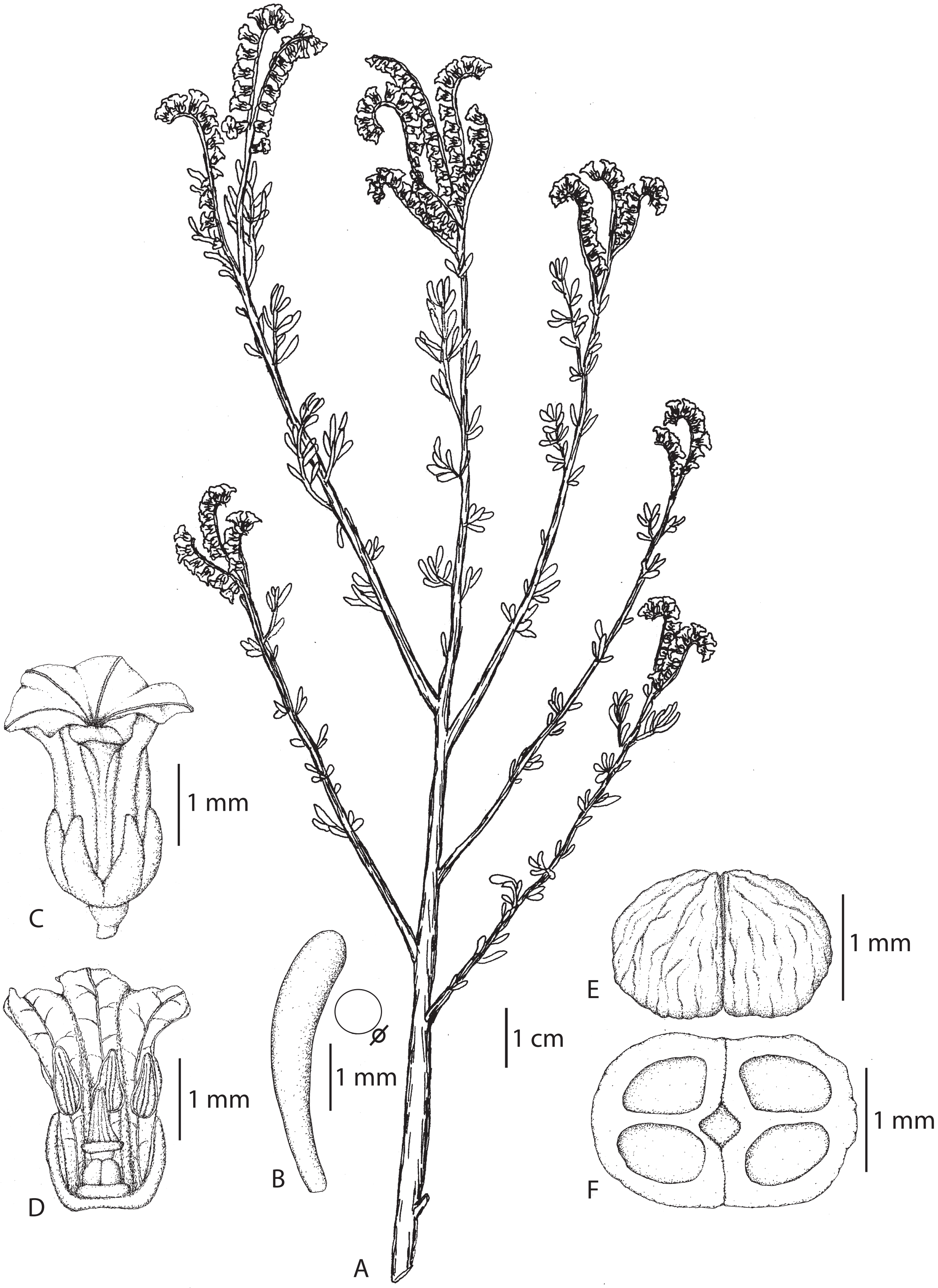

Figure 6.8: *Heliotropium jaffuelii.* A, Flowering branch; B, Leaf; C, Flower - outer view; D, Flower - inner view; E, Fruit - dorsal view; F, Fruit - transversal view. (All from *Jaffuel* 2524, G). Drawn by Anja Salchow.

Figure 6.9: Distribution of *Heliotropium jaffuelii* (●) and *H. glutinosum*(□).

solitary or grouped in fascicles of up to 9 leaves, sessile, linear-oblong, 8 – 23 × 1.5 – 6 mm; lamina glutinous with evident red glands and few simple hairs, green or greyish-green, margin sinuate, revolute, base attenuated, apex acute, with the main and secondary veins conspicuous. *Inflorescences* terminal, elongate, dichotomically branched, to ca. 4 cm long. *Flowers* sessile or shortly pedicellated, alternate, erect, aromatic. Calyx cylindric, pale green; calyx lobes linear, fused only at the base, hirsute and glandulous outside, strigose within, 1.5 – 3.5 × 0.5 – 1.5 mm, free portion 1.5 – 3.5 mm long, apex obtuse. Corolla infundibuliform, hispid outside, dull white with yellow throat; limb horizontally spreading, 4.5 – 6.5 mm wide, lobes rounded; tube as long as or shortly longer than the calyx, 3.5 – 5 mm long. Stamens included or exserted at late anthesis; filaments adnate to petals; anthers oblong, glabrous, base cordate, apex obtuse, 1 – 1.5 mm long, overlapping the stigmatic head. Ovary glabrous, subglobose, ca. 0.7 mm diam., with a basal nectar ring. Style glabrous, ca. 0.2 mm long, shorter than the stigmatic head. Stigmatic head conic, glabrous, 1 – 1.5 × 0.4 – 0.6 mm. *Fruits* dry, ellipsoid, rugose, glabrous, light brown, ca.

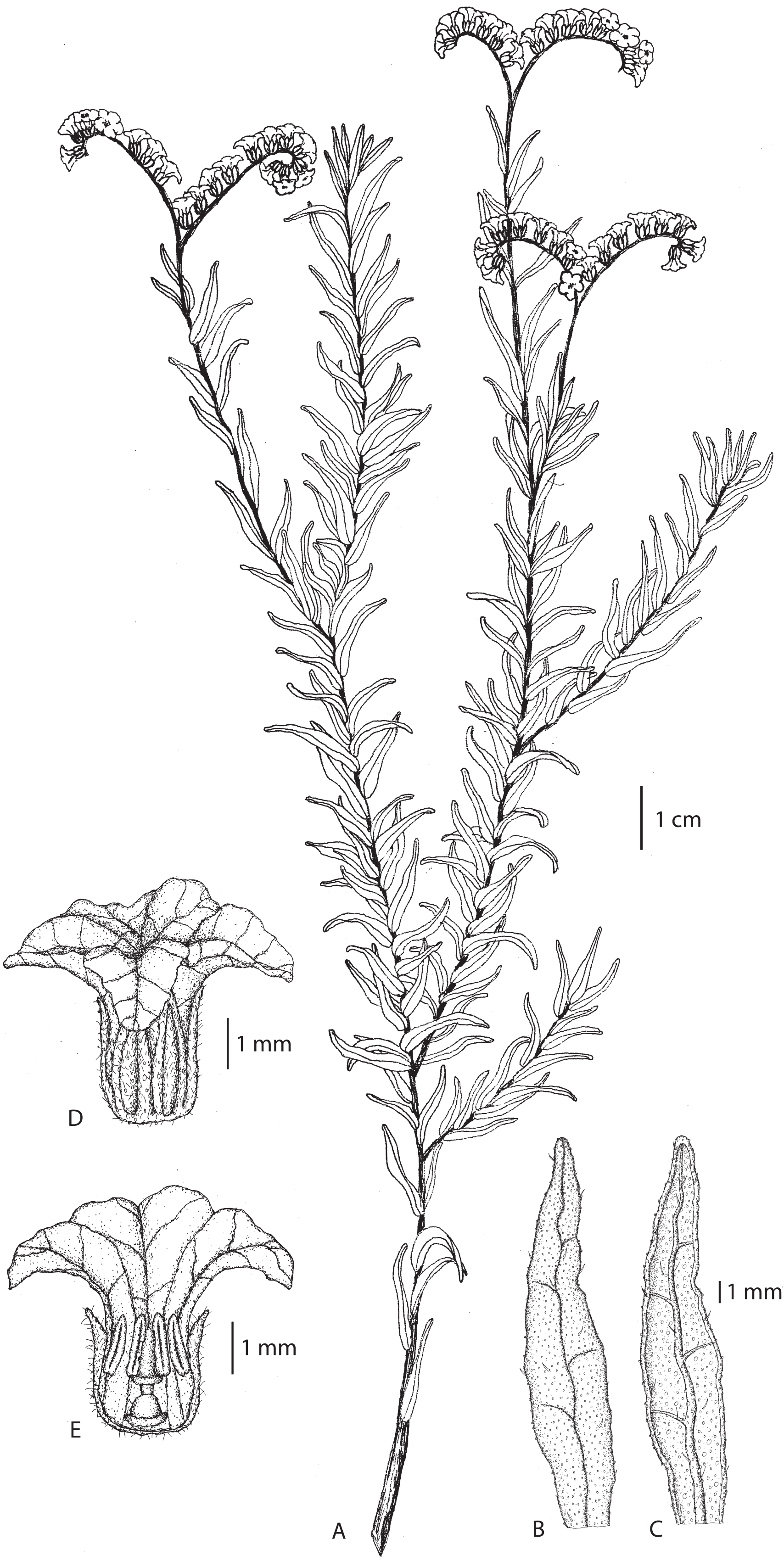

Figure 6.10: *Heliotropium glutinosum.* A, Flowering branch; B, Leaf - adaxial surface; C, Leaf - abaxial surface; D, Flower - outer view; E, Flower - inner view. (All from *Luebert & Torres* 1970, BSB). Drawn by Anja Salchow.

1.6 × 1.3 mm diam., falling apart at maturity into two 2-seeded nutlets, each ca. 1.6 × 0.8 mm diam. Fig. 6.10.

*Pollen* prolate, 18.3 – 20.2 × 9.5 – 10.8 $\mu$m (from *Luebert & Torres* 1970, BSB).

**DISTRIBUTION**. Endemic to the Andean foothills of the province of Chañaral (Región de Atacama) in Chile, 26°22' – 27°10' S (Fig. 6.9). A further north locality is cited by Johnston (1928b) from a specimen collected by *Gigoux* (GH) at Quebrada Doña Inés Chica (26°1'S), but I failed to find the material at the Harvard Herbaria or to collect the species in that area. The specimens *Johnston* 3698 and 4749 were not found at the Harvard Herbaria, but only elsewhere.

**SPECIMENS EXAMINED.** See Appendix E (p. 300).

**HABITAT**. Ravines or alluvial plains of the Andean foothills in a matrix of barren Desert, between 1195 and 2200 m. The species is locally common but not dominant. The vegetation is a Desert scrub dominated by *Atriplex* spec. (Amaranthaceae), *Nolana leptophylla* (Miers) I.M.Johnst. (Solanaceae) and *Encelia canescens* Lam. (Asteraceae).

**CONSERVATION STATUS**. Endangered (EN), after the application of both IUCN (2001) criteria of extent of the presence (B1) and area of occupancy (B2) (see Section 6.2).

**FLOWERING TIME**. Throughout the year provided sufficient moisture.

**ETYMOLOGY**. The epithet *glutinosum* refers to its resinous foliage.

**VERNACULAR NAME**. Palo negro (Spanish).

**USES**. No uses are reported in the literature, but Modak et al. (2007) indicate antoxidant activity of the resinous exudates.

**NOTES**. This species is readily distinct from the other members of sect. *Cochranea* due to the presence of conspicuous glandular trichomes on the leaf's surface, as well as its geographic distribution and elevation. Only *Heliotropium chenopodiaceum* can be rarely found at the same geographical area, but the latter species has smaller leaves and flowers and the glandular trichomes are not apparent with naked eye.

*Heliotropium glutinosum* was resolved as sister to the main polytomous group in the phylogeny of sect. *Cochranea* (Luebert and Wen, 2008). Such a sister relationship of a species from the Andean foothills was also recovered for *Nolana sessiliflora* Phil. (Dillon et al., 2007; Tu et al., 2008), which is distributed about the same geographical area of *Heliotropium glutinosum* (Dillon et al., 2009). It can be hypothesised that the species of *Heliotropium* from the coastal range had an ancestor in the Andean foothills, which has already been suggested for *Malesherbia* Ruiz & Pav. sect. *Malesherbia* (Malesherbiaceae; Gengler-Nowak, 2002b), *Nolana* L.f. (Solanaceae; Dillon et al., 2007) and *Gypothamnium* Phil. (Asteraceae; Luebert et al., 2009).

Toro and Moldenke (1979) indicate that *Heliotropium glutinosum* (erroneosuly cited as *H. stenophyllum*) is pollinated by two Colletidae species: *Chilicola deserticola* Toro & Moldenke, 1979 and *C. erithropoda* Toro & Moldenke, 1979.

**5. Heliotropium sinuatum** (*Miers*) *I.M.Johnst.* (Johnston, 1928b: 26); Förther (1998: 219). Type: Chile, 'Coquimbo', *T. Bridges* s.n. (lectotype BM [photo GH], selected by Johnston (1928b: 27); possible duplicates BM, P not seen [digital photograph!]).

*Cochranea sinuata* Miers (1868: 127); Philippi (1895: 342). Type as above.

*Heliophytum floridum* A.DC. var. *bridgesii* A.DC. (de Candolle, 1845: 553). Type: Chile, 'in prov. Coquimbo' [dry valleys and hills between Huasco and Copaipó], [Sept. 1841], *T. Bridges* 1342 (holotype G-DC [photo SGO 11770, photo F neg. n° 27073: F, GH, US]; isotypes BM, E not seen [digital photograph!], G, K [photo SGO 2255], P not seen [digital photograph!, photo MSB], W not seen).

*Heliotropium floridum* (A.DC.) Clos var. *bridgesii* (A.DC.) Clos, in Gay (1849: 457). Type as for *Heliophytum floridum* var. *bridgesii*.

*Cochranea conferta* Miers var. *auriculata* Miers (1868: 126). Type: N. Chile, *W. Lobb* 442 (holotype K; isotype BM).

*Heliotropium rosmarinifolium* Phil. (Philippi, 1873: 514). Type: Chile, Región de Atacama, Prov. Huasco, Huasco, Oct. 1866, *R.A. Philippi* s.n. (holotype SGO 42229 [fragm. GH, photo F, GH, MSB, NY, US]; isotype B† [photo F neg. n° 27072: F, GH, US]).

*Cochranea rosmarinifolia* (Phil.) Phil. (Philippi, 1895: 349). Type as for *Heliotropium rosmarinifolium*.

*Heliotropium izagae* Phil. (Philippi, 1895: 355). Type: Chile, Región de Atacama, Prov. Huasco, Chañarcito prope Carrizal, Sept. 1885, *F. Philippi* s.n. (lectotype SGO 42231 [photo F, GH, MSB, NY, US], selected by Förther (1998: 201); duplicates B† [photo F neg. n° 17344: F, NY, US], BM, GH [fragm.], SGO 54378 [photo MSB]; possible duplicates K [photo SGO 2257], WU not seen [photo MSB]).

*Erect shrubs*, 0.5 – 1.5 (– 2.6) m tall, profusely branched, densely foliose to the apex. Stems and foliage strongly glutinous. *Leaves* alternate, solitary or grouped in fascicles of up to 25 leaves, sessile, linear-oblong to lnear spathulate, 9 – 65 × 1 – 7 mm; lamina glutinous, sparsely strigose, dark-green or dark brownish-green, margin sinuate, revolute, base attenuated, apex acute, with the main and secondary veins conspicuous. *Inflorescences* terminal, elongate, dichotomically branched, to ca. 5 cm long. *Flowers* sessile or shortly pedicellated (pedicel up to 2 mm), alternate, erect, aromatic. Calyx cylindric, pale green; calyx lobes linear, fused only at the base or free, hirsute and glandulous outside, sparsely strigose within, 2 – 4.5 × 0.5 – 0.7 mm, free portion 0.5 – 3.5 mm long, apex obtuse. Corolla infundibuliform, hispid outside, white with yellow throat; limb horizontally spreading, 5 – 10 mm wide, lobes rounded; tube longer than the calyx, 3.5 – 8.5 mm long. Stamens included or exserted at late anthesis; filaments adnate to petals; anthers oblong, glabrous, base cordate, apex obtuse, ca. 1 mm long, overlapping the stigmatic head. Ovary glabrous, subglobose, ca. 0.5 mm diam., with a basal nectar ring. Style glabrous, ca. 1 mm long, as long as or slightly shorter than the stigmatic head. Stigmatic head conic, glabrous, ca. 0.8 - 1 × 0.4 – 0.6 mm. *Fruits* dry, ellipsoid, rugose, light orange brown or cream, ca. 2,5 × 1.5 mm diam., falling apart at maturity into two 2-seeded nutlets, each ca. 1.2 × 2 mm diam.

*Pollen* prolate, 24.5 – 27.5 × 14.5 – 16.5 $\mu$m. Endoapertures ca. 3.5 $\mu$m diam. in polar direction and contracted at the centre. Exine thickness ca. 1 $\mu$m, slightly thicker at the poles (from *Ricardi & Marticorena* 3882 in Marticorena, 1968).

**DISTRIBUTION**. Coast and interior of the north of the province of Elqui (Región de Coquimbo) and provinces of Huasco and Copiapó (Región de Atacama), Chile, 27°40' – 29°39' S, (Fig. 6.11). The assertion of Johnston (1928b: 34) that there are no reliable records of the species in the province of Coquimbo, where the plant occurs in sympatry with what Johnston (1928b) called *Heliotropium huascoense*, is certainly not valid any longer. The locality in *Zöllner* 4472 from the province of Arica is certainly erroneously given.

**SPECIMENS EXAMINED**. See Appendix E (p. 300).

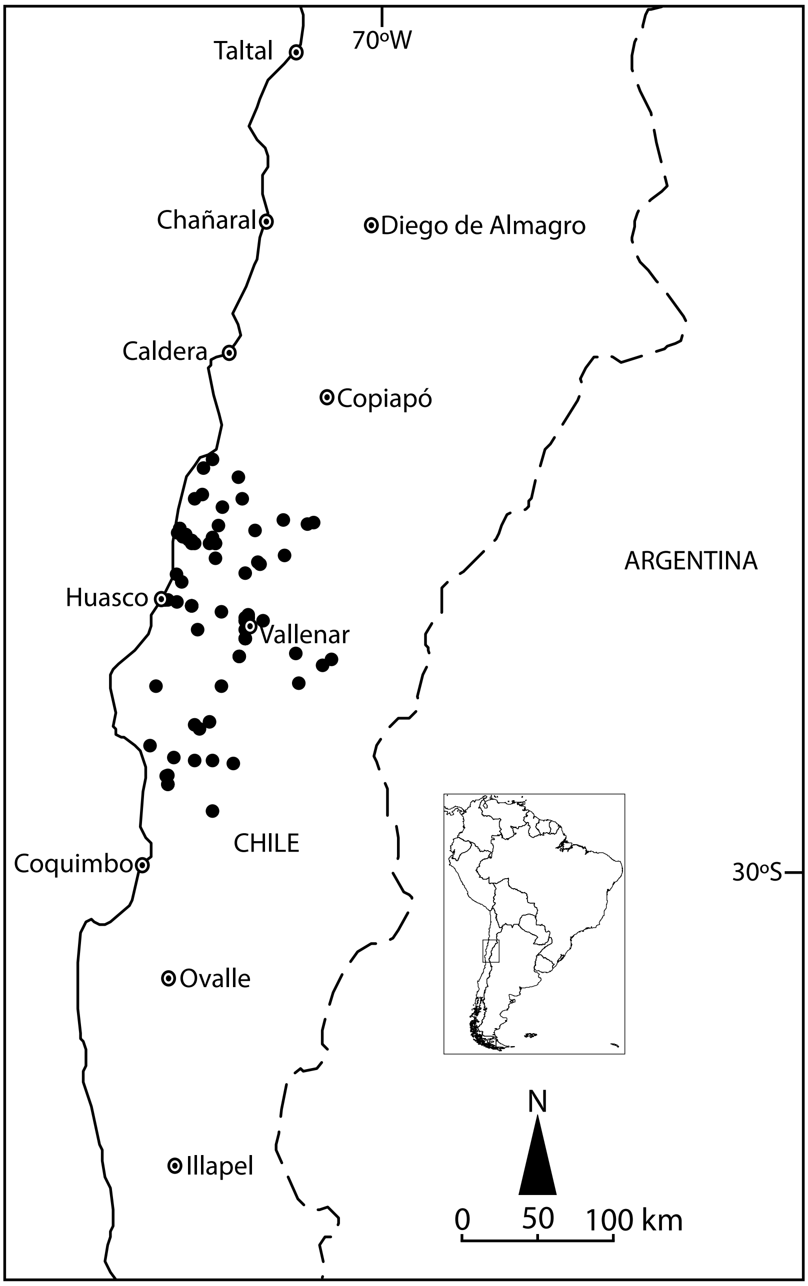

Figure 6.11: Distribution of *Heliotropium sinuatum*.

**HABITAT**. Coastal ravines and rocky hillsides, between the sea level and 1500 m, where it can be dominant in desert scrubs together with *Adesmia argentea* Gill. ex Hook., *Balbisia peduncularis*, *Frankenia chilensis* C.Presl, *Nolana albescens* (Phil.) I.M.Johnst., *Oxalis virgosa*, *Pleocarphus revolutus* D.Don, among others. The species can occur in local sympatry with *Heliotropium filifolium*, *H. floridum*, *H. longistylum*, *H. megalanthum* and *H. stenophyllum*.

**CONSERVATION STATUS**. Least concern (LC), criterion B2(c), see Chapter 5.

**FLOWERING TIME**. September to November, but throughout the year provided sufficient moisture.

**ETYMOLOGY**. The epithet *sinuatum* refers to its sinuate leaves.

**VERNACULAR NAME**. Palo negro, monte negro (Spanish).

**USES**. Chemical compounds of the resinous exudates of *Heliotropium sinuatum* have shown to have antibacterial (Modak et al., 2004b), as well as antioxidant (Modak et al., 2003) properties. Riedemann et al. (2006) suggest its potential use as ornamental.

**NOTES**. This species is unique in *Heliotropium* sect. *Cochranea*, for its strongly rugose, sinuate, leaves, with non forked secondary veins and its geographical distribution, where no other species of the section with rugose leaves occur. However, Reiche (1907a, 1910) considered it in a broader sense under the name *Heliotropium rugosum* Phil., a synonym of *H. taltalense*. *Heliotropium taltalense* was distinguished from the present species by subsequent authors (Johnston, 1928b; Förther, 1998; Luebert and Pinto, 2004), which is the criterion followed here. Apart from its geographical distribution, *Heliotropium sinuatum* is clearly distinguished from *H. taltalense* in that the latter has forked secondary veins and more pubescent leaves. Both are resinous, erect, shrubs with sinuate and rugose levaes.

Förther (1998) indicated that no lectotype had been selected, but he probably overlooked Johnston (1928b). The type specimen of *Cochranea sinuata* (*Bridges* s.n.) and that of *Heliophytum floridum* var. *bridgesii* (*Bridges* 1342) probably come from the same collection, as they are morphologically very similar. While there is no evidence that Bridges collected more than six specimens of *Heliotropium* in northern Chile, Johnston (1928a) pointed out that part of Bridges materials, while corresponding to his numbered collections, may have been distributed without numbers, causing the impression that they are different gatherings. The type material at BM (*Bridges* s.n.) has several small envelopes, one of which is annotated as '*Bridges* 1342'. That would confirm the assertion of Johnston (1928a) and the identity between the types of *Cochranea sinuata* and *Heliophytum floridum* var. *bridgesii*.

The F negative n° 27072 (*H. rosmarinifolium*) was distributed under the heading 'Types of the Delessert Herbarium' (G); Förther (1998) cites it as from B, Johnston (1928b) refers to an isotype of *H. rosmarinifolium* at B, and no isotype of *H. rosmarinifolium* is to be found at G. One specimen at K labelled as *H. rosmarinifolium* (photo SGO 2258) was collected in Vallenar, probably by F. Philippi in 1885 and is therefore not a type.

In the protologue of *Heliotropium izagae* Philippi (1895) indicated that the plant comes from Carrizal Bajo, which was followed by Johnston (1928b), Muñoz (1960) and Förther (1998). The specimens from that locality at SGO (42230 and 54376) were, however, determined by Philippi as *Heliotropium rosmarinifolium*. The type material of *Heliotropium izagae* comes from Chañarcito, and the specimens that serve as type of this name are coincident with the description of Philippi (1895) and with other materials collected in that area. All them have larger and less sinuate and rugose leaves than the type of *Heliotropium rosmarinifolium*, intermixed with smaller and more rugose and sinuate leaves that make it possible to include the name in the synonymy of the present species. The locality given in the protologue of *Heliotropium izagae* (Philippi, 1895) is thus probably erroneous.

**6. Heliotropium taltalense** (*Phil.*) *I.M.Johnst.* (Johnston, 1928b: 27); Marticorena (1968: 47); Förther (1998: 223). Type: Chile, Región de Antofagasta, Prov. Antofagasta, prope Taltal, Oct. 1889, *L. Darapsky* 30 (holotype SGO 54432 [fragm. GH, photo F, GH, MSB, NY]).

*Cochranea taltalensis* Phil. (Philippi, 1895: 349). Type as above.

*Heliotropium rugosum* Phil. (Philippi, 1860a: 38), **nom. illegit.**, non M.Martens & Galeotti (1844: 336); Reiche (1907a: 239); Reiche (1910: 197). Type: Chile, Región de Antofagasta, Prov. Antofagasta, Paposo, Dec. 1853, *R.A. Philippi* s.n. (holotype SGO 54381 [fragm. GH, photo F, GH, MSB, NY]; isotypes B† [photo F neg. n° 17347: F, GH, NY, US], W not seen [photo F neg. n° 31913: F, GH]).

*Cochranea rugosa* (Phil.) Phil. (Philippi, 1895: 351). Type as for *Heliotropium rugosum*.

*Erect shrubs*, 0.65 – 1.0 (– 1.8) m tall, profusely branched, densely foliose to the apex. Stems and foliage glutinous. *Leaves* alternate, solitary or grouped in fascicles of up to 20 leaves, sessile, linear-oblong to linear-lanceolate, 12 – 45 (– 50) × 1 – 5.5 mm; lamina glutinous, pubescent on both sides, sparsely strigose on the adaxial surface, tomentose on the abaxial surface, dark-green or dark greyish-green, margin sinuate, revolute, base attenuated, apex obtuse, with the main and secondary veins conspicuous, the later forked toward the margin. *Inflorescences* terminal, elongate, dichotomically branched, to ca. 8 cm long. *Flowers* sessile or shortly pedicellated, alternate, erect, aromatic. Calyx cylindric, pale green; calyx lobes linear, free or fused only at the base, villous outside, glabrous or sparsely hirsute within, 2 – 5 × 0.5 – 1 mm, free portion 1.5 – 5 mm long, apex acute. Corolla infundibuliform, hispid outside, dull white with yellow throat; limb horizontally spreading, 3.5 – 7 mm wide, lobes rounded; tube longer than the calyx, 3.5 – 7.5 mm long. Stamens included or exserted at late anthesis; filaments adnate to petals; anthers linear-lanceolate, glabrous, base cordate, apex acute, 1.5 – 2 mm long, overlapping the stigmatic head. Ovary glabrous, subglobose, ca. 0.7 mm diam., with a basal nectar ring. Style glabrous, 0.5 – 1.8 mm long, as long as or shorter than the stigmatic head. Stigmatic head conic, glabrous, 1 – 1.8 × 0.5 – 0.7 mm. *Fruits* dry, ellipsoid, rugose, glabrous, light brown, ca. 1.5 – 3.5 × 1 – 2 mm diam., falling apart at maturity into two 2-seeded nutlets, each ca. 1 – 2 × 1 – 2 mm diam. Fig. 6.12.

*Pollen* prolate, 29.5 – 31 × 18 – 18.5 $\mu$m. Endoapertures 3 × 5 $\mu$m diam., contracted at the centre. Exine thickness ca. 1.3 $\mu$m, slightly thicker at the poles (from *Ricardi* 2614 in Marticorena, 1968).

**DISTRIBUTION**. Coastal hills of the province of Antofagasta (Región de Antofagasta), Chile, most common between the localities of Miguel Díaz and Taltal, 24°30' – 25°29'S (Fig. 6.13).

**SPECIMENS EXAMINED**. See Appendix E (p. 302).

**HABITAT**. Dry hillsides of the coastal Cordillera, usually outside the fog zone (Johnston, 1929a), generally above it, between 50 and 1060 m. It forms part of the coastal desert scrub (Luebert and Pliscoff, 2006), where it is usually rare, but it can be locally dominant in the vegetation (Reiche, 1911), along with *Balbisia peduncularis* (Ledocarpaceae), *Copiapoa tenebrosa* F.Ritter (Cactaceae), *Euphorbia lactiflua* Phil. (Euphorbiaceae), *Nolana divaricata* I.M.Johnst., *Nolana incana* I.M.Johnst. (both Solanaceae), *Ophryosporus triangularis* Meyen (Asteraceae), *Tetragonia maritima* (Aizoaceae), among others.

**CONSERVATION STATUS**. Vulnerable (VU), criterion B2(c), see Chapter 5.

**FLOWERING TIME**. September to November.

**ETYMOLOGY**. Th epithet *taltalense* refers to Taltal, the type locality.

**VERNACULAR NAME**. Palo negro, monte negro (Spanish).

**USES**. Recently Modak et al. (2009a) reported antoxidant activity of the resinous exudate. It is locally used (Matancilla) as infusion against stomachache. Riedemann et al. (2006) suggest its potential use as ornamental.

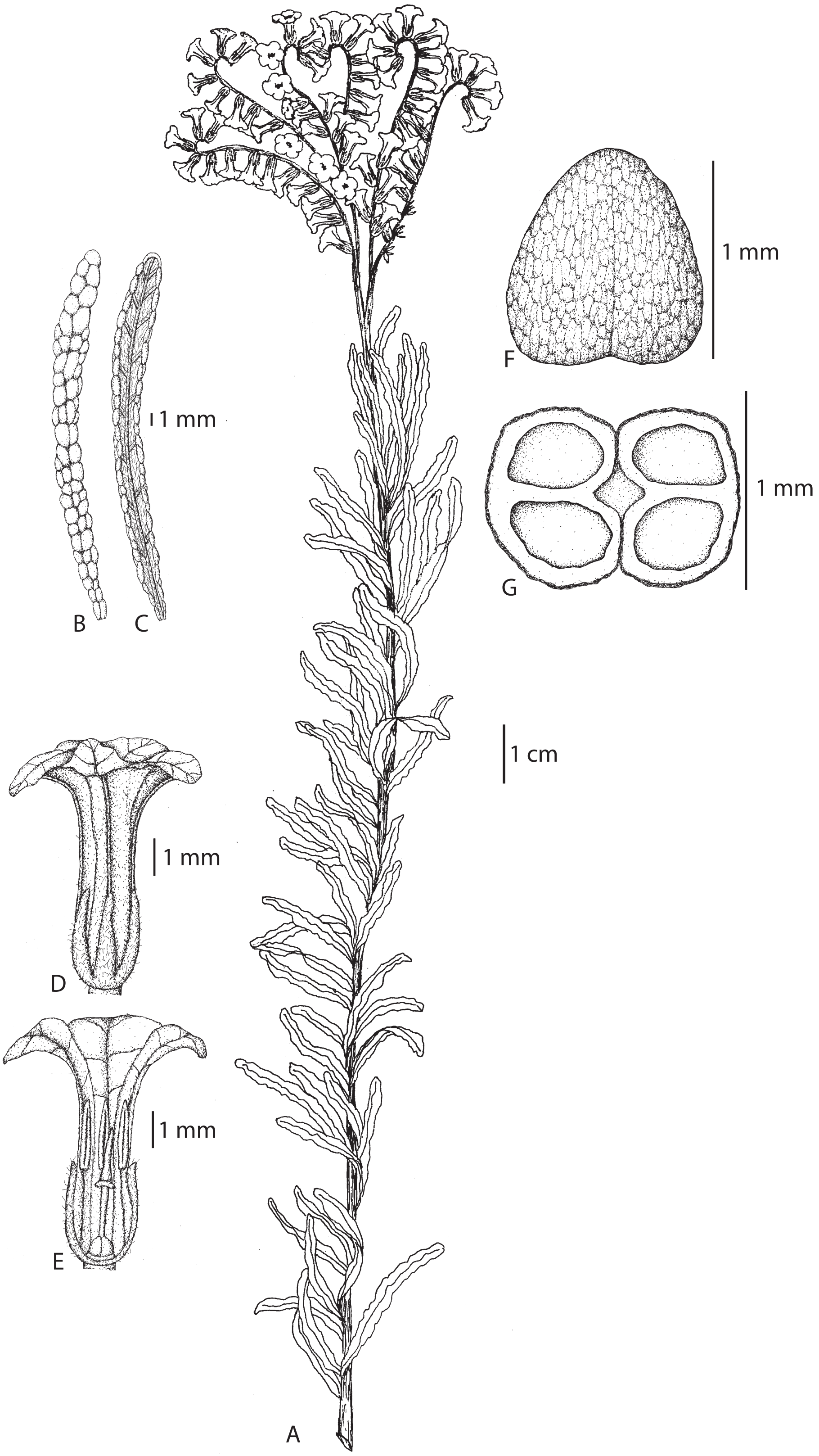

Figure 6.12: *Heliotropium taltalense.* A, Flowering branch; B, Leaf - adaxial surface; C, Leaf - abaxial surface; D, Flower - outer view; E, Flower - inner view; F, Fruit - dorsal view; G, Fruit - transversal view. (All from *Luebert et al.* 2083, BSB). Drawn by Anja Salchow.

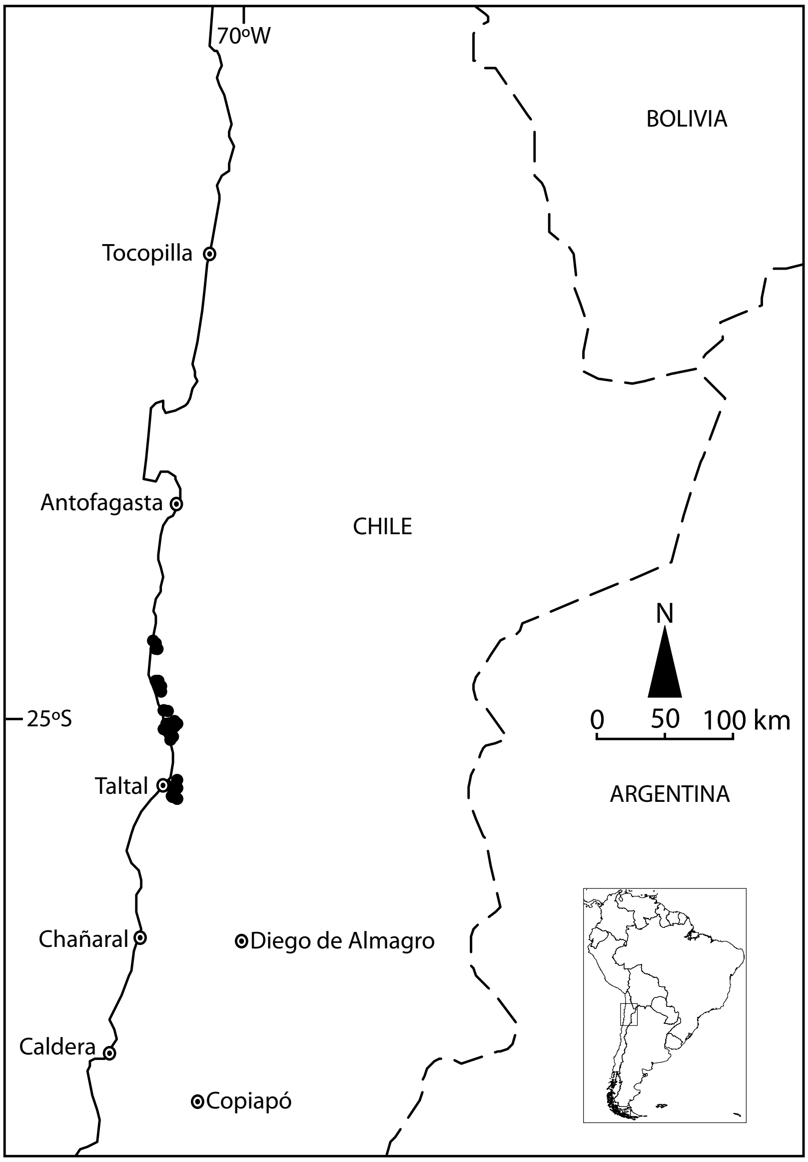

Figure 6.13: Distribution of *Heliotropium taltalense*.

**NOTES**. This species is a distinct inhabitant of the coastal hills of the areas around Taltal and Paposo. According to Johnston (1928b), *Heliotropium krauseanum* could be considered a variety of the present species, but they differ in flower size and indument and have different geographic ranges. Phylogenetic analyses (Luebert and Wen, 2008; Chapter 2) resolve *H. taltalense* and *H. krauseanum* in different grades. On the other hand, Reiche (1907a, 1910) considered *Heliotropium sinuatum* as falling into the variability of *H. taltalense* (treated as *H. rugosum* Phil.). Although the latter two species are phylogentically closely related (Luebert and Wen, 2008; Chapter 2), I concur with Johnston (1928b) in treating them apart (Luebert and Pinto, 2004; see discussion under *Heliotropium sinuatum*).

In the protologue of *Heliotropium rugosum* (Philippi, 1860a), two localities are mentioned, Hueso Parado and Paposo. Although the species certainly occurs in both localities, no material collected by R.A. Philippi in the former one has been found in SGO nor in any other herbarium, and Muñoz (1960) cites only one specimen (SGO 54381), which is considered the holotype, in accordance with Förther (1998). The photo F neg. n° 17347 (ex B) of *Heliotropium rugosum* at US has an annotation of I.M. Johnston 'not a type', which is certainly erroneous. Förther (1998) cites a possible isotype of *Heliotropium rugsum* at BM as well as a photo F neg. n° 31913 (ex W) at US, which are not to be found there.

**7. Heliotropium krauseanum** *Fedde* (1906: 72) subsp. **krauseanum**; Johnston (1928b: 28); Macbride (1960: 561); Ferreyra (1961: 111); Brako and Zarucchi (1993: 220); Förther (1998: 202); Galán de Mera et al. (2003: 331); Weigend et al. (2003); Luebert and Pinto (2004). Type: Peru, Depto. Arequipa, prope Mollendo, in saxosis, 50 – 100 m, Oct., A. Weberbauer 1552 (holotype B† [photo F neg. n° 17327: F, GH, NY, US]; isotype GH not seen). Replacement name for *Heliotropium saxatile*.

*Heliotropium saxatile* K.Krause (1906: 633), **nom. illegit.**, non Brandegee (1905: 218). Type as above.

*Erect shrubs*, 0.5 – 1.5 m tall, profusely branched, densely foliose to the apex. Stems and foliage glutinous. *Leaves* alternate, solitary or grouped in fascicles of up to 17 leaves, sessile, linear-oblanceolate to oblong, 10 – 55 (– 60) × 1.2 – 9 (– 10.5) mm; lamina glutinous, pubescent on both sides, sparsely strigose on the adaxial surface, tomentose on the abaxial surface, dark-green or dark greyish-green, margin sinuate, revolute, base attenuated, apex obtuse, with the main and secondary veins conspicuous, the later forked toward the margin. *Inflorescences* terminal, elongate, dichotomically branched, to ca. 5 cm long. *Flowers* sessile or shortly pedicellated, alternate, erect, aromatic. Calyx cylindric, pale green; calyx lobes linear, free or fused only at the base, sparsely hirsute outside, glabrous or sparsely hirsute within, 1.5 – 3 × 0.3 – 1 mm, free portion 1.5 – 3 mm long, apex acute. Corolla infundibuliform, hispid outside, dull white with yellow throat; limb horizontally spreading, 2.5 – 5 mm wide, lobes rounded; tube longer than the calyx, 2.5 – 4.5 (– 6) mm long. Stamens included or exserted at late anthesis; filaments adnate to petals; anthers linear-lanceolate, glabrous, base cordate, apex acute, 1 – 1.5 mm long, overlapping the stigmatic head or above it. Ovary glabrous, subglobose, ca. 0.5 mm diam., with a basal nectar ring. Style glabrous, 0.5 – 0.9 mm long, longer than the stigmatic head. Stigmatic head conic, bilobate and sometimes papillose at the apex, 0.3 – 0.7 × 0.3 – 0.7 mm. *Fruits* dry, ellipsoid, rugose, glabrous, light brown, ca. 0.5 – 1 × 0.9 – 1.2 mm diam., falling apart at maturity into two 2-seeded nutlets, each ca. 0.7 × 1 mm diam. Fig. 6.14.

**DISTRIBUTION**. Coastal range of the Departments of Tacna, Moquegua and Arequipa in southern Peru (Johnston, 1928b; Macbride, 1960; Ferreyra, 1961; Galán de Mera et al., 2003; Weigend et al., 2003). Two outliers have recently been found in the Andean foothills of the province of Yauyos, Department of Lima, Peru (Weigend et al., 2003) and in the coast of the province of Tamarugal, Región de Tarapcá, Chile (Luebert and Pinto, 2004). Between 12°37' and 19°37'S. This is the only species of section *Cochranea* that ranges into Peru (Fig. 6.15).

**SPECIMENS EXAMINED**. See Appendix E (p. 303).

**HABITAT**. Foggy coastal lomas formations, usually on sandy and rocky slopes (Ferreyra, 1961; Weigend et al., 2003; Luebert and Pinto, 2004), 0 – 780 (– 1734) m. The populations of the province of Yauyos in the Department of Lima from part of the vegetation dominated by cacti in the dry Andean valleys, above 1200 m (Weigend et al., 2003).

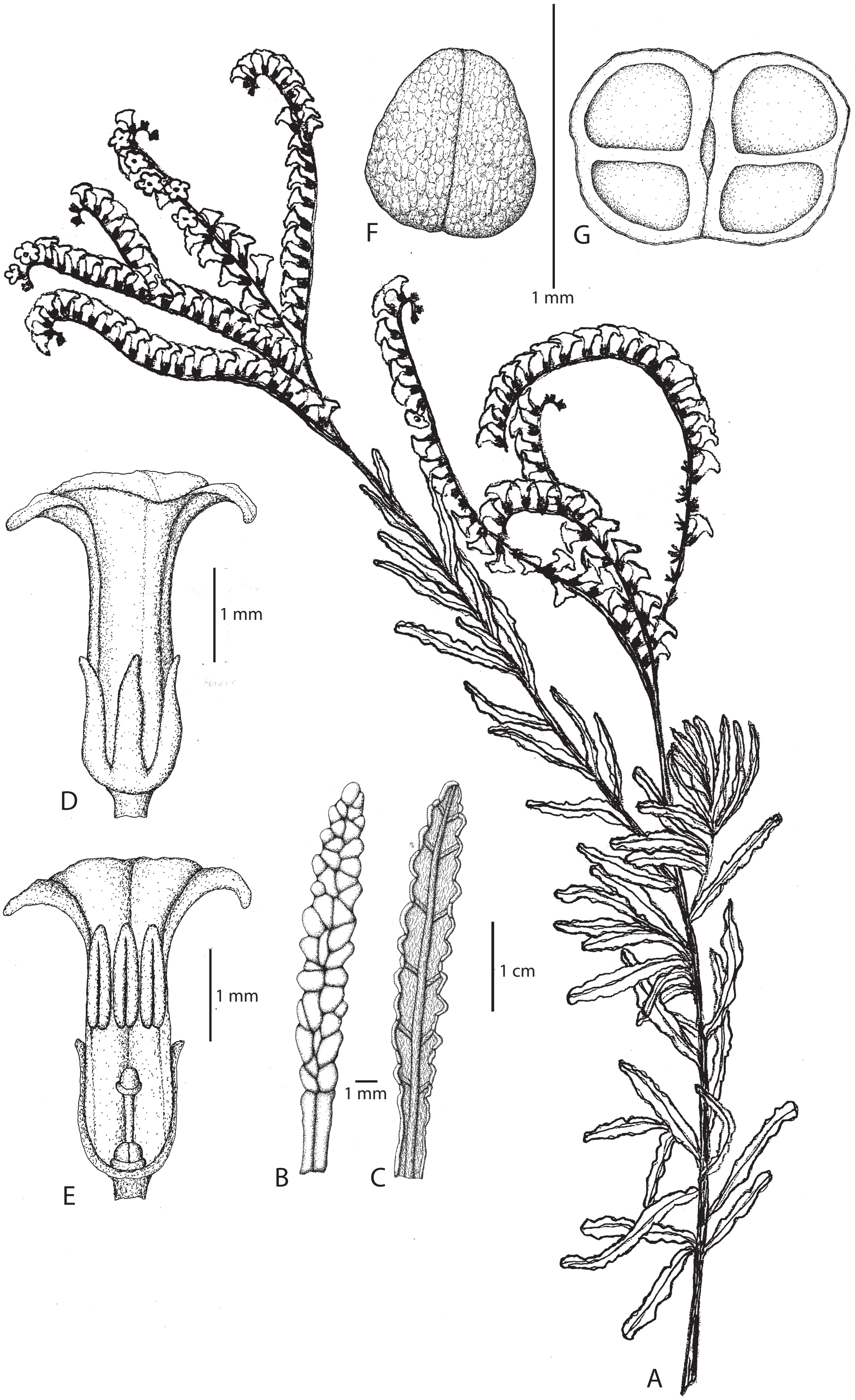

Figure 6.14: *Heliotropium krauseanum.* A, Flowering branch; B, Leaf - adaxial surface; C, Leaf - abaxial surface; D, Flower - outer view; E, Flower - inner view; F, Fruit - dorsal view; G, Fruit - transversal view. (All from *Dostert & Cáceres* 1025, BSB). Drawn by Anja Salchow.

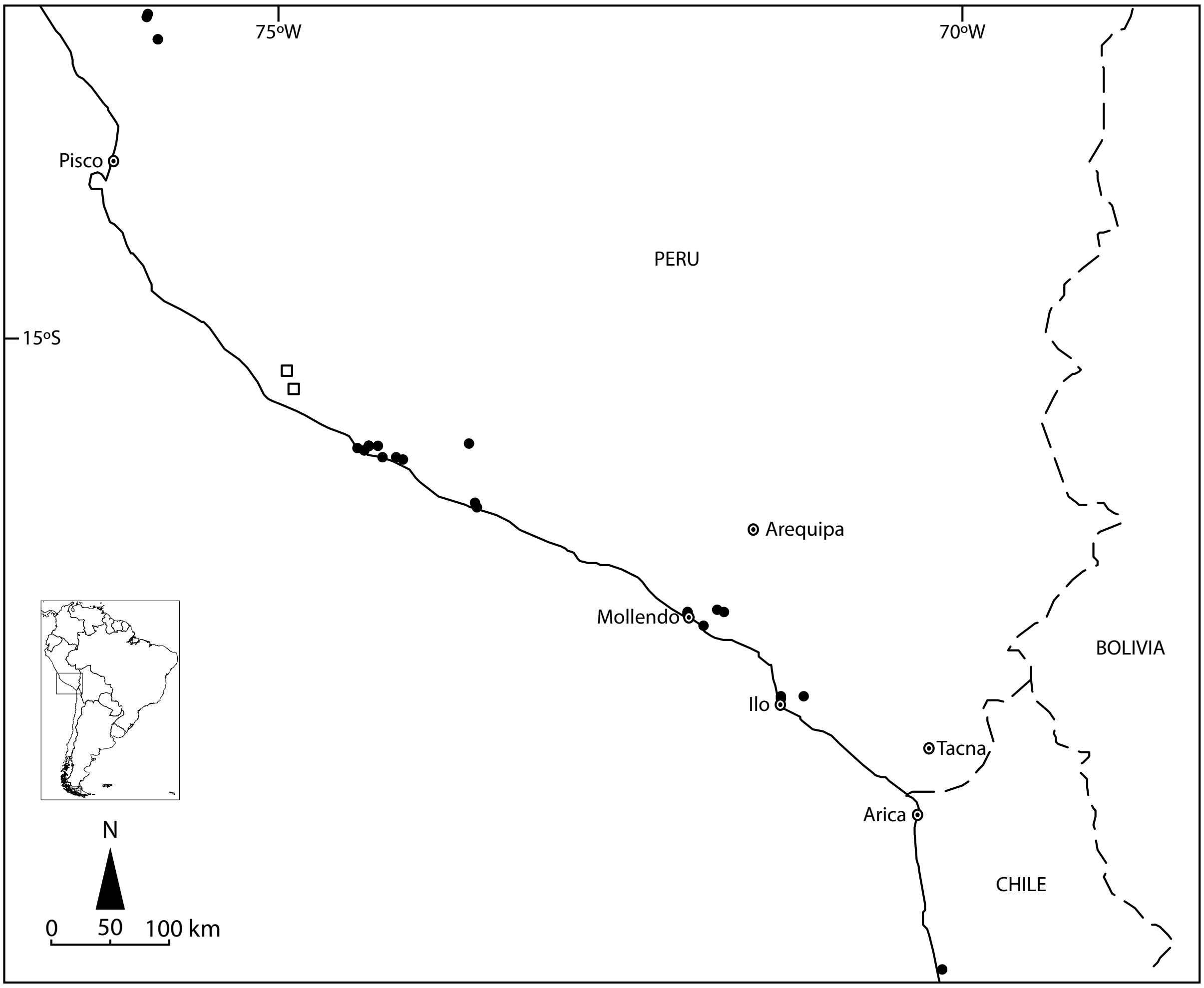

Figure 6.15: Distribution of *Heliotropium krauseanum* subsp. *krauseanum* (●) and *H. krauseanum* subsp. *jahuay* (□).

**CONSERVATION STATUS**. Least concern (LC), criterion B2(c), see Chapter 5.
**FLOWERING TIME**. Throughout the year provided sufficient moisture.
**ETYMOLOGY**. The name was dedicated to Kurt Krause, who described the species first time.
**NOTES**. In his description of *Heliotropium saxatile*, Krause (1906) associated this species with *H. lanceolatum* Ruiz & Pav. (Ruiz and Pavón, 1799) from the section *Heliothamnus*. Johnston (1928b), however, placed the former species in section *Cochranea*, which was followed by subsequent authors (Macbride, 1960; Förther, 1998; Weigend et al., 2003; Luebert and Pinto, 2004) based on morphology. Molecular phylogenetc analyses (Luebert and Wen, 2008; Luebert et al., in press; see Chapers 2 and 3) have shown that *H. krauseanum* is a member of section *Cochranea* and is only distantly related to section *Heliothamnus*.

The material *Cuming* 955 cited here as ‘indefinite’ has been referred to as from Chile (Cobija, Iquiqui [sic] et Arica) or Peru (Lima) (see Johnston, 1928b: 28). The former corresponds to the printed labels of Bentham, while the latter to the Hooker herbarium, whose label seems to have the Cuming’s handwriting (N. Hind, personal communication). In the original list of Cuming’s material examined at K (Plant Lists vol. 33), Nr. 955 appears under the heading ‘Peru’ and it is therefore not possible to ascertain whether the material comes from northern Chile or the Department of Lima, Peru, moreover when the species has recently been found in both areas (Weigend et al., 2003; Luebert and Pinto, 2004). It is also possible that Cuming gathered the plant somewhere in southern Peru, where it is very common and he certainly collected (Dance, 1980). The date (1831) corresponds to the arrival of the material in London.

**7a. Heliotropium krauseanum** *Fedde* subsp. **jahuay** *Luebert*, **subsp. nov.** *a subspecie krauseanum differt foliis supra dense pubescentibus, nervis secundariis non furcatis.* Typus: Peru. Depto. Arequipa, Prov. Caravelí, Lomas de Jahuay, ca. 52 km S Nazca, near border with Depto. Ica [15°22'S, 74°54'W], 365 - 380 m, 1 Nov. 1983, *M.O. Dillon & D. Dillon* 3766 (holotypus F; isotypus MSB).

This subspecies is superficially similar to the subspecies *krauseanum*, and it is undoubtlessly conspecific with it, but it differs from the the subspecies *krauseanum* in its densely pubescent adaxial leaf surface and in the secondary nerves not forked. Conversely the subspecies *krauseanum* has the adaxial leaf surface only sparsely strigose (Weigend et al., 2003) and the secondary veins are clearly forked.

**DISTRIBUTION**. Endemic to the vicinity of Lomas de Jahuay (15°22'S, 74°54'W), in the north of the province of Caravelí, Depto. Arequipa, Peru (Fig. 6.15).
**SPECIMENS EXAMINED**. See Appendix E (p. 303).
**HABITAT**. Lomas formations, between 300 and 500 m.
**CONSERVATION STATUS**. Conservation status of this subspecies has not been evaluated yet, but due to its restricted geographic range in may be tentatively classified as endangered (EN).
**ETYMOLOGY**. The name refers to the type locality.
**NOTES**. On the label of the paratype specimen *Sandeman* 4019, there is an annotation of I.M. Johnston 'sp. inet.'. Because of the collection date (1943), this annotation was made after Johnston published his revision of South American *Heliotropium* (Johnston, 1928b) and was therefore not included in his tratment. Furthermore, all collections so far revised are posterior to the Johnston's revision. Had Johnston seen material before he published his treatment in 1928, it may be that he would have recognised this taxa,.

This seems to be a case of peripatric incomplete speciation (Losos and Glor, 2003), since the only localities from where this subspecies is reported are peripheral to the core of the distribution of *Heliotropium krauseanum* along the coast of southern Peru (Fig. 6.15).

**8. Heliotropium inconspicuum** *Reiche* (1907a: 245); Reiche (1910: 203); Johnston (1928b: 28); Marticorena (1968: 44); Förther (1998: 200). Type: Chile, Región de Antofagasta, Prov. Antofagasta, Breas in deserto Atacama, 1888, *A. Larrañaga* s.n. (holotype SGO 54431 [fragm. GH, photo F, GH, MSB, NY, US]). Replacement name for *Cochranea parviflora.*

*Cochranea parviflora* Phil. (Philippi, 1895: 350), non *Heliotropium parviflorum* L. (Linnaeus, 1771: 201). Type as above.

*Erect shrubs*, 0.3 – 1 m tall, profusely branched, densely foliose to the apex. Stems and foliage glutinous. *Leaves* alternate, solitary or grouped in fascicles of up to 11 leaves, sessile or with short petiole, linear-oblanceolate to linear-spathulate, 4 – 10 × 0.7 – 2 mm; lamina glutinous, pubescent on both sides, sparsely strigose on the adaxial surface, white-tomentose on the abaxial surface, dark-green or dark greyish-green, with two white bands on the abaxial surface when dried, margin entire, revolute, base attenuated, apex obtuse, with only the main vein conspicuous. *Inflorescences* terminal, elongate, dichotomically branched, to ca. 5 cm long. *Flowers* sessile, alternate, erect. Calyx cylindric, green; calyx lobes linear, glutinous, free or fused only at the base, sparsely strigose outside, glabrous within, 1 – 2 × 0.3 – 1 mm, free portion 0.8 – 2 mm long, apex acute. Corolla infundibuliform, hispid outside, dull white with yellow throat; limb horizontally spreading, 3 – 4 mm wide, lobes rounded; tube longer than the calyx, 2.5 – 4.5 mm long. Stamens included; filaments adnate to petals; anthers linear-lanceolate, glabrous, base cordate, apex acute, ca. 1 mm long, overlapping the stigmatic head or above it. Ovary glabrous, subglobose, ca. 0.5 mm diam., with a basal nectar ring. Style glabrous, ca. 0.7 – 0.8 mm long, equal to or slightly longer than the stigmatic head. Stigmatic head conic, bilobate, ca. 0.7 × 0.7 mm. *Fruits* dry, ellipsoid, rugose, glabrous, light brown, ca. 2.5 – 3 × 4.5 mm diam., falling apart at maturity into two 2-seeded nutlets, each ca. 3 × 3 mm diam.

*Pollen* prolate, 28 – 30.5 × 15.5 – 18 $\mu$m. Amb lobes not deep. Endoapertures ca. 3.5 $\mu$m diam., circular. Exine thickness ca. 1 $\mu$m at the equator and ca. 1.3 $\mu$m at the poles (from *Ricardi* 3122 in Marticorena, 1968).

**DISTRIBUTION**. Coastal hills of the provinces of Antofagasta (Región de Antofagasta) and Chañaral (Región de Atacama), Chile, between 25°5'S and 26°8'S (Fig. 6.16).
**SPECIMENS EXAMINED**. See Appendix E (p. 304).
**HABITAT**. Gravelly hillsides of the coastal Atacama Desert, 100 – 780 m, where is usually scarce or rarely locally abundant. It forms part of the coastal scrub in the fog zone, where the dominant species are *Eulychnia iquiquensis* (Cactaceae), *Euphorbia lactiflua* (Euphorbiaceae), *Balbisia peduncularis* (Ledocarpaceae), *Nolana ramosissima* I.M. Johnst. (Solanaceae), *Oxalis gigantea* Barnéoud (Oxalidaceae), among others.
**CONSERVATION STATUS**. Vulnerable (VU), criterion B2(c), see Chapter 5.
**FLOWERING TIME**. September to November.
**USES**. The presence of saponin in the leaves of *Heliotropium inconspicuum* (Ricardi et al., 1958) may give a pharmacological potential to this species.
**NOTES**. This species is easily recognizable on herbarium specimens by its two white bands on the the abaxial leaf surface after drying (Johnston, 1928b), which are not developed by any other species of section *Cochranea*. However it is frequently confounded in herbaria, even with the very different species *Heliotropium philippianum* and *H. taltalense*. Although these two species have a similar geographic range to *H. inconspicuum*, they are morphologically very distinct. *H. philippianum* has leaves usually > 1 cm long, while in *H. inconspicuum* the leaves are not longer than 1 cm. *H. taltalense* has also larger leaves, the leaf surface is rugose and the margin sinuate, while *H. inconspiccum* has leaves not rugose and the margin is straight. *Heliotropium inconspicuum* has also been confounded with *H. filifolium* and *H. chenopodiaceum*, both with small leaves, but different geographic ranges. From the former it differs in having the style equal to or longer than the stigmatic head and leaves not terete (versus sessile stigmatic head and leaves terete in *H. filifolium*); from the latter differs in its leaves with rounded apex and in having the style equal to or longer than the stigmatic head (versus acute leaves and style shorter than the stigmatic head in *H. chenopodiaceum*).

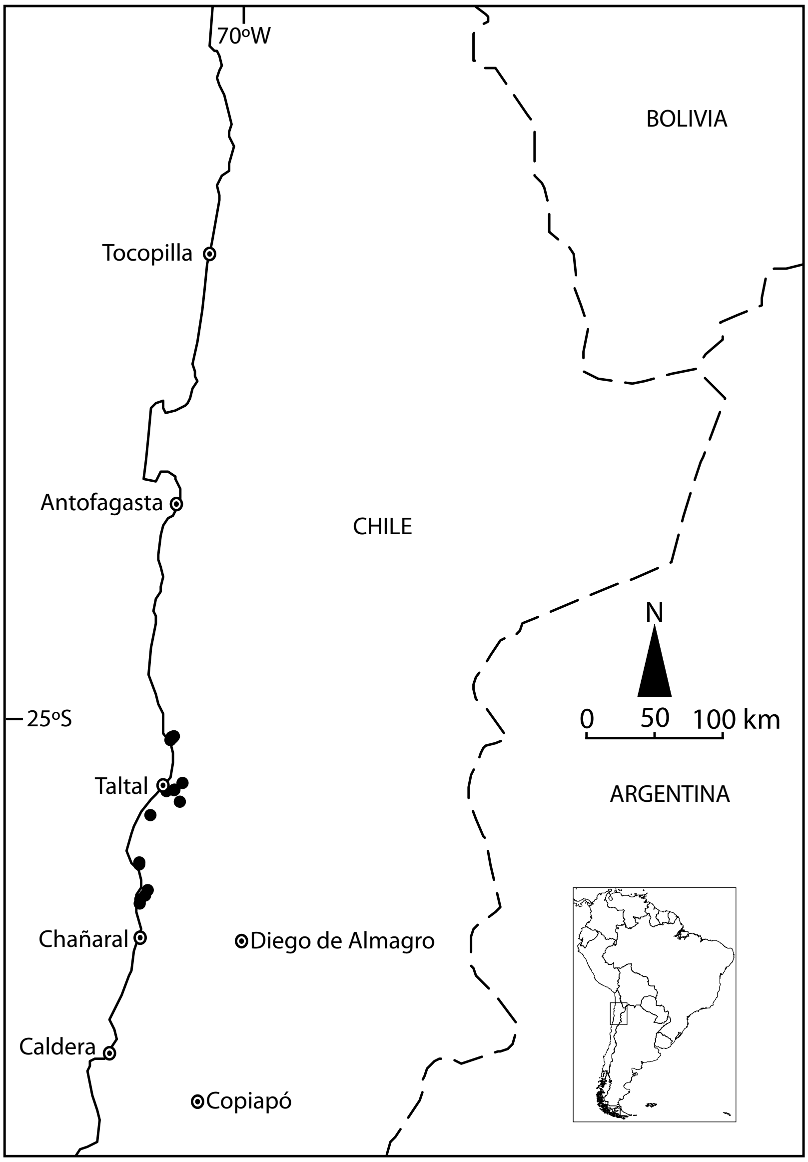

Figure 6.16: Distribution of *Heliotropium inconspicuum.*

**9. Heliotropium megalanthum** *I.M.Johnst.* (Johnston, 1928b: 35); Marticorena (1968: 44); Förther (1998: 206). Type: Chile, in prov. Coquimbo [dry valleys and hills between Huasco and Copiapó], [Sept. 1841], *T. Bridges* 1341 (lectotype BM [photo GH], selected by Johnston (1928b: 35); duplicates E not seen [digital photograph!], K [photo SGO 2266]). Replacement name for *Cochranea corymbosa.*

*Cochranea corymbosa* Miers (1868:126); Philippi (1895: 340). Type as above.

*Heliotropium corymbosum* (Miers) Reiche (1907a: 242), **nom. illegit.**, non *H. corymbosum* Ruiz & Pav. (Ruiz and Pavón, 1799: 2); Reiche (1910: 200). Type as above.

*Heliotropium crassifolium* Phil. (Philippi, 1873: 515), **nom. illegit.**, non *H. crassifolium* Boiss. & Noë, in Boissier (1856: 131); Reiche (1907a: 240); Reiche (1910: 198). Type: Chile, Región de Atacama, Prov. Huasco, Huasco, Oct. 1866, *R.A. Philippi* s.n. (lectotype SGO 54364 [photo F, GH, MSB, NY, US], selected by Förther (1998: 188); duplicates B † [photo F neg. n° 17331: F, GH, NY, US, photo SGO 67287], GH [fragm.], SGO 54365 [photo MSB!], W not seen [photo F neg. n° 31929: F, GH, US])

*Cochranea crassifolia* (Phil.) Phil. (Philippi, 1895: 349). Type as for *Heliotropium crassifolium* Phil.

*Decumbent shrubs*, 0.09 – 0.4 m tall, with ascending branches, densely foliose to the base of the inflorescence. Stems and foliage glabrous or sparsely strigose. *Leaves* alternate, somewhat succulent, solitary or grouped in fascicles of up to 12 leaves, sessile, oblanceolate to ovate-spathulate, 13 – 44 (– 50) × 3.5 – 10.5 (– 12) mm; lamina glabrous with hirsute (pustulate) pubescence only on the margin, dark-green, margin entire, revolute, base attenuated in a pseudopetiole, apex obtuse, with only the main vein conspicuous. *Inflorescences* terminal, elongate, dichotomically branched, to ca. 15 cm long. *Flowers* sessile or shortly pedicellated, alternate, erect. Calyx cylindric, green; calyx lobes linear, glutinous, fused only at the base, hirsute only on the margin outside, strigose within, (2 –) 2.5 – 6.5 × 0.5 – 1 mm, free portion 3 – 6 mm long, apex acute. Corolla infundibuliform, sparsely strigose to glabrous outside, dull white with yellow or orange-yellow throat; limb horizontally spreading, 7.5 – 12.5 mm wide, lobes rounded; tube longer than the calyx, 6.5 – 11 mm long. Stamens included or exserted at late anthesis; filaments adnate to petals; anthers linear-lanceolate, glabrous, base cordate, apex acute, ca. 1 mm long, overlapping the stigmatic head. Ovary glabrous, subglobose, ca. 0.5 mm diam., with a basal nectar ring. Style glabrous, ca. 1 – 1.5 mm long, equal to or slightly longer than the stigmatic head. Stigmatic head conic, elongated, bilobate, ca. 1 × 0.7 mm. *Fruits* dry, ellipsoid, rugose, glabrous, pale brown to yellowish, ca. 1.5 × 2 mm diam., falling apart at maturity into two 2-seeded nutlets, each ca. 1.5 × 1.5 mm diam.

*Pollen* prolate, 28 – 32.5 × 19.5 – 24 $\mu$m. Amb almost 3-lobate. Mesocolpi concave in the polar view. Colpiferous sides convex. Endoapertures 3 – 3.5 $\mu$m diam., contracted at the center. Exine thickness ca. 1 $\mu$m uniform in the whole of its extension (from *Ricardi* 2300 in Marticorena, 1968).

**DISTRIBUTION**. Litoral and interior areas of the provinces of Copiapó and Huasco (Región de Atacama, Chile), between 27°42'S and 28°38'S (Fig. 6.17). The material cited from Fray Jorge (*Kummerow* s.n.) is probably erroneously given.
**SPECIMENS EXAMINED**. See Appendix E (p. 304).
**HABITAT**. Coastal and interior sand plains and rocky outcrops of the south-central Atacama Desert, 0 – 620 m. It forms part of the scrub vegetation dominated by *Atriplex clivicola* (Amaranthaceae), *Eulychnia breviflora* (Cactaceae), *Oxalis virgosa* (Oxalidaceae), among others. *Heliotropium megalanthum* loses almost all its above-ground structures (i.e., flowers and leaves) in dry years, when it is not possible to recognise it. In rainy years it leafs and flowers and only some few leaves persist to the next dry year.
**CONSERVATION STATUS**. Vulnerable (VU), criterion B2(c), see Chapter 5.
**FLOWERING TIME**. September to October, with a flowering peak in September (Vidiella et al., 1999).
**ETYMOLOGY**. The epithet *megalanthum* refers to the large flowers this species possesses.
**VERNACULAR NAME**. Heliotropio amarillo (Spanish; Riedemann, 2004; erroneously cited as *Heliotropium linariifolium*).
**USES**. According to Riedemann (2004) and Riedemann et al. (2006) this species has potential as ornamental. Johnston (1928b) considered it a beautiful plant, a characteristic probably derived from the size of its flowers and inflorescences and its yellow to orange, sometimes spreading, corolla throat.

Figure 6.17: Distribution of *Heliotropium megalanthum*.

**NOTES**. This species is characteristic for its large flowers with a yellow to orange corolla throat and its decumbent habit. The other two decumbent species in section *Cochranea* (*Heliotropium linariifolium* and *H. eremogenum*) have strigose lamina (versus glabrous lamina with pustulate pubescence only on the margin in *H. megalanthum*), definitely orange corollas (*H. linariifolium*) or smaller flowers (*H. eremogenum*), and both are distributed north of the geographic range of *H. megalanthum*, with which they do not overlay. In its area of distribution, *H. megalanthum* might be confounded with *H. floridum*, but the latter has strigose lamina and erect habit and the style longer than the stigmatic head.

Förther (1998: 228-229) considers a material *Bridges* 1341 at B as the holotype of *Cochranea corymbosa*. This is not possible because in the original description of Miers (1868) only two specimens from BM and K are mentioned ('*in herb. Mus. Brit. et Hook.*').

The necessary lectotypification was undertaken by Johnston (1928b). There is not material of this collection of Bridges at B, and the Filed Museum negative n° 17331, cited by Förther (1998), corresponds to an isotype of *Heliotropium corymbosum* Phil.

**10. Heliotropium chenopodiaceum** (*A.DC.*) *Clos*, in Gay (1849: 458); Reiche (1907a: 243); Reiche (1910: 201); Johnston (1928b: 29); Marticorena (1968: 42); Arroyo et al. (1984: 7); Förther (1998: 206). Type: Chile, prov. Coquimbo, 1837 – 1836[?], *Gay* s.n. (lectotype G-DC [photo F neg. n° 7768: F, GH, NY, US; photo SGO 67285], selected by Miers (1868: 132) and narrowed by Förther (1998: 231); possible duplicates BM, F 515900 [fragm.], G, GH, K, LE not seen, P not seen [digital photograph!, mixed with *Heliotropium myosotifolium*, photo MSB]).

*Heliophytum chenopodiaceum* A.DC. (de Candolle, 1845: 553). Type as above.
*Cochranea chenopodiacea* (A.DC.) Miers (1868: 132); Philippi (1895: 348). Type as above.
*Heliotropium chenopodiaceum* (A.DC.) Clos var. *genuinum* I.M.Johnst. (Johnston, 1928b: 29), **nom. invalid.** Type as above.
*Cochranea ericoidea* Miers (1868: 130), **synon. nov.**; Philippi (1895: 344). Type: Chile, in prov. Coquimbo [mountains near the Andes valleys of Copiapó], [Sept. 1841], *T. Bridges* 1339 (BM [fragm. + photo GH], selected by Johnston (1928b: 29); isotypes E not sen (digital photograph!), K, P not seen [digital photograph, fragm. F 515811, photo MSB]).
*Heliotropium chenopodiaceum* (A.DC.) Clos. var. *ericoideum* (Miers) Reiche (1907a: 244); Reiche (1910: 202); Johnston (1928b: 29); Förther (1998: 185). Type as for *Cochranea ericoidea.*
*Heliotropium pearcei* Phil. (Philippi, 1861: 65), **synon. nov.** Type: Chile, Coquimbo, *R. Pearce* s.n. (holotype SGO 42236 [photo GH, MSB]).
*Cochranea pearcei* (Phil.) Phil. (Philippi, 1895: 352). Type as for *Heliotropium pearcei.*
*Heliotropium sclerocarpum* Phil. (Philippi, 1873: 515); Johnston (1928b: 30); Marticorena (1968: 45); Förther (1998: 218). Type: Chile, Región de Atacama, Prov. Huasco, Huasco, Oct. 1866, *R.A. Philippi* s.n. (SGO 54348 [photo GH, MSB, NY, US], selected by Förther (1998: 218); isotypes B† [photo F neg. n° 17343: F, GH, NY, US], GH [fragm.], SGO 42241 [photo MSB]).
*Cochranea sclerocarpa* (Phil.) Phil. (Philippi, 1895: 351). Type as for *Heliotropium sclerocarpum.*
*Heliotropium chenopodiaceum* (A.DC.) Clos var. *sclerocarpum* (Phil.) Reiche (1907a: 244); Reiche (1910: 202). Type as for *Heliotropium sclerocarpum.*
?*Eritrichum glabratum* Phil. (Philippi, 1891: 56), **synon. nov.** Possible type: Chile, Región de Atacama, Prov. Copiapó, Quebrada de Puquios, 1885, *F. Philippi* s.n. (SGO 54401).
*Cochranea sentis* Phil. (Philippi, 1895: 351), **synon. nov.** Type: Chile, Región de Atacama, Prov. Copiapó, Piedra Colgada, Sept. 1885, *F. Philippi* s.n. (SGO 54434 [photo F, GH, MSB, NY], selected by Johnston (1928b: 31) and narrowed here; isotype BM, GH [fragm.], SGO 42226 [photo MSB]).

*Erect shrubs*, 0.2 – 0.8 (– 1) m tall, with ascending thin and reddish brown branches, densely foliose to the base of the inflorescence. Stems and foliage glabrous or hirsute, glutinous. *Leaves* alternate, solitary or, more frequently, grouped in fascicles of up to 13 leaves, sessile, linear-lanceolate, 2.5 – 12.5 × 0.5 – 2 (– 3) mm; lamina glabrous to hirsute, green or brownish-green, margin entire, revolute, base attenuate, apex acute, with only the main vein conspicuous. *Inflorescences* terminal, elongate, dichotomically branched, to ca. 5 cm long. *Flowers* sessile, alternate, erect, aromatic. Calyx cylindric, green; calyx lobes linear, glutinous, fused to the half of their length, glabrous or hirsute outside, strigose within, 1 – 3.5 × 0.3 – 1 (– 1.5) mm, free portion 0.2 – 2 mm long, apex acute. Corolla infundibuliform, sparsely strigose, dull white with yellow throat; limb horizontally spreading, 1.5 – 4.5 (– 5.5) mm wide, lobes rounded; tube longer than the calyx, 2 – 4.5 mm long. Stamens included or exserted at late anthesis; filaments adnate to petals; anthers oblong-lanceolate, glabrous, base cordate, apex acute, ca. 1 mm long, overlapping the stigmatic head. Ovary glabrous, subglobose, ca. 1 mm diam., with a basal nectar ring. Style glabrous, ca. 0.3 – 0.5 mm long, shorter than the stigmatic head. Stigmatic head conic, elongated, bilobate, ca. 1 – 2 × 0.7 mm. *Fruits* dry, ellipsoid, dorsally sulcate, glabrous, pale brown to yellow, ca. 3 × 2 mm diam., falling apart at maturity into two 2-seeded nutlets, each ca. 1.5 × 2 mm diam.

*Pollen* prolate, 18 – 21 × 13 – 14 $\mu$m. Endoapertures 3.5 – 4 $\mu$m diam., circular. Exine thickness ca. 1 $\mu$m (from *Ricardi & Marticorena* 3994 and 4370/955 (as 4730/955) in Marticorena, 1968).

**DISTRIBUTION**. Inland mountains and Andean foothills of the provinces of Chañaral, Copiapó, Huasco (Región de Atacama), Elqui, Limarí and Choapa (Región de Coquimbo), Chile. Together with *Heliotropium krauseanum* this is the species with the largest geographic range in section *Cochranea*, between 26°14'S and 31°30'S (Fig. 6.18). The norhernmost collections cited by Johnston (1928b: 30, 1929a: 97) from El Rincón (24°56'S; *Johnston* 5545) and Panulcito (24°48'S; *Johnston* 5477), isolated from the rest of the geographic range of the species, were not seen at GH.

**SPECIMENS EXAMINED**. See Appendix E (p. 305).

**HABITAT**. Rocky hillsides and sandy soils of the Andean Atacama Desert, 200 – 2250 m. *Heliotropium chenopodiaceum* is usually found in open dwarf scrubs, where is usually dominant, especially in the northern portion of its distribution, together with *Aphyllocladus denticulatus* Cabrera, *Encelia canescens* (both Asteraceae) and *Nolana leptophylla* (Solanaceae) in the northern part, and with *Flourensia thurifera* DC. (Asteracae), *Opuntia sphaerica* Foerster (Cactaceae), *Fagonia chilensis* Hook. & Arn. (Zygophyllaceae), among others, in the southern part.

**CONSERVATION STATUS**. Least concern (LC), criterion B2(c), see Chapter 5.

**FLOWERING TIME**. September to November, but with early (late) rains it can also flower from August (to January).

**ETYMOLOGY**. The epithet *chenopodiaceum* refers, acccording to de Candolle (1845), to its habit, similar to a Chenopodiaceae.

**USES**. Riedemann et al. (2006) suggest its potential use as ornamental.

**NOTES**. *Heliotropium chenopodiaceum* is treated here in a broad sense. Reiche (1907a, 1910), Johnston (1928b) and Förther (1998) recognised var. *ericoideum*, which differs from the typical variety in having pubescent leaves. Earlier authors (Miers, 1868; Philippi, 1895) treated the former variety at the species level. The geographic range of these varieties is similar. Field observations have revealed that individuals with glabrous and pubescent leaves coexist in the same geographic area and even in the same populations, making the taxonomic differentiation of *Heliotropium chenopodiaceum* var. *ericoideum* unsustainable under the present taxon concept (see Section 6.3). All names associated with specimens referable to this species with pubescent leaves have therefore been placed under the synonymy of *Heliotropium chenopodiaceum*. Förther (1998) considers *Bridges* 1339 (BM) as the holotype of *Cochranea ericoidea*. Since Miers (1868) mentions two specimens in his description, the above mentioned material must be considered a lectotype, according to Johnston (1928b).

Johnston (1928b) and Förther (1998) recognised *Heliotropium sclerocarpum* as a distinct species, in agreement with Philippi (1895), while Reiche (1907a, 1910) reduced it to a variety of *Heliotropium chenopodiaceum*. The type specimen of *Heliotropium scleocarpum* is an aberrant form of the pubescent *H. chenopodiaceum*, with lanose pubescence, but it cannot otherwise be distinguished from the later species as here defined.

The closest related species to *H. chenopodiaceum* seems to be *H. myosotifolium*, as suggested by Johnston (1928b). Both fall in a polytomous group in the phylogeny of *Heliotropium* sect. *Cochranea* (Luebert and Wen, 2008; see Chapter 2). *Heliotropium chenopodiaceum* and *H. myosotifolium* are morphologically very similar and in some cases very difficult to distinguish from each other. *Heliotropium chenopodiaceum* tend to have smaller flowers and leaves than *H. myosotifolium*, but during rainy years, populations of the former can develop flowers and leaves that are as large as those of the latter species. The most consistent characters to differentiate these two species seems to be the calyx lobes, which are fused to the half of their length in *H. chenopodiaceum* and are almost totally free in *H. myosotifolium*, an a denser pubescence in the foliage of the latter, which is not glutinous. Even so, in some geographic areas this character seems to be very variable from one individual to another and intermediate stages are often found. The geographic areas of both species are parapatric (Fig. 6.18), and present zones of contact in the eastern portion of the geographic range of *H. myosotifolium* (alluvial plains between Vallenar and Copiapó), which coincides with the western boundary of the geographic range of *H. chenopodiaceum*. These species probably diverged recently and may still hybridize in these areas of contact in rainy years, when the geographic range of both species is fully expressed. In dry years, flowering individuals of *Heliotropium chenopodiaceum* are restricted to the ravines of the Andean foothills, while *H. myosotifolium* does not develop any vegetative or reproductive structure.

Probably as a result of the difficulty to differentiate *Heliotropium chenopodiaceum* from *H. myosotifolium*, Johnston (1928b) cited the name *Cochranea sentis* under the synonymy of *H. myosotifolium*. According to the present species concept of *Heliotropium chenopodiaceum* and to the lectotypification of *Cochranea sentis* made by Johnston (1928b), the latter name should be placed in the synonymy of *H. chenopodiaceum*, because it has the calyx lobes fused. Reiche (1907a, 1910) cited *Cochranea sentis* in the synonymy of *Heliotropium chenopodiaceum* var. *filifolium* (≡*Heliotropium filifolium* ≡*Cochranea filifolia*), which does not agree with the original description and type material of the former name. Since Reiche did probably not see the type material of *Cochranea filifolia*, he was confused with its description, which stems from one of the syntypes of *Heliotropium chenopodiaceum*. Evidence of that is the recognition of *Heliotropium kingi* by Reiche (1907a, 1910), which is conspecific with *H. filifolium*. An additional source of confusion is the lectotypification of *Cochranea sentis* made by Förther (1998). This author used a different syntype as the lectotype (*Albert* s.n., SGO 54433), a specimen that corresponds to *Heliotropium myosotifolium*. This lectotypification must be superseded against Johnston's one, who clearly indicated Philippi's material as the type of *Cochranea sentis* (Art. 9.17). Since two Philippi's specimens of *Cochranea sentis* are found at SGO, the lectotypification of Johnston (1928b) is narrowed here to the more complete of them (Art. 9.15).

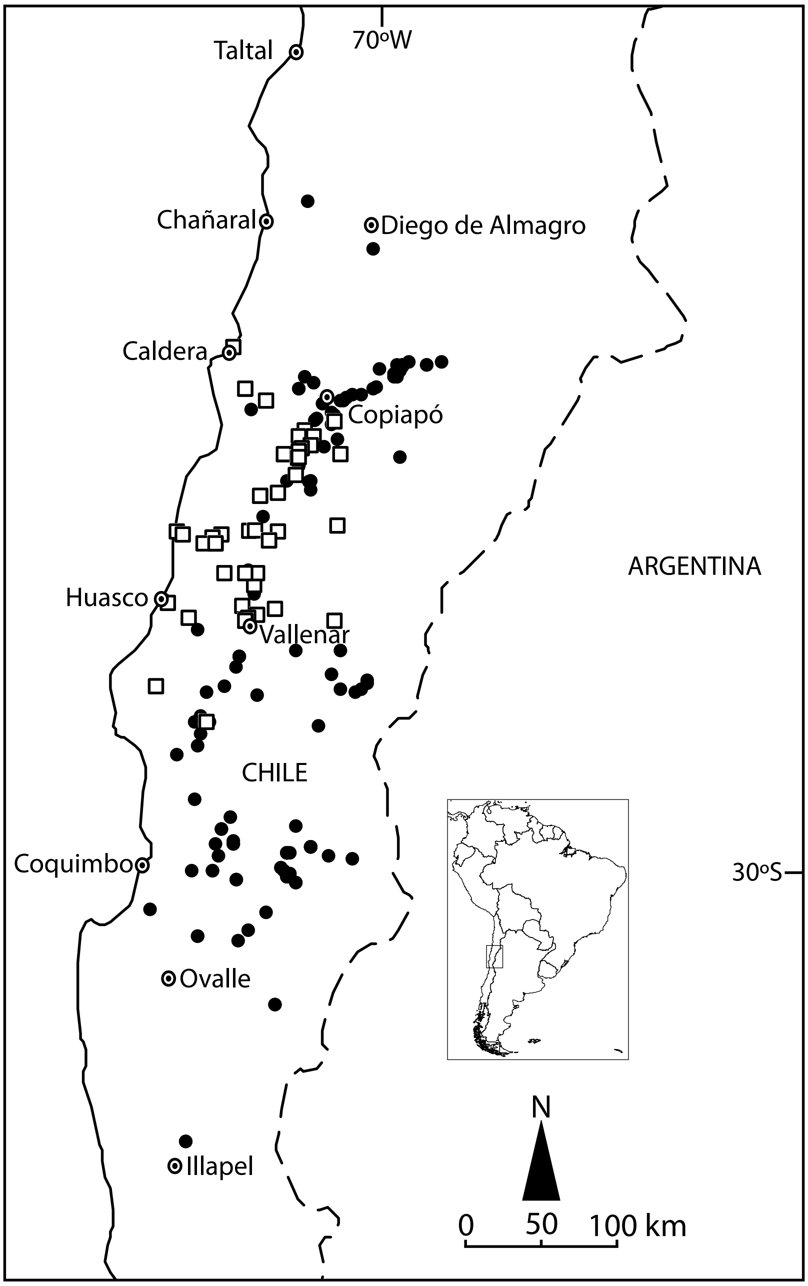

Figure 6.18: Distribution of *Heliotropium chenopodiaceum* (●) and *H. myosotifolium* (☐).

Förther (1998: 231) lectotypified *Heliophytum chenopodiaceum* with the material of Gay at G-DC. Such a lectotyificaton had already been undertaken by Miers (1868) 120 years earlier, by segregating *Bridges* 1343, a syntype of *H. chenopodiaceum*, as the type of *Heliotropium filifolium*. Although identical, the lectotypification must therefore be attributed to Miers (1868).

Förther (1998) cites specimens at P and LE collected by Gay as isotypes of *Heliotropium chenopodiaceum*. It is not clear, however, whether these specimens are actually duplicates of the lectotype collection, since Gay was in direct contact with de Candolle (Marticorena, 1995) and communicated specimens directly to him (Barros Arana, 1876), at a time (1830s) that de Candolle was long settled back in Geneva (Gray, 1863), so that these specimens did not necessarily go through Paris. The material at G-DC does not have indication of precise locality, nor it has a collector number. The materials at P, however come from a precise locality (Arqueros) and have collector number (*C. Gay* 294). The specimens at F and GH are duplicates sent from P. The material at BM does not have collector number but it has locality (Arqueros), so that it can also be identified with the materials at P. The materials at G and K does neither have collector number nor precise locality. I did not see the specimen at LE. Since Gay probably collected more than one specimen (there is one more specimen at SGO with the number *Gay* 1075), it is not possible to ascertain whether all the cited duplicate materials (BM. F, G, GH, K, P) correspond to the same gathering as that of G-DC.

Following Johnston (1928b), *Eritrichum glabratum* have been placed in the synonymy of *Heliotropium chenopodiaceum*. However, neither Johnston (1928b) nor Muñoz (1960) assigned any material from SGO to the former name. The specimen cited here (SGO 54401) as type of *Eritrichum glabratum*, though coincident with locality, collector and collection date, do not exactly match the description provided by Philippi (1891), and must therefore be regarded as tentative.

**11. Heliotropium myosotifolium** (*A.DC.*) *Reiche* (1907a: 243); Reiche (1910: 201); Johnston (1928b: 31); Marticorena (1968: 45); Förther (1998: 208). Type: Chile, Coquimbo, [barren and stony hills between Huasco and Copiapó], [Sept. 1841], *T. Bridges* 1338 (holotype G-DC [photo SGO 11767]; isotypes BM [photo GH], E not seen (digital photograph!), G, GH, K [photo SGO 2262], P not seen [digital photograph!, fragm. F 515813, photo MSB], W not seen).

*Heliophytum stenophyllum* (Hook. & Arn.) A.DC. var. *myosotifolium* A.DC. (de Candolle, 1845: 552). Type as above.

*Heliotropium stenophyllum* Hook. & Arn. var. *myosotifolium* (A.DC.) Clos, in Gay (1849: 456). Type as above.

*Cochranea myosotifolia* (A.DC.) Miers (1868: 128); Philippi (1895: 343). Type as above.

*Cochranea hebecula* Miers (1868: 130); Philippi (1895: 343). Type: Chile, Coquimbo, *T. Bridges* s.n. (holotype BM [photo GH]; possible isotypes BM, BR not seen (digital photograph!, photo + fragm. MSB!), F515813, P not seen [digital photograph!]).

*Cochranea hispidula* Miers (1868: 132); Philippi (1895: 347). Type: In Chile boreali, *W. Lobb* 440 (holotype K; isotype BM).

*Heliotropium hispidulum* (Miers) Reiche (1907a: 243), **nom. illegit.**, non *H. hispidulum* Phil. (Philippi, 1895: 356); Reiche (1910: 201). Type as for *Cochranea hispidula*.

*Heliotropium canum* Phil. (Philippi, 1895: 356). Type: Chile, in valle Carrizal loco dicto Yerbabuena, Sept. 1885, [*A. Borchers*] s.n. (lectotype SGO 54347 [photo F, GH, MSB, NY, US], selected by Förther (1998: 189); duplicates B† [photo F neg. n° 17334: F, GH, NY, US], BM, GH [fragm.], K (ex Herb. Ball), K [photo SGO 2261], SGO 42222 [photo MSB], US 942362, WU not seen).

*Heliotropium hispidulum* Phil. (Philippi, 1895: 356). Type: Chile, Valle del Carrizal, Sept. 1885, *F. Philippi* s.n. (holotype SGO 54345 [photo F, GH, MSB, NY, US])

*Erect shrubs*, 0.1 – 0.5 m tall, with ascending thin branches, densely foliose to the base of the inflorescence. Stems and foliage strigose or villous, usually densely so, non glutinous. *Leaves* alternate, solitary or grouped in fascicles of up to 10 leaves, sessile, linear to oblong-linear, 5 – 20 (– 30) × 0.7 – 2.5 (– 4) mm; lamina strigose or villous, grewish- or brownish-green, margin entire, revolute, base attenuate, apex obtuse, with only the main vein conspicuous. *Inflorescences* terminal, elongate, dichotomically branched, to ca. 5 cm long. *Flowers* sessile, alternate, erect, aromatic. Calyx cylindric, green or greyish-green; calyx lobes linear, glutinous, fused only at the base or free, strigose on both sides, 2 – 5 × 0.5 – 0.7 mm, free portion 2 – 3 mm long, apex acute. Corolla infundibuliform, sparsely strigose, dull white with yellow throat; limb horizontally spreading, 5 – 7 (– 8) mm wide, lobes rounded; tube as long as the the calyx, 3 – 5 mm long. Stamens included or exserted at late anthesis; filaments adnate to petals; anthers oblong-lanceolate, glabrous, base cordate, apex acute, ca. 1 mm long, overlapping the stigmatic head. Ovary glabrous, subglobose, 0.5 – 1 mm diam., with a basal nectar ring. Style glabrous, ca. 0.2 – 0.5 mm long, shorter than the stigmatic head. Stigmatic head conic, elongated, bilobate, ca. 1.3 – 2.2 × 0.7 mm. *Fruits* dry, ellipsoid, rugose, glabrous, dark brown, falling apart at maturity into two 2-seeded nutlets.

*Pollen* prolate, 22 – 23 × 11.5 – 14.5 $\mu$m. Amb 6-lobate. Endoapertures 2.5 $\mu$m diam. Exine thickness 1 $\mu$m at the mesocolpia and 1.5 $\mu$m ate the apocolpia. Colpifeorus sides almost parallel (from *Ricardi & Marticorena* 4393/788 in Marticorena, 1968).

**DISTRIBUTION**. Inland pampa of the provinces of Copiapó and Huasco, Región de Atacama, Chile, largely restricted to the plains located between the cities of Vallenar and Copiapó, between 27°30'S and 29°9'S (Fig. 6.18). The locality given in the collection of *Albert* s.n. ('Quinteros', Región de Valparaíso, Chile) is certainly erroneous.

**SPECIMENS EXAMINED**. See Appendix E (p. 307).

**HABITAT**. Dry inland sandy plains, subject to rain-shadow effect of the coastal mountains, 170 – 700 (– 1500) m. These areas are largely devoid of vegetation during dry years, but both woody and herbaceous plants emerge in the spring of rainy years giving rise to the so-called blooming desert. The vegetation of these areas has been studied by Kohler (1967, 1968). It consists of a scrub dominated by *Atriplex deserticola* Phil. (Amaranthaceae) and *Skytanthus acutus* Meyen (Apocynaceae), with a dense layer of ephemeral plants, such as *Nolana baccata* Dunal (Solanaceae) and *Cistanthe longiscapa* (Barnéoud) Carolin ex Hershkovitz (Portulacaceae), where *Heliotropium myosotifolium* is usually scarce.

**CONSERVATION STATUS**. Least concern (LC), criterion B2(c), see Chapter 5.

**FLOWERING TIME**. September to October.

**ETYMOLOGY**. The epithet *myosotifolium* refers to its leaves similar to some species of the genus *Myosotis* L. (Boraginaceae).

**USES**. Riedemann et al. (2006) suggest its potential use as ornamental.

**NOTES**. This species is very similar to *Heliotropium chenopodiaceum* (see discussion under the latter species). It also has sometimes been confounded with *Heliotropium floridum*, from which it is easily distinguished by its style shorter than the stigmatic head (versus style longer than the stigmatic head in *H. floridum*). The latter species has the leaves more succulent than *Heliotropium myosotifolium*, and is distributed west of the range of *H. myosotifolium*, closer to the coast.

Förther (1998) indicates the presence of two isotypes (*Bridges* 1338) housed at P. However, only one of them has collector number. The other specimen, *Bridges* s.n., as well as the duplicate material at F (ex P), may more likely be a duplicate of the type of *Cochranea hebecula*. It is possible that these latter materials correspond to the same collection as *Bridges* 1338 that were distributed dissociated from their original number (Johnston, 1928a).

Förther (1998) selected a lectotype of *Heliotropium hispidulum* Phil. (SGO 54345). However, as already indicated by Johnston (1928b), this specimen constitutes the holotype, since is the only one at SGO that can be associated with the description of Philippi (1895), who indicates that the material comes from 'Valle de Carrizal'. The other specimens (SGO 42225 and SGO 54346), cited by Muñoz (1960) and Förther (1998) as isotypes of *H. hispidulum* Phil., are labelled as from 'Chañarcito', as well as several duplicates of the latter at BM, GH and K, which are not type specimens.

**12. Heliotropium stenophyllum** *Hook. & Arn.* (Hooker and Arnott, 1830: 38); Steudel (1840: 744); Clos, in Gay (1849: 456); Reiche (1907a: 241); Reiche (1910: 199); Johnston (1928b: 33); Marticorena (1968: 47); Förther (1998: 220). Type: Chile, Región de Coquimbo, Prov. Elqui, Panamericana S of Coquimbo, *F. Luebert & C. Becker* 2910 (neotype SGO, selected here; duplicate BSB).

*Heliophytum stenophyllum* (Hook. & Arn.) A.DC. (de Candolle, 1845: 552). Type as above.
*Cochranea stenophylla* (Hook. & Arn.) Miers (1868: 128); Philippi (1895: 343). Type as above.
*Meladendron chilense* Molina (1810: 143), non *Heliotropium chilense* Bertero (1829: 647) = *H. curassavicum* L. (Linnaeus, 1753: 130). Type not designated (?BOLO), see Förther (1998: 233).
*Heliotropium rosmarinifolium* Bertero ex Steud. (Steudel, 1840: 744), **nomen nudum**.
*Heliophytum rosmarinifolium* Bertero ex A.DC. (de Candolle, 1845: 552), **nomen nudum**.
*Heliophytum stenophyllum* (Hook. & Arn.) A.DC. var. *rosmarinifolium* DC. (de Candolle, 1845: 552); Reiche (1907a: 242); Reiche (1910: 200). Type: Chile, loco dicto La Calera Quillota, Oct. 1829, *C. Bertero* 1042 (holotype G-DC [photo SGO 11766]; isotypes BM, BREM not seen, F 1547440, F 515750, ?F 997919, FI not seen, G, GH, HAL not seen, HOH not seen, KIEL not seen, L not seen, LE not seen, M, NY, P not seen (digital photograph!), PR not seen, PRC not seen, TUB not seen, W 284993 not seen).
*Heliotropium stenophyllum* Hook. & Arn. var. *rosmarinifolium* (DC.) Clos, in Gay (1849: 456). Type as for *Heliophytum stenophyllum* var. *rosmarinifolium*.
*Cochranea conferta* Miers (1868: 125); Philippi (1895: 339). Type: Chile, Cuesta de Llaillay, *J. Miers* s.n. (lectotype BM, selected by Johnston, 1928b: 34).
*Cochranea congesta* Miers (1868: 126), **nomen nudum**. Probably a typo of Miers (1868) intended to refer to *Cochranea conferta*.
*Heliotropium huascoense* I.M.Johnst. (Johnston, 1928b: 34), **synon. nov.**; Förther (1998: 200). Type: Región de Atacama, Prov. Huasco, Huasco, 1920, *R.E. López* s.n. (holotype GH).

*Erect shrubs*, 0.6 – 2 m tall, with ascending branches, densely foliose to the base of the inflorescence. Stems and foliage finely strigose or glabrous, glutinous. *Leaves* alternate, solitary or grouped in fascicles of up to 20 leaves, sessile, linear to linear-spathulate, 9.5 – 35 (– 60) × 0.7 – 3 mm; lamina glabrous or finely strigose, dark green, margin entire, revolute, base attenuate, apex acute or obtuse, with only the main vein conspicuous. *Inflorescences* terminal, elongate, dichotomically branched, to ca. 5 cm long. *Flowers* sessile, alternate, erect, aromatic. Calyx cylindric, green or greyish-green; calyx lobes linear, fused only at the base or free, glutinous, with ciliated margins, strigose outside, glabrous or strigose within, 1 – 4.5 × 0.5 – 1 mm, free portion 1.5 – 4.5 mm long, apex acute. Corolla infundibuliform, sparsely strigose, dull white with yellow throat, becoming bluish at late anthesis; limb horizontally spreading, 4.5 – 9 (– 10) mm wide, lobes rounded; tube longer than the calyx, 2.5 – 7.5 mm long. Stamens included or exserted at late anthesis;

filaments adnate to petals; anthers oblong-lanceolate, glabrous, base cordate, apex acute, ca. 1.2 – 1.5 mm long, overlapping the stigmatic head. Ovary glabrous, subglobose, 0.4 – 0.6 mm diam., with a basal nectar ring. Style glabrous, ca. 0.8 – 1.5 mm long, as long as or slightly shorter than the stigmatic head. Stigmatic head conic, elongated, bilobate, ca. 1 – 1.8 × 0.7 mm. *Fruits* dry, ellipsoid, rugose, glabrous, light brown or cream, ca. 2.5 × 1.5 mm diam., falling apart at maturity into two 2-seeded nutlets, ca. 2 × 1.5 mm diam. Fig. 6.19.

*Pollen* prolate, 24.5 – 30.5 × 16.5 – 18.5 $\mu$m. Endoapertures 4 × 5 $\mu$m diam., lalongate. Exine thickness 1 $\mu$m at the mesocolpia and 1.5 $\mu$m at the apocolpia. (from *Ricardi & Marticorena* 4332/717 in Marticorena, 1968).

**DISTRIBUTION**. Coastal and island areas of the provinces of Huasco (Región de Atacama), Elqui, Limarí, Choapa (Región de Coquimbo), Petorca, San Felipe and Quillota (Región de Valparaíso), Chile. It is broadly distributed between 28°28'S and 32°50'S (Fig. 6.20). It has been cited for Arica (*Jaffuel* 12), 'Conception' (*Caldcleugh* s.n.), Valdivia (*Bridges* 595) and even 'Perou' (*s.col.*), but these localities are all certainly erroneous. The material of Bridges at NY is probably his number 235 from the province of Quillota, whose label could have been confounded with 595. In the catalogues of the plants of Bridges at BM and K, number 595 actually comes from Valdivia, but the species mentioned there is not a *Heliotropium* (but 'Cineraria?'), which Bridges knew well, since it is mentioned under his numbers 235 and 1338-1343.

**SPECIMENS EXAMINED**. See Appendix E (p. 308).

**HABITAT**. Hillsides, usually on dry slopes, and sandy and rocky coastal areas, 5 – 1200 m. In the coast it is usually dominant, together with *Oxalis virgosa* (Oxalidaceae) (see Weisser and Rundel, 1980), while in inland areas it is usually restricted to dry north-facing slopes, where is sometimes dominant together with *Bridgesia incisifolia* Bertero ex Cambess. (Sapindaceae) *Cordia decandra* (Cordiaceae) and *Flourensia thurifera* (Asteraceae) (Gajardo, 1978; Etienne et al., 1982).

**CONSERVATION STATUS**. Least concern (LC), criterion B2(c), see Chapter 5.

**FLOWERING TIME**. August to November, but throughout the year provided sufficient moisture (Olivares and Squeo, 1999).

**ETYMOLOGY**. The epithet *stenophyllum* refers to its narrow leaves.

**VERNACULAR NAME**. Palo negro, monte negro (Spanish).

**USES**. Riedemann and Aldunate (2001) and Riedemann et al. (2006) suggest its potential use as ornamental. Villarroel et al. (1991) determined antioxidat activity of the resin exudates of *Heliotropium stenophyllum*. The leaves are locally (Pichasca) used for preparing vaginal washes.

**NOTES**. In the work of Förther (1998), *Gaudichaud* 64 is cited as the type of *Heliotropium stenophyllum*. This specimen comes from Coquimbo, Chile, the type locality given by Hooker and Arnott (1830), where the species actually grows. Gaudichaud, however, collected at Coquimbo during the expedition of l'Herminie (1831 – 1833) in 1832 (Lasègue, 1845), two years later than the description of the species. Therefore, this material cannot be part of the type. The specimens upon which the species of the Beechey's Voyage were described, were collected by the naturalists Lay and Collie (Hooker and Arnott, 1841). The type material of *Heliotropium stenophyllum* is not to be found at the Hooker herbarium (now at K) at least since the 1860s (Miers, 1868). Both the Arnott herbarium and part of the Hooker herbarium of the Beechey's voyage are now at E (Stafleu and Cowan, 1979). However, according to Noltie (2010), the type specimen of

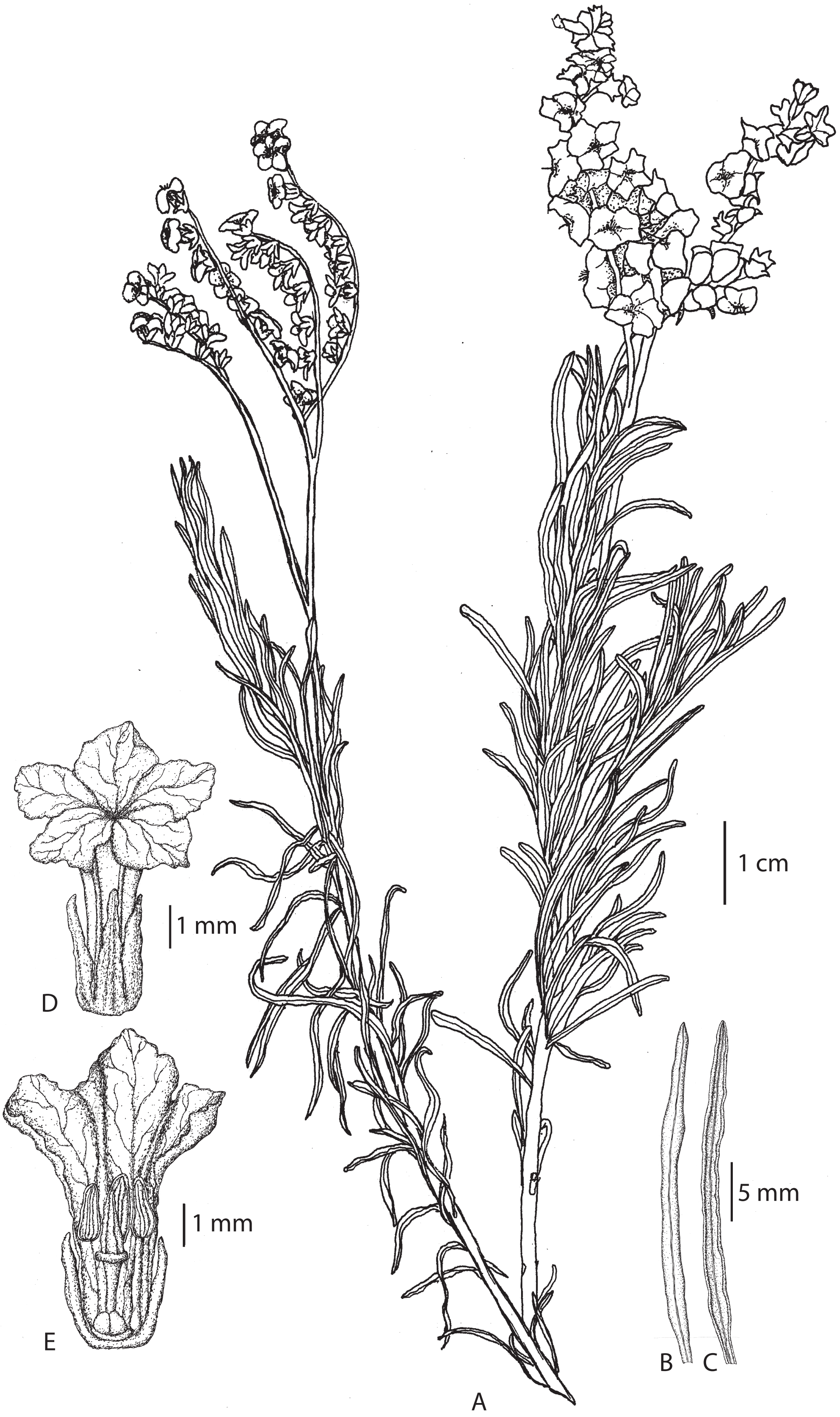

Figure 6.19: *Heliotropium stenophyllum.* A, Flowering branch; B, Leaf - adaxial surface; C, Leaf - abaxial surface; D, Flower - outer view; E, Flower - inner view. (All from *Luebert & Becker* 2910, BSB). Drawn by Anja Salchow.

*Heliotropium stenophyllum* should be regarded as missing, as is not to be found at E. A neotype have thus been selected here from modern material coming from the same locality cited by Hooker and Arnott (1830) and agreeing with the protologue and with the way Hooker applied the name to other material of his herbarium, which corresponds to the historical and current application of the name.

In his description of *Heliotropium huascoense*, Johnston (1928b) indicated that his new species is closely related to *Heliotropium stenophyllum*, but that it differs from the latter 'in its narrowly spathulate leaves, smaller corolla, shorter style, as well as more northern range'. Examination of more material reveals that none of these characters is consistent across the geographic range of both species, although the northernmost populations tend to have more spathulate leaves, but as a part of a rather gradual transition than a discrete change. Also, some specimens from the middle of the range of *Heliotropium stenophyllum* (e.g., *Luebert & Becker* 2918) have also spathulate leaves. Moreover, Johnston (1928b: 34) based his geographic differentiation of *Heliotropium huascoense* partially on the assumption that *Heliotropium sinuatum*, that was mixed in the same sheet of two paratype specimens (*Pearce* s.n. and *Lobb* 442, both K) along with material attributed to *H. huascoense*, does not occur in the region of Coquimbo, from which the mentioned specimens were labelled to come from. Modern material of *Heliotropium sinuatum* show that this assumption is false, and that what could be called *Heliotropium huascoense* occurs in the same geographic range of *Heliotropium stenophyllum* sensu Johnston (1928b). Due to this fact and the failure to consistently differentiate both species, *Heliotropium huascoense* is placed here under the synonymy of *H. stenophyllum*.

**13. Heliotropium longistylum** *Phil.* (Philippi, 1873: 515); Reiche (1907a: 240); Reiche (1910: 198); Johnston (1928b: 34); Förther (1998: 205). Type: Chile, Región de Atacama, Prov. Huasco, Carrizal Bajo, Dec. 1871, *T. King* s.n. (lectotype SGO 54363 [photo F, G, GH, MSB, NY, US], selected by Förther (1998: 205); duplicates GH [fragm.], K [photo SGO 2265], SGO 42221 [photo GH, MSB])

*Cochranea longistyla* (Phil.) Phil. (Philippi, 1895: 349). Type as above.

*Heliotropium vernicosum* Phil. (Philippi, 1895: 355). Type: Chile, Región de Atacama, Prov. Huasco, Carrizal Bajo, Sept. 1885, *F. Philippi* s.n. (lectotype SGO 54362 [photo F, GH, MSB, NY, US], selected by Förther (1998: 226); duplicates GH [fragm.], SGO 42218 [photo MSB]).

*Erect shrubs*, 0.4 – 1.2 m tall, with ascending branches, densely foliose to the base of the inflorescence. Stems and foliage finely strigose or glabrous, glutinous. *Leaves* alternate, solitary or grouped in fascicles of up to 12 leaves, sessile, linear to linear-elliptic, 12 – 62 × 1 – 6 (– 7) mm; lamina glabrous, dark green, margin entire, revolute, base attenuate, apex obtuse, with only the main vein conspicuous. *Inflorescences* terminal, elongate, dichotomically branched, to ca. 10 cm long. *Flowers* sessile, alternate, erect, aromatic. Calyx cylindric, green or greyish-green; calyx lobes linear, fused only at the base, glutinous, with ciliated margins, strigose outside, glabrous within, 3 – 6.5 × 0.5 – 1 mm, free portion 3.5 – 6 mm long, apex acute. Corolla infundibuliform, sparsely strigose, dull white with yellow throat; limb horizontally spreading, 7.5 – 12.5 mm wide, lobes rounded; tube longer than the calyx, 6 – 8.5 mm long. Stamens included or exserted at late anthesis; filaments adnate to petals; anthers oblong-lanceolate, glabrous, base cordate, apex acute, ca. 1 – 1.2 mm long, overlapping the stigmatic head. Ovary glabrous, subglobose, 0.3 –

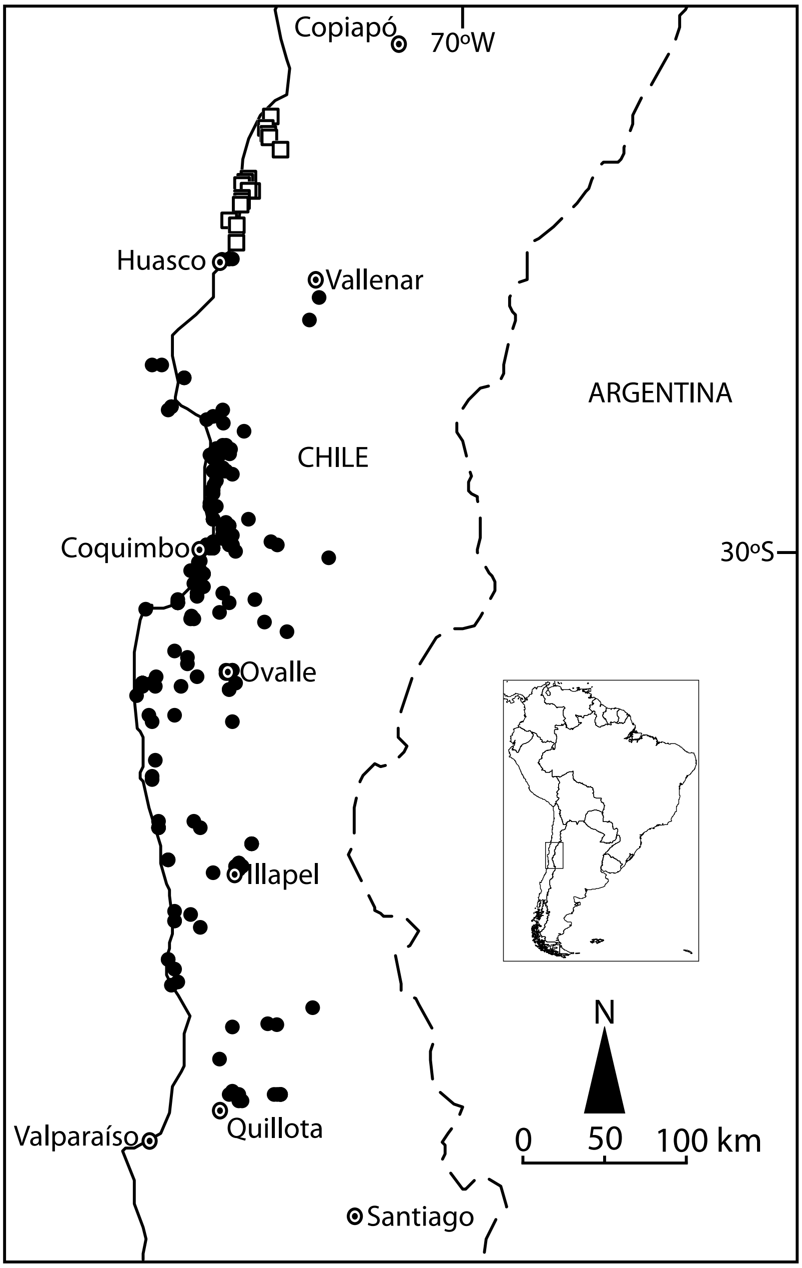

Figure 6.20: Distribution of *Heliotropium stenophyllum* (●) and *H. longistylum* (□).

0.8 mm diam., with a basal nectar ring. Style glabrous, ca. 1.1 – 2 mm long, longer than the stigmatic head. Stigmatic head conic, elongated, bilobate, ca. 0.8 – 1.2 × 0.7 mm. *Fruits* dry, ellipsoid, rugose, glabrous, light brown or cream, ca. 3.5 × 2 mm diam., falling apart at maturity into two 2-seeded nutlets, ca. 2 × 2 mm diam.

*Pollen* prolate, 21.4 – 25.1 × 16.5 – 19.3 μm (from *Ackermann* 518, BSB).

**DISTRIBUTION**. Endemic to the coastal areas or the provinces of Copiapó and Huasco (Región de Atacama, Chile), between 27°43'S and 28°22'S (Fig. 6.20).
**SPECIMENS EXAMINED**. See Appendix E (p. 312).
**HABITAT**. Sandy plains, coastal rocks and ravines, always near the coast, 5 – 400 m. Usually scarce and rarely dominant, in a shrubby vegetation dominated by *Atriplex*

*mucronata* (Amaranthaceae), *Eulychnia breviflora* (Cacataceae), *Heliotropium sinuatum* (Heliotropiaceae) and *Oxalis virgosa* (Oxalidaceae).
**CONSERVATION STATUS**. Endangered (EN), criterion B2(c), see Chapter 5.
**FLOWERING TIME**. September to October.
**ETYMOLOGY**. The epithet *longistylum* refers to its long style.
**USES**. Riedemann et al. (2006) suggest its potential use as ornamental.
**NOTES**. This species is closest to *Heliotropium stenophyllum*, from which it differs in its larger leaves and flowers, as well as in its style longer than the stigmatic head (versus style shorter than or as along as the stigmatic head in *H. stenophyllum*). *Heliotropium longistylum* is distributed north of the northernmost populations of *H. stenophyllum* (Fig. 6.20). Aberrant, small individuals of *Heliotropium longistylum* with strigose leaves can be confounded with *H. floridum*, but it can distinguished from the latter in its glutinous foliage (versus non-glutinous in *H. floridum*). The possibility of hybridization between *Heliotropium longistylum* and *H. floridum* cannot be ruled out, as they grow in local parapatry at some localities (e.g., Carrizal Bajo). Both species fall in an unresolved polytomous group in the phylogeny of section *Cochranea* (Luebert and Wen, 2008; see Chapter 2).

In the protologue of *Heliotropium longistylum* is indicated that the plant was collected by T. King. It should be noted that the lectotype specimen (SGO 54363) does not have collector's name on its label. However, Muñoz (1960) cites it among the syntypes and its collection date coincides with the other specimen (SGO 42221), which does have collector's name.

**14. Heliotropium floridum** (*A. DC.*) *Clos*, in Gay (1849: 457); Reiche (1907a: 240); Reiche (1910: 198); Johnston (1928b: 37); Marticorena (1968: 44); Förther (1998: 195). Type: Chile. ad Coquimbo, 1839 [1837?], *C. Gay* 1182 (holotype G-DC! [photo F neg. n° 7769: F, GH, NY, US, photo SGO 67284]; isotypes GH, P not seen [digital photograph!, fragm. F 515902, F 970065, photo MSB]) probable isotypes [Chili, *Gay* (1834-1842)] G, [Chili *Gay*] K, P not seen [digital photograph!, photo MSB])

*Heliophytum floridum* A.DC. (de Candolle, 1845: 553). Type as above.
*Cochranea florida* (A.DC.) Miers (1868: 129). Type as above.
*Heliotropium floridum* (A. DC.) Clos var. *latifolium* Phil. (Philippi, 1873: 516). Type: Chile, Región de Atacama, Prov. Huasco, Carrizal Bajo, Dec. 1871, *T. King* s.n. (lectotype SGO 54384 [photo F, GH, MSB, NY, US], selected by Förther (1998: 195); duplicates GH [fragm.], SGO 54385 [photo MSB], possible duplicate K)

*Erect shrubs*, 0.15 – 0.8 (– 1) m tall, with ascending branches, densely foliose to the base of the inflorescence. Stems and foliage strigose. *Leaves* alternate, solitary or grouped in fascicles of up to 13 leaves, sessile, succulent linear to linear-spathulate, 6.5 – 30 (– 40) × 1 – 9.5 (– 11) mm; lamina strigose, green or greyish-green, margin entire, revolute, base attenuate, apex obtuse, with only the main vein conspicuous. *Inflorescences* terminal, elongate, dichotomically branched, congested, to ca. 6 (– 9) cm long. *Flowers* sessile or shortly (<1 mm) pedicellate, alternate, erect. Calyx cylindric, green or brownish-green; calyx lobes linear, fused only at the base or free, strigose on both sides, 2.5 – 5.5 × 0.5 – 1.5 mm, free portion 2 – 5.5 mm long, apex acute. Corolla infundibuliform, sparsely strigose, dull white with yellow to orange throat, becoming bluish at late anthesis; limb horizontally spreading, 5.5 – 11.5 mm wide, lobes rounded; tube longer than the calyx, 5 – 9 mm long. Stamens included or exserted at late anthesis; filaments adnate to petals; anthers oblong-

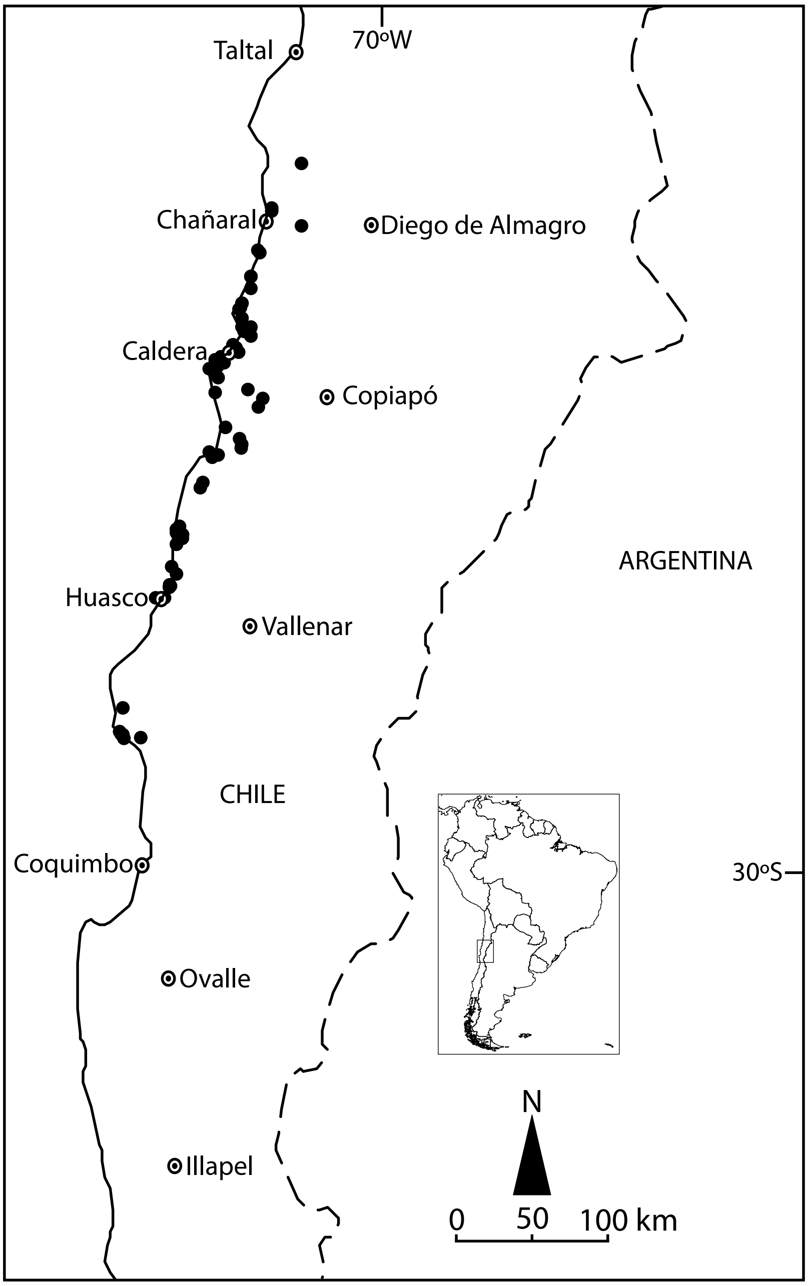

Figure 6.21: Distribution of *Heliotropium floridum.*

lanceolate, glabrous, base cordate, apex acute, ca. 1.2 – 1.5 mm long, overlapping the stigmatic head. Ovary glabrous, subglobose, 0.4 – 0.6 mm diam., with a basal nectar ring. Style glabrous, ca. 1.5 – 2 mm long, longer than the stigmatic head. Stigmatic head conic, elongated, bilobate, ca. 0.7 – 1 × 0.7 mm. *Fruits* dry, ellipsoid, rugose, glabrous, brown, ca. 2.5 × 1.5 mm diam., falling apart at maturity into two 2-seeded nutlets, ca. 1.5 × 1.5 mm diam.

**DISTRIBUTION**. Coastal range of the provinces of Chañaral, Copiapó, Huasco (Región de Atacama) and Elqui (Región de Coquimbo), Chile, between 26°2'S and 29°15'S (Fig. 6.21).
**SPECIMENS EXAMINED**. See Appendix E (p. 312).

**HABITAT**. Coastal dunes, rocky hills and sandy plains, 0 – 270 m. In the sandy plains the vegetation is usually a scrub with columnar cacti, where *Heliotropium floridum* can be dominant together with *Atriplex clivicola* (Amaranthaceae) and *Eulychnia breviflora* (Cactaceae). In the coastal dunes it can also be dominant together with *Chuquiraga ulicina* (Hook. & Arn.) Hook. & Arn. (Asteraceae) and *Cristaria glaucophylla* Cav. (Malvaceae).
**CONSERVATION STATUS**. Least concern (LC), criterion B2(c), see Chapter 5.
**FLOWERING TIME**. September to November.
**ETYMOLOGY**. The epithet *floridum* refers to its congested inflorescence.
**USES**. Riedemann et al. (2006) suggest its potential use as ornamental.
**NOTES**. This species might be locally confounded with *Heliotropium longistylum* and *H. megalanthum* (see discussion under these species). In herbaria it is frequently confounded with *Heliotropium linariifolium*. The latter has orange flowers and decumbent habit (versus white flowers and erect habit in *H. floridum*), but these characters are difficult to see in herbarium specimens. Both species overlay their geographic areas in the coastal range between the towns of Caldera and Chañaral, and material coming from that area is usually difficult to distinguish in herbarium specimens, unless there is indication of flower colour or habit.

It can also be confounded with *Heliotropium philippianum*, with which does not overlay its geographic range. *Heliotropium philippianum* is distributed from Paposo (ca. 25°S) northwards, while *H. floridum* from Chañaral (ca. 26°S) southwards. *Heliotropium philippianum* is a shrub usually taller than 0.6 m, while *H. floridum* is almost always shorter. Both species were recovered in an unresolved clade in the phylogeny of section *Cochranea* (Luebert and Wen, 2008; see Chaptee 2).

**15. Heliotropium linariifolium** *Phil.* (Philippi, 1860a: 38); Philippi (1895: 354); Reiche (1907a: 239); Reiche (1910: 197); Johnston (1928b: 37); Marticorena (1968: 44); Förther (1998: 203). Type: Chile, in regioni litorali deserti herbosa ad Cachinal de la Costa, 13 Dec. 1853, *R.A. Philippi* s.n. (lectotype SGO 42217 [photo F, GH, MSB, NY, US], selected by Johnston (1928b: 37); duplicate B† [photo F neg. n° 17329: F, GH, NY, US]).

*Heliotropium linearifolium* F.Phil. (Philippi, 1881: 212), by mistake.
*Heliotropium longiflorum* Phil. (Philippi, 1895: 354), **nom. illegit.**, non *H. longiflorum* (A.DC.) Jaub. & Spach (Jaubert and Spach, 1852: 96, pl. 360). Type: Chile, in deserto Atacama ad Breas, 1888, *A. Larrañaga* s.n. (holotype SGO 54350 [photo F, GH, MSB, NY, US]; isotype SGO 54352).

*Decumbent shrubs*, 0.15 – 0.3 (– 0.6) m tall, with ascending branches, densely foliose to the base of the inflorescence. Stems and foliage strigose. *Leaves* alternate, solitary or grouped in fascicles of up to 13 leaves, sessile, linear to linear-spathulate, 8.5 – 40 × 1 – 5.5 mm; lamina strigose, green or greyish-green, margin entire, revolute, base attenuate, apex acute or obtuse, with only the main vein conspicuous. *Inflorescences* terminal, elongate, dichotomically branched, congested, to ca. 8 (– 14) cm long. *Flowers* sessile or shortly (ca. 1 mm) pedicellate, alternate, erect. Calyx cylindric, green or brownish-green; calyx lobes linear, fused only at the base or free, strigose on both sides, 3 – 6 × 0.5 – 0.7 mm, free 2.5 – 6 mm portion, apex acute. Corolla infundibuliform, sparsely strigose, orange; limb horizontally spreading, 5.5 – 10 mm wide, lobes rounded; tube longer than the calyx, 6 – 8.5 mm long. Stamens included or exserted at late anthesis; filaments adnate to petals; anthers oblong-lanceolate, glabrous, base cordate, apex acute, ca. 1.5 mm long, above the

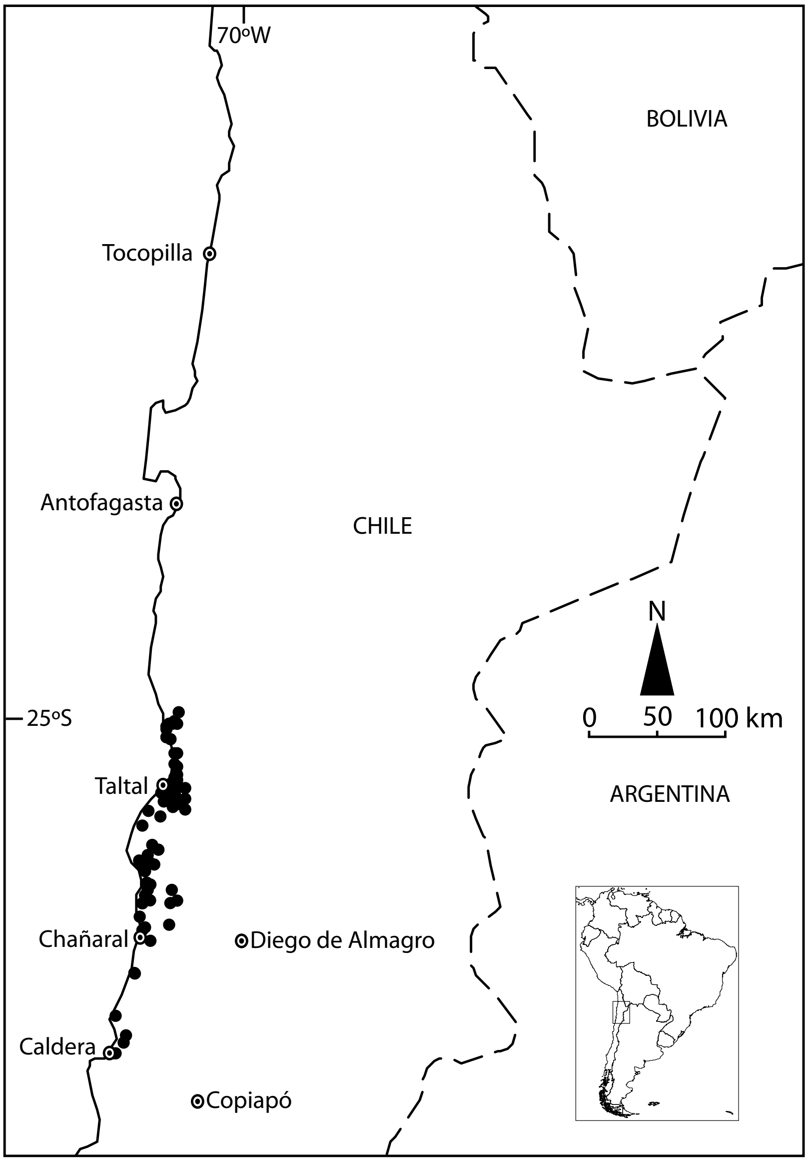

Figure 6.22: Distribution of *Heliotropium linariifolium*.

apex of or overlapping the stigmatic head. Ovary glabrous, subglobose, ca. 0.4 mm diam., with a basal nectar ring. Style glabrous, ca. 0.7 – 1.8 mm long, longer than the stigmatic head. Stigmatic head conic, elongated, bilobate, ca. 0.5 – 1.5 × 0.5 – 0.7 mm. *Fruits* dry, ellipsoid, rugose, glabrous, brown, ca. 2 × 1.5 mm diam., falling apart at maturity into two 2-seeded nutlets, ca. 1.5 × 1.5 mm diam.

*Pollen* prolate, 26.5 – 28 × 15 – 17 $\mu$m. Endoapertures ca. 3.5 $\mu$m diam., circular or contracted at the centre. Exine thickness ca. 1.3 $\mu$m. Amb lobes not deep. Colpifereous sides convex (from *Ricardi* 3144 in Marticorena, 1968).

**DISTRIBUTION**. Coastal range of the provinces of Antofagasta (Región de Antofagasta), Chañaral and Copiapó (Región de Atacama), Chile, between 24°56'S and 27°4'S (Fig. 6.22). The collection of *Zalensky* XV-866, given for Lago Chingará (ca. 4200 m) is certainly erroneous.

**SPECIMENS EXAMINED**. See Appendix E (p. 313).

**HABITAT**. Rocky slopes, sandy plains and gravely stream-ways, out of the fog zone, 0 – 1000 (– 1300) m. It can be found at low elevations under the fog zone, high elevations above the fog zone or leeward of the coastal mountains. It is seldom dominant, though in rainy years can become very abundant. Forms part of the coastal scrubs where *Heliotropium pycnophyllum* (Heliotropiaceae), *Gypothamnium pinifolium*, *Oxyphyllum ulicinum* Phil. (both Asteraceae), and *Gymnophyton foliosum* Phil. (Apiaceae) are the dominant species. Kohler (1970) reports it as part of the vegetation of dunes, where *Tetragonia maritima* (Aizoaceae), *Nolana divaricata* (Lindl.) I.M.Johnst. and *N. carnosa* Miers ex Dunal (Solanaceae) are dominant.

**CONSERVATION STATUS**. Least concern (LC), criterion B2(c), see Chapter 5.

**FLOWERING TIME**. September to November.

**ETYMOLOGY**. The epithet *linariifolium* refers to its leaves similar to species of the genus *Linaria* Mill. (Plantaginaceae).

**USES**. Johnston (1928b) and Riedemann et al. (2006) suggest its potential use as ornamental.

**NOTES**. In the protologue of *Heliotropium linariifolium*, Philippi (1860a) cites three syntypes, one from Miguel Díaz (SGO 42220), one from Paposo (SGO 42216), and one from Cachinal de la Costa (SGO 42217). In the protologue, the species is decribed as being 1.2 m tall, leaves 25 – 30 mm long, 3.7 – 4.2 mm wide, calyx 4.2 mm long, corolla white 7.5 mm long. These characters corresponds to what Johnston (1928b) described as *Heliotropium philippianum*, whose paratypes are the two first mentioned Philippi 's specimens. Johnston (1928b) lectotypified *Heliotropium linariifolium* with the material of Cachinal de la Costa, which is a decumbent shrub, not taller than 0.5 m, with orange corollas. This lectotype is therefore in conflict with the protologue and should be superseded in favor of one of the other Philippi's specimens (Art. 9.17). In this case *Heliotropium philippianum* should be treated as synonym of *H. linariifolium*. However, such a change would contradict Art. 57.1, because the name *H. linariifolium* has been, since Reiche (1907a), persistently applied to the species with orange flowers. The lectotypification of Johnston (1928b), though in conflict with the protologue of *Heliotropium linariifolium*, is here accepted. As a consequence, *Heliotropium philippianum* is the only valid name available for the species with white flowers.

*Heliotropium linariifolium* is easily distinguished from the other species of section *Cochranea* for its orange corollas. Since corolla colour is sometimes difficult to appreciate in dry material, herbarium specimens of this species can be confounded with *Heliotropium floridum* (see discussion under this species), *H. philippianum*, and, eventually, *H. eremogenum*. These four species are phylogenetically closely related (Luebert and Wen, 2008; see Chapter 2). From the latter it clearly differs in its larger leaves, but it is otherwise very similar. The citation of Johnston (1932: 7) of *Heliotropium linariifolium* for Iquique was probably due to their similarity. The material of Iquique is here treated under *Heliotropium eremogenum*, described by Johnston (1937) later on. From *Heliotropium philippianum*, herbarium specimens are almost indistinguishable when there is no indication of flower colour or habit. *Heliotropium philippianum* is an erect shrub with white flowers, while *H. linariifolium* is a decumbent shrub with orange flowers. This is particularly problematic in the area around Paposo, where both species occur.

**16. Heliotropium philippianum** *I.M.Johnst.* (Johnston, 1928b: 36); Förther (1998: 212). Type: Chile, Región de Antofagasta, Prov. Antofagasta, Vicinity of Paposo, hill directly back of Punta Grande, 29 Nov. 1925, *I.M. Johnston* 5233 (holotype GH; isotypes E not seen (digital photograph!), K [photo SGO 2267], US 1495296).

*Erect or subscandent shrub*, 0.6 – 1.5 (– 2) m tall, with ascending branches, densely foliose to the base of the inflorescence. Stems and foliage strigose. *Leaves* alternate, solitary or grouped in fascicles of up to 8 leaves, sessile, linear-spathulate, linear-elliptic or elliptic, 5 – 30 × 1 – 6 mm; lamina strigose, green or greyish-green, margin entire, revolute, base attenuate, apex acute or obtuse, with the main vein conspicuous and the secondary veins sometimes visible. *Inflorescences* terminal, elongate, dichotomically branched, congested, to ca. 5 cm long. *Flowers* sessile or shortly (<1 mm) pedicellate, alternate, erect, aromatic. Calyx cylindric, green or brownish-green; calyx lobes linear, free, strigose outside, glabrous or strigose within, (1.5 –) 3.5 – 5 × 0.1 – 1 (– 2) mm, free portion 3.5 – 5 mm long, apex acute. Corolla infundibuliform, sparsely strigose, white with orange or yellow throat; limb horizontally spreading, 5.5 – 9 mm wide, lobes rounded; tube longer than the calyx, 4 – 7.5 mm long. Stamens included or exserted at late anthesis; filaments adnate to petals; anthers oblong-lanceolate, glabrous, base cordate, apex acute, ca. 1 – 1.5 mm long, above the apex of or overlapping the stigmatic head. Ovary glabrous, subglobose, ca. 0.6 mm diam., with a basal nectar ring. Style glabrous, ca. 1.8 – 2.5 mm long, longer than the stigmatic head. Stigmatic head conic, elongated, bilobate, ca. 1.5 – 2 × 0.7 mm. *Fruits* dry, ellipsoid, smooth or rugose, glabrous, brown, ca. 2 × 1.5 mm diam., falling apart at maturity into two 2-seeded nutlets, ca. 1 × 1.5 mm diam.

**DISTRIBUTION**. Endemic to the coastal range of the area between Paposo and Blanco Encalada (province of Antofagasta, Región de Antofagasta, Chile), between 24°26'S and 25°6'S (Fig. 6.23).
**SPECIMENS EXAMINED**. See Appendix E (p. 315).
**HABITAT**. Gravelly and rocky hillsides and gravelly stream-ways of the fog zone, where is never dominant. It forms part of the coastal scrub typically dominated by *Euphorbia lactiflua* (Euphorbiaceae) and *Eulychnia iquiquensis* (Cactaceae) (Johnston, 1929a; Luebert and Pliscoff, 2006).
**CONSERVATION STATUS**. Critically endangered (CR). According to the criterion of extent of occurrence (B1), this species should be classified as critically endangered; after the application of the criterion of area of occupancy is classified as endangered (EN). Tho more critical of them has been selected according to the recommendations of IUCN (2001).
**FLOWERING TIME**. September to November.
**ETYMOLOGY**. The epithet *philippianum* honours Rodulfo A. Philippi, the first collector of the species.
**NOTES**. This species is morphologically similar and probably closely related to *Heliotropium floridum*, *H. linariifolium* and *H. eremogenum*. See discussion under the two former species. From *Heliotropium eremogenum*, this species differs from its generally longer leaves, erect habit (versus decumbent habit in *H. eremogenum*) and more southern geographic range (Fig. 6.23).

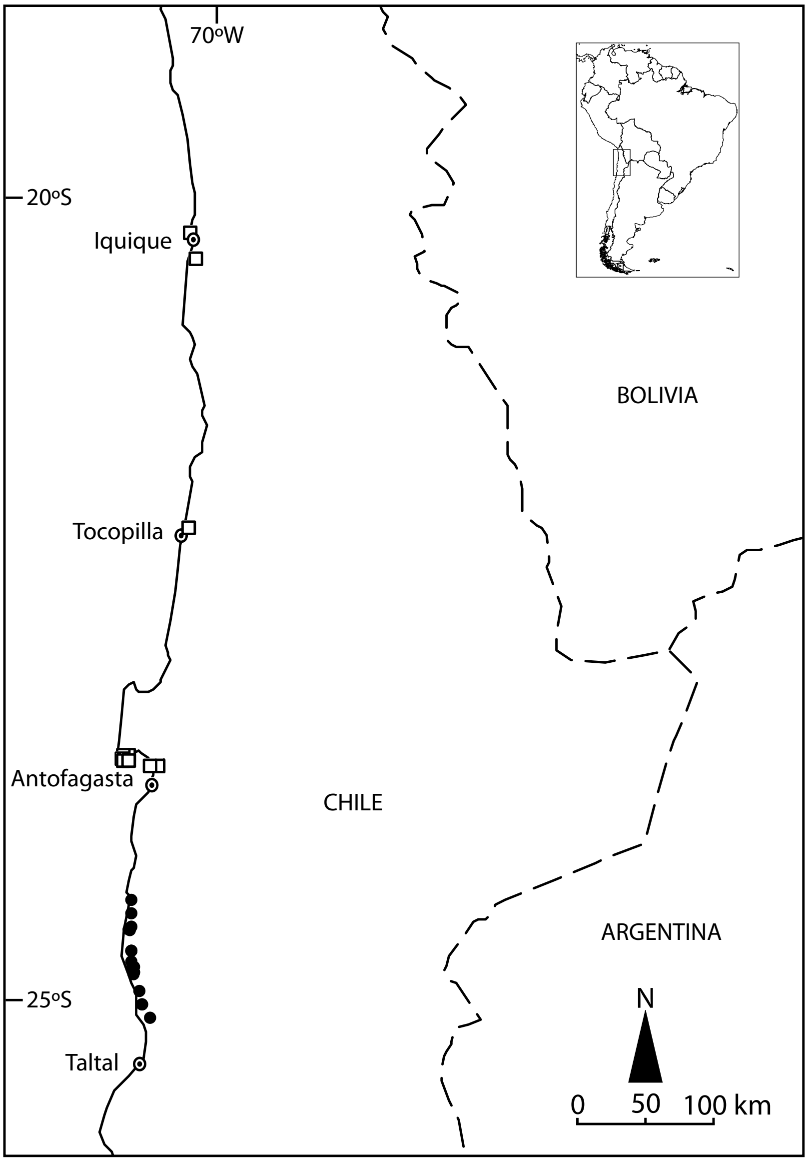

Figure 6.23: Distribution of *Heliotropium philippianum* (●) and *H. eremogenum* (□).

**17. Heliotropium eremogenum** *I.M.Johnst.* (Johnston, 1937: 20); Förther (1998: 192). Type: Región de Antofagasta, Prov. Antofagasta, Antofagasta, 29 Oct. 1930, *F. Jaffuel* 1120 (holotype GH).

*Decumbent shrubs*, 0.1 – 0.3 m tall, with ascending branches, densely foliose to the base of the inflorescence. Stems and foliage strigose. *Leaves* alternate, solitary or grouped in fascicles of up to 5 leaves, sessile, linear-oblaceolate or linear-elliptic, 2 – 6.5 × 1 – 2 mm; lamina strigose, green or greyish-green, margin entire, revolute, base attenuate, apex acute, with only the main vein conspicuous. *Inflorescences* terminal, elongate, dichotomically branched, congested, to ca. 3 cm long. *Flowers* sessile, alternate, erect. Calyx cylindric, green or brownish-green; calyx lobes linear, free, strigose outside, glabrous or strigose within, (1 –) 2.5 – 3.5 (– 4.5) × 0.5 – 0.7 mm, free portion 2.5 – 3.5 mm long, apex acute. Corolla infundibuliform, sparsely strigose, white with yellow throat; limb horizontally spreading, 5 – 7 mm wide, lobes rounded; tube longer than the calyx, 4.5 – 6 mm long. Stamens included or exserted at late anthesis; filaments adnate to petals; anthers oblong-lanceolate, glabrous, base cordate, apex acute, 1.5 – 2 mm long, above the apex of or overlapping the stigmatic head. Ovary glabrous, subglobose, ca. 0.6 mm diam., with a basal nectar ring. Style glabrous, ca. 1.5 – 2.5 mm long, longer than the stigmatic head. Stigmatic head conic, elongated, bilobate, ca. 1 – 2 × 0.7 mm. *Fruits* dry, ellipsoid, smooth or rugose, glabrous, brown, ca. 1.5 × 1 mm diam., falling apart at maturity into two 2-seeded nutlets, ca. 0.7 × 1 mm diam.

*Pollen* prolate, 21.5 – 24.8 × 11.3 – 12 $\mu$m (from *Luebert & García* 2575/969, BSB).

**DISTRIBUTION**. Endemic to the coastal range of the area of Antofagasta (Cerro Moreno – La Chimba, 23°28'S – 23°39'S, province of Antofagasta, Región de Antofagasta, Chile), with two isolated stations in the surroundings of Tocopilla (22°3'S, province of Tocopilla, Región de Antofagasta, Chile) and Iquique (20°13'S – 20°22'S, province of Iquique, Región de Tarapacá, Chile) (Fig. 6.23). The locality of the collection of *Kuschel* s.n. (Putre) is very doubtful. A search in the database of the Natural History Museum in Santiago (SGO), showed that Kuschel actually collected in La Chimba just before his trip to Putre. It is therefore very likely that this specimen was erroneously labelled.
**SPECIMENS EXAMINED**. See Appendix E (p. 316).
**HABITAT**. Coastal hills, on rocky slopes of the fog zone in a very arid area, between 100 – 1020 m, where several years without rain are common. All materials from Tocopilla and Iquique are fragmentary, probably due to long periods of aridity. The vegetation corresponds to a desert scrub dominated by *Ephedra breana* (Ephedraceae), *Euplychnia iquiquensis* (Cactaceae) and *Nolana peruviana* (Gaudich.) I.M.Johnst. (Solanaceae) (Johnston, 1929b; Luebert et al., 2007).
**CONSERVATION STATUS**. Critically endangered (CR). The same reasoning as for *Heliotropium philippianum* is applied to this species.
**FLOWERING TIME**. September to November.
**ETYMOLOGY**. The epithet *eremogenum* probably refers to the very arid areas where this species grows.
**NOTES**. The closest relative of this species seems to be *Heliotropium philippianum*. It is also morphologically smilar and phylogentically related to *Heliotropium floridum* and *H. linariifolium*. See discussion under these species.

This species was mentioned by Johnston in several works as an undescribed *Heliotropium* species (Johnston, 1928b, 1929b, 1932), until Jaffuel's material became available. Johnston (1937) suggests that the materials from Iquique and Tocopilla are closely allied to this species, but, due to its fragmentary nature, he did not include them, saying that good collections will prove that it corresponds to a different species. While such good collections have not become available yet, these populations are provisionally regarded here as part of *Heliotropium eremogenum*. Material from Iquique was included in the phylogenetic analysis of Luebert and Wen (2008). It falls in an unresolved clade together with most species of section *Cochranea*.

### 6.4.13 Excluded Names

*Cochranea anchusaefolia* (Poir.) Gürke (1893: 97) ≡ *Heliotropium anchusaefolium* Poir. (Poiret, 1813: 23) = ***Heliotropium amplexicaule*** Vahl (1794: 21) (sect. *Heliotrophytum*)

*Cochranea anchusaefolia* (Poir.) Gürke var. *latifolia* Hicken (1910: 194) ≡ *Heliophytum anchusaefolium* (Poir.) DC. var. *latifolium* DC. (de Candolle, 1845: 554) = ***Heliotropium amplexicaule*** Vahl (sect. *Heliotrophytum*)

*Heliotropium macrostachyum* (DC.) Hemsl. (Hemsley, 1881-1882: 375) ≡ *Heliophytum macrostachyum* DC. (de Candolle, 1845: 556). Johnston (1939) regarded this species as a member of section *Cochranea*. The examination of the type material (G-DC) reveals that this species has few common morphological characters with the members of section *Cochranea*. The leaves of *Heliotropium macrostachyum* are broadly elliptic ca. 8 × 3 cm or larger, denselly pubescent, with a petiole of ca. 2 cm long, while in section *Cochranea* the leaves are usually linear or narrowly elliptic and very rarely wider than 1 cm, in which case are never densely pubescent; the leaves in *Cochranea* are at most shortly petiolate and mostly sessile. The inflorescences of *Heliotropium macrostachyum* are no or one-time divided and up to 20 or even 30 cm long. In section *Cochranea* the inflorescences are two or more timed divided and are never longer than 15 cm. The corolla tube is villous inside and pubescent outside in *Heliotropium macrostachyum*, while in *Cochranea* is always glabrous inside and hirsute or villous outside. The fruits of *Heliotropium macrostachyum* are apically bi-horned, globose, ca. 3 mm diam., with 2 cells empty, falling into two one-seeded nutlets, while in *Cochranea* fruits are never bi-horned, usually 1-2 cm diam., without empty cells, and falling into two two-seeded nutlets. *Heliotropium macrostachyum* and section *Cochranea* have totally different geographic ranges, the former occurring only in Mesoamerica. For its morphology *Heliotropium macrostachyum* may be rather a member of section *Tiaridium* from the *Tournefortia* clade of Luebert et al. (in press; see Chapter 3) and its systematic placement in phylogenetic analyses remains to be seen.

*Heliotropium genovefae* I.M.Johnst. (Johnston, 1939: 378). Johnston (1939) described this species as a member of section *Cochranea*. However it has a few or no character that allows associating it with the latter section. In gross aspect is similar to *Heliotropium macrostachyum* and the description of the fruits by Johnston (1939) apparently agrees in size with the latter species, although in *H. genovefae* there are no empty cells. I have only seen an isotype specimen (K), which bears no fruits. It is only known from its type collection made at Port à L'Ecu, Haiti. It probably belongs to the *Tournefortia* clade (Luebert et al., in press; Chapter 3), perhaps to section *Tiaridium*, but it has never been included in phylogenetic analyses.

# 7. Epitypification of *Heliotropium arborescens* L. (Heliotropiaceae)[a]

## Abstract

The plate designated as lectotype of the name *Heliotropium arborescens* L. (1759) does not permit a precise application of the name. The herbarium material associated with that illustration was examined in order to clarify the identity of the type material and an epitype was selected. The epitype corresponds in morphology to the taxon called *Heliotropium urbanianum* K.Krause (1906) in the recent literature, which is here lectotypified and synonymized with *H. arborescens*. The name *Heliotropium arborescens* has been misapplied to a predominantly Peruvian species, which should now be correctly called *Heliotropium corymbosum* Ruiz & Pav. (1799). The epitypification here proposed will ensure nomenclatural stability for most material from cultivation, where the name *Heliotropium arborescens* is widely used.

## 7.1 Introduction

The most commonly cultivated species of the widespread genus *Heliotropium* L. is a shrubby species from South America that belongs to the Andean *Heliotropium* sect. *Heliothamnus* I.M. Johnst., and is usually known under the name *Heliotropium arborescens* L. (Linnaeus, 1759) or under its homotypic synonym *Heliotropium peruvianum* L. (Linnaeus, 1762; see Jarvis, 2007). The name *Heliotropium arborescens* L. was established on the basis of a plate by Miller (1757: pl. 144, erroneously cited by Linnaeus as plate 143, see McClintock and Fryxell (1979)). The plate (available on-line from the Digital Library of the Real Jardín Botánico of Madrid, `http://bibdigital.rjb.csic.es/Imagenes/Of_MIL_Fig_Pl_1/MIL_Fig_Pl_1_247.pdf`, accessed 11 December 2009) was based on a plant cultivated at that time in the Chelsea Physic Garden, where Miller worked as gardener from 1722 to 1772 (Underwood, 1963). This plate was designated as lectotype for *H. arborescens* L. by Riedl (1997: 102; see Jarvis 2007). Johnston (1928b) indicated the presence of a herbarium specimen at BM, and considered it as the type of 'Miller's plant from the Chelsea Gardens'. However, the latter cannot be considered as a valid lectotypification, because in the description of *H. arborescens* by Linnaeus (1759) only the plate of Miller (1757: pl. 144) is cited, and there is no evidence that Linnaeus ever saw any of Miller's specimens, to which Johnston (1928b) refers. These specimens are thus not part of the original material. In consequence, the lectotypification by Riedl (1997) can not be superseded in spite of the presence of the herbarium specimens.

*Heliotropium arborescens* is the type of *Heliotropium* sect. *Heliothamnus*, a group of ca. eleven Andean and Central American species (Johnston, 1928b; Förther, 1998) with a particularly complex taxonomy and difficult species delimitation. According to Johnston

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[a] Published as: Luebert, F., Weigend, M. and Hilger, H.H. 2010. Epitypification of *Heliotropium arborescens* L. (Heliotropiaceae). *Taxon* 59(4): 1263-1266.

(1928b), the morphology of the style stigma complex, as well as the presence of glandular trichomes on the surface of the ovary are the most important characters to key out the species within *Heliotropium* sect. *Heliothamnus*. Unfortunately, the morphology of the gynoecium is not depicted in the lectotype plate of Miller (1757: pl. 144), nor is it mentioned in the accompanying description. It therefore cannot be identified for the purposes of precise application of the name *Heliotropium arborescens*. It seems hence evident that the name *Heliotropium arborescens* needs to be unambiguously applied through the designation of an epitype. A suitable epitypification would be both nomenclaturally stabilizing and taxonomically clarifying. In this note, we establish the connection between Miller's (1757) plate, and the specimens housed at BM mentioned by Johnston (1928b) and select one of them as the epitype of *Heliotropium arborescens*.

## 7.2 Miller's Specimens and Epitypification

There are three main sources of herbarium material of Miller's plants (Britten, 1913; Stearn, 1972, 1974): (1) the Sloane Herbarium, (2) the Miller Herbarium, acquired by Joseph Banks after Miller's death and (3) the specimens sent from the Chelsea Physic Garden to the Royal Society of London. All of them can now be found in the herbarium of the Natural History Museum in London (BM). Some additional specimens of Miller are also held at the Linnaean Herbarium, LINN (Stafleu and Cowan, 1981).

Since the first reference to *Heliotropium arborescens* in Miller's works dates to 1757, it is not possible that any of Miller's herbarium specimen of the species under study is found in the Sloane Herbarium, because it only contains plants given by Miller to Sloane between 1727 and 1739 (Dandy, 1958). Two specimens deposited in the general collection of BM correspond to the other two sources of Miller's material: (1) One of them consists of a single fragment of a flowering branch and is labelled as sent to the Royal Society of London with the number 1770; according to Wilmer (1758), this number corresponds to a specimen that, holding the same name Miller gave to the plate (Miller, 1757: pl. 144), was sent to the Royal Society of London in 1757, which is the same year Miller first published the plate. It is very likely that this specimen had been taken directly from the plant cultivated at Chelsea from which the plate was drawn. (2) The other material, doubtlessly conspecific with the latter, consists of several flowering branches; it probably was part of Miller's herbarium as it is labelled as 'Hort. Chels.' on the reverse side (Britten, 1913); it also has the annotations 'Stylus breviformis' and 'Mill. Dict. 6', which is the number of the species in subsequent editions of the Gardeners Dictionary (Miller, 1759, 1768). In the Linnaean Herbarium there is one specimen labelled as *Heliotropium peruvianum* (LINN 179.1; original not seen, digital photograph!); whether this specimen was obtained from Miller is not possible to ascertain, at least not from the letters from Miller in the Linnaean correspondence. In any case, Linnaeus published the name *Heliotropium peruvianum* only in 1762, so that this specimen should not be treated as original material of *Heliotropium arborescens*.

The two specimens deposited in the general collection of BM can be directly linked to Miller's plate. We have therefore chosen the better of them as the epitype of *Heliotropium arborescens*.

## 7.3 Application of the Name *Heliotropium arborescens*

Kunth (1818), de Candolle (1845) and Bentham (1846: 233–240) explicitly considered *Heliotropium arborescens* (under the name *H. peruvianum*) to be a species from the Andes of Ecuador. However, Johnston (1928b: 40) applied the name *Heliotropium arborescens* var. *arborescens* [as var. '*genuinum*'] to a species 'from the region about Lima', Peru. Upon examination of Miller's specimens at BM, it becomes clear that they do not correspond to the plants 'known only from the Department of Lima, Peru', as suggested by Johnston (1928b: 40). They belong to a different species of *Heliotropium* sect. *Heliothamnus*, native to the Andes of southern Ecuador and northern Peru, as previous authors correctly assumed. Johnston (1928b) referred the specimens corresponding to that taxon to *Heliotropium urbanianum* K.Krause, which should therefore be placed under the synonymy of *H. arborescens*. This latter taxon differs from the species from Lima in having a style shorter than or equal to the stigmatic head, calyx lobes acute, not long acuminate (Fig. 7.1A – B), leaves generally smaller and with the surface more rugose and with more deeply impressed veins, as well as a different geographic range (Johnston, 1928b) and perfectly agrees with the Miller specimens in BM. Conversely, the taxon that is common in the area around Lima is characterized by having the style twice as long as the stigmatic head and by its acute and long acuminate sepals, especially in the fruiting stage (Fig. 7.1C – D). These characters coincide with the geographical origin, the description and the type material (B!, MA!) of *Heliotropium corymbosum* Ruiz & Pav. (Ruiz and Pavón, 1799), which is the oldest name available for this Peruvian species.

## 7.4 Formal Nomenclature

***Heliotropium arborescens*** L., Syst. Nat., ed. 10, 2: 913. 1759 ≡ *Heliotropium peruvianum* L., Sp. Pl., ed. 2, 1: 187: 1762, nom. illeg. – Lectotype (designated by Riedl, 1997: 102): [icon] '*Heliotropium, foliis ovato lanceolatis, spicis plurimis confertis caule fruticoso*' in Miller, Fig. Pl. Gard. Dict. 1: 96, t. 144. 1957. Epitype (designated here): Hort. Chels. N°1 [ex Herb. Miller] (BM! [barcode N° BM000953070]).

= *Heliotropium urbanianum* K.Krause in Bot. Jahrb. Syst. 37: 633. 1906 - Holotype: Ecuador, in lichten Buschwerken um Pulilio [Pelileo] und Cuero [Quero], int[. . . ?] Thal von Amboto [Ambato] 2300 – 2800 m, *F.C. Lehmann 5779* (B, destroyed [photo F. neg nr. 17349!]) – Lectotype (designated here): Ecuador, Pelileo and Quero, valley of the Ambato, 2300 – 2800 m, *F.C. Lehmann 5779* (K!; duplicates of the lectotype: F!, US!).

## 7.5 *Heliotropium arborescens* in horticulture

In cultivation the application of the name *Heliotropium arborescens* is considerably more complex than in the wild, partly because of the history of its cultivation, partly because characters such as leaf size and pubescence are variable in cultivation (e.g., Anonymous, 1884) and because of the existence of both interspecific hybrids and horticultural varieties (Anonymous, 1849; Morren, 1852; Bailey, 1909; Randhawa and Mukhopadhyay, 1986). The publication of the Miller's (1757) plate is the first mention of the species in cultivation in Europe. From this, and the fact that Miller did not mention this species in

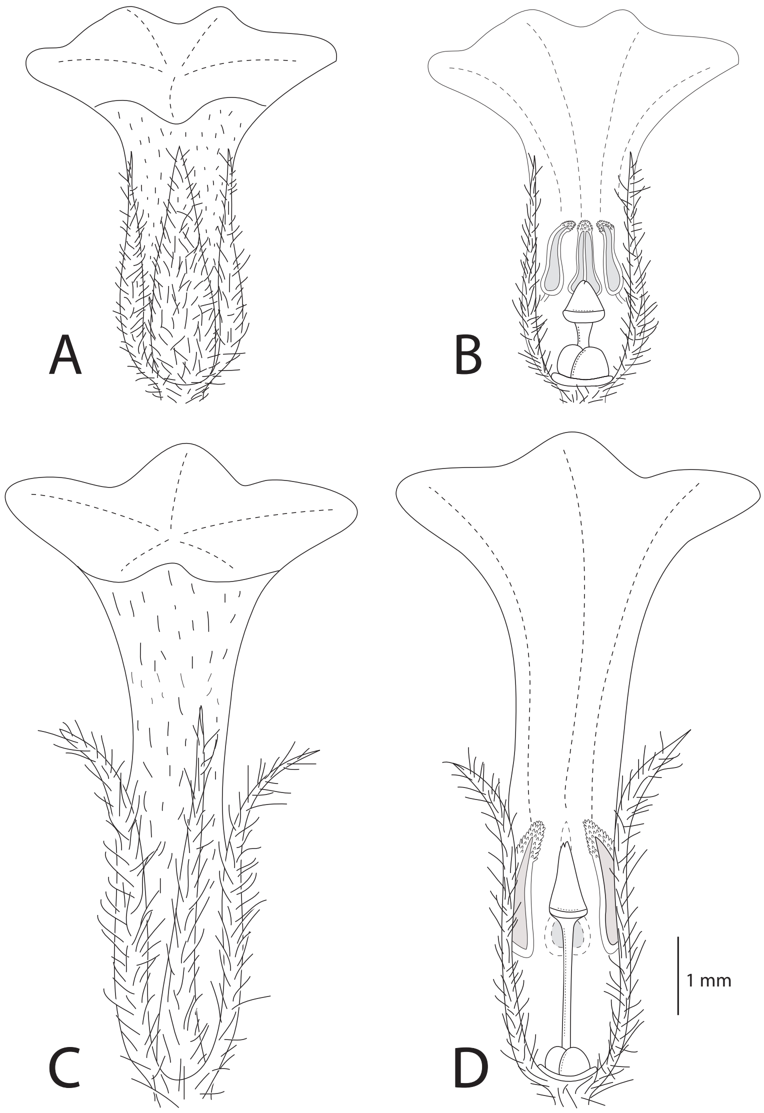

Figure 7.1: Flower morphology of *Heliotropium arborescens* L. and *Heliotropium corymbosum* Ruiz & Pav. A – B, *H. arborescens*, from the Andes of southern Ecuador (Prov. Tungurahua, Ambato and Baños); = *Heliotropium urbanianum* K.Krause sensu Johnston (1928b); it corresponds to Miller's material at BM; from *Lehmann 362a* (G). C – D, *H. corymbosum*, from the region about Lima (Depto. Lima, Pachacamac); = *Heliotropium arborescens* L. sensu Johnston (1928b); from *Weigend & Förther 97/550* (BSB).

previous editions of the Gardeners Dictionary (Miller, 1752, 1754), it must be assumed that the plant was introduced into Europe sometime during the first half of the 1750s (see Stearn, 1974). The species was rapidly propagated and distributed to other gardens across Europe (e.g., Curtis, 1790; Trattinnick, 1816; see Appendix F for selected specimens from cultivation).

The introduction of *Heliotropium corymbosum* took place in 1808 (Donn, 1811; Redouté, 1833; Morren, 1852) and it was also soon propagated in the gardens of Europe. Donn (1811) Bonpland (1813), Sims (1814), Loiseleur-Deslongchamps (1817), Schrank (1817), Redouté (1833), Morren (1852) and Bailey (1909) report the cultivation of *Heliotropium corymbosum* (or its synonym *Heliotropium grandiflorum* Donn ex Schrank; fide de Candolle, 1845; Johnston, 1928b; Förther, 1998). However, *H. corymbosum* was apparently not cultivated as widely as *H. arborescens* and may have soon been lost again from cultivation (see Appendix F for selected specimens from cultivation) - we have not seen modern material of *H. corymbosum* from horticulture. However, artificial crossings to obtain hybrids between *Heliotropium arborescens* and *Heliotropium corymbosum* were undertaken as early as 1815 ('*Heliotropium* × *hybridum*' = *H. arborescens* × *H. corymbosum*; Morren, 1852), and some plants later cultivated may go back to hybrid stock. Moreover, Anonymous (1849) and Morren (1852) provide evidence of the existence of horticultural varieties that were circulated in the horticulture at least as early as 1850, but it remains unclear whether these are of hybrid origin, or represent selections based on morphologically aberrant seedlings or newly introduced wild accessions. The situation is further complicated by the introduction of additional species of *Heliotropium* sect. *Heliothamnus* into Europe during the second half of the nineteenth century; for instance, *Heliotropium submolle* Klotzsch (1852) and *H. argenteum* Lehm. (Anonymous, 1884), which may have also been used to generate hybrids.

During the twentieth century the cultivation of the garden heliotrope became common around the world. Most regional taxonomic revisions mention it as *Heliotropium arborescens* or *Heliotropium peruvianum* (e.g., Johnston, 1951; Frohlich, 1981; Verdcourt, 1991; Riedl, 1997; but see Britton and Wilson, 1930). Consequently, all herbarium material from cultivated plants is generally referred to *Heliotropium arborescens* (or *H. peruvianum*), regardless of flower morphology. In order to clarify this aspect and to illustrate the historical application of the names *Heliotropium arborescens* (*peruvianum*) and *H. corymbosum* (*grandiflorum*) we provide some examples from herbarium specimens taken from plants in cultivation with their original determinations (Appendix F). From the examples given in the Appendix F, it seems that both names, *Heliotropium arborescens* and *H. corymbosum*, were quite consistently applied during the nineteenth century. Most modern material from horticulture agrees with the type of *Heliotropium arborescens*, but we cannot discard the possibility that some cultivated strains ultimately go back to artificial hybrids/backcrosses. Johnston's (1928b) definition of *Heliotropium arborescens* (as identical to *H. corymbosum* from Peru) would necessitate a name change for the (majority of the) cultivated material, which would then have to be called *H. urbanianum*. Since the name *H. arborescens* is widely (and in our view correctly) used for the domesticated species in horticulture this would be contrary to Art. 57.1. of the ICBN (McNeill et al., 2006). The epitypification and re-definition of *H. arborescens* here proposed based on morphological evidence thus also contributes to the stabilization of a widely used and commonly known taxon name.

# 8. Towards a Historical Plant Geography of the Atacama Desert[a]

## Abstract

The concept of floristic element is essential in historical biogeography. In an attempt to identify floristic elements of the Atacama Desert, a review of the phylogenetic literature was carried out and integrated with the knowledge about the geographical distribution of lineages present in the Atacama Desert. Four floristic elements were identified: (i) Neotropical, (ii) Central Chilean, (iii) Trans-Andean and (iv) Antitropical. These elements are discussed in the context of possible geographical origins of the Atacama Desert flora.

## 8.1 Introduction

Boundaries of the Atacama Desert and biogrographical relationships of its flora have been studied by several authors (see Chapter 1, Sections 1.2.1 and 1.2.2). However, identification of floristic elements from the point of view of the biogeographical relationships of lineages present in the Atacama Desert has not been completed to date. Examination of the biogeographical relationships of several Atacama Desert groups can help to place the biogeography of *Heliotropium* sect. *Cochranea* into perspective, and provide a more complete understanding of the origin of the Atacama Desert flora. In the following chapter, the biogeographical relationships of several plant lineages that occur in the Atacama Desert are presented, in an attempt to identify floristic elements of the Atacama Desert.

## 8.2 Biogeographical Relationships of Lineages from the Atacama Desert

Phylogenies of taxa that include species distributed in the Atacama Desert were compiled. The studies included here were those which provided sufficient representation of taxa, high levels of resolution, and statistical support. Phylogenies with low representation or not fully resolved were discarded. A total of 53 lineages were reviewed, representing ca. 40% of the vascular flora of the Atacama Desert.

### 8.2.1 Areas

To each species of a supraspecific taxon, an area or areas were assigned according to the taxonomic literature available. The biogeographical relationships were determined for each lineage as a function of the areas occupied by the taxa related to the Atacama Desert species at the level of the stem node. Consequently, when all species of a lineage occurred

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in the Atacama Desert, the distribution of the sister group was considered. The following areas were taken into account for the analysis:

- A Tropical Andes: Andean zones above ∼2500 m of elevation of northern Chile, northwestern Argentina, Bolivia, Peru, Ecuador, Colombia and Venezuela.
- B Peruvian Desert: Includes low-elevation zones (∼< 2500 m) of the western versant of the Andes of Peru and southern Ecuador.
- C Galapagos Islands.
- D NW South America: Low-elevation zones (∼< 2500 m) of central and northern Ecuador, Colombia, Venezuela and extending to Panama
- E Central America.
- F Caribbean.
- G North America: Northern Mexico and southern United States.
- H Chaco: Low-elevation zones (∼< 2500 m) of the eastern flank of the Andes of central and northern Argentina, southern Bolivia and southern Paraguay.
- I Paraná Region: Southeastern Brazil, Uruguay, and northeastern Argentina.
- J Central Chile: Low-elevation zones (∼< 2000 m) of central Chile between 31° and 38°S.
- K Mediterranean Andes : Andean zones above ∼2000–2500 m of elevation of central Chile and Argentina, between 25°S and 38°S.
- L Patagonia: Steppes of the eastern versant of the Andes (< 500 m) of southern Argentina (south of 36°S) and marginally southern Chile.
- M Southern Chile: Zone of Valdivian, North Patagonian, Subantarctic and Magellanean forests of southern Chile and Argentina.
- N Juan Fernández Archipelago.
- O Indo-Pacific Region : Oceania, Malay Archipelago, southern Asia, Madagascar and easternmost Africa.

For each taxon primary and marginal distribution areas were identified. Marginal distribution is defined as a small portion (<10%) of the geographic range of a taxon in one of the extremes of its distribution.

### 8.2.2 Taxa

In the following list, phylogenetic relationships and distribution areas of the studied taxa are described. The number of species present in the Atacama Desert and the total number of the taxon are indicated in square brackets. The latter value was generally obtained from the references indicated. When marked with '$^M$', the total number of species was obtained from Mabberley (2008). Figures 8.1–8.3 depict examples of phylogenies decribed in the text. These figures do not include phylogenies with only two species involved (i.e., one species from the Atacama Desert and its sister species). Table 8.1 shows a summary of the phylogenies described in the text.

(1) *Argemone* L. [4 / ∼30$^M$] (Papaveraceae): Fig. 8.1A. All four species present in Chile occur in the Atacama Desert. Two of them extend their distribution over central Chile, the Peruvian Desert, the Tropical Andes and the Chaco and Paraná regions (Ownbey, 1961; Zuloaga et al., 2008). Three of them were included in the phylogenetic analysis based on ITS of Schwarzbach and Kadereit (1999). They were recovered in a clade together with *A. subinermis* (G.B. Ownbey) Schwarzbach, from the Chaco and Paraná regions (Ownbey, 1961).

Table 8.1: Taxa present in the Atacama Desert with phylogenetic studies and distribution of related groups. X indicates primary distribution, x indicates marginal distribution. For details see text. TA, Tropical Andes; PD, Peruvian Desert; GA, Galapagos Islands; NW, North-Western South America; CA, Central America; CB, Caribbean; NA, North America; CH, Chaco Region; PR, Paraná Region; CC, Central Chile; MA, Mediterranean Andes, PA, Patagonia; SC, Southern Chile; JF, Juan Fernández Archipelago; IP, Indo-Pacific Region

| Taxon | TA | PD | GA | NW | CA | CB | NA | CH | PR | CC | MA | PA | SC | JF | IP |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Tropical Relationships** | | | | | | | | | | | | | | | |
| *Bomarea* | X | | | | | | | | | | | | | | |
| *Chuquiraga* | X | | | | | | | X | | | | | | | |
| *Cistanthe* sect. *Amaranthoides* | | X | | | | | | | | | x | | | | |
| *Cleome* | X | | | x | X | | | | | | | | | | |
| *Croton* | X | | | x | x | | | | | | | | | | |
| *Encelia* | | X | X | | | | | | | | | | | | |
| *Eremocharis* | X | X | | | | | | | | | | | | | |
| *Gypothamnium* | X | x | | | | | | X | | | | | | | |
| *Heliotropium* sect. *Cochranea* | X | X | x | x | X | X | X | X | X | | X | x | | | X |
| *Hoffmannseggia prostrata* | | X | | | | | | | | | | | | | |
| *Krameria* | X | x | | | | | | | | x | | | | | |
| *Malesherbia* sect. *Malesherbia* | X | X | | | | | | | | | | | | | |
| *Nasa* | X | X | | | | | | | | | | | | | |
| *Nolana* | x | X | x | | | | | | | x | | | x | | |
| *Oxalis* | X | x | | | x | | | | | x | | | | | |
| *Oziroë* | X | X | | | | | | X | | X | | | | | |
| *Palaua* | | X | | | | | | | | | | | | | |
| *Pasithea* | X | | | | | | | | | | | | | | X |
| *Prosopis* ser. *Cavenicarpae* | X | | | | | | | | | | | | | | |
| *Solanum* sect. *Lycopersicon* | X | X | x | | | | | | | | | | | | |
| *Solanum* sect. *Regmandra* | | X | | | | | | | | x | | | | | |
| *Tarasa* | X | X | | | | | | | | | | | | | |
| **Mediterranean Relationships** | | | | | | | | | | | | | | | |
| *Asteriscium* | x | | | | | | | x | | X | X | x | | | |
| *Chaetanthera* | x | | | | | | | | | X | X | | x | | |
| *Cistanthe* (*Grandiflora*-group) | | | | | | | | | | X | x | | | | |

Table 8.1: continued

| Taxon | TA | PD | GA | NW | CA | CB | NA | CH | PR | CC | MA | PA | SC | JF | IP |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Conanthera* |  |  |  |  |  |  |  |  |  |  | X |  |  |  |  |
| *Ephedra* | x |  |  |  |  |  |  | X | x | X | X | X | x |  |  |
| *Homalocarpus* |  | x |  |  |  |  |  |  |  | X |  |  |  |  |  |
| *Loasa* ser. *Macrospermae* |  | x |  |  |  |  |  |  |  | X | x |  |  |  |  |
| *Lobelia* sect. *Tupa* |  |  |  |  |  |  |  |  |  | X |  |  | X | X |  |
| *Malesherbia* sect. *Parvistella* |  |  |  |  |  |  |  |  |  | X |  |  |  |  |  |
| *Mathewsia* |  | x |  |  |  |  |  |  |  | X |  |  |  |  |  |
| *Montiopsis* subg. *Montiopsis* | x |  |  |  |  |  |  |  |  | x | X |  |  |  |  |
| *Oxyphyllum* | x | x |  |  |  |  |  |  |  | X | X |  |  |  |  |
| *Puya* ('yellow' *Puya*) |  |  |  |  |  |  |  |  |  | X |  |  |  |  |  |
| *Schizanthus* |  |  |  |  |  |  |  |  |  | X | X |  | x |  |  |
| *Schizopetalon* |  |  |  |  |  |  |  |  |  | X | X |  |  |  |  |
| *Tecophilaea* |  |  |  |  |  |  |  |  |  | X |  |  |  |  |  |
| *Tropaeolum* sect. *Chilensia* |  |  |  |  |  |  |  |  |  | X | X | x | x |  |  |
| *Zephyra* |  |  |  |  |  |  |  |  |  | X |  |  |  |  |  |
| **Trans-Andean Disjunctions** |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Aristolochia* |  |  |  |  |  |  |  | X | X | x |  |  |  |  |  |
| *Balsamocarpon* |  |  |  |  |  |  |  | X |  |  |  |  |  |  |  |
| *Bulnesia* |  |  |  |  |  |  |  | X |  |  |  |  |  |  |  |
| *Dinemandra/Dinemagonum* |  |  |  |  | X |  |  | X | X |  |  |  |  |  |  |
| *Fuchsia* |  |  |  |  |  |  |  |  | X | X |  |  | X |  |  |
| *Monttea* |  |  |  |  |  |  |  | X |  | x | X |  |  |  |  |
| *Suaeda* |  | X |  |  |  |  |  | X |  |  |  | x |  |  |  |
| **Antitropical Disjunctions** |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Bryantiella* |  | X |  |  |  |  | X |  |  |  |  |  |  |  |  |
| *Cistanthe* (*Rosulatae*-goup) |  | X |  |  |  |  | x |  |  | x | X |  |  |  |  |
| *Fagonia* |  | X |  |  |  |  | X |  |  |  |  |  |  |  |  |
| *Hoffmannseggia glauca* | X |  |  |  |  |  | X | X |  |  | X | X |  |  |  |
| *Pintoa* |  | x |  |  |  |  | X | X |  | x |  | x |  |  |  |
| *Tiquilia* subg. *Tiquilia* |  | X | x |  |  |  | x |  |  |  |  |  |  |  |  |

(2) *Aristolochia* L. [2 / $120^M$] (Aristolochiaceae). One of two species present in the Atacama Desert (*A. chilensis* Bridges ex Lindl.) was included in the work of Neinhuis et al. (2005), based on *trnL-trnF* sequences, where it was resolved as sister to *A. fimbriata* Cham. The latter is distributed in the the Chaco and Paraná regions (Ahumada, 1967, 1975).

(3) *Asteriscium* Cham. & Schltdl. (incl. *Gymnophyton* Clos) [6 / 14] (Apiaceae): Fig. 8.2A. The study of Nicolas and Plunkett (2009), based on the plastid regions *rpl*16 and *trnD-trnT*, shows a well-supported clade that includes species traditionally ascribed to the genera *Asteriscium* and *Gymnophyton*. This clade is sister to the genus *Pozoa* Lag. According to Mathias and Constance (1962), the species of this clade not present in the Atacama Desert are mainly distributed in Central Chile and in the Mediterranean Andes, with marginal representation in the Chaco Region, Tropical Andes and Patagonia.

(4) *Balsamocarpon* Clos [1 / 1] (Fabaceae). In the *trnL-trnF* analysis of Bruneau et al. (2008), this monotypic genus is resolved, with moderate support, as sister to *Zuccagnia* Cav., another monotypic genus distributed in the Chaco region (Ulibarri, 2005).

(5) *Bomarea* Mirb. (incl. *Leontochir* Phil.) [1 / $\sim 100^M$] (Alstroemeriaceae). The phylogenetic studies of Aagesen and Sanso (2003) and Alzate et al. (2008) show that *Bomarea* is paraphyletic with respect to *Leontochir*. The latter is endemic to the Atacama Desert and, based on a molecular phylogeny with ITS, *trnH-psbA*, *rpoB-trnC* and *matK*, sister to *Bomarea involucrosa* Baker (89% bootstrap support, Alzate et al., 2008), distributed in the Andes of southern Peru and northern Chile (Ricardi, 1961).

(6) *Bryantiella* J.M.Porter [1 / $2^M$] (Polemoniaceae): Fig. 8.3D. This genus has two species, one of them in the Atacama Desert, and was resolved as polyphyletic in the phylogenetic analysis with ITS and *trnL-trnF* of Porter et al. (2010). The Atacama species (*B. glutinosa* (Phil.) J.M.Porter) is also distributed in the Peruvian Desert (Gibson, 1967) and appears to be related to the genus *Dayia* J.M.Porter from SW North America (Mabberley, 2008). It would be therefore an antitropical disjunction.

(7) *Bulnesia* Gay [1 / ∼9] (Zygophyllaceae): Fig. 8.3A. The analysis of Comas et al. (1998), based on electrophoresis of seed proteins, shows *Bulnesia chilensis* Gay, endemic to the Atacama Desert, in a clade with species distributed mainly in the Chaco region, with marginal representation in the Tropical Andes.

(8) *Chaetanthera* Ruiz & Pav. [7 / 44] (Asteraceae): Fig. 8.2B. Hershkovitz et al. (2006a), using ITS sequences, show the monophyly of *Chaetanthera*. The species present in the Atacama Desert are in their Clade B, which has its centre of diversity in Central Chile and the Mediterranean Andes, with some species also present in the Puna province and in Southern Chile (Davies, 2010).

(9) *Chuquiraga* Juss. (incl. *Doniophyton* Wedd.) [1 / 25] (Asteraceae): Fig. 8.1B. Gruenstaeudl et al. (2009), based on 7 plastid and one nuclear marker, show that the only species present in the Atacama Desert, *C. ulicina* (Hook. & Arn.) Hook. & Arn., is associated with species with distribution in Central Chile, Mediterranean Andes, Patagonia and Chaco region (Gruenstaeudl et al., 2009).

(10) *Cistanthe* Spach sects. *Amaranthoides* (Reiche) Carolin ex Hershk. (excl. *Cistanthe ambigua* (S. Watson) Carolin ex Hershk. (Hershkovitz, 2006)) and *Philippiamra* (Kuntze) Hershk. [∼5 / ∼5] (Montiaceae): Fig. 8.1C. This clade, resolved on the basis of ITS and *ycf3-trnS* (Hershkovitz, 2006), has species distributed in the Ata-

cama Desert, some of which extend their distribution over the Peruvian Desert (*C. calycina* (Phil.) Carolin ex Hershk.) and marginally to the Mediterranean Andes (*C. densiflora* (Barnéoud) Hershk.) (Hershkovitz, 1991).

(11) *Cistanthe* Spach sect. *Cistanthe* (*Grandiflora*-group (Hershkovitz, 2006)) [∼5 / ∼8] (Montiaceae): Fig. 8.2C. Monophyletic group (based on *ycf3*; Hershkovitz, 2006) with species present in the Atacama Desert, Central Chile and marginally in the Mediterranean Andes (Hershkovitz, 1991, 2006).

(12) *Cistanthe* Spach sect. *Cistanthe* (*Rosulatae*-group (Hershkovitz, 2006)) [∼9 / ∼20] (Montiaceae): Fig. 8.3E. Monophyletic group (based on ITS and *ycf3*; Hershkovitz, 2006) that, apart from including species present in the Atacama Desert, is distributed primarily in the Peruvian Desert (not included in the analysis of Hershkovitz (2006)) and in the Mediterranean Andes, with marginal presence in central Chile, and in Baja California (*C. maritima* (Nutt.) Carolin ex Hershk.) (Hershkovitz, 1991).

(13) *Cleome* L. ('Andean clade', incl. *Podandrogyne* Ducke (Sánchez-Acebo, 2005; Inda et al., 2008b)) [1 / ∼27] (Cleomaceae): Fig. 8.1D. On the basis of a phylogenteic study using sequences of *trnH-psbA*, the species of the 'Andean clade' (Sánchez-Acebo, 2005) cluster together with *C. chilensis* DC., endemic to the Atacama Desert. Most species in this clade are mainly distributed in the Tropical Andes and in Central America (Sánchez-Acebo, 2005; Woodson, 1948).

(14) *Conanthera* Ruiz & Pav. [2 / $5^M$] (Tecophilaeaceae): Fig. 8.2D. Genus probably monophyletic (after a phylogeny based on *rbcL*, Brummitt et al., 1998), whose species are distributed in the Atacama Desert and Central Chile (Zuloaga et al., 2008).

(15) *Croton* L. [1 / 800-$1200^M$] (Euphorbiaceae): Fig. 8.1E. *C. chilensis* Müll.Arg., endemic to the Atacama Desert, froms a clade with species of tropical Andean distribution, according to a phylogeny based on ITS and *trnL-trnF* (Berry et al., 2005).

(16) *Dinemandra* A.Juss. ex Endl. [1 / 1] and *Dinemagonum* A.Juss. [1 / 1] (Malpighiaceae): Fig. 8.3C. These two monotypic Atacama Desert endemic genera (Simpson, 1989b) are resolved as sister to each other in a phylogeny based on *CYC2B* sequences. They are sister to the genera *Ptilochaeta* Turcz. (5 species) and *Lasiocarpus* Leibm. (4 species) (Zhang et al., 2010). The former is distributed in the Chaco and Paraná regions, while the latter in Central America (Niedenzu, 1928), forming a double disjunction.

(17) *Encelia* Adans. [1 / 13-$14^M$] (Asteraceae). The only species present in the Atacama Desert, *E. canescens* Lam., extends its distribution over the Peruvian Desert (Brako and Zarucchi, 1993) and is sister to *E. hispida* Anderss., endemic to the Galapagos Islands (94% bootstrap support in a molecular phylogeny based on ITS and ETS; Fehlberg and Ranker, 2007).

(18) *Ephedra* L.[3 / ∼50] (Ephedraceae): Fig. 8.2E. The South American species form a clade in the phylogenetic analysis of Rydin and Korall (2009) with seven molecular markers (but see Ickert-Bond et al. (2009)). Two subclades have species present in the Atacama Desert. In one of them, *E. rupestris* Benth. is related to species from the Tropical Andes and the Chaco and Paraná regions (Hunziker, 1995). In the other clade, where *E. breana* Phil. y *E. gracilis* Phil. are included, the distributions are primarily in the Mediterranean Andes, Central Chile and Patagonia, but also in the Tropical Andes, the Chaco region as well as Southern Chile (Hunziker, 1995; Matthei, 1995)

(19) *Eremocharis* Phil. (incl. *Domeykoa* Phil.) [3 / 13] (Apiaceae): Fig. 8.1F. Based on the plastid markers *rpl*16 and *trnD*-*trnT*, Nicolas and Plunkett (2009) show that *Domeykoa* and *Eremocharis* form a clade. In total, three species are present in the Atacama Desert, while the rest are distributed mainly in the Peruvian Desert and in the Tropical Andes of Peru (Mathias and Constance, 1962).

(20) *Fagonia* L. [1 / 34] (Zygophyllaceae): Fig. 8.3F. This genus has a well-supported clade with sequences of ITS and *trnL* (Beier et al., 2004) that includes the species present in the Atacama Desert (*F. chilensis* Hook. & Arn.) and a group of species distributed in southwestern North America (Beier, 2005). According to Beier (2005), *F. chilensis* extends is distribution over the Peruvian Desert.

(21) *Fuchsia* L. [1 / 106$^{M}$] (Onagraceae): Fig. 8.3B. This genus has one species in the southern portion of the Atacama Desert (*F. lycioides* Andrews). The phylogenetic analysis of Berry et al. (2004) with nuclear and plastid markers show it in sister relation to *Fuchsia* sect. *Quelusia* (Vand.) DC. (9 species), disjunctly distributed in Central and Southern Chile and in the Paraná region (Berry, 1989).

(22) *Gypothamnium* Phil. [1 / 1] (Asteraceae): Fig. 8.1G. Monotypic genus and endemic to the Atacama Desert. It was placed in a clade in which the species are distrubuted in the Tropical Andes and in the Chaco region, as well as in the Atacama Desert, according to a study with four molecular markers (Luebert et al., 2009). One of the related genera has been recently found in the Peruvian Desert (Schwarzer et al., 2010).

(23) *Heliotropium* L. sect. *Cochranea* (Miers) Kuntze [17 / 17] (Heliotropiaceae). This monophyletic group is endemic to the Atacama Desert with one species in the Peruvian Desert (Luebert and Wen, 2008; Chapter 2). Its sister group is widely distributed in the Neotropics, absent in Central Chile, and some species are present in the Indo-Pacific region (Luebert et al., in press; Chapters 3 and 4).

(24) *Hoffmannseggia* Cav. [2 / 24$^{M}$] (Fabaceae): Fig. 8.3G. Genus with one species endemic of the Atacama and Peruvian Deserts (*H. prostrata* Lag. ex DC.), whose sister species (*H. miranda* Sandwith) is distributed in the Peruvian Desert (Simpson and Ulibarri, 2006), a well-supported relationship based on a phylogeny with ITS, *trnL*-*trnF* and *rbcL* (Simpson et al., 2005). The data of Simpson et al. (2004a) indicate that *H. arequipensis* Ulibarri, also from the Peruvian Desert (Simpson and Ulibarri, 2006), could be in the same clade. *H. glauca* (Ortega) Eifert also reaches the Atacama Desert, and has an antitropical distribution with presence in North America, the Chaco region and Patagonia (Simpson and Ulibarri, 2006), and takes part in a clade with species of tropical Andean, Mediterranean Andean, Chacoan and Patagonian distribution (Simpson et al., 2005).

(25) *Homalocarpus* Hook. & Arn. [3 / 6] (Apiaceae). Monophyletic group (Nicolas and Plunkett, 2009) with three species in the Atacama Desert and the rest in Central Chile (Mathias and Constance, 1965). Schwarzer et al. (2010) have recently reported the presence of *Homalocarpus digitatus* (Phil.) Math. & Const. in the Peruvian Desert.

(26) *Krameria* Loefl. [1 / 18] (Krameriaceae). Using ITS sequences and morphology, Simpson et al. (2004b) identified a sister relationship between the only species of this genus present in the Atacama Desert (*K. cistoidea* Hook. & Arn.) and *K. lappacea* (Dombey) Burdet & B.B. Simpson. The former extends its distribution marginally over Central Chile, while the latter has a tropical Andean distribution with some localities in the Peruvian Desert (Simpson, 1989a).

(27) *Loasa* Adans. ser. *Macrospermae* Urb. & Gilg [1 / ∼7] (Loasaceae): Fig. 8.2F. This series appears well-supported as monophyletic in the analysis of Weigend et al. (2004) with *trnL*. One species (*L. nitida* Desr.) occurs in the Atacama and Peruvian Deserts (Grau and Bayer, 1994), while the rest are concentrated in Central Chile and the Mediterranean Andes, and marginally in Southern Chile (Grau, 1996).

(28) *Lobelia* L. sect. *Tupa* (G.Don) Benth. [2 / 4] (Campanulaceae): Fig. 8.2H. Monophyletic group after a phylogeny based on the plastid region *atpB-rbcL* (Knox et al., 2008). Two species reach the Atacama Desert, which in turn are distributed in Central Chile, while the other two species occur in Central Chile, Juan Fernández, and Southern Chile (Lammers, 2000).

(29) *Malesherbia* Ruiz & Pav. sect. *Malesherbia* [3 / 13] (Malesherbiaceae): Fig. 8.1I. A phylogeny based on ITS Gengler-Nowak (2003) supports the monophyly of this section, with three species present in the Atacama Desert, while the remainders are distributed in the Tropical Andes as well as the Peruvian Desert (Ricardi, 1967).

(30) *Malesherbia* sect. *Parvistella* Gengler [1 / 1] (Malesherbiaceae). Clade composed of one species (Gengler-Nowak, 2003) distributed in the Atacama Desert and Central Chile (Ricardi, 1967; Gengler-Nowak, 2002a).

(31) *Mathewsia* Hook. & Arn. [5/10] (Brassicaceae): Fig. 8.2G. Genus apparently monophyletic according to a phylogenetic study with ITS and *ndhF* (Warwick et al., 2009), with species distributed in the Atacama Desert and mainly in Central Chile, though some reach marginally the Peruvian Desert (Rollins, 1966).

(32) *Monttea* Gay [1 / $3^M$] (Plantaginacae). The avilable phylogeny for this genus, based on three plastid markers (*trnL-trnF*, *rps*16, *matK-trnK*), only includes the Atacama Desert species (*M. chilensis* Gay, which extends marginally over Central Chile), which is sister to the monotypic genus *Melosperma* Benth. (Albach et al., 2005). The affinities among the species of *Monttea* and *Melosperma* are additionally supported by their unusual type of nectary and the presence of elaiophores (Sérsic and Cocucci, 1999). *Melosperma* is distributed in the Mediterranean Andes, while the remaining species of *Monttea* in the Chaco region (Sérsic and Cocucci, 1999; Zuloaga et al., 2008).

(33) *Montiopsis* Kuntze subg. *Montiopsis* [3 / ∼15] (Montiaceae): Fig. 8.2I. According to a phylogenetic analysis of based on ITS and *ycf3* (Hershkovitz, 2006), this subgenus is monophyletic, with a centre of diversity in the Mediterranean Andes and marginal distribution in the Tropical Andes and Central Chile (Hershkovitz, 2006; Ford, 1993).

(34) *Nasa* Weigend (*Nasa poissoniana*-group (Henning and Weigend, 2009)) [1 / 7] (Loasaceae): Fig. 8.1H. This group was individualized as monophyletic in the *trnL* analysis of Weigend et al. (2004) and is consistently retrieved as monophyletic in subsequent analyses with more molecular markers (Tilo Henning, personal communication). One species (*N. urens* (Jacq.) Weigend) reaches the Atacama Desert, while the rest are distributed both in the Tropical Andes of Peru and Bolivia and in the Peruvian Desert (Henning and Weigend, 2009).

(35) *Nolana* L. f. [49 / 89] (Solanaceae): Fig. 8.1J. This genus is composed of six major clades (Tu et al., 2008). Some of them are mainly distributed in the Atacama Desert, and other have their distribution centered in the Peruvian Desert, with incursions into the Galapagos Islands and in the Tropical Andes; two Atacama clades extend their distribution marginally over Central Chile, while one species (*N. paradoxa* Lindl., Clade ‘LFY A’) occurs even in Southern Chile (Dillon et al., 2009).

(36) *Oxalis* L. sects. *Carnosae* Reiche and *Giganteae* Lourteig [12 / 14] (Oxalidaceae). These two sections form a monophyletic group, according to the phylogenetic analysis based on *rbcL*, *trnT-trnF*, *psbA-trnH*, *trnS-trnG* and ITS, centered in the Atacama Desert and marginally in the Peruvian Desert and Central Chile (Heibl et al., in press). Its sister group, the '*Oxalis tuberosa* alliance' (Heibl et al., in press), has a distribution centered in the Tropical Andes, and reached marginally Central America (Emshwiller, 2002).

(37) *Oxyphyllum* Phil. [1 / 1] (Asteraceae). Monotypic genus that, according to a phylogenetic analysis with four molecular markers, is related to species whose centre of distribution is Central Chile (Luebert et al., 2009), though also extend marginally over the tropical and Mediterranean Andes (Crisci, 1974, 1976; Ricardi and Weldt, 1974).

(38) *Oziroë* Raf. [1 / 5] (Asparagaceae). Genus probably monophyletic (Pfosser and Speta, 1999), whose species are mainly distributed in the Tropical Andes, the Chaco region, the Peruvian Desert, and Central Chile (Guaglianone and Arroyo-Leuenberger, 2002).

(39) *Palaua* Cav. [4 / 15] (Malvaceae): Fig. 8.1L. This genus has been confirmed as monophyletic in an analysis with *psbA-trnH* and ITS (Huertas et al., 2007). The species have their centre of distribution in the Peruvian Desert, while four reach the Atacama Desert (Marticorena, 2005).

(40) *Pasithea* D.Don [1 / 1] (Xanthorrhoeaceae). This monotypic genus is frequent in Central Chile and reaches the Atacama and also the Peruvian Desert. Phylogenetic analyses with four plastid markers (*atpB*, *ndhF*, *rbcL*, *trnL-trnF;* Wurdack and Dorr, 2009) show that this genus is sister to a clade of tropical Andean and Indo-Pacific distribution.

(41) *Pintoa* Gay [1 / 1] (Zygophyllaceae). Monotypic genus endemic to the Atacama Desert. On the basis of phylogenetic analyses with *rbcL* it has been suggested that this genus is sister to *Larrea* Cav. (Lia et al., 2001). The latter has a disjunct distribution mainly in the Chaco region and in North America, with some populations in the Peruvian Desert, Central Chile and Patagonia (Hunziker et al., 1972).

(42) *Prosopis* L. ser. *Cavenicarpae* (Burkart) Burkart [1 / 2] (Fabaceae). This series is composed of two species which form a clade in the phylogenetic analysis with *matK-trnK*, *trnL-trnF*, *trnS-psbC*, G3pdh and NIA of Catalano et al. (2008). One of the species, *P. tamarugo* Phil., is endemic to the Atacama Desert, while the other, *P. ferox* Griseb., is distributed in the Andes of northern Argentina and southern Bolivia (Burkart, 1976).

(43) *Puya* Molina ('yellow' *Puya* (Jabaily and Sytsma, 2010)) [3 / 3] (Bromeliaceae). The species of this group are distributed in the Atacama Desert and extend their distribution over Central Chile. Is a well-resolved clade, according to a molecular phylogeny based on *PHYC* sequences (Jabaily and Sytsma, 2010). It is possible that these species are also related with the 'blue' *Puya* group (phylogeny based on sequences of *matK*+*trnS-trnG*+*rps*16+*PHYC*; Jabaily and Sytsma, 2010), distributed primarily in Central Chile, although hybridization and/or chloroplast capture events seem to be confounding the plastid and nuclear phylogenetic signals.

(44) *Schizanthus* Ruiz & Pav. [5 / 12] (Solanaceae): Fig. 8.2K. This genus, whose phylogenetic relationships were studied in the analyses with ITS, *waxy* and *trnF/ndhJ* sequences of Pérez et al. (2006), has five species in the Atacama Desert, while the rest

are distributed in the Mediterranean Andes and Central Chile, reaching marginally Southern Chile (Grau and Gronbach, 1984).

(45) *Schizopetalon* Sims [7 / 10] (Brassicaceae): Fig. 8.2G. Group probably monophyletic (according to the phylogenetic analysis with ITS and *ndhF* of Warwick et al., 2009), whose species are mainly distributed in the Atacama Desert, and extend over Central Chile and the Mediterranean Andes (Al-Shehbaz, 1989).

(46) *Solanum* L. sect. *Lycopersicon* (Mill.) Wettst. [4 / 13] (Solanaceae): Fig. 8.1K. This section is a monophyletic group with four species present in the Atacama Desert; the rest are mainly distributed in the Peruvian Desert and the Tropical Andes of Peru ans Ecuador, reaching the Galapagos Islands (Spooner et al., 2005; Peralta et al., 2008).

(47) *Solanum* L. sect. *Regmandra* Ugent ex D'Arcy [8 / 11] (Solanaceae). Morphologically homogeneous (Bennett, 2008) and apparently monophyletic group, according to a phylogenetic analysis with *ndhF* (Bohs, 2005). Apart from the species present in the Atacama Desert, this group extends its distribution mainly over the Peruvian Desert and marginally over Central Chile (Bennett, 2008).

(48) *Suaeda* Forssk. ex J.F.Gmel. [2 / $\sim 100^{M}$] (Chenopodiaceae). One of the species present in the Atacama Desert (*S. foliosa* Moq.) was resolved as sister to *S. divaricata* Moq. in a phylogenetic analysis with *atpB-rbcL* and *psbB-psbH* (Schütze et al., 2003). *S. foliosa* extends its distribution to the Peruvian Desert (Teillier, 1996), while *S. divaricata* is distributed in the Chaco region and, marginally, in Patagonia (Tolaba, 2006; Zuloaga et al., 2008).

(49) *Tarasa* Phil. [4 / 30] (Malvaceae). This genus, of primarily tropical Andean distribution, seems to be polyphyletic (Tate and Simpson, 2003). Four species reach the Atacama Desert in its upper altitudinal portion (Marticorena, 2005). They are related, according to a phylogentic analysis based on ITS, *psbA-trnH*, *trnT-trnL* and *matK-trnK* sequences (Tate and Simpson, 2003), to species distributed in the Tropical Andes, and one of them (*T. operculata* (Cav.) Krapov.) is nested in a separate clade in sister relationship with *T. thyrsoidea* Krapov. from the Peruvian Desert. Two species from the Atacama Desert (*T. congestiflora* (I.M. Johnst.) Krapov. and *T. pediculata* Krapov.) appear to be related, in the plastid phylogeny, to the genus *Nototriche* Turcz., also of tropical Andean distribution, which could indicate gene flux between *Tarasa* and *Nototriche* in southern Peru (Tate and Simpson, 2003).

(50) *Tiquilia* Pers. subg. *Tiquilia* [5 / 19] (Ehretiaceae): Fig. 8.3H. Monophyletic subgenus based on a phylogenetic analysis with *matK*, *ndhF*, *rps*16, ITS, and *waxy* sequences (Moore et al., 2006). The species present in the Atacama Desert form clades that are extended over the Peruvian Desert. They are related to disjunct species from North America and the Galapagos Islands (Richardson, 1977; Moore et al., 2006).

(51) *Tecophilaea* Bertero ex Colla [1 / $2^{M}$] (Tecophilaeaceae): Fig. 8.2D. Apparently polyphyletic genus (Brummitt et al., 1998), in which the species present in the Atacama Desert (*T. violiflora* Bertero ex Colla), as well as the other related taxa, have their centre of distribution in Central Chile (Zuloaga et al., 2008).

(52) *Tropaeolum* L. sect. *Chilensia* Sparre (excl. *Tropaeolum speciosum* Poepp. & Endl., incl. *Magallana* Cav. (Andersson and Andersson, 2000; Hershkovitz et al., 2006b)) [6 / 22] (Tropaeolaceae): Fig. 8.2J. Hershkovitz et al. (2006b) provide molecular evidence with ITS sequences for the monophyly and phylogenetic relationships in this section. Seven species are present in the Atacama Desert, while the related species

are mainly distributed in Central Chile and the Mediterranean Andes, extending marginally over Patagonia and Southern Chile (Sparre and Andersson, 1991).

(53) *Zephyra* D.Don [2 / $2^M$] (Tecophilaeaceae): Fig. 8.2D. This genus, endemic to the Atacama Desert (Zuloaga et al., 2008), seems to be related, on the basis of a phylogeny with *rbcL* (Brummitt et al., 1998), with other genera primarily distributed in Central Chile.

Several phylogenetic studies, which include plant representatives of the Atacama Desert, were also consulted, but not considered in the present analysis, either because they were rather incomplete or lack phylogenetic resolution. Studies that were incomplete include treatments on the members of the Cactaceae *Browningia* Britton & Rose, *Copiapoa* Britton & Rose and *Eulychnia* Phil. (Nyffeler, 2002; Ritz et al., 2007), *Bridgesia* Bertero ex Cambess. (Sapindaceae) (Buerki et al., 2009), *Skytanthus* Meyen (Apocynaceae) (Potgieter and Albert, 2001), *Sicyos* L. (Cucurbitaceae) (Kocyan et al., 2007) and *Bakerolimon* Lincz. (Plumbaginaceae) (Lledó et al., 2005). Studies that lacked sufficient phylogenetic resolution included the genera *Alstroemeria* L. (Alstroemeriaceae) (Aagesen and Sanso, 2003), *Cordia* L. (Cordiaceae) (Gottschling et al., 2005), *Euphorbia* L. (Euphorbiaceae) (Steinmann and Porter, 2002), *Huidobria* Gay (Loasaceae) (Hufford et al., 2003; Weigend et al., 2004), *Phrodus* Miers (Solanaceae) (Levin and Miller, 2005), *Sisymbrium* L. s.l. and *Sibara* Greene (Warwick et al., 2002, 2009; Al-Shehbaz, 2010; Couvreur et al., 2010).

## 8.3 Floristic Elements and Possible Origins of the Atacama Desert Flora

In Table 8.1 taxa have been grouped according to patterns of biogeographical relationships defined by primary distribution areas of the related lineages to those present in the Atacama Desert. Four patterns of distribution of related lineages were identified: Tropical relationships (Fig. 8.1), Mediterranean relationships (Fig. 8.2), trans-Andean disjunctions (Fig. 8.3A-C) and antitropical disjunctions (Fig. 8.3D-H). These patterns are an arbitrary generalization, but may be useful to guide a discussion on their meaning in terms of the history and origins of the Atacama Desert flora, and to relate them to what other authors have written on the topic (reviewed in section 1.2.2, p. 18).

The four patterns may be considered as the floristic elements the Atacama Desert flora, i.e., (i) Neotropical element, (ii) central Chilean element, (iii) trans-Andean element, and (iv) antitropical element, respectively. It is clear, however, that these elements are not mutually exclusive, and that in their heterogeneity are overlapping to one another. The biogeographical relationships proposed so far by other authors are reflected in these floristic elements. Affinities with the Peruvian Desert correspond to the Neotropical element; phytogeographical relationships with the Chaco region correspond to the trans-Andean element; biogeographical relationships with North America correspond to the antitropical element (previously mentioned by Rundel et al., 1991). Surprisingly, the central Chilean element of the Atacama Desert is little mentioned in the literature, though it seems obvious given the adjacent geographical situation between Central Chile and the Mediterranean Andes and the Atacama Desert. Moreover, results confirm the ideas proposed by Katinas et al. (1999) and Morrone (2004, 2006) on the mixed biogeographical character of the area where the Atacama Desert is located.

In the context of the Neotropical element, the presence of related lineages in the Atacama and the Peruvian Deserts seems natural, given the contiguity of both territories.

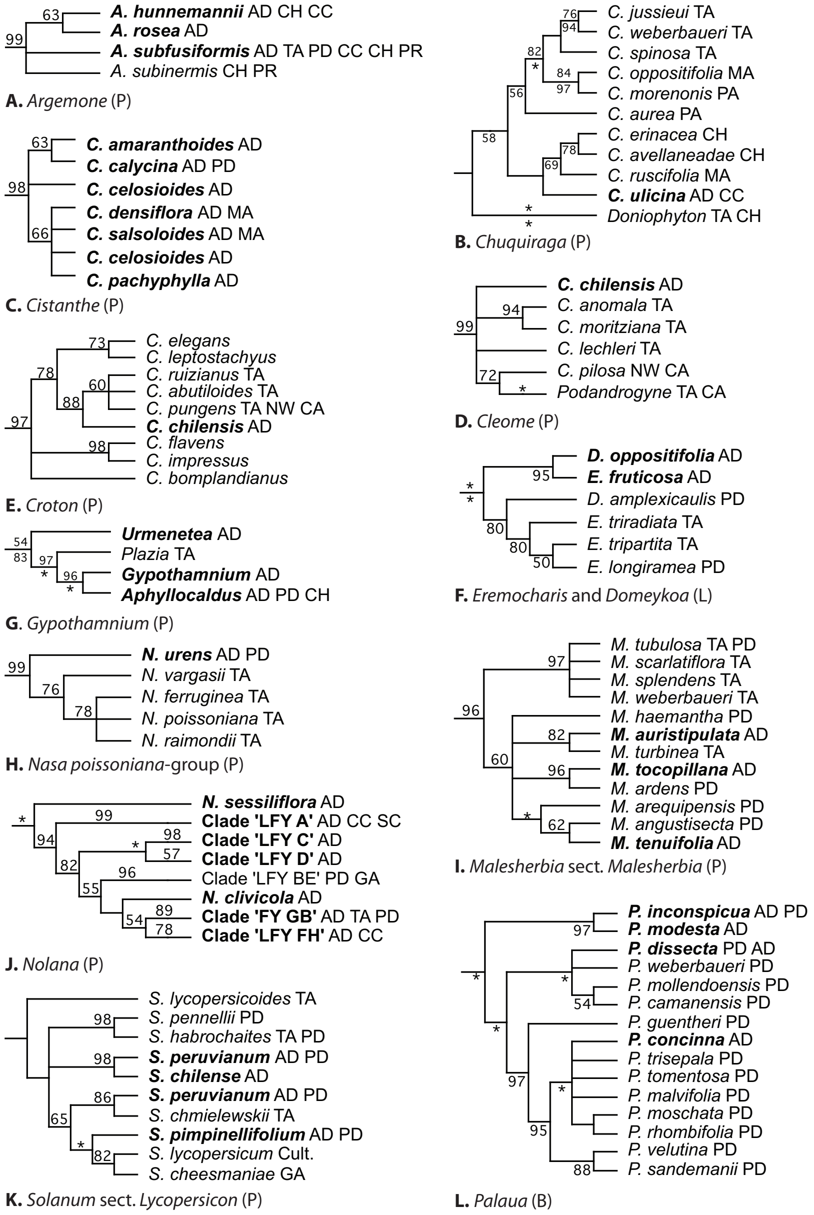


Figure 8.1: Phylogenies of taxa present in the Atacama Desert with tropical affinities. Taxa present in the Atacama Desert are marked in bold. The acronyms to the right of taxon names represent their areas of distribution (abbreviated as in Table 8.1; AD, Atacama Desert; for details see the text). Under the phylogenies and between brackets to the right of the taxon name, (P) indicates parsimony analysis, (L) indicates likelihood analysis, and (B) indicates Bayesian analysis. Only bootstrap values (above branches) and Bayesian posterior probabilities (below branches) are indicated when are provided in the original references and are greater than 50%; asterisk indicates 100%. A, *Argemone*, after Schwarzbach and Kadereit (1999; Fig. 4); B, *Chuquiraga*, after Gruenstaeudl et al. (2009; Fig. 2 derecha); C, *Cistanthe* sects. *Amaranthoides* and *Philippiamra*, after Hershkovitz (2006; Fig. 10); D, *Cleome*, after Sánchez-Acebo (2005; Fig. 1); E, *Croton*, after Berry et al. (2005; Fig. 4); F, *Eremocharis* and *Domeykoa*, after Nicolas and Plunkett (2009; Fig. 4); G, *Gypothamnium*, after Luebert et al. (2009; Fig. 2); H, *Nasa poissoniana*-group, after Weigend et al. (2004; Fig. 1); I, *Malesherbia* sect. *Malesherbia*, after Gengler-Nowak (2003; Fig. 2); J, *Nolana*, after Tu et al. (2008; Fig. 2); K, *Solanum* sect. *Lycopersicon*, after Spooner et al. (2005; Fig. 9); L, *Palaua*, after Huertas et al. (2007; Fig. 5).

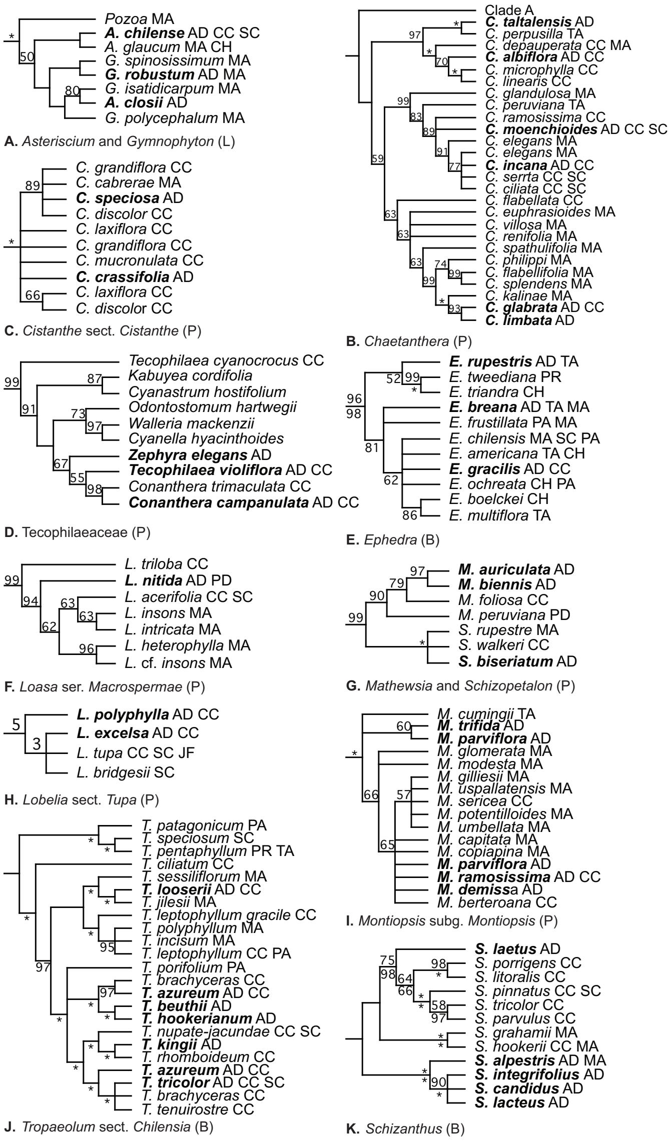
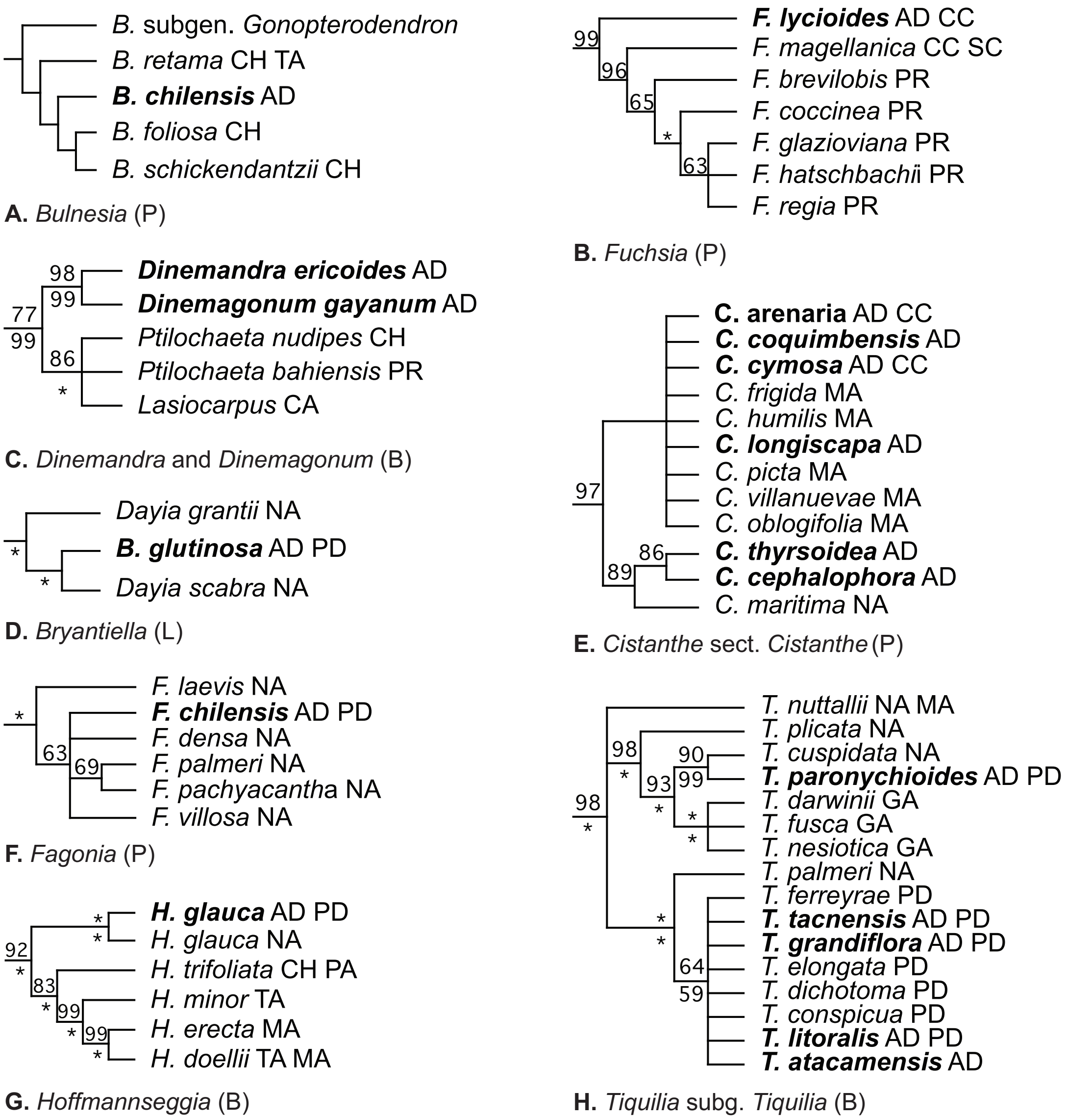


Figure 8.2: Phylogenies of taxa present in the Atacama Desert with Mediterranean affinities. Taxa present in the Atacama Desert are marked in bold. The acronyms to the right of taxon names represent their areas of distribution (abbreviated as in Table 8.1; AD, Atacama Desert; for details see the text). Under the phylogenies and between brackets to the right of the taxon name, (P) indicates parsimony analysis, (L) indicates likelihood analysis, and (B) indicates Bayesian analysis. Only bootstrap values (above branches) and Bayesian posterior probabilities (below branches) are indicated when are provided in the original references and are greater than 50% (except in G where decay values are indicated); asterisk indicates 100%. A, *Asteriscium* and *Gymnophyton*, after Nicolas and Plunkett (2009; Fig. 4); B, *Chaetanthera*, after Hershkovitz et al. (2006a; Fig. 3); C, *Cistanthe* sect. *Cistanthe* (*Grandiflora*-group), after Hershkovitz (2006; Figs. 2 and 12); D, Tecophilaeaceae, after Brummitt et al. (1998; Fig. 11 (weighted bootstrap)); E, *Ephedra*, after Rydin and Korall (2009; Fig. 2); F, *Loasa* ser. *Macrospermae*, after Weigend et al. (2004; Fig. 1); G, *Mathewsia* and *Schizopetalon*, after Warwick et al. (2009; Fig. 3); H, *Lobelia* sect. *Tupa*, after Knox et al. (2008; Fig. 1); I, *Montiopsis* subg. *Montiopsis*, after Hershkovitz (2006; Fig. 19); J, *Tropaeolum* sect. *Chilensia*, after Hershkovitz et al. (2006b; Fig. 2); K, *Schizanthus*, after Pérez et al. (2006; Fig. 2A).



**A.** *Bulnesia* (P)

**B.** *Fuchsia* (P)

**C.** *Dinemandra* and *Dinemagonum* (B)

**D.** *Bryantiella* (L)

**E.** *Cistanthe* sect. *Cistanthe* (P)

**F.** *Fagonia* (P)

**G.** *Hoffmannseggia* (B)

**H.** *Tiquilia* subg. *Tiquilia* (B)

Figure 8.3: Phylogenies of taxa present in the Atacama Desert with trans-Andean (A-C) and antitropical (D-H) affinities. Taxa present in the Atacama Desert are marked in bold. The acronyms to the right of taxon names represent their areas of distribution (abbreviated as in Table 8.1; AD, Atacama Desert; for details see the text). Under the phylogenies and between brackets to the right of the taxon name, (P) indicates parsimony analysis, (L) indicates likelihood analysis, and (B) indicates Bayesian analysis. Only bootstrap values (above branches) and Bayesian posterior probabilities (below branches) are indicated when are provided in the original references and are greater than 50%; asterisk indicates 100%. A, *Bulnesia*, after Comas et al. (1998; Fig. 1b); B, *Fuchsia*, after Berry et al. (2004; Fig. 2); C, *Dinemandra and Dinemagonum*, after Zhang et al. (2010; Fig. 2 (*CYC2B*)); D, *Bryantiella*, after Porter et al. (2010; Fig. 5); E, *Cistanthe* sect. *Cistanthe*(*Rosulatae*-group), after Hershkovitz (2006; Figs. 3 and 16); F, *Fagonia*, after Beier et al. (2004; Fig. 4); G, *Hoffmannseggia galuca*, after Simpson et al. (2005; Fig. 1); H, *Tiquilia* subg. *Tiquilia*, after Moore et al. (2006; Fig. 4).

However, the existence of a floristic break at the latitude of the Chilean-Peruvian administrative border (Rundel et al., 1991; Galán De Mera et al., 1997; Dillon, 2005b; Pinto and Luebert, 2009) seems to be in contradiction with that. This break has been, nonetheless, proposed only for the coastal floras. It seems to be caused by the aridity gradient observed in the coast of Chile and Peru, which reaches its maximum towards the Chilean-Peruvian border, both in terms of rainfall (Galán De Mera et al., 1997; Luebert and Pliscoff, 2006) and coastal fog (Cereceda and Schemenauer, 1991), as well as relief conditions favourable for the condensation of the air masses from the ocean (Paskoff, 1979).

It is interesting to note some patterns associated with the Neotropical element, such as the joint presence of several lineages in the Peruvian and Atacama Deserts, as well as in the tropical Andes (Table 8.1). This may indicate that the biotic exchanges between both deserts might have occurred through the western Andean foothills, as proposed by several authors (Moreno et al., 1994; Gengler-Nowak, 2002b; Luebert et al., 2009; Pinto and Luebert, 2009). Different lines of evidence support this hypothesis. First, the western Andean foothills receive more moisture than the coast, due to the lower influence of the Humboldt Current. Summer rainfall generated in the Amazonian basin, and convective storms originated in the Andes (Garreaud, 2009) occasionally reach the western versant of the Andes, hence generating a trend of increasing precipitation with elevation in northern Chile (Houston and Hartley, 2003). These conditions of higher moisture may promote permanent occurrence of north-south floristic exchange along the western Andean foothills. It is possible that such conditions have been stable since the Pliocene, when the effect of the Humboldt Current intensified (Ibaraki, 1997). Intensification of the effect of the Humboldt Current probably occurred in concomitance with the Andean uplift (Sepulchre et al., 2009), which reached its current elevation during the same period (Garzione et al., 2008; see Chapter 4). Second, molecular divergence time estimations of lineages with tropical relationships are consistent with Plicoene species diversification (Gengler-Nowak, 2002b; Moore and Jansen, 2006; Luebert and Wen, 2008). Third, recent floristic evidence indicates several plant species of sub-Andean distribution in northern Chile (i.e., in the Precordillera) also extend their distribution over the Precordillera of southern Peru (e.g., *Aphyllocladus denticulatus* Cabrera (Asteraceae), *Reyesia juniperoides* (Werderm.) D'Arcy (Solanaceae), *Tiquilia tacnensis* A.T. Richardson (Ehretiaceae), Schwarzer et al., 2010). These data have recently become available due to increased botanical collecting in this region.

The presence of lineages shared between the Atacama Desert and the Tropical Andes, without occurrence in other areas (Table 8.1) also accounts for possible Andean connections. The colonization of coastal environments from the Andes seems to be a relatively simple process, for example, through landslides or alluvia that could transport propagules down-slope. The opposite process, i.e. the colonization of Andean environments from the coast, may be more difficult. On the one hand, passive transport of propagules from the coast to the Andes can occur through upslope winds. Upslope winds have been reported to occur daily along the valleys central and northern Chile (Kalthoff et al., 2002; Rutllant et al., 2003; Houston, 2006b), as well as in northern Peru (Howell, 1953). On the other hand, because the present conditions of aridity between the coast and the Andes, the absolute desert could constitute a barrier for movements from the coast to the Andes. Such conditions of aridity do not seem to have changed, at least during the 3000 years (Holmgren et al., 2008). The transport of seeds and propagules in either direction could be effected by the movement of animals, both native (guanacos) or introduced livestock (sheep and goats). Several phylogenetic studies show direct Andes-coast connections between closely related lineages in northern Chile (Gengler-Nowak, 2002b; Luebert and Wen, 2008; Luebert et al., 2009; Tu et al., 2008). But these studies do not explain the existence of closely related species separated by hundreds of kilometers in the coastal Atacama Desert and the central and northern Tropical Andes (e.g., *Cleome*, *Croton*). One hypothesis to explain the distribution of these lineages is past continuity of the geographic range and secondary extinction in the southernmost Tropical Andes, or, as put forward by other authors (Schwarzer et al., 2010), long-distance dispersal.

Some lineages of the Neotropical element are continuously distributed in the Atacama Desert, the Tropical Andes, the Chaco region, and, in some cases, other areas of South America. Possible causes of such distribution pattern may respond to similar factors to those of trans-Andean disjunctions. Also, several lineages with essentially Neotropical distributions extend to North America from Central America and/or the Caribbean. This distribution pattern could shed light on the causes of antitropical disjunctions. Both patterns are discussed below.

The central Chilean element is perhaps the easiest to explain, although the least mentioned in the literature. Palynological studies (e.g., Villagrán and Varela, 1990; Villa-Martínez and Villagrán, 1997) detected dry phases during the Holocene of Central Chile, which seem to be related with the expansion of lineages from the Atacama Desert to the south. Floristic north-south exchanges, both along the coast and the coastal and Andean Cordilleras, seem possible given the absence of physical barriers for such exchanges. As expected, the majority of the Atacama species of the central Chilean element tend to be distributed in the southern portion of the Atacama Desert, and in some cases extend marginally over the Peruvian Desert or the Tropical Andes (Table 8.1). Many of these lineages have originated in the driest environments of Central Chile and have dispersed toward the more humid areas of the Atacama Desert, either through the coast or the Andes. The presence of several Central Chilean lineages in the Andes suggests that migrations along the Andean foothills, with posterior colonization of coastal environments may have occurred in a similar way to what was already mentioned for the Tropical Andes. In the analysis of Urtubey et al. (2010), based on phylogenies of genera of Asteraceae, the Atacama Desert is related to Central Chile, the Mediterranean Andes, Patagonia, Southern Chile and the Monte province of the Chaco region. Some lineages of the central Chilean element analysed here coincide with that pattern (see Table 8.1), but it is necessary to emphasize that this is not the only one.

The lineages of the trans-Andean disjunct element are generally distributed in arid and semiarid zones on both sides of the Andes. The most parsimonious explanation for these distributions seems to be Andean vicariance, i.e., the formation of the disjunctions is produced as a consequence of the Andean uplift, which generates a barrier for dispersion, promoting population differentiation on both Andean versants. Roig-Juñent et al. (2006) propose this hypothesis for the fauna of arthropods in the arid zones of South America. The chronology of the Andean uplift is currently a matter of controversy (compare for example, Garzione et al., 2008; Ehlers and Poulsen, 2009; see Chapter 4), but there seems to be agreement in the conclusion that the present elevation of the Andes was reached toward the late Miocene or early Pliocene. No molecular dating studies are known to the author for the studied lineages, but other works on lineages disjunctly distributed on both sides of the Andes (e.g., *Drimys* J.R.Forst. & G.Forst.) estimate the origin of the disjunction toward the middle or late Miocene (Marquínez et al., 2009). The lineages distributed in the Atacama Desert, the Chaco region and the tropical and/or Mediterranean Andes may be explained in the same way. Colonization of Andean areas from the basal areas of one or both sides of the Andes after the vicariance events had occurred can be hypothesised. In these cases, long-distance dispersal, via trans-Andean corridors, cannot be ruled out a priori.

Finally, the antitropical disjunctions constitute, at the first glance, the most difficult pattern to be explained, because of the long distance separating North and South America. Lineages continuously distributed in the Neotropics and in North America (i.e., with continuous presence in Central America) provide evidence about posible floristic exchanges between both sub-continents via Mesoamerica. Such exchanges have been broadly documented for plants via Panama Isthmus (Morley, 2003; and references therein). The Panama Isthmus has been available since the middle Pliocene (Marshall et al., 1979) and islands of dry habitats in Central America and northwestern South America may have been used by desert plants for steping-stone dsipersal (Solbrig, 1972). Secondary extinctions in Central America may explain the disjunct distribution observed today. Long-distance dispersal can also explain this pattern, as has been suggested by several authors (e.g., Raven, 1963; Hunziker, 1975; Dillon, 1984; Simpson et al., 2005; Moore et al., 2006). The latter seems likely since most disjunct groups are absent in the dry Andean valleys of northwestern South America and in the tropical dry scrub vegetation of Central America. Transport of propagules on or in birds has been invoked as likely means of long-distance dispersal between North and South America (Cruden, 1966). However, Solbrig (1972) argued that birds are not a very likely source of dispersal between dry areas, because no migrators are birds of desert areas and one should assume that they stop either in the centre or in the periphery of desert areas.

The present review intends to put in context the biogeography of *Heliotropium* sect. *Cochranea* and to contribute to the systematization of the knowlege on the origin of the Atacama Desert flora. It seems natural that the next step in this direction is the integration of this knowledge through more formal methods of biogeographical analysis (e.g., analysis of compatibility of area cladograms, analysis of lineage diversification rates) that enable a better understanding of the biogeoggraphical evolution of the Atacama Desert biota. However, basic information is still lacking. Many critical areas have never been floristically inventoried in detail (e.g., the southern portion of the Atacama Desert, the Precordillera of the Atacama administrative region, the coastal area of the Huasco administrative province). Such inventories can enable a better assessment of the boundaries and floristic transitions both within the Atacama desert and with its neighbour areas. Many plant groups have not been phylogenetically studied, or the available phylogenies are incomplete, or lack resolution at the species level. Among them there are groups with high species richness in the Atacama Desert, such as *Atriplex* L. (Amaranthaceae), *Copiapoa* (Cactaceae), *Cristaria* Cav. (Malvaceae), *Cryptantha* Lehm. ex G.Don (Boraginaceae), *Cruckshanksia* Hook. & Arn. (Rubiaceae), *Haageocereus* Backeb. (Cactaceae), *Lycium* L. (Solanaceae), *Spergularia* (Pers.) J.Presl & C.Presl (Caryophyllaceae), *Tillandsia* L. (Bromeliaceae), and *Viola* L. (Violaceae). If advances in the biogeography of the Atacama Desert flora are to be achieved, these aspects need to be accomplished.

# 9. Conclusions

## 9.1 Systematics of *Heliotropium* sect. *Cochranea*

### 9.1.1 Systematic Relationships in *Heliotropium* sect. *Cochranea*

*Heliotropium* sect. *Cochranea* is a monophyletic group of shrubs and subshrubs, endemic to the Pacific Desert of South America on the western versant of the Andes. In its current circumscription, it is composed of 17 species and one subspecies, which can be found in the Atacama Desert. Only *Heliotropium krauseanum* and its subspecies occur in the Peruvian Desert. Most species are narrow endemics with small ranges within the Atacama Desert, except *Heliotropium chenopodiaceum*, *H. krauseanum* and *H. stenophyllum*, whose distributions extend for more than three degrees of latitude. Further, majority of species are restricted to the coastal range, with the exception of *Heliotropium chenopodiaceum* and *H. glutinosum* that are distributed along the Andean foothills of the Atacama Desert, but never above 2.200 m. *Heliotropium krauseanum*, *H. sinuatum* and *H. stenophyllum* occasionally reach inland sites (see Chapters 2, 5 and 6).

Molecular phylogenetic studies (Chapters 2 and 3) have recovered two major lineages in *Heliotropium* sect. *Cochranea*. The first comprises only *Heliotropium pycnophyllum* and the other is composed of the remaining 16 species (Fig. 9.1). *Heliotropium pycnophyllum* is morphologically distinct from the other species in flower and fruit. It is the only species in section *Cochranea* with a pubescent style and stigmatic head, and possessing a persistent calyx that is dispersed along with the fruit, which does not fall apart[a]. *Heliotropium pycnophyllum* has also a distinctive leaf morphology with revolute margins (Fig. 6.4B, p. 121) that give the appearance of being terete or subterete. It is an extreme xerophyte distributed in the fog-free coastal zone of northern Chile (Fig. 6.5, p. 122), sometimes in sympatry or local parapatry with other species of section *Cochranea*, such as *Heliotropium eremogenum*, *H. inconspicuum*, *H. linariifolium*, *H. philippianum* or *H. taltalense*.

The second lineage is composed of the remaining 16 species and forms an unresolved tetratomy with *Heliotropium krauseanum*, *H. filifolium*, *H. glutinosum* and a well-suported polytomous group of 12 species (Fig. 9.1). *Heliotropium jaffuelii*, was not included in the phylogenetic analyses due to unavailability of material. Despite a through search of herbaria, the ultimate gathering of this species dates to 1964 and along with the type, mark the only known material. *Heliotropium jaffuelii* is endemic to the surroundings of the coastal town of Tocopilla (ca. 22°S, see Fig. 6.9, p. 129) and from its characteristic morphology (i.e., leaves terete and subsessile stigma, Fig. 6.8, p. 128) it is best associated with *Heliotropium filifolium* (Fig. 6.6, p. 124), also a narrow endemic from the coastal areas around Carrizal Bajo (ca. 28°S, see Fig. 6.7, p. 126), some 700 km to the south. The other two species that fall outside the polytomous group, *H. krauseanum* and *H. glutinosum*, are distributed in the coastal areas of northernmost Chile and southern Peru

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[a] This combination of characters is also found in *Heliotropium supinum* L. (Hilger, 1987) and *Heliotropium drepanophyllum* Baker (≡ *Nogalia drepanophylla* (Baker) Verdc.; Verdcourt, 1988). Both species are closely related (Hilger and Diane, 2003) and inhabit arid or semiarid environments of the Old World, but are phylogenetically distantly related to *Heliotropium pycnophyllum*.

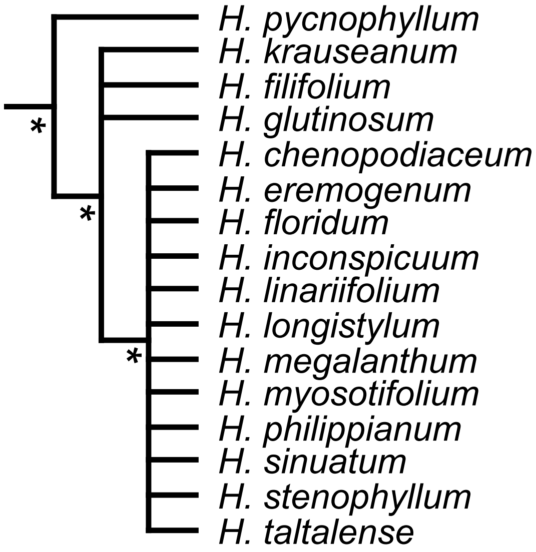

Figure 9.1: Phylogenetic relationships of *Heliotropium* sect. *Cochranea* as currently understood. Asterisks indicate well supported clades.

and in the Andean foothills of the surroundings of Potrerillos (ca. 28°S), respectively, and in the absence of all other members of the section. Based on its floral and leaf morphology, *Heliotropium krauseanum* can be associated with *H. sinuatum* and *H. taltalense* (Johnston, 1928b; Luebert and Pinto, 2004; Fig. 6.2, p. 114). *Heliotropium glutinosum* seems to be morphologically isolated from the other members of *Cochranea*, being the only species in the section with densely glandular leaves (Fig. 6.10, p. 130).

Among the species of the polytomy, no resolution has been achieved in the phylogenetic analyses (Chapters 2 and 3), thus conjectures about their systematic affinities must be based only on the morphological and chorological information available. Similarities between *Heliotropium sinuatum* and *H. taltalense*, both with rugose, sinuate leaves, were already mentioned. These species have non-overlapping geographical distributions (Fig. 2.1H, p. 32).

At least three other morphological groups can be recognised. One is composed of *Heliotropium chenopodiaceum* and *H. myosotifolium*. They are very similar to each other in habit, floral morphology and leaf characteristics, but are slightly different in flower and leaf size (both larger in *H. myosotifolium*) and in the more resinous and less pubescent leaves of *H. chenopodiaceum*. Both species are distributed along similar latitudinal range. Their distributions can be considered parapatric (Fig 6.18, p. 149), with *H. chenopodiaceum* at higher elevations than *H. myosotifolium*. In the contact zones it is often difficult to distinguish them, especially during rainy years when *H. chenopodiaceum* tends to develop larger leaves and flowers.

The second morphological group is composed of five species. Four of them (*Heliotropium floridum*, *H. linariifolium*, *H. philippianum* and *H. eremogenum*) have pubescent leaves and styles longer than the stigmatic head, and are distributed along the coast between 23°S and 29°S (Figs. 6.21–6.23). They form a continuum with overlapping distributions at the extreme of each geographical range, where it is still possible to differentiate them, even in locally sympatric areas. *Heliotropium linariifolium* is the most distinct species and is unique in the section *Cochranea* for having orange corollas. It is a decumbent subshrub, similar in habit to *H. megalanthum*, with which it does not overlap in distribution. *Heliotropium megalanthum* can sometimes have showy pale orange or yellow corollas, leaves pubescent only on the margins, and the style equaling the stigmatic head. This is in contrast to the other four species that are pubescent on the whole leaf surface and the styles are evidently longer. *Heliotropium floridum* has an erect habit and white flowers, and encompasses the geographic range of *H. megalanthum* (see Figs. 2.1C-D, p. 32), which possesses a decumbent habit and white flowers. The former species has an overlapping distribution at the northern terminus of its range with the southern range of *H. linariifolium*, a decumbent, orange-flowered species, at around 27°S. *Heliotropium linariifolium*, in turn, shares its northern terminus with the southern range of *H. philippianum* at ∼25°S, yet another species with erect habit and white flowers. At the northern extreme of this continuum, *Heliotropium eremogenum*, with white corollas and decumbent habit, is distributed in the regions of Antofagasta, Tocopilla and Iquique (Fig. 6.23, p. 163). However, the fragmentary nature of the available material makes it impossible to ascertain whether the northernmost populations of Tocopilla and Iquique represent different species as suggested by Johnston (1929b, 1932, 1937).

The third morphological group is composed of *Heliotropium stenophyllum* and *H. logistylum*. Both are erect shrubs with long and narrow leaves with sparse pubescence, but they differ in the style : stigma ratio (greater in *H. longistylum*), as well as in their different geographic ranges (Fig. 6.20, p. 156). Their ranges are separated by a corridor of less than 50 km along the coast. The geographic area occupied by *H. longistylum* is smaller than that of *H. stenophyllum*, which is widely distributed south of Huasco (ca. 28°30'S).

*Heliotropium inconspicuum* is the only species that appears to be morphologically isolated in the polytomous group. Johnston (1928b) associated it with *H. chenopodiaceum* based on leaf and flower size; however, a close examination of more abundant material reveals that they differ both in leaf and floral morphology, as well as in habit and geographical distribution (Fig. 2.1B-C, p. 32). Its short style and its minute, revolute leaves, suggest that it can be derived from *Heliotropium filifolium*. Indeed, the main flavonoid present in the resin of *H. incospicuum*, seems to be a derivative of filifolinol (R. Torres, personal communication), a constituent of the resin of *H. filifolium* (Torres et al., 1994).

### 9.1.2 Taxonomy of *Heliotropium* sect. *Cochranea*

Compared with the previous taxonomic treatments of *Heliotropium* sect. *Cochranea* (Johnston, 1928b), the present revision (Chapter 6) differs only in few aspects. Synonymy and typification were fully revised here, especially concerning the bulk of type material of European herbaria to which Johnston (1928b) did not have access, resulting in one new narrowed lectotype (*Cochranea sentis*), one neotype (*Heliotropium stenophyllum*), and several corrections to the typifications of Förther (1998).

*Heliotropium huascoense* is placed in the synonymy of *H. stenophyllum*, due to the absence of discreet characters to differentiate these two taxa. More detailed field studies may lead to the conclusion that these two entities are actually different taxa. *Heliotropium sclerocarpum* and *H. chenopodiaceum* var. *ericoideum* are placed in the synonymy of *H. chenopodiaceum*. The former taxon was difficult to distinguish using the key provided by Johnston (1928b) and was known to him only from the type collection made by R.A. Philippi in 1866 from the Andean foothills near Vallenar (ca. 28°35'S). This collection is potentially an aberrant form of *H. chenopodiaceum*. *Heliotropium chenopodiaceum* var.

*ericoideum* was stated to differ from the typical form of *H. chenopodiaceum* only by its pubescence. Observations at the type locality of this variety suggest that both glabrous and pubescent forms co-occur within the same population and that pubescence is variable, even on the same individual.

A new subspecies of *Heliotropium krauseanum* is described from the Lomas de Jahuay in southern Peru and is restricted to the most northern end of the continuous range of *H. krauseanum*. The material upon which this new subspecies is based was not known to Johnston (1928b) and differs from the typical form of *H. krauseanum* in its densely pubescent and less divided veins on the leaves.

Finally, *Heliotropium eremogenum* and *H. jaffuelii*, both described by Johnston (1937) and with no sectional placement in the work of Förther (1998), are included in section *Cochranea*. Johnston (1937) suggested this assignment and phylogenetic analyses (Chapters 2 and 3) confirm it for *Heliotropium eremogenum*. Although *Heliotropium jaffuelii* was not included in the phylogenetic analyses, its morphology and distribution make a different sectional placement very unlikely.

### 9.1.3 Systematic Relationships of ***Heliotropium*** sect. ***Cochranea*** and other ***Heliotropium*** Clades

The closest relatives of *Heliotropium* sect. *Cochranea* occur in South America. The sister clade is composed of *Tournefortia* sect. *Tournefortia* and most sections of Neotropical *Heliotropium* (excl. sect. *Orthostachys* ≡ *Euploca*), except section *Heliothamnus*. While this sister relationship would imply taxonomic rearrangements in *Heliotropium*, it is not clear how they should be executed (compare Diane et al., 2002; Hilger and Diane, 2003; Craven, 2005; see Chapter 3, Section 3.4.4, p. 67). This sister clade has been informally termed the '*Tournefortia* clade' and it has its centre of distribution in the Neotropics, from southern Patagonia to southern United States. Most species of *Tournefortia* occur in the humid tropics, especially along the Andes, Mesoamerica and the Caribbean, and also a few representatives in the Indo-Pacific region. Most of the geographical distribution of section *Cochranea* does not overlap with the distribution of its sister clade. Exceptions are *H. angiospermum* (sect. *Schobera*), occasionally found in southern Peru, and the cosmopolitan *H. curassavicum* (sect. *Platygyne*) that occurs on saline soils across the whole range of section *Cochranea*. The latter species is broadly distributed across the Neotropics, and has been introduced into all continents.

Morphologically, it is not simple to differentiate *Heliotropium* sect. *Cochranea* from its sister clade. The *Tournefortia* clade is more variable in habit, fruit morphology, as well as in pollen morphology, but it is not necessarily more variable than *Heliotropium* sect. *Cochranea* in leaf morphology (Chapter 3). Habit of the *Tournefortia* clade ranges from ephemeral herbs to small trees, while *Cochranea* consists of only shrubs and sub-shrubs. Pollen morphology in the *Tournefortia* clade is very variable (Nowicke and Skvarla, 1974; Scheel et al., 1996), but is constant in section *Cochranea* (Marticorena, 1968), falling into one of the several pollen types defined for the *Tournefortia* clade (Nowicke and Skvarla, 1974). The leaves tend to be smaller, long and narrow in section *Cochranea*, but such characters are also found in some representatives of the *Tournefortia* clade. Fruit morphology in the *Tournefortia* clade varies from dry to fleshy, and from falling apart into one to four syn-mericarpids. In section *Cochranea*, only dry fruits falling apart into two syn-mericarpids (except the above-mentioned *H. pycnophyllum*) are found. One of the few characters with systematic value might be the presence of 'empty chambers' in the fruits. They are absent in section *Cochranea* but present in the *Tournefortia* clade, as well as in the Old World *Heliotropium* (Hilger and Diane, 2003). However, not all species of the *Tournefortia* clade present this feature (Hilger, 1992). Apart from the investigations of Hilger (1987, 1989, 1992), little is known about the systematic distribution of fruit characters and its development in *Heliotropium*, a topic that deserves further study.

Most phylogenetic analyses show the Neotropical *Heliotropium* sect. *Heliothamnus* as sister to the remaining *Heliotropium* clades. Section *Heliothamnus*, a group of Andean and Central American shrubs, is only distantly related to *Heliotropium* sect. *Cochranea*, in spite of their ecological and geographical affinities and the fact that both are shrubby groups. There are several differences in fruit, flower and leaf morphology that separate sections *Cochranea* and *Heliothamnus* (see Förther, 1998; and references therein for details). Fruits of section *Heliothamnus* fall apart into four nutlets (versus two in section *Cochranea*), and the leaves are larger and the limb expanded in *Heliothamnus* (versus small and reduced in section *Cochranea*).

## 9.2 Ecology of *Heliotropium* sect. *Cochranea*

*Heliotropium* sect. *Cochranea* is distributed in arid environments of the Atacama Desert. The distribution of the species of section *Cochranea* is largely controlled by winter precipitation (Chapter 5). The exception is *Heliotropium krauseanum*, the only species of section *Cochranea* under the influence of truly tropical desert climate. In Peru and northernmost Chile (north of Iquique, ca. 20°S) rainfall, although rare, tends to occur in summer (December-March, Schulz, 2009). Conversely, south of Iquique, especially along the coast, rainfall tends to occur in winter (June-September, Luebert and Pliscoff, 2006; Schulz, 2009), a typical feature of Mediterranean-type climates (Rivas-Martínez, 2008). Most species of *Heliotropium* sect. *Cochranea* are under the influence of Mediterranean climate and winter precipitation is therefore an important factor for their distribution. The majority of species have very narrow distribution along the rainfall gradient, concentrated around values of precipitation in the environmental space (see Fig. 5.2, p. 97). This suggests that precipitation is a limiting factor for the distribution of the species. The distribution of section *Cochranea* under more favourable conditions (i.e., higher amounts of rainfall) may be limited by competition with other species who outperform them in more humid habitats. *Heliotropium chenopodiaceum* and *H. stenophyllum* have the widest ranges of available precipitation, and also the greatest latitudinal ranges for any species in the section. This may be the result of increased fitness under more favourable rainfall conditions. This observation is in contradiction with the theoretical prediction that niche breadth should increase as resource availability decreases (Pianka, 1979). A positive relationship between niche breadth and amount of rainfall was also found in *Leucadendron* L. (Proteaceae) in the Cape Region (Thuiller et al., 2004b).

Minimum temperature of the coldest month, and maximum temperature of the warmest month of the year are also important variables, limiting the distribution of the species in *Heliotropium* sect. *Cochranea*. Species tend to have wider distributions and to be more differentiated along temperature gradients than along precipitation gradients (see Fig. 5.2, p. 97). However most species grow near the coast, where the ocean exerts a thermal regulatory influence on local climate, preventing the occurrence of extreme values of both maximum and minimum temperatures. This may be indicative of differential tolerance to temperature conditions. Especially during the warmest period, high evapotranspiration rates may be a critical factor for plant survival in arid environments due to plant water storage limitations (Woodward, 1987). At the scale of the individual, however, transpiration is controlled by stomatal conductance (Jarvis and McNaughton, 1986; Kimball and Bernacchi, 2006). Plants can exhibit adaptations is leaf characteristics, such as hypostomatry, in order to face conditions favoring high evapotranspiration in arid environments.

Species of *Heliotropium* sect. *Cochranea* possess vegetative morphology and phenology that may be considered as adaptations to survival under extremely arid conditions. (Diane et al., 2003; Brokamp, 2006; see Chapters 3 and 6). Such characters are:

- Microphylly (all species)
- High leaf length : width ratio (all species)
- Revolute margins (all species, but especially *H. pycnophyllum*)
- Low stomatal density on the adaxial surface (all species)
- Hypostomatous leaves with high trichome density on the abaxial surface of the leaves (*H. inconspicuum*, *H. krauseanum*, *H. sinuatum*, *H. taltalense*)
- Dense leaf pubescence (*H. eremogenum*, *H. floridum*, *H. linariifolium*, *H. philippianum*, *H. pynophyllum*)
- Resin exudation (*H. chenopodiaceum*, *H. filifolium*, *H. glutinosum*, *H. inconspicuum*, *H. krauseanum*, *H. longistylum*, *H. sinuatum*, *H. stenophyllum*, *H. taltalense*)
- Leaf succulence (*H. filifolium*, *H. floridum*, *H. linariifolium*, *H. megalanthum*, *H pycnophyllum*)
- Loss of above-ground structures during dry years (*H. eremogenum*, *H. linariifolium*, *H. megalanthum*, *H. myosotifolium*, *H. philippianum*)
- Superficial laterally expanded root systems (reported for *H. pycnophyllum* and *H. stenophyllum* Rundel et al., 1980; Olivares and Squeo, 1999; and *H. floridum*, personal field observations)

## 9.3 Evolution of ***Heliotropium*** sect. ***Cochranea***

The central hypothesis of this study is an evolutionary hypothesis (see p. 26, Chapter 1): that the origin and diversification of *Heliotropium* sect. *Cochranea* was associated with the development of the Atacama Desert, and that the group experienced an adaptive radiation in the Atacama Desert. Most analyses carried out in this work are in line with this hypothesis.

The age estimate for the origin of *Heliotropium* sect *Cochranea*, using two different datasets and molecular dating methods (Chapters 2 and 4), is middle to late Miocene. This age is coincident with the major uplift of the Andes, as postulated by several authors (see references in Chapters 2 and 4). The Andes are one of the major factors contributing to aridity in the Atacama Desert, either by generating a rain shadow effect (Rech et al., 2010) or by a decrease in eastern Pacific surface temperatures (Sepulchre et al., 2009). The uplift of the Andes is also a powerful barrier to dispersal. The origin of *Heliotropium* sect. *Cochranea* may also be linked to the Andes as vicariant barrier. *Heliotropium* sect.

*Cochranea* is the only group of South American *Heliotropium* that is restricted to the western versant of the Andes (Fig. 4.2, p. 72), and their uplift could have isolated populations of the ancestor of *Heliotropium* sect. *Cochranea* on its western side. These populations later diversified and produced the diversity that is observed today in this section.

A second major diversification event appears to have occurred in the early Pliocene, the time period coincident with a postulated reinforcement of aridity in the Atacama Desert as a result of an intensification of the effect of the Humboldt Current (see Section 1.2.3, p. 20). Whether this diversification occurred gradually or was rather sudden, is connected with the second part of the hypothesis of this study. Several lines of evidence indicate that *Heliotropium* sect. *Cochranea* actually experienced an adaptive radiation in the Atacama Desert in the early Pliocene.

As mentioned in Section 1.3.2, adaptive radiations are characterized by three major features: (i) common ancestry, (ii) adaptation (phenotype-environmental correlation and trait utility) and (iii) extraordinary diversification. In Chapters 2 and 3 the monophyly of section *Cochranea* is well-supported with broad taxon samplings, including 16 out of 17 species of section *Cochranea*, all sections of Neotropical *Heliotropium*, representatives of Old World *Heliotropium*, *Euploca*, *Myriopus* and *Ixorhea*, as well as members of closely related families within Boraginales. As a consequence, the first feature of an adaptive radiation is met by section *Cochranea*, since monophyly is one of the aspects of the broader concept of common ancestry (Schluter, 2000; Glor, 2010).

Phenotype-environmental correlation is usually more difficult to assess. In the previous Section (9.2), some morphological characters of species of *Heliotropium* sect. *Cochranea* were mentioned as phenotypic adaptations to better survive in arid environments. A major limiting climatic factor for the distribution of species of *Heliotropium* sect. *Cochranea* is precipitation (Chapter 5). These characters are related to the environments, in which species of *Heliotropium* sect. *Cochranea* grow because they contribute to tolerate aridity. These features help to reduce transpiration rates, increase water storage, avoid dry periods or increase efficiency in water uptake. Most leaf characters are mentioned by Napp-Zinn (1984) as indications of xeromorphy.

Microphylly and high leaf length : width ratio may be considered as adaptations to aridity because plants with reduced leaf area have less surface exposed, thus reducing transpiration (Woodward, 1987). Low stomatal density on the abaxial surface and hypostomatry may help reducing transpiration (Foster and Smith, 1986). Abaxial leaf surface in *Cochranea* is usually more pubescent than adaxial surface and the leaves are revolute, thus helping reducing transpiration (O'Toole et al., 1979) through modification of leaf boundary air layers and by protecting stomata against high radiation levels (Manetas, 2003). Some species with higher density of simple hairs (*Heliotropium eremogenum*, *H. floridum*, *H. linariifolium*, *H. philippianum*) do not have glandular trichomes. Glandular trichomes seem to be responsible of resin exudation. Resin exudation causes the effect of protecting leaf surface from direct contact with air, thus contributing to the reduction of water loss (Meinzer et al., 1990). Leaf succulence, usually associated with an increase in the number of spongy parenchyma layers, is a mechanism to increase water storage (Zimmermann and Milburn, 1982). Loss of above-ground structures during dry years may be seen as a mechanism to avoid unfavourable - extremely arid - periods. Superficial root systems may also be seen as arid adapted. In arid environments, plants with well-developed lateral root systems can utilize the rains penetrating only to the upper zones of the soil, where competition can be intense during rainy periods (Drew, 1979).

Extraordinary diversification has several facets. It can be seen in high absolute number of species of a clade, high morphological diversity, diversification rates, and rapid bursts of diversification (rapid speciation) (Schluter, 2000; Glor, 2010). Sister group comparison offers a framework to asses extraordinary diversification, because sister groups are, by definition, of the same age (Barraclough et al., 1998). *Heliotropium* sect. *Cochranea* may then be compared with the *Tournefortia* clade, which is its sister group (see Chaper 3).

Absolute number of species in section *Cochranea* is less than in the *Tournefortia* clade (17 versus ca. 160 species). In spite of its lower number of species, leaf morphological diversity in *Heliotropium* sect. *Cochranea* is at least as high as in the *Tournefortia* clade, indicating that leaf morphology in *Cochranea* is extraordinarily diverse. Estimates of disparity may be seen, when not confounded by phylogeny (see Chapter 3), as rates of morphological diversification (Collar et al., 2005; O'Meara et al., 2006). Considering the younger age of the onset of diversification of *Cochranea*, in comparison with the *Tournefortia* clade ($\sim$ 16 Ma versus $\sim$ 31 Ma, Chapter 4), high leaf morphological diversity is further amplified.

On the other hand, considering crown ages of section *Cochranea* and the *Tournefortia* clade and absolute number of species for simple estimation of diversification rates (Magallón and Sanderson, 2001), rate of diversification in section *Cochranea* results 20% greater than in the *Tournefortia* clade. Lack of phylogenetic resolution of the polytomous group of section *Cochranea* (12 species, see Chapters 2 and 3) is interpreted as indication of rapid speciation in the early Pliocene. Preliminary studies on timing of diversification of *Cochranea* using the $\gamma$ statistic (Pybus and Harvey, 2000) suggest that internal nodes of the polytomous group tend to be concentrated close to the root node, exhibiting a slowdown of lineage diversification rate towards the present. Such slowdowns have been interpreted as signature of adaptive radiations (Schluter, 2000; Harmon et al., 2003; Phillimore and Price, 2008; Rabosky and Lovette, 2008). Furthermore, according to preliminary analyses, slightly differentiated climatic niches among species of section *Cochranea* (Chapter 5) are not associated with patristic phylogenetic distance. They rather appear to be related to co-distribution (sympatry, parapatry or allopatry), indicating that some species have tended to diverge in sympatry (Graham et al., 2004). Taken together, evidence provided here tend to support the hypothesis of adaptive radiation of *Heliotropium* sect. *Cochranea* in the Atacama Desert. However, the preliminary results still require further study.

Why did *Heliotropium* sect. *Cochranea* diversify rapidly in the early Pliocene and then slow its diversification rate towards the present-day? One possible explanation is diversity-dependence cladogenesis after initial diversification (Phillimore and Price, 2008; Rabosky and Lovette, 2008). The increase of aridity during the early Pliocene possibly created new environments, triggering speciation processes in plants as a consequence of ecological differentiation. As the Atacama Desert is essentially a resource-limited environment, carrying capacity may become saturated soon, placing a limit for further diversification (Rabosky, 2009), thus reducing rates of speciation toward the present. This working hypothesis can be used as a guide to address future evolutionary studies in *Heliotropium* sect. *Cochranea*.

## 9.4 ***Heliotropium*** **sect.** ***Cochranea*** **and the Biogeography of the Atacama Desert**

Several ecological and geological processes, discussed in previous sections, can help explaining the present distribution of *Heliotropium* sect. *Cochranea*. These processes, such as the development of hyperaridity in the Atacama Desert and the uplift of the Andes, may be common to several Atacama lineages with similar distributions. However, different distribution patterns (floristic elements) can be found in the Atacama Desert flora, namely Neotropical, central Chilean, trans-Andean and antitropical elements (Chapter 8). These elements are summarized in Fig. 9.2.

*Heliotropium* sect. *Cochranea* is included in the Neotropical element, along with several lineages whose close relatives are continuously distributed in the Peruvian Desert, the Tropical Andes and subtropical eastern South America (see Table 8.1, p. 175). Floristic exchanges between the Peruvian Desert and the Atacama Desert along the western Andean foothills and long-distance dispersal may be put forward to partially explain this distribution pattern. Andean vicariance and colonization of high-Andean environment from either side of the Andes can also be proposed to explain the joint presence of lineages on both sides of the Andes and in the high-Andean environments. They are also possible explanations for the Trans-Andean element (lineages disjunctly distributed on both sides of the Andes), where long-distance dispersal via trans-Andean corridors cannot be discarded.

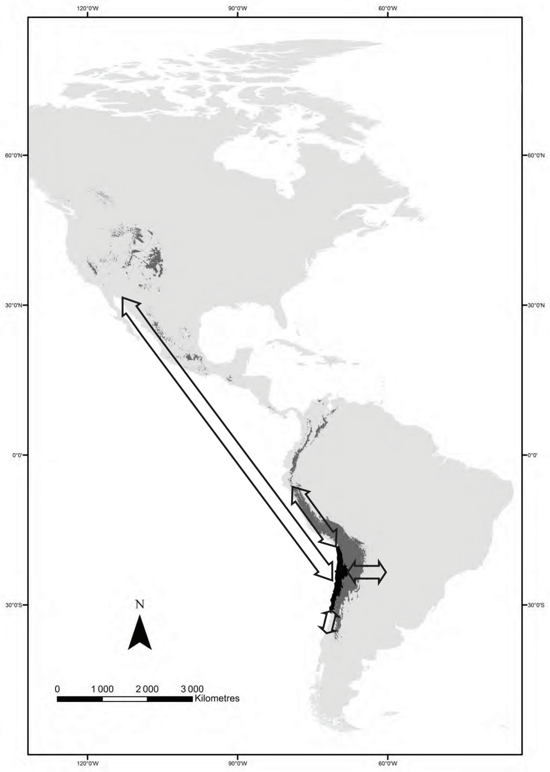

Figure 9.2: Floristic elements of the Atacama Desert (black area). Arrows indicate biogeographical affinities. The dark grey area indicates zones higher than 3000 m, showing the major extension of the Andes.

Biogeographical affinities between the Atacama Desert and Central Chile and the Mediterranean Andes (central Chilean element) are supported by several lineages having such distribution (see Table 8.1, p. 175). Given the contiguity of both areas, past climatic fluctuations, causing expansion and contraction of the geographical ranges of Atacama and Central Chilean taxa can explain these affinities.

The antitropical element, lineages disjunctly distributed in arid zones of South and North America, with presence in the Atacama Desert, is represented by few groups. Pliocene or later steping-stone dispersal via Panama Isthmus, or long-distance dispersal, can be invoked to explain this distribution pattern.

## 9.5 Prospects for the Systematic Studies of *Heliotropium*

Some aspects regarding the study of *Heliotropium* sect. *Cochranea* in particular and of the genus *Heliotropium* in general can be identified, to which future research may be addressed. Some of them have been mentioned throughout this work, but others came out as a product of a global appreciation of the state of the art of the systematics of Heliotropiaceae.

Phylogenetic resolution is still very poor within *Heliotropium* sect. *Cochranea*. Improving phylogenetic resolution is essential to test hypotheses of rapid diversification in a phylogenetic framework, and to implement comparative evolutionary methods in order to generate robust tests about the links between phylogenetic relatedness, morphological and environmental diversification, and modes of geographic speciation. Several ways to improve phylogenetic resolution can be suggested. Preliminary results with six molecular markers (5 chloroplast regions and ITS) do not show changes in resolution. In other members of the Atacama Desert flora (e.g., *Nolana*; Tu et al., 2008), low-copy nuclear markers, such as the LEAFY second intron (Frohlich and Meyerowitz, 1997), have been used to infer more robust phylogenies. This might be seen as an immediate next step in *Heliotropium* sect. *Cochranea*.

To better understand in detail the interspecific relationships and speciation mechanisms, it will be necessary to approach at the population/species level and focus on species trees (Maddison, 1997; Slowinski and Page, 1999; Edwards, 2009; Knowles, 2009) with explicit consideration of coalescent processes (Avise, 2004). To this end, intensive field work is required, especially in those areas where several closely related species of *Heliotropium* sect. *Cochranea* grow in sympatry.

Beyond *Heliotropium* sect. *Cochranea*, almost all groups of *Heliotropium* still require basic study. Ongoing research objectives will attempt to clarify the classification of section *Heliothamnus*. Most species in this group were described by Ruiz and Pavón (1799), Krause (1906) and Johnston (1928b). While Johnston's (1928b) material is clear, Ruiz and Pavón (1799) names still need to be typified. Type specimens of *Heliotropium* at the herbarium of the Jardín Botánico de Madrid, where most Ruiz & Pavón's material is housed, were already revised. All type specimens of Krause (1906) at Berlin were destroyed and a work of lectotypification is therefore required. Chapter 7 is also a first step in this direction. Since the last taxonomic revision of *Heliotropium* sect. *Heliothamnus* by Johnston (1928b), numerous specimens have been collected in Peru and Ecuador, where section *Heliothamnus* has its centre of diversity. Several of theses specimens cannot be accommodated in the treatment of Johnston (1928b) and need to be described as new species. Phylogenetic resolution in *Heliotropium* sect. *Heliothamnus* is also low and more phylogenetic research must be carried out in this group.

One of the most challenging groups in *Heliotropium* is the *Tournefortia* clade. Several species that likely belong to this clade have never been included in phylogenetic analyses, especially narrow endemics from Central America and eastern South America (Argentina, Brazil, Paraguay, Uruguay). More problematic are the species of *Tournefortia* sect. *Tournefortia*, with over 300 species names. This group has never been taxonomically revised and species delineation is difficult. Current estimates of species diversity in the *Tournefortia* clade are therefore provisional, and a taxonomic revision is urgently needed before more evolutionary and ecological studies are undertaken.

To date, no comprehensive taxonomic work is available for any section in the Old World *Heliotropium* (*Heliotropium* II clade, Hilger and Diane, 2003; see Chapter 3), where only regional treatments have been published (e.g., Verdcourt, 1991; Akhani and Förther, 1994; Craven, 1996). The genera *Euploca* and *Myriopus* also lack taxonomic revisions (Hilger and Diane, 2003). The placement of the monotypic genus *Ixorhea* in the phylogeny of Heliotropiaceae is still unclear (Chapter 3). In spite of considerable progress in the knowledge of the systematics of these genera made in the last decade (Diane et al., 2002; Hilger and Diane, 2003), infrageneric relationships of these groups are still unresolved.

More research is also needed at the level of the family Heliotropiaceae. Its monophyly is well-supported, but its placement within the order Boraginales is still unresolved (compare Ferguson, 1999; Gottschling et al., 2001; Moore and Jansen, 2006; Luebert and Wen, 2008), as well as the placement and composition of Boraginales in the lamiid clade (Angiosperm Phylogeny Group, 2009). Future studies will attempt to contribute to the classification at all hierachial levels.

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# Zusammenfassung

## Systematik, Ökologie und Evolution von *Heliotropium* sect. *Cochranea* (Heliotropiaceae) und die Biogeographie der Atacama-Wüste

*Heliotropium* sect. *Cochranea* ist ein in der chilenischen Atacama und angrenzenden peruanischen Wüste endemisches Taxon der Heliotropiaceae. In dieser Arbeit werden Systematik, Ökologie und Evolution der Gruppe unter der Hypothese untersucht, dass *Heliotropium* sect. *Cochranea* eine adaptive Radiation in der Atacama-Wüste erfahren hat und dass die Entstehung und Diversifizierung von *Heliotropium* sect. *Cochranea* in ummittelbarer Verbindung mit Entstehung und Veränderung der Wüste stehen.

Damit werden folgende wissenschaftliche Fragen angesprochen:

(1) Welche Arten können innerhalb von *Heliotropium* sect. *Cochranea* anerkannt werden?

(2) Ist *Heliotropium* sect. *Cochranea* monophyletisch?

(3) Welche Hauptclades können innerhalb von *Heliotropium* sect. *Cochranea* identifziert werden?

(4) Mit welcher anderen *Heliotropium*-Gruppe ist die Sektion nahe verwandt?

(5) Wann diversifizierten sich die Hauptclades von *Cochranea* und verwandten Gruppen?

(6) Ist die morphologische Vielfalt von *Cochranea* mit ihrem Lebensraum verbunden?

(7) Durch welche klimatisch limitierenden Faktoren wird die Verbreitung von *Heliotropium* sect. *Cochranea* kontrolliert?

Um diese Fragen klären zu können, wurden folgende Methoden verwendet: Moderne Ansätze zur phylogenetischer Systematik, traditionelle Alpha-Taxonomie und morphologische Analysen. Weiterhin wurden phylogenetische Zeitabschätzungen und ereignisbasierte biogeographische Analysen durchgeführt. Die ökologische Nische-Modellierung wurde verwendet, um klimatische Faktoren, die die Verbreitung der Arten der *Heliotropium* sect. *Cochranea* kontrollieren, identifizieren zu können.

Diese Dissertation ist eine kumulative Arbeit, die aus bereits veröffentlichten, bereits akzeptierten, eingereichten oder in Vorbereitung befindendlichen Manuskripten besteht. Deshalb wurden die Kapitel 2 bis 8 als Zeitschriftartikeln strukturiert, wobei jedes eine separate ,,Material und Methoden"-Sektion enthält. Die zitierte Literatur wird am Ende zusammen aufgelistet.

Kapitel 1 ist eine allgemeine Einleitung. Die bisherigen Kenntnisse über Sektion *Cochranea* und die Atacama-Wüste werden dargestellt, Hypothesen, wissenschaftliche

Fragen, und Forschungsziele werden formuliert, und eine Übersicht der Dissertation wird gegeben.

Kapitel 2 ist eine vorläufige phylogenetische Studie von *Heliotropium* sect. *Cochranea.* Ziele dieses Kapitels sind, die Monophylie von Sektion *Cochranea* einzuschätzen, Hauptlinien innerhalb von *Cochranea* zu identifizieren, und eine erste Abschätzung der Divergenzzeiten zu ermöglichen. Eine phylogenetische Analyse mit vier molekularen Markern (*ndhF*, *trnL-trnF*, *rps*16 und ITS) und drei unterschiedlichen Methoden (Maximum Parsimony, Maximum Likelihood und Baysian Inference) wurde durchgeführt, um die Monophylie zu testen und phylogenetische Beziehungen zu identifizieren. Eine Fossilien-kalibrierte Maximum Likelihood *ndhF*-Phylogenie der Boraginales und die Penalized Likelihood-Methode wurden verwendet, um Divergenzzeiten der Hauptlinien von *Heliotropium* sect. *Cochranea* abzuschätzen. Die Ergebnisse zeigen, dass *Cochranea* monophyletisch ist, während des Miozäns entstand und sich während des Pliozäns diversifiziert hat.

Phylogenetische Beziehungen zwischen der Sektion *Cochranea* und anderen *Heliotropium*-Gruppen sind im Kapitel 3 angesprochen. Eine erweiterter Datensatz von *Heliotropium* unter besonderer Berücksichtigung der neotropischen Arten wurde verwendet, um auf Verwandtschaftskreise rückschließen zu können. Maximum Parsimony, Maximum Likelihood und Bayesian Inference wurden für die Analyen von fünf molekularen Marker (*trnL-trnF*, *rps*16, *psbA-trnH*, *trnS-trnG* and ITS) verwendet. Drei neotropische Hauptclades in *Heliotropium* wurden identifiziert, eine davon ist *Heliotropium* sect. *Cochranea.* Für diese Clades wurde die morphologische Vielfalt basierend auf vegetativen Merkmalen der Wuchsform und der Blätter untersucht. Diese Diversität ist auch zwischen den Sippen trockener und feuchter Lebensräumen der Neotropis verglichen worden. *Heliotropium* sect. *Cochranea* weist eine große morphologische Vielfalt im Blattbau auf und ist daran genau so variabel wie ihre viel artenreichere Schwestergruppe. Die morphologischen Diversität tendiert dazu, bei Arten trockener Gebiete höher zu sein als in feuchten Lebensräumen, besonders in Bezug auf die Blattmorphologie. Innerhalb der neotropischen *Heliotropium*-Arten trockener Lebensräume trägt Sektion *Cochranea* in einem besonders großen Maß zur blattmorphologischen Vielfalt bei.

Im Kapitel 4 werden Divergenzzeit und biogeographische Beziehungen der Hauptclades der südamerikanischen *Heliotropium*-Arten mit einer auf drei Markern (*trnL-trnF*, *rps*16 and *trnS-trnG*) basierenden Phylogenie untersucht. Vertreter aus den Familien Ehretiaceae und Cordiaceae der („holzigen“) Boraginales wurden mit einbezogen, um eine Kalibrierung mehrerer Knoten zu ermöglichen. Eine bayesische, unkorrelierte und lognormale Uhr wurde verwendet, um Divergenzzeiten abzuschätzen. Parsimony und Maximum Likelihood-Ansätze wurden kombiniert, um ursprüngliche Verbreitungsgebiete der Clades in der Phylogenie abzuschätzen. Das Kapitel fokussiert dann auf die Rolle, die die Anden-Hebung und die Entstehung arider Lebensräumen in Südamerika auf die Diversifizierung von *Heliotropium* ausübten. Mindestens fünf unabhängige andine und außerandine Diversifizierungsereignisse während des Spätmiozäns und Frühpliozäns wurden nachgewiesen. Sie stimmen mit der Hypothese überein, dass die Anden und die ariden Lebensräume Südamerikas sich schnell und in der jüngsten Vergangenheit entwickelt haben.

Eine Modellierung der Artenverbreitung mit Klimadaten wurde im Kapitel 5 durchgeführt. Mehre Modellierungstechniken mit sechs Klimadatensätze wurden verwendet. Endgültige Modelle sind für jede Art via Ensemble Forecasting aufgebaut worden. Die Wichtigkeit jeder Variablen und die Nische-Differenzierung zwischen den Arten wurden bewertet. Effekte des Klimawandels auf den Bedrohungsgrad und mögliche

Auswirkungen von Klimadatensätzen auf Modellierungsergebnisse wurden abgeschätzt. Winterniederschläge und Winterminimum-Temperaturen waren die wichtigsten Variablen für die Verbreitung der Mehrheit der Arten von *Heliotropium* sect. *Cochranea*, aber auch Sommermaximum-Temperaturen sind für mehrere Arten wichtig. Diese Ergebnisse stehen in Einklang mit der Erwartung, dass die Verbreitung der Arten der Sektion *Cochranea* durch saisonale Schwankungen von Niederschlägen und erst sekundär durch die Temperatur kontrolliert wird. Die Klima-Nische der *Heliotropium* sect. *Cochranea* Arten differieren leicht voneinander. Die Szenarien des Klimawandels variieren deutlich im Hinblick auf die potentielle Verbreitung der Arten; und die Klimadatensätze haben große Auswirkungen auf die Modelle der Artenverbreitung.

Kapitel 6 ist eine taxonomische Revision von *Heliotropium* sect. *Cochranea*. Siebzehn Arten werden anerkannt und eine neue Unterart beschrieben. Zwei bisher eigenständige Arten (*H. huascoense* und *H. sclerocarpum*) werden in die Synonymie von *H. stenophyllum* und *H. chenopodiaceum* gestellt. Jeder Protolog und jede Typifizierung wurde sorgfältig revidiert, und ein Lecto- und ein Neotypus werden vorgeschlagen. Zwei Arten (*H. eremogenum* und *H. jaffuelii*) werden zum ersten Mal in der Sektion *Cochranea* einbezogen. Verbreitungskarten und neue Abbildungen wurden für alle Arten erstellt. Diese Revision stellt eine Synthese des gegenwärtigen Kenntnisstands der Sektion *Cochranea* dar.

Kapitel 7 und 8 gehen über *Heliotropium* sect. *Cochranea* hinaus. Kapitel 7 wird als erster Schritt zur einer systematischen Studie weiterer neotropischer *Heliotropium* Arten betrachtet. In diesem Kapitel wird der Name *Heliotropium arborescens* L. (die Typusart von Sektion *Heliothamnus*) epitypifiziert. Dies schafft taxonomische Klarheit und nomenklatorische Stabilität für die Art, damit komplexe Artabgrenzungen und Verwandtschaftskreise auch formal eindeutig untersucht werden können.

Kapitel 8 ist ein Review bisheriger phylogenetischer Arbeiten über Arten aus der Atacama-Wüste und ihrer Areale. Ziel ist es, Florenelemente der Atacama-Wüste aufgrund phylogenetischer Beziehungen und der Verbreitung zu identifizieren. Vier Florenelemente (neotropisch, mittelchilenisch, transandin und antitropisch) wurden identifiziert, und im Kontext möglicher geographischen Ursprünge der Flora der Atacama-Wüste diskutiert.

Im abschließenden Kapitel 9 werden die Hauptaspekte der Systematik, Ökologie und Evolution von *Heliotropium* sect. *Cochranea*, die in den vorherigen Kapiteln diskutiert wurden, zusammengefasst. Es wird nachgewiesen dass *Heliotropium* sect. *Cochranea* eine adaptive Radiation in der Atacama-Wüste erfahren hat. Weitere im Rahmen der Arbeit deutlich gewordene systematische, ökologische und evolutive Aspekte von *Heliotropium* sect. *Cochranea* und nahe verwandter Arten werden vorgestellt und als zukünftige Projekte diskutiert.

# Contribution to Chapters

**Chapter 2**: Luebert, F. and Wen, J. 2008. Phylogenetic analysis and evolutionary diversification of *Heliotropium* sect. *Cochranea* (Heliotropiaceae) in the Atacama Desert. *Systematic Botany* 33: 390-402.

Own contributions: Designed work (together with J. Wen), collected material (most), performed laboratory work and statistical analyses, and wrote the manuscript.

**Chapter 3**: Luebert, F., Brokamp, G., Wen, J., Weigend, M and Hilger, H.H. Phylogenetic relationships and morphological diversity in Neotropical *Heliotropium* (Heliotropiaceae). *Taxon* (accepted, 07.09.2010).

Own contributions: Designed work (together with H. H. Hilger and M. Weigend), collected material (in part), performed laboratory work (in part) and statistical analyses, and wrote the manuscript.

**Chapter 4**: Luebert, F., Hilger, H.H. and Weigend, M. Diversification in the Andes: Age and origins of South American *Heliotropium* lineages (Heliotropiaceae, Boraginales).

Own contributions: Designed work (together with H. H. Hilger and M. Weigend), collected material (in part), performed laboratory work and statistical analyses, and wrote the manuscript.

**Chapter 5**: Pliscoff, P., Luebert, F.. Hilger, H.H. and Guisan, A. Climatic control on distribution, niche differentiation, extinction risk, climate change effects and uncertainties associated with variable selection in *Heliotropium* sect. *Cochranea* a group of rare species from the Atacama Desert.

Own contributions: Designed work (together with P. Pliscoff), revised material and built databases, performed statistical analyses (in part), and wrote the manuscript (together with P. Pliscoff).

**Chapter 6**: Luebert, F. Revision of *Heliotropium* sect. *Cochranea* (Heliotropiaceae).

Single authorship.

**Chapter 7**: Luebert, F., Weigend, M. and Hilger, H.H. 2010. Epitypification of *Heliotropium arborescens* L. (Heliotropiaceae). *Taxon* 59(4): 1263-1266.

Own contributions: Designed work, performed literature research, revised material, and wrote the manuscript.

**Chapters 1 and 8**: Luebert, F. Hacia una fitogeografía histórica del Desierto de Atacama. *Revista de Geografía Norte Grande* (invited contribution, submitted, 08.07.2010).

Single authorship.

# Curriculum Vitae

For reasons of data protection, the curriculum vitae is not included in the online version

# Publication List

## *Heliotropium*

(1) Luebert, F. Revision of *Heliotropium* sect. *Cochranea* (Heliotropiaceae). in prep.

(2) Pliscoff, P., Luebert, F.. Hilger, H.H. and Guisan, A. Climatic control on distribution, niche differentiation, extinction risk, climate change effects and uncertainties associated with variable selection in *Heliotropium* sect. *Cochranea* a group of rare species from the Atacama Desert. in prep.

(3) Luebert, F., Hilger, H.H. and Weigend, M. Diversification in the Andes: Age and origins of South American *Heliotropium* lineages (Heliotropiaceae, Boraginales). in prep.

(4) Diane, N., Luebert, F., Förther, H., Weigend, M. and Hilger, H.H. Heliotropiaceae. In: Families and genera of vascular plants (Kubitzki, K., ed.). Springer, Berlin. accepted.

(5) Luebert, F., Brokamp, G., Wen, J., Weigend, M and Hilger, H.H. Phylogenetic relationships and morphological diversity in Neotropical *Heliotropium* (Heliotropiaceae). *Taxon* (accepted, 07.09.2010).

(6) Luebert, F., Weigend, M. and Hilger, H.H. 2010. Epitypification of *Heliotropium arborescens* L. (Heliotropiaceae). *Taxon* 59(4): 1263–1266.

(7) Luebert, F. and Wen, J. 2008. Phylogenetic analysis and evolutionary diversification of *Heliotropium* sect. *Cochranea* (Heliotropiaceae) in the Atacama Desert. *Systematic Botany* 33(2): 390–402.

(8) Modak, B., Rojas, M., Torres, R., Rodilla, J. and Luebert, F. 2007. Antioxidant activity of a new Aromatic Geranyl Derivative of the resinous exudates from *Heliotropium glutinosum* Phil. *Molecules* 12(5): 1057–1063.

(9) Luebert, F. and Pinto, R. 2004. Nota sobre la presencia de *Heliotropium krauseanum* Fedde (Heliotropiaceae) en Chile. *Gayana Botánica* 61(2): 60–62.

## Atacama Desert

(1) Luebert, F. Hacia una fitogeografía histórica del Desierto de Atacama. *Revista de Geografía Norte Grande* (invited contribution, submitted, 08.07.2010)

(2) Pinto, R. and Luebert, F. 2009. Datos sobre la flora vascular del desierto costero de Arica y Tarapacá, Chile, y sus relaciones fitogeográficas con el sur de Perú. *Gayana Botánica* 66(1): 28–49.

(3) Luebert, F., Wen, J. and Dillon, M.O. 2009. Systematic placement and biogeographical relationships of the monotypic genera *Gypothamnium* and *Oxyphyllum* (Asteraceae: Mutisioideae) from the Atacama Desert. *Botanical Journal of the Linnean Society* 159(1): 32–51.

(4) Luebert, F., García, N. and Schulz, N. 2007. Observaciones sobre la flora y vegetación de los alrededores de Tocopilla (22°S, Chile). *Boletín Museo Nacional de Historia Natural* 56: 27–52.

(5) Dillon, M.O., Arancio, G. and Luebert, F. 2007. Five new species of *Nolana* (Solanaceae- Nolaneae) from Chile. *Arnaldoa* 14: 191–212.

(6) García, N. and Luebert, F. 2005. Hallazgo de *Malesherbia tocopillana* Ricardi (Malesherbiaceae) en su localidad tipo. *Chloris Chilensis* 8(2). URL: `http:/www.chlorischile.cl`.

(7) Luebert, F. 2004. Apuntes sobre la vegetación de bosque y matorral del desierto precordillerano de Tarapacá (Chile). *Chloris Chilensis* 7(1). URL: `http:/www.chlorischile.cl`.

## Other topics (since 2006)

(1) Tecklin, D., DellaSala, D.A., Luebert, F. and Pliscoff, P. 2010. From Gondwana to New World: Valdivian temperate rainforests of Chile and Argentina. In: Temperate and Boreal Rainforests of the World. Ecology and conservation (DellaSala, D.A., ed.), Island Press, Washington DC. in press.

(2) Luebert, F. and Pliscoff, P. 2010. Settings biodiversity conservation priorities in Chile. *Ecoengen* 12: 17–25.

(3) Weigend, M. and Luebert, F. 2009. Weeding the Nettles I: Clarifying species limits in perennial, rhizomatous *Urtica* (Urticaceae) from southern and central Chile and Argentina. *Phytotaxa* 2: 1–12.

(4) Luebert, F. and Pliscoff, P. 2009. Depuración y estandarización de la cartografía de pisos de vegetación de Chile. *Chloris Chilensis* 12(1). URL: `http:/www.chlorischile.cl`.

(5) García, N. and Luebert, F. 2008. Aporte al conocimiento de la flora y la vegetación del río Mosco, Villa O'Higgins, ∼48° S (Región de Aysén, Chile). *Chloris Chilensis* 11(2). URL: `http:/www.chlorischile.cl`.

(6) Pliscoff, P. and Luebert, F. 2006. Una nueva propuesta de clasificación de la vegetación de Chile y su aplicación en la evaluación del estado de conservación de los ecosistemas terrestres. *Ambiente y Desarrollo* 22(1): 41–45.

(7) Luebert, F. and Pliscoff, P. 2006. Los límites del clima mediterráneo en Chile. *Chagual* 4: 64–69.

(8) Luebert, F. and Pliscoff, P. 2006. Sinopsis bioclimática y vegetacional de Chile. Editorial Universitaria, Santiago.

(9) Pliscoff, P. and Luebert, F. 2006. Ecosistemas terrestres. In: Biodiversidad de Chile: Patrimonio y desafíos, pp. 78–91. Comisión Nacional del Medio Ambiente, Santiago.

# Congress Contributions

(1) Pliscoff P., Luebert F., Hilger H.H. and Guisan A. Exploring structure and evolution of climatic realized niche in *Heliotropium* from the Pacific Desert of South America. Niche Evolution Conference, Zürich, Switzeralnd, 3-4 July 2009 (Poster).

(2) Luebert, F., Brokamp, G., Weigend, M., and Hilger, H.H. Phylogeny and age estimates of the South American *Heliotropium* (Heliotropiaceae). 60° Congresso Nacional de Botânica, Feria de Santana, Brazil, 28 June-3 July 2009 (Poster).

(3) Luebert, F., Hilger, H.H. and Pliscoff, P. 2008. Integrating molecular phylogenetics, distribution, and climatic modelling to infer evolutionary processes of *Heliotropium* sect. *Cochranea* (Heliotropiaceae) in the Atacama Desert. Systematics 2008: 10th Annual Meeting of the German Society of Plant Systematics, 8th International Symposium 'Biodiversity and Evolutionary Biology' of the German Botanical Society, Göttingen, Germany, 7-11 April 2008 (Talk).

(4) Pliscoff, P., Hilger, H.H. and Luebert, F. 2008. Ecological modelling and GIS analysis to evaluate the conservation status and protection level of *Heliotropium* sect. *Cochranea* species (Heliotropiaceae) in Chile and Peru. Systematics 2008: 10th Annual Meeting of the German Society of Plant Systematics, 8th International Symposium 'Biodiversity and Evolutionary Biology' of the German Botanical Society, Göttingen, Germany, 7-11 April 2008 (Poster).

(5) Torres, R., Véjar, N., Modak, B., Luebert, F. and Faini, F. 2006. Flavonoides y ácido carrizaloico en el exudado resinoso de *Heliotropium longystylum* y su relación con *H. huascoense*. XVII Reunión Anual de la Sociedad de Botánica de Chile, Talca, Chile, 16-19 Jan. 2006 (Poster).

(6) Torres, R., Modak, B. and Luebert, F. 2005. Género *Heliotropium* en Chile: Sistemática, química y biología, guíada por los exudados resinosos. V Reunión de la Sociedad Latinoamericana de Fitoquímica, Montevideo, Uruguay, 28 Nov.–2 Dec. de 2005 (Poster).

(7) Torres, R., Modak, B. and Luebert, F. 2005. Un nuevo tipo de derivados espiranicos de la resina de *Heliotropium inconspicuum* y sus actividades antioxidantes. V Reunion de la Sociedad Latinoamericana de Fitoquímica, Montevideo, Uruguay, 28 Nov.–2 Dec. de 2005 (Poster).

(8) Luebert, F. 2003. Patrones de distribución en *Heliotropium* sect. *Cochranea* (Heliotropiaceae). XXIX Jornadas Argentinas de Botánica and XV Reunión Anual de la Sociedad Botánica de Chile. San Luis, Argentina, 19-23 Oct. 2003 (Poster).

# Appendix A: Supplementary data to Chapter 2

## Plant material used in the phylogenetic analysis of *Heliotropium* sect. *Cochranea*

Voucher specimens and GenBank accessions are indicated. Samples followed by * were used only in the combined ITS1+*trnL* intron analysis. Samples followed by ** were used in the *ndhF* age estimate analysis. Herbaria voucher abbreviations: Departamento de Botánica, Universidad de Concepción, Concepción, Chile (CONC), Field Museum of Natural History, Chicago, Illinois, U.S.A. (F), Museo Nacional de Historia Natural, Santiago, Chile (SGO), Smithsonian Institution, Washington, D.C., U.S.A. (US). Data for each collection is presented in the following order: taxon, voucher or reference, ITS or ITS1 GenBank, *rps*16 GenBank, *ndhF* GenBank, *trnL-trnF* or *trnL* intron GenBank.

***Heliotropium* sect. *Cochranea* (Ingroup)**: *Heliotropium* sp., *Luebert, Becker, García & Pinto 2159* (SGO)**, EF688880, EF688983, EF688933, EF688827. *Heliotropium chenopodiaceum* (A.DC.) Clos, *Luebert & García 2462/856* (SGO)**, EF688869, EF688972, EF688921, EF688816. *Heliotropium chenopodiaceum* (A.DC.) Clos, *Luebert & García 2501/895* (SGO)**, EF688872, EF688975, EF688924, EF688819. *Heliotropium eremogenum* I. M. Johnst., *Luebert & García 2575/969* (SGO)**, EF688865, EF688968, EF688917, EF688812. *Heliotropium filifolium* (Miers) I. M. Johnst., *Luebert, Becker & García 2015* (SGO)**, EF688900, EF689002, EF688951, EF688848. *Heliotropium filifolium* (Miers) I. M. Johnst., *Luebert & Torres 1973* (SGO)**, EF688882, EF688985, EF688935, EF688829. *Heliotropium floridum* (A.DC.) Clos, *Luebert, Becker & García 2031* (SGO)**, EF688893, EF688996, EF688946, EF688840. *Heliotropium floridum* (A.DC.) Clos, *Luebert & Torres 1974* (SGO)**, EF688884, EF688987, EF688937, EF688831. *Heliotropium floridum* (A.DC.) Clos, *Luebert & Becker 2838* (SGO)**, EF688861, EF688964, EF688913, EF688808. *Heliotropium glutinosum* Phil., *Luebert & Torres 1970* (SGO)**, EF688885, EF688988, EF688938, EF688832. *Heliotropium glutinosum* Phil., *Luebert & Becker 2161* (SGO)**, EF688879, EF688982, EF688932, EF688826. *Heliotropium huascoense* I. M. Johnst., *Luebert & Becker 2902* (SGO)**, EF688873, EF688976, EF688925, EF688820. *Heliotropium* cf. *huascoense* I. M. Johnst., *Luebert & Becker 2909* (SGO)**, EF688874, EF688977, EF688926, EF688821. *Heliotropium* cf. *huascoense* I. M. Johnst., *Luebert & Becker 2168* (SGO)**, EF688877, EF688980, EF688930, EF688824. *Heliotropium inconspicuum* Reiche, *Luebert, Becker & García 2081* (SGO)**, EF688891, EF688994, EF688944, EF688838. *Heliotropium inconspicuum* Reiche, *Luebert, Becker & García 2095* (SGO)**, EF688890, EF688993, EF688943, EF688837. *Heliotropium inconspicuum* Reiche, *Luebert & García 2783/1177* (SGO)**, EF688862, EF688965, EF688914, EF688809. *Heliotropium krauseanum* Fedde, *Dillon 8779* (F)**, EF688894, EF688997, EF688947, EF688841. *Heliotropium krauseanum* Fedde, Hilger and Diane (2003)*, AF396909, n/a, n/a, AY376195. *Heliotropium linariifolium* Phil., *Luebert, Becker & García 2054* (SGO)**, EF688892, EF688995, EF688945, EF688839. *Heliotropium linariifolium* Phil., *Luebert & García 2731/1125* (SGO)**, EF688863, EF688966, EF688915, EF688810. *Heliotropium linariifolium* Phil., *Luebert & Becker 2844A* (SGO)**, EF688870, EF688973, EF688922, EF688817. *Heliotropium longistylum* Phil., *Luebert, Becker & García 2020* (SGO), EF688901, EF689003, EF688952, EF688849. *Heliotropium longistylum* Phil., *Luebert & Torres 1971* (SGO)**, EF688883, EF688986, EF688936, EF688830. *Heliotropium megalanthum* I. M. Johnst., *Teillier* (SGO 154510)*, EF688897, n/a, n/a, EF688844, *Heliotropium megalanthum* I. M. Johnst., *Luebert & Becker 2165* (SGO)**, EF688876, EF688979, EF688929, EF688823. *Heliotropium myosotifolium* (A.DC.) Reiche, *Luebert & Becker 2162* (SGO)**, EF688878, EF688981, EF688931, EF688825. *Heliotropium philippianum* I. M. Johnst., *Luebert, Becker & García 2124* (SGO)**, EF688887, EF688990, EF688940, EF688834. *Heliotropium philippianum* I. M. Johnst., *Luebert, Becker & García 2131* (SGO)**, EF688886, EF688989, EF688939, EF688833. *Heliotropium pycnophyllum* Phil., *Luebert & García 2620/1014* (SGO)**, EF688866, EF688969, EF688918, EF688813. *Heliotropium pycnophyllum* Phil., *Luebert & García 2813/1207* (SGO)**, EF688868, EF688971, EF688920, EF688815. *Heliotropium pycnophyllum* Phil., Hilger and Diane (2003)*, AY377812, n/a, n/a, AY376208. *Heliotropium* cf. *sclerocarpum* Phil., *Luebert & Becker 2907* (SGO)**, EF688864, EF688967, EF688916, EF688811. *Heliotropium sinuatum* (Miers) I. M. Johnst., *Luebert & Torres 1972* (SGO)**, EF688881, EF688984, EF688934, EF688828. *Heliotropium sinuatum* (Miers) I. M. Johnst., *Luebert & García 2492/886* (SGO)**, EF688871, EF688974, EF688923, EF688818. *Heliotropium stenophyllum* Hook. & Arn., *Luebert & Becker 1990* (SGO)**, EF688899, EF689001, EF688950, EF688847. *Heliotropium stenophyllum* Hook. & Arn., *Luebert & Becker 2911* (SGO)**, EF688875, EF688978, EF688928, EF688822. *Heliotropium stenophyllum* Hook. & Arn., *Luebert & Becker 2910* (SGO)**, n/a, n/a, EF688927, n/a. *Heliotrapium taltalense* (Phil.) I. M. Johnst., *Luebert, Becker & García 2083* (SGO)**, EF688889, EF688992, EF688942, EF688836. *Heliotropium taltalense* (Phil.) I. M. Johnst., *Luebert, Becker & García 2101* (SGO)**, EF688888, EF688991, EF688941, EF688835. *Heliotropium taltalense* (Phil.) I. M. Johnst., *Luebert & García 2650/1044* (SGO)**, EF688867, EF688970, EF688919, EF688814. **Outgroups**: **Heliotropiaceae**: *Euploca campestris* (Griseb.) Diane & Hilger, *Nee & Wen 53873* (US)**, EF688856, EF688959, EF688908, EF688803. *Heliotropium adenogynum* I. M. Johnst., Hilger and Diane (2003)*, AY377792, n/a, n/a, AY376172. *Heliotropium aegyptiacum* Lehm., Hilger and Diane (2003)*, AF396918, n/a, n/a, AY376173. *Heliotropium amplexicaule* Vahl, Hilger and Diane (2003)*, AY176076, n/a, n/a, AY376174. *Heliotropium arbainense* Fresen., Hilger and Diane (2003)*, AF396916, n/a, n/a, AY376176. *Heliotropium arborescens* L., *Dillon 8838* (F)**, EF688859, EF688962, EF688911, EF688806. *Heliotropium asperrimum* R.Br., Hilger and Diane (2003)*, AF402586, n/a, n/a, AY376178. *Heliotropium confertiflorum* Boiss. & Noe, Hilger and Diane (2003)*, AY377798, n/a, n/a, AY376184. *Heliotropium curassavicum* L., *Luebert & García 2521/915* (SGO)**, EF688896, EF688999, EF688949, EF688843. *Heliotropium curassavicum* subsp. *oculatum* (A. Heller) Thorne, Hilger and Diane (2003)*, AF396897, n/a, n/a, AY376186. *Heliotropium curassavicum* var. *argentinum* I. M. Johnst., Hilger and Diane (2003)*, AF396898, n/a, n/a, AY376185. *Heliotropium digynum* (Forssk.) Asch. ex C. Christensen, Hilger and Diane (2003)*, AF396915, n/a, n/a, AY376188. *Heliotropium elongatum* Hoffm. ex Roem. & Schult., *Nee & Wen 53844* (US)**, EF688855, EF688958, EF688907, EF688802. *Heliotropium europaeum* L., Hilger and Diane (2003)*, AF402587, n/a, n/a, AY376193. *Heliotropium foertherianum* Diane & Hilger, Hilger and Diane (2003)*, AF396900, n/a, n/a, AY376222. *Heliotropium giessii* Friedr.-Holzh., Hilger and Diane (2003)*, AF396917, n/a, n/a, AY376194, *Heliotropium gnaphalodes* L., Hilger and Diane (2003)*, AF396903, n/a, n/a, AY376226. *Heliotropium hirsutissimum* Grauer, Hilger and Diane (2003)*, AF396912, n/a, n/a, AY376190. *Heliotropium incanum* Ruiz & Pav., Hilger and Diane (2003)*, AY176077, n/a, n/a, AY376192. *Heliotropium luzonicum* (I. M. Johnst.) Craven, Hilger and Diane (2003)*, AF396899, n/a, n/a, AY376228. *Heliotropium mandonii* I. M. Johnst., Hilger and Diane (2003)*, AF396895, n/a, n/a, AY376197. *Heliotropium messerschmidioides* Kuntze, Hilger and Diane (2003)*, AY377791, n/a, n/a, AY376171. *Heliotropium microstachyum* Ruiz & Pav., Hilger and Diane (2003)*, AF396908, n/a, n/a, AY376199. *Heliotropium nicotianaefolium* Poir., Hilger and Diane (2003)*, AY377807, n/a, n/a, AY376201. *Heliotropium nicotianifolium* Poir., *Nee & Wen 53843* (US)**, EF688854, EF688957, EF688906, EF688801. *Heliotropium nicotianifolium* Poir., *Nee & Wen 53890* (US)**, EF688857, EF688960, EF688909, EF688804. *Heliotropium oliverianum* Schinz, Hilger and Diane (2003)*, (AF396913), n/a, n/a, (AY376202). *Heliotropium paronychioides* A.DC, *Luebert & Teillier 2241* (CONC)**, EF688895, EF688998, EF688948, EF688842. *Heliotropium paronychioides* A.DC, Hilger and Diane (2003)*, AY377808, n/a, n/a, AY376204. *Heliotropium patagonicum* (Speg.) I. M. Johnst., Hilger and Diane (2003)*, AY377809, n/a, n/a, AY376205. *Heliotropium pilosum* Ruiz & Pav., *Dillon 8819* (F), EF688902, EF689004, EF688953, EF688850. *Heliotropium pinnatisectum* R.L.Pérez-Mor., Hilger and Diane (2003)*, AY377810, n/a, n/a, AY376206. *Heliotropium verdcourtii* Craven, Hilger and Diane (2003)*, AF396901, n/a, n/a, AY376227. *Heliotropium verdcourtii* Craven, *Wen 8706* (US)*, EF688898, n/a, n/a, EF688845. *Heliotropium veronicifolium* Griseb., Hilger and Diane (2003)*, AY377818, n/a, n/a, AY376215. *Heliotropium zeylanicum* (Burm. f.) Lam., Hilger and Diane (2003)*, AY377819, n/a, n/a, AY376216. *Ixorhea tschudiana* Fenzl, Hilger and Diane (2003)*, AF396880, n/a, n/a, AY376218. *Myriopus* *salzmannii* (DC.) Diane & Hilger, *Nee & Wen 53848* (US)**, EF688853, EF688956, EF688905, EF688800. *Myriopus volubilis* (L.) Small, Hilger and Diane (2003)*, AF396882, n/a, n/a, AY376233. *Tournefortia acutiflora* M. Martens & Galeotti, Ferguson (1999)**, n/a, n/a, AF047813, n/a. *Tournefortia breviloba* Krause, Hilger and Diane (2003)*, AY377824, n/a, n/a, AY376223. *Tournefortia* cf. *buchtienii* Killip, *Nee & Wen 53944* (US)**, EF688858, EF688961, EF688910, EF688805. *Tournefortia chinchensis* Killip, Hilger and Diane (2003)*, AY377825, n/a, n/a, AY376224. *Tournefortia fuliginosa* Kunth, Hilger and Diane (2003)*, AY377826, n/a, n/a, AY376225. *Tournefortia rubicunda* Salzm. ex DC, *Nee & Wen 53846* (US)**, EF688852, EF688955, EF688904, EF688799. *Tournefortia ternifolia* Kunth, Hilger and Diane (2003)*, AY377830, n/a, n/a, AY376231. *Tournefortia undulata* Benth., Hilger and Diane (2003)*, AY377831, n/a, n/a, AY376232. **Cordiaceae**: *Cordia decandra* Hook. & Arn., *Luebert & Kritzner 1873* (SGO EIF)**, EF688903, EF689005, EF688954, EF688851. *Cordia nodosa* Lam., Ferguson (1999)**, n/a, n/a, AF047808, n/a. **Boraginaceae**: *Borago officinalis* L., Olmstead and Reeves (1995)**, n/a, n/a, L36393, n/a. *Borago officinalis* L., Bremer et al. (2002), n/a, AJ431019, n/a, AJ430896. *Borago officinalis* L., Winkworth et al. (2002), AY092898, n/a, n/a, n/a. *Cryptantha flavoculata* Payson, Ferguson (1999)**, n/a, n/a, AF047803, n/a. **Ehretiaceae**: *Bourreria costaricensis* (Standl.) A. H. Gentry, Ferguson (1999)**, n/a, n/a, AF047797, n/a. *Bourreria succulenta* Jacq., Moore and Jansen (2006)**, n/a, n/a, DQ197257, n/a. *Coldenia procumbens* L., Moore and Jansen (2006)**, n/a, n/a, DQ197255, n/a. *Ehretia anacua* I.M. Johnst., Moore and Jansen (2006)**, n/a, n/a, DQ197256, n/a. *Ehretia ovalifolia* Hassk., Ferguson (1999)**, n/a, n/a, AF047800, n/a. *Tiquilia canescens* (DC.) A. T. Richardson, Moore and Jansen (2006)**, n/a, n/a, DQ197258, n/a. *Tiquilia hispidissima* (Torr. & A. Gray) A. T. Richardson, Moore and Jansen (2006)**, n/a, n/a, DQ197268, n/a. *Tiquilia nuttallii* (Benth.) A. T. Richardson, Moore and Jansen (2006)**, n/a, n/a, DQ197282, n/a. *Tiquilia paronychioides* (Phil.) A. T. Richardson, *Dillon 8798* (F)**, EF688860, EF688963, EF688912, EF688807. **Hydrophyllaceae**: *Codon schenckii* Schinz, Ferguson (1999)**, n/a, n/a, AF047776, n/a. *Eriodictyon californicum* Greene, Ferguson (1999)**, n/a, n/a, AF047820, n/a. *Hydrophyllum virginianum* L., Ferguson (1999)**, n/a, n/a, AF019646, n/a. *Nama demissum* A. Gray, Ferguson (1999)**, n/a, n/a, AF047767, n/a. *Phacelia congesta* Hook., Ferguson (1999)**, n/a, n/a, AF047780, n/a. *Romanzoffia californica* Greene, Ferguson (1999)**, n/a, n/a, AF047804, n/a. *Tricardia watsonii* Torr. ex S. Watson, Ferguson (1999)**,n/a, n/a, AF047775, n/a. *Wigandia urens* Urb., Ferguson (1999)**. n/a, n/a, AF047763, n/a. *Wigandia urens* Urb., Ferguson unpubl., AF091212, n/a, n/a, n/a. *Wigandia urens* Urb., *Wen 8671* (US), n/a, EF689000, n/a, EF688846. **Vahliaceae**: *Vahlia capensis* Thunb., Bremer et al. (2002)**, n/a, n/a, AJ429112, n/a. **Solanaceae**: *Nicotiana tabacum* L., Wakasugi et al. (1998)**, n/a, n/a, Z00044, n/a. **Gentianaceae**: *Gentiana procera* T. Holm, Olmstead and Reeves (1995)**, n/a, n/a, L36400, n/a. **Loganiaceae**: *Logania vaginalis* (Labill.) F. Muell., Backlund et al. (2000)**, n/a, n/a, AJ235837, n/a. **Rubiaceae**: *Luculia gratissima* Sweet, Oxelman et al. (1999)**, n/a, n/a, AJ011987, n/a.

# Appendix B: Supplementary data to Chapter 3

## B.1 Plant material included in the phylogenetic study of Neotropical *Heliotropium*

Information is given in the following order: Taxon; Reference and/or Voucher specimen; *rps*16 GenBank accession; *trnL-trnF* GenBank accession; *trnH-psbA* GenBank accession; *trnS-trnG* GenBank accession; ITS GenBank accession

**Ingroup - Neotropical species, *Heliotropium* sect. *Cochranea***: *H. chenopodiaceum* (A.DC.) Clos; Luebert and Wen (2008), *Luebert & García 2501/895* (SGO); EF688975; EF688819; HQ286167; HQ286046; EF688872. *H. eremogenum* I.M.Johnst.; Luebert and Wen (2008), *Luebert & García 2575/969* (SGO); EF688968; EF688812; HQ286168; HQ286047; EF688865. *H. filifolium* (Miers) I.M.Johnst.; Luebert and Wen (2008), *Luebert & Torres 1973* (SGO); EF688985; EF688829; HQ286169; HQ286048; EF688882. *H. floridum* (A.DC.) Clos; Luebert and Wen (2008), *Luebert & Torres 1974* (SGO); EF688987; EF688831; HQ286170; HQ286049; EF688884. *H. glutinosum* Phil.; Luebert and Wen (2008), *Luebert & Torres 1970* (SGO); EF688988; EF688832; HQ286171; HQ286050; EF688885. *H. inconspicuum* Reiche; Luebert and Wen (2008), *Luebert, Becker & García 2081* (SGO); EF688994; EF688838; HQ286172; HQ286051. EF688891. *H. krauseanum* Fedde; Luebert and Wen (2008), *Dillon 8779* (F); EF688997; EF688841; HQ286173; HQ286052; EF688894. *H. linariifolium* Phil.; Luebert and Wen (2008), *Luebert, Becker & García 2054* (SGO); EF688995; EF688839; HQ286174; HQ286053; EF688892. *H. longistylum* Phil.; Luebert and Wen (2008), *Luebert & Torres 1971* (SGO); EF688986; EF688830; HQ286175; HQ286054; EF688883. *H. megalanthum* I.M.Johnst.; Luebert and Wen (2008), *Luebert & Becker 2165* (SGO); EF688979; EF688823; HQ286176; HQ286055; EF688876. *H. myosotifolium* (A.DC.) Reiche; *Luebert, Becker & García 2011* (SGO); HQ286228; HQ286135; HQ286177; HQ286056; HQ286107. *H. philippianum* I.M.Johnst.; Luebert and Wen (2008), *Luebert, Becker & García 2124* (SGO); EF688990; EF688834; HQ286178; HQ286057; EF688887. *H. pycnophyllum* Phil.; Luebert and Wen (2008), *Luebert & García 2813/1207* (SGO); EF688971; EF688815; HQ286179; HQ286058; EF688868;. *H. sinuatum* (Miers) I.M.Johnst.; Luebert and Wen (2008), *Luebert & Torres 1972* (SGO); EF688984; EF688828; HQ286180; HQ286059; EF688881. *H. stenophyllum* Hook. et Arn.; Luebert and Wen (2008), *Luebert & Becker 1990* (SGO); EF689001; EF688847; HQ286181; HQ286060; EF688899. *H. taltalense* (Phil.) I.M.Johnst.; Luebert and Wen (2008), *Luebert, Becker & García 2083* (SGO); EF688992; EF688836; HQ286182; HQ286061; EF688889. ***Heliotropium* sect. *Coeloma***: *H. patagonicum* (Speg.) I.M.Johnst.; *Weigend et al. 6012* (BSB); HQ286229; HQ286136; HQ286183; HQ286062; HQ286108. *H. veronicifolium* Griseb.; *Hilger et al. 95/29* (BSB); HQ286230; HQ286137; HQ286184; HQ286063; HQ286109. *H. transalpinum* Vell.; *Hilger et al. 95/23* (BSB); HQ286231; HQ286138; HQ286185; HQ286064; HQ286110. ***Heliotropium* sect. *Heliothamnus***: *H. adenogynum* I.M.Johnst.; *Cano 10058* (USM); HQ286232; HQ286139; HQ286186; HQ286065; HQ286111. *H. arborescens* L.; *Schwerdtfeger 2443* (cult. BGBM) (B); HQ286233; HQ286140; HQ286187; HQ286066; HQ286112. *H. incanum* Ruiz & Pav.; *Weigend 00/162* (NY); HQ286234; HQ286141; HQ286188; HQ286067; HQ286113. *H.* cf. *lippioides* Krause; *Weigend et al. 8545* (M); HQ286235; HQ286142; HQ286189; HQ286068; -. *H. mandonii* I.M.Johnst.; *Hilger K04/02* (B); HQ286236; HQ286143; HQ286190; HQ286069; HQ286114. *H. submolle* Klotzsch; *Weigend et al. 2000/719* (BSB); -; HQ286144; HQ286191; HQ286070; -. *H.* spec.; *Weigend et al. 8621* (BSB); HQ286237; -;

HQ286192; HQ286071; HQ286115. ***Heliotropium*** **sect.** ***Heliotrophytum***: *H. amplexicaule* Vahl; *Hilger et al. 95/70* (BSB); HQ286238; HQ286145; HQ286193; HQ286072; -. *H. nicotianifolium* Poir.; Luebert and Wen (2008), *Nee & Wen 53843* (US); EF688957; EF688801; HQ286194; HQ286073; EF688854. *H. phylicoides* Cham.; *Hilger et al. 95/09* (BSB); HQ286239; HQ286146; HQ286195; HQ286074; HQ286116. ***Heliotropium*** **sect.** ***Hypsogenia***: *H. abbreviatum* Rusby; *de la Barra 286* (BSB); HQ286240; HQ286147; HQ286196; HQ286075; HQ286117. *H. microstachyum* Ruiz & Pav.; *Weigend et al. 97/320* (BSB); HQ286241; HQ286148; HQ286197; HQ286076; HQ286118. ***Heliotropium*** **sect.** ***Plagiomeris***: *H. kurtzii* Gangui; *Weigend et al. 5914* (BSB); HQ286242; HQ286149; HQ286198; HQ286077; HQ286119. *H. paronychioides* A.DC.; Luebert and Wen (2008), *Luebert & Teillier 2241* (SGO); EF688998; EF688842; HQ286199; HQ286078; EF688895. *H. pinnatisectum* Pérez-Mor.; *Weigend et al. 5901* (BSB); HQ286243; HQ286150; HQ286200; HQ286079; HQ286120. ***Heliotropium*** **sect.** ***Platygyne***: *H. curassavicum* L.; Luebert and Wen (2008), *Luebert & García 2521* (SGO); EF688999; EF688843; HQ286201; HQ286080; EF688896. ***Heliotropium*** **sect.** ***Schobera***: *H. angiospermum* Murray; *Gillis 8155* (FTG); HQ286244; HQ286151; HQ286202; HQ286081; HQ286121. *Hilger 99/44* (BSB); -; -; -; -; HQ286122. ***Heliotropium*** **sect.** ***Tiaridium***: *H. elongatum* (Lehm.) I.M.Johnst.; Luebert and Wen (2008), *Nee & Wen 53844* (US); EF688958; EF688802; HQ286203; HQ286082; EF688855. *H. indicum* L.; *Hilger 1584* (BSB); HQ286245; -; HQ286204; HQ286083; HQ286123. *Heliotropium without sectional placement*: *H. glabriusculum* (Torr.) A.Gray; *Warnock 15067* (LL); -; HQ286152; HQ286205; HQ286084; -. *H. molle* (Torr.) I.M.Johnst.; *Turner 25-139* (TEX); HQ286246; HQ286153; HQ286206; HQ286085; HQ286124. ***Touneforita*** **sect.** ***Tournefortia***: *T. argentea* L.f.; *Tillich 3555* (MSB); HQ286247; HQ286154; HQ286207; HQ286086; HQ286125. *T.* cf. *buchtienii* Killip; Luebert and Wen (2008), *Nee & Wen 53944* (US); EF688961; EF688805; HQ286208; HQ286087; EF688858. *T. chinchensis* Killip; *Weigend et al. 5809* (BSB); HQ286248; HQ286155; HQ286209; HQ286088; HQ286126. *T. gnaphalodes* (L.) Kunth; *Hilger 99/34* (BSB); HQ286249; HQ286156; HQ286210; HQ286089; HQ286127. *T. hirsutissima* L.; *Stenzel 96/32* (BSB); HQ286250; AY376227; HQ286211; HQ286090; HQ286128. *T. hirsutissima* L.; Luebert and Wen (2008); -; -; -; -; EF688898. *T. microcalyx* (Ruiz & Pav.) I.M.Johnst.; *Weigend & Dostert 97/5* (MSB); HQ286251; HQ286157; HQ286212; HQ286091; HQ286129. *T. polystachya* Ruiz & Pav.; *Weigend* 3869 (BSB); HQ286252; HQ286158; HQ286213; HQ286092; HQ286130. *T. ternifolia* Kunth; *Weigend et al.* 5675 (BSB); HQ286253; HQ286159; HQ286214; HQ286093; HQ286131. *Ingroup - Old World species, Heliotropium sect. Heliotropium*: *H. europaeum* L.; Hilger & Diane (2003), *Hilger 97/06* (BSB); HQ286253; HQ286160; HQ286215; HQ286094; AF396914. *H. giessii* Friedr.-Holz; Hilger & Diane (2003), *Hilger 93/03* (BSB); HQ286255; HQ286161; HQ286216; HQ286095; AF396917. ***Heliotropium*** **sect.** ***Odontotropium***: *H. arbainense* Fresen.; Hilger & Diane (2003), *Förther 4049* (BSB); HQ286256; HQ286162; HQ286217; HQ286096; AF396916. ***Heliotropium*** **sect.** ***Pterotropium***: *H. erosum* Lehm.; *Zippel 00/69* (BSB); HQ286257; HQ286163; HQ286218; HQ286097; HQ286132. ***Heliotropium*** **sect.** ***Zeylanica***: *H. zeylanicum* (Burm.f.) Lam.; Hilger & Diane (2003), *Hilger 94/04* (BSB); HQ286258; HQ286164; HQ286219; HQ286098; AY377819. ***Ceballosia***: *C. fruticosa* (L.f.) Kunkel ex Förther; *Weigend & Weigend 8703* (B); HQ286259; HQ286165; HQ286220; HQ286099; HQ286133. **Outgroups, Heliotropiaceae**: *Euploca procumbens* (Mill.) Diane & Hilger[a]; Luebert and Wen (2008), *Nee & Wen 53873* (US); EF688959; EF688803; HQ286221; HQ286100; EF688856. *Heliotropium pilosum* Ruiz & Pav.; Luebert and Wen (2008), *Dillon 8819* (F); EF689004; EF688850; HQ286222; -; EF688902. *Ixorhea tschudiana* Fenzl; *Hilger et al. 95/65* (BSB); HQ286260; HQ286166; HQ286223; HQ286101; HQ286134. *Myriopus salzmannii* (DC.) Diane & Hilger; Luebert and Wen (2008), *Nee & Wen 53848* (US); EF688956; EF688800; HQ286224; HQ286102; EF688853. *Tournefortia rubicunda* Salzm.; Luebert and Wen (2008), *Nee & Wen 53846* (US); EF688955; EF688799; HQ286225; HQ286103; EF688852. **Ehretiaceae**: *Tiquilia paronychioides* (Phil.) A.T.Richardson; Luebert and Wen (2008), *Dillon 8798* (F); EF688963; EF688807; HQ286226; HQ286104; EF688860. **Cordiaceae**: *Cordia decandra* Hook. & Arn.; Luebert and Wen (2008), *Luebert & Kritzner 1873* (SGO); EF689005; EF688851; HQ286227; HQ286105; EF688903. **Hydrophyllaceae**: *Wigandia urens* Urb.; Luebert and Wen (2008), *Wen 8671* (US); EF689000; EF688846; -; HQ286106; AF091212.

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[a] Cited by Luebert and Wen (2008) as *Euploca campestris* (Griseb.) Diane & Hilger

## B.2 Data sources for morphological analyses

### B.2.1 Data sources for LM and SEM analyses

*Heliotropium amplexicaule* (Diane et al., 2003), *H. angiospermum* (*Hilger 99/44*, BSB), *H. curassavicum*, *H. elongatum* (Diane et al., 2003), *H. indicum* (*Hilger 99/22*, BSB), *H. kurtzii* (Weigend et al. 5914, BSB), *H. microstachyum* (*Weigend et al. 97/320*, BSB), *H. nicoteanifolium* (*Hilger et al. 95/56*, BSB), *H. paronychioides* (*Hilger e al. 95/83*, BSB), *H. patagonicum*, *H. pinnatisectum*, *H. transalpinum* (Diane et al., 2003), *H. veronicifolium* (*Hilger et al. 95/29*, BSB), *Tournefortia argentea*, *T. bicolour*, *T. glabra*, *T. gnaphalodes*, *T. hirsutissima*, *T. luzonica*, *T. microcalyx*, *T. rollotii*, *T. ternifolia* (Diane et al., 2003), *Heliotropium chenopodiaceum* (*Luebert 1736*, BSB), *H. eremogenum* (*Luebert & García 2575/969*, BSB), *H. filifolium* (*Luebert & Torres 1977*, BSB), *H. floridum* (*Luebert & Torres 1974*, BSB), *H. glutinosum* (*Luebert & Torres 1970*, BSB), *H. huascoense* (*Luebert & Becker 2168*, BSB), *H. inconspicuum* (*Luebert et al. 2081*, BSB), *H. krauseanum* (*Weigend et al. 7202*, BSB), *H. linariifolium* (*Luebert et al. 2079*, BSB), *H. longistylum* (*Luebert & Kritzner 1811*, BSB), *H. megalanthum* (*Luebert & Becker 2165*, BSB), *H. myosotifolium* (*Luebert et al. 2011*, BSB), *H. philippianum* (*Luebert et al. 2124*, BSB), *H. pycnophyllum* (*Luebert & Torres 1966*, BSB), *H. sinuatum* (*Luebert & Torres 1972*, BSB), *H. stenophyllum* (*Luebert & Becker 1990*, BSB), *H. taltalense* (*Luebert et al. 2083*, BSB), *Ceballosia fruticosa*, *H. arbainense*, *H. erosum*, *H. europaeum*, *H. giessii*, *H. zeylanicum*, *H. adenogynum*, *H. arborescens* (Diane et al., 2003), *H. corymbosum* (*Ackermann & Cáceres 432*, B), *H. incanum*, *H. mandonii*, *H. rufipilum*, *H. submolle*, *Euploca procumbens*, *Myriopus salzmannii*, *Ixorhea tschudiana* (Diane et al., 2003).

### B.2.2 Data sources for leaf length, leaf width and plant height

*Heliotropium abbreviatun* (15, 20). *H. amplexicaule* (1. 3,8, 11, 24, 25, 27, 31, 34, 36, 37). *H. angiospermum* (8, 28, 34, 39, 40, 41). *H. curassavicum* (1, 3, 5, 6, 8, 9, 11, 22, 24, 25, 26, 27, 28, 30, 31, 32, 34, 35, 36, 37, 38, 39, 40, 41). *H. elongatum* (1, 3, 8, 11, 30). *H. indicum* (1, 3, 5, 6, 8, 11, 22, 24, 26, 27, 28, 29, 30, 32, 33, 34, 37, 38, 39, 40, 41). *H. kurtzii* (9, 11). *H. microstachyum* (11, 35, 37, 41). *H. nicoteanifolium* (1,8, 11, 36, 37). *H. paronychioides* (9, 11, 35). *H. patagonicum* (9, 11, 17). *H. phylicoides* (1, 11, 36). *H. pinnatisectum* (9, 18). *H. transalpinum* (1,8, 11, 12, 37, 39, 40). *H. veronicifolium* (1, 11, 37). *Tournefortia argentea* (3,5, 32). *T. bicolour* (23, 26, 28, 38, 39, 40, 41, 45). *T. buchtienii* (41, 45). *T. chinchensis* (41, 45). *T. glabra* (26, 28, 38, 39, 40, 41). *T. gnaphalodes* (28, 39, 40, 45). *T. hirsutissima* (22, 26, 28, 38, 39, 40, 41, 45). *T. luzonica* (2,3). *T. microcalyx* (41, 45). *T. polystachya* (41, 45). *T. rollotii* (45). *T. ternifolia* (41, 45, F). *H. chenopodiaceum* (35, 49, H, F). *H. eremogenum* (21, H, F). *H. filifolium* (35, H, F). *H. floridum* (35, H, F). *H. glutinosum* (35, H, F). *H. huascoense* (13, H, F). *H. inconspicuum* (35, 49, H, F). *H. jaffuelii* (21, H). *H. krauseanum* (10, 41). *H. linariifolium* (35, 49, H, F). *H. longistylum* (35, H, F). *H. megalanthum* (35, H, F). *H. myosotifolium* (35, H, F). *H. philippianum* (13, 49, H, F). *H. pycnophyllum* (35, 49, H, F). *H. sinuatum* (H, F). *H. stenophyllum* (35, H, F). *H. taltalense* (49, H, F). *Ceballosia fruticosa* (42, 43, 44, 47). *H. arbainense* (5,14, 16). H. erosum (5, 47). *H. europaeum* (4, 14, 16, 27, 29, 31, 34). *H. giessii* (6). *H. zeylanicum* (4, 5, 6, 29, 30, 32). *H. adenogynum* (13, 41). *H. arborescens* (3, 41, H). *H. corymbosum* (41, H). *H. incanum* (41, H). *H. mandonii* (13, 41, H). *H. rufipilum* (19, 28, 39, 40, 41). *H. submolle* (48, H). *Euploca procumbens* (1, 22, 26, 27, 28, 36, 37, 38, 39, 40, 41). *Myriopus salzmannii* (1,7, 37). *Tournefortia rubicunda* (1,7, 37). *Ixorhea tschudiana* (7, 46).

References: 1: Pérez-Moreau (1994): 2: Johnston (1935b); 3: Riedl (1997); 4: Akhani and Förther (1994); 5: Baker and Wright (1906); 6: Verdcourt (1991); 7: Ariza-Espinar (2006); 8: Melo and Semir (2008); 9: Correa (1999); 10: Weigend et al. (2003); 11: Gangui (1955); 12: di Fulvio and Ariza-Espinar (2004); 13: Johnston (1928b); 14: Feinbrun-Dothan (1978); 15: di Fulvio (2003); 16: Boissier (1879); 17: Spegazzini (1902); 18: Pérez-Moreau (1963); 19: Macbride (1916); 20: Rusby (1895); 21: Johnston (1937); 22: Richardson and King (2009); 23: Johnston (1935a); 24: Craven (1996); 25: Munz and Keck (1965); 26: Nowicke (1969); 27: Correll and Johnston (1970); 28: Miller (2001); 29: Riedl and Edwards (2006); 30: Martins (1990); 31: Brummitt (1972); 32: Nowicke and Miller (1991); 33: Taton (1971); 34: Johnston (1964); 35: Reiche (1907a); 36: Dawson (1965); 37: Pérez-Moreau and Cabrera (1983); 38: Miller (1988); 39: Gibson (1970); 40: Frohlich (1981); 41: Macbride (1960); 42: Förther (1998); 43: Kunkel (1974); 44: Kunkel (1977); 45: Killip (unpubl.); 46: di Fulvio (1982); 47: Schönfelder and Schönfelder (1997); 48: Klotzsch (1852); 49: Johnston (1929c); H: Direct measurements on herbarium specimens; F: Direct measurements in the field.

## B.3 Mean, minimum and maximum values of Partitioned Bremer Support for the clades of Heliotropiaceae

Clades correspond to those depicted in Figure 3.4C. Section names are given in parenthesis when correspond. Major clades are highlighted.

| | Average | | Minimum | | Maximum | |
|---|---|---|---|---|---|---|
| **Clade** | **plastid** | **ITS** | **plastid** | **ITS** | **plastid** | **ITS** |
| *Tiquilia paronychioides* + *Cordia decandra* | 20.69 | 11.31 | 12 | 3 | 29 | 20 |
| *Tournefortia rubicunda* + *Myriopus salzmannii* (*Myriopus*) | 45.99 | 47.01 | 38 | 39 | 54 | 55 |
| *Myriopus* + *Euploca procumbens* | 26.82 | 0.18 | 18 | -9 | 36 | 9 |
| *Heliotropium adenogynum* + *H. mandonii* | 1.85 | -0.85 | -6 | -9 | 10 | 7 |
| ***Heliothamnus*** | 20.29 | 8.71 | 12 | 1 | 28 | 17 |
| *Heliotropium giessii* + *H. arbainense* | 3.05 | -2.05 | -5 | -10 | 11 | 6 |
| *Heliotropium giessii* + *H. arbainense* + *H. europaeum* | 8.24 | 0.76 | 0 | -7 | 16 | 9 |
| *Heliotropium giessii* + *H. arbainense* + *H. europaeum* + *H. erosum* | 7.92 | -5.92 | 0 | -14 | 16 | 2 |
| *Heliotropium giessii* + *H. arbainense* + *H. europaeum* + *H. erosum* + *H. zeylanicum* | 4.31 | 0.69 | -4 | -7 | 12 | 9 |
| ***Heliotropium* II-clade** | 12.35 | 3.65 | 3 | -9 | 14 | 8 |
| *Tournefortia chinchensis* + *T. microcalyx* + *T.* cf. *buchtienii* | 5.95 | -0.95 | -3 | -9 | 14 | 8 |
| *Tournefortia chinchensis* + *T. microcalyx* + *T.* cf. *buchtienii* + *T. polystachya* | 0.38 | 1.62 | -8 | -3 | 5 | 10 |
| *Tournefortia argentea* + *T. gnaphalodes* | 0.12 | 4.88 | -8 | -1 | 6 | 13 |
| *Heliotropium paronychioides* + *H. pinnatisectum* | 3.5 | -2.5 | -3 | -5 | 6 | 4 |
| *Heliotropium paronychioides* + *H. pinnatisectum* + *H. kurtzii* (*Plagiomeris*) | 10.72 | 5.28 | 4 | 2 | 14 | 12 |
| *Heliotropium microstachyum* + *H. abbreviatum* (*Hypsogenia*) | 15.42 | 3.58 | 7 | -2 | 21 | 12 |
| *Heliotropium phylicoides* + *H. nicotianifolium* (*Heliotrophytum*) | 15.78 | 2.22 | 9 | 0 | 18 | 9 |
| *Heliotropium veronicifolium* + *H. transalpinum* (*Coeloma*) | 18.5 | 9.5 | 12 | 6 | 22 | 16 |
| *Heliotropium elongatum* + *H. indicum* (*Tiaridium*) | 20.17 | 11.83 | 14 | 9 | 23 | 18 |
| *Heliotropium curassavicum* + *H. patagonicum* (*Platygyne*) | 14.41 | 12.59 | 8 | 10 | 17 | 19 |
| *Tournefortia* clade (except *Heliotropium angiospermum*) | 2.37 | 0.37 | -4 | -3 | 5 | 6 |
| ***Tournefortia* clade** | 8.24 | 3.76 | -1 | -4 | 16 | 13 |
| *Heliotropium eremogenum* + *H. philippianum* | 1.1 | 0.1 | -7 | -8 | 9 | 8 |
| *Heliotropium chenopodiaceum* + *H. linariifolium* + *H. myosotifolium* + *H. sinuatum* | 3.23 | -0.23 | -5 | -8 | 11 | 8 |
| *Heliotropium chenopodiaceum* + *H. linariifolium* + *H. myosotifolium* + *H. sinuatum* + *H. stenophyllum* | 1.89 | 0.11 | -6 | -8 | 10 | 8 |
| *Heliotropium eremogenum* + *H. philippianum* + *H. chenopodiaceum* + *H. linariifolium* + *H. myosotifolium* + *H. sinuatum* + *H. stenophyllum* + *H. floridum* + *H. huascoense* + *H. inconspicuum* + *H. longistylum* + *H. megalanthum* + *H. taltalense* | 1.15 | -0.15 | -7 | -8 | 9 | 8 |
| *Heliotropium eremogenum* + *H. philippianum* + *H. chenopodiaceum* + *H. linariifolium* + *H. myosotifolium* + *H. sinuatum* + *H. stenophyllum* + *H. floridum* + *H. huascoense* + *H. inconspicuum* + *H. longistylum* + *H. megalanthum* + *H. taltalense* + *H. filifolium* + *H. glutinosum* + *H. krauseanum* | 1.3 | 1.7 | -7 | -6 | 9 | 10 |
| ***Cochranea*** | 7.29 | 1.71 | -1 | -5 | 14 | 10 |
| ***Cochranea* + *Tournefortia* clade** | 7.69 | 3.31 | 1 | -1 | 12 | 10 |
| ***Cochranea* + *Tournefortia* clade + *Heliotropium* II-clade** | 1.88 | 2.12 | -6 | -6 | 10 | 10 |
| ***Cochranea* + *Tournefortia* clade + *Heliotropium* II-clade + *Heliothamnus*** | 18.46 | 7.54 | 11 | -1 | 27 | 15 |
| ***Cochranea* + *Tournefortia* clade + *Heliotropium* II-clade + *Heliothamnus* + *Ixorhea*** | 1.68 | -0.68 | -7 | -8 | 9 | 8 |

## B.4 Character states of the species used in the morphological analysis ordered by clade

The asterisk indicates species included in the phylogenetic analysis. Characters 1–17 as in Table 3.2. The last six columns indicate the analysis in which the species was included as follows: O, Overall morphological analysis; L, Leaf morphological analysis; G, Habit analysis; H, Plant height analysis; F, Leaf form analysis; S, Leaf size analysis

| | **Clade** | **Species** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **O** | **L** | **G** | **H** | **F** | **S** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| * | Tournefortia | *Heliotropium abbreviatun* | 2.43 | 3.97 | 1 | ? | ? | 0 | ? | ? | ? | ? | ? | ? | 1 | 0 | E | R | 1.30 | | | x | x | x | x |
| * | Tournefortia | *Heliotropium amplexicaule* | 3.75 | 3.97 | 1 | I | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | E | F | 1.60 | x | x | x | x | x | x |
| * | Tournefortia | *Heliotropium angiospermum* | 2.93 | 4.43 | 1 | S | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | E | F | 1.92 | x | x | x | x | x | x |
| * | Tournefortia | *Heliotropium curassavicum* | 4.69 | 3.58 | 0 | S | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | D | T | 1.44 | x | x | x | x | x | x |
| * | Tournefortia | *Heliotropium elongatum* | 1.69 | 4.56 | 1 | B | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | E | F | 1.74 | x | x | x | x | x | x |
| * | Tournefortia | *Heliotropium indicum* | 1.38 | 4.92 | 1 | S | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | E | F | 1.90 | x | x | x | x | x | x |
| * | Tournefortia | *Heliotropium kurtzii* | 15.6 | 2.49 | 1 | S | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | D | F | 1.30 | x | x | x | x | x | x |
| * | Tournefortia | *Heliotropium microstachyum* | 3.00 | 3.44 | 1 | I | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | E | R | 1.18 | x | x | x | x | x | x |
| * | Tournefortia | *Heliotropium nicoteanaefolium* | 2.17 | 4.39 | 1 | S | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | E | F | 1.60 | x | x | x | x | x | x |
| * | Tournefortia | *Heliotropium paronychioides* | 8.25 | 2.62 | 1 | I | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | D | F | 0.95 | x | x | x | x | x | x |
| * | Tournefortia | *Heliotropium patagonicum* | 0.83 | 2.93 | 0 | S | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | D | T | 1.18 | x | x | x | x | x | x |
| * | Tournefortia | *Heliotropium phylicoides* | 1.88 | 3.18 | 1 | ? | ? | 1 | ? | ? | ? | ? | ? | ? | 0 | 0 | E | F | 1.71 | | | x | x | x | x |
| * | Tournefortia | *Heliotropium pinnatisectum* | 4.00 | 2.79 | 1 | I | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | D | F | 0.54 | x | x | x | x | x | x |
| * | Tournefortia | *Heliotropium transalpinum* | 2.26 | 4.68 | 1 | B | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | E | F | 2.08 | x | x | x | x | x | x |
| * | Tournefortia | *Heliotropium veronicifolium* | 1.45 | 3.82 | 1 | S | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | D | F | 1.60 | x | x | x | x | x | x |
| * | Tournefortia | *Tournefortia argentea* | 3.00 | 5.06 | 1 | ? | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | E | F | 2.74 | x | x | x | x | x | x |
| | Tournefortia | *Tournefortia bicolour* | 1.94 | 4.81 | 1 | B | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | E | F | 2.60 | x | x | x | x | x | x |
| * | Tournefortia | *Tournefortia buchtienii* | 2.47 | 4.75 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | E | F | 2.48 | | | x | x | x | x |
| * | Tournefortia | *Tournefortia chinchensis* | 2.63 | 4.08 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | E | F | 2.30 | | | x | x | x | x |
| | Tournefortia | *Tournefortia glabra* | 1.93 | 5.11 | 1 | B | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | E | F | 2.88 | x | x | x | x | x | x |
| * | Tournefortia | *Tournefortia gnaphalodes* | 15.6 | 3.50 | 0 | S | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | E | F | 2.22 | x | x | x | x | x | x |
| * | Tournefortia | *Tournefortia hirsutissima* | 2.48 | 4.93 | 1 | B | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | S | F | 2.60 | x | x | x | x | x | x |
| | Tournefortia | *Tournefortia luzonica* | 1.71 | 4.56 | 1 | B | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | S | F | ? | x | x | x | | x | x |

| | **Clade** | **Species** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **O** | **L** | **G** | **H** | **F** | **S** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| * | Tournefortia | *Tournefortia microcalyx* | 3.11 | 4.30 | 1 | B | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | E | F | 2.18 | x | x | x | x | x | x |
| * | Tournefortia | *Tournefortia polystachya* | 1.41 | 5.33 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | E | F | 2.70 | | | x | x | x | x |
| | Tournefortia | *Tournefortia rollotii* | 1.53 | 5.03 | 1 | B | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | E | F | 2.00 | x | x | x | x | x | x |
| * | Tournefortia | *Tournefortia ternifolia* | 2.53 | 4.86 | 1 | B | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | E | F | 2.10 | x | x | x | x | x | x |
| * | Cochranea | *Heliotropium chenopodiaceum* | 2.00 | 2.55 | 0 | I | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | E | F | 1.76 | x | x | x | x | x | x |
| * | Cochranea | *Heliotropium eremogenum* | 2.83 | 1.90 | 0 | S | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | D | F | 1.48 | x | x | x | x | x | x |
| * | Cochranea | *Heliotropium filifolium* | 6.50 | 1.91 | ? | I | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | E | F | 1.85 | x | x | x | x | x | x |
| * | Cochranea | *Heliotropium floridum* | 3.48 | 3.08 | 0 | I | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | E | F | 1.66 | x | x | x | x | x | x |
| * | Cochranea | *Heliotropium glutinosum* | 4.13 | 2.86 | 1 | I | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | E | F | 1.75 | x | x | x | x | x | x |
| * | Cochranea | *Heliotropium inconspicuum* | 5.19 | 2.07 | 0 | S | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | E | F | 1.89 | x | x | x | x | x | x |
| | Cochranea | *Heliotropium jaffuelii* | 7.94 | 1.86 | ? | I | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | E | F | ? | | | x | | x | x |
| * | Cochranea | *Heliotropium krauseanum* | 5.46 | 3.46 | 1 | B | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | E | F | 2.10 | x | x | x | x | x | x |
| * | Cochranea | *Heliotropium linariifolium* | 7.00 | 2.97 | 0 | I | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | D | F | 1.57 | x | x | x | x | x | x |
| * | Cochranea | *Heliotropium longistylum* | 10.6 | 3.21 | 0 | I | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | E | F | 1.96 | x | x | x | x | x | x |
| * | Cochranea | *Heliotropium megalanthum* | 4.07 | 3.40 | 0 | I | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | D | F | 1.28 | x | x | x | x | x | x |
| * | Cochranea | *Heliotropium myosotifolium* | 5.78 | 2.27 | 0 | I | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | E | F | 1.40 | x | x | x | x | x | x |
| * | Cochranea | *Heliotropium philippianum* | 5.43 | 2.92 | 0 | S | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | E | F | 2.02 | x | x | x | x | x | x |
| * | Cochranea | *Heliotropium pycnophyllum* | 13.3 | 3.05 | 0 | I | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | E | F | 1.97 | x | x | x | x | x | x |
| * | Cochranea | *Heliotropium sinuatum* | 10.8 | 3.09 | 1 | B | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | E | F | 2.23 | x | x | x | x | x | x |
| * | Cochranea | *Heliotropium stenophyllum* | 15.4 | 2.55 | 0 | S | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | E | F | 2.18 | x | x | x | x | x | x |
| * | Cochranea | *Heliotropium taltalense* | 8.69 | 3.06 | 1 | B | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | E | F | 2.17 | x | x | x | x | x | x |
| * | Heliotropium-II | *Ceballosia fruticosa* | 7.20 | 4.15 | 1 | S | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | E | F | 2.40 | x | x | x | x | x | x |
| * | Heliotropium-II | *Heliotropium arbainense* | ? | ? | 1 | S | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | E | ? | 1.48 | x | x | x | x | | |
| * | Heliotropium-II | *Heliotropium erosum* | ? | ? | 1 | S | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | D | T | 1.48 | x | x | x | x | | |
| * | Heliotropium-II | *Heliotropium europaeum* | 1.70 | 4.13 | 1 | S | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | E | T | 1.51 | x | x | x | x | x | x |
| * | Heliotropium-II | *Heliotropium giessii* | 3.44 | 4.34 | 1 | I | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | E | T | 1.85 | x | x | x | x | x | x |
| * | Heliotropium-II | *Heliotropium zeylanicum* | 6.13 | 3.69 | 1 | S | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | E | T | 1.72 | x | x | x | x | x | x |
| * | Heliothamnus | *Heliotropium adenogynum* | 2.00 | 3.89 | 1 | B | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | E | F | 1.70 | x | x | x | x | x | x |
| * | Heliothamnus | *Heliotropium arborescens* | 1.77 | 4.37 | 1 | B | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | E | F | 2.18 | x | x | x | x | x | x |
| | Heliothamnus | *Heliotropium corymbosum* | 2.00 | 4.35 | 1 | B | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | E | F | 2.13 | x | x | x | x | x | x |

|  | **Clade** | **Species** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **O** | **L** | **G** | **H** | **F** | **S** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| * | Heliothamnus | *Heliotropium incanum* | 2.00 | 4.20 | 1 | B | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | E | F | 2.15 | x | x | x | x | x | x |
| * | Heliothamnus | *Heliotropium mandonii* | 2.47 | 4.75 | 1 | B | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | E | F | 2.16 | x | x | x | x | x | x |
|  | Heliothamnus | *Heliotropium rufipilum* | 2.77 | 4.57 | 1 | B | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | E | F | 2.18 | x | x | x | x | x | x |
| * | Heliothamnus | *Heliotropium submolle* | 2.16 | 5.33 | 1 | B | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | E | F | 2.26 | x | x | x | x | x | x |
| * | Euploca | *Euploca procumbens* | 1.67 | 3.76 | 1 | B | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | D | ? | 1.74 | x | x | x | x | x | x |
| * | Myriopus | *Tournefortia rubicunda* | 2.22 | 4.15 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | S | ? | 2.40 |  |  | x | x | x | x |
| * | Myriopus | *Myriopus salzmannii* | 1.77 | 4.37 | 1 | B | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | S | ? | 2.60 | x | x | x | x | x | x |
| * | Ixorhea | *Ixorhea tschudiana* | 3.00 | 3.93 | 1 | I | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | E | ? | 2.24 | x | x | x | x | x | x |

## B.5 Ranges of leaf length, leaf width and plant height

Data obtained from the literature, herbarium specimens and field measurements. All values are given in cm.

| Species | Leaf length | Leaf width | Plant height |
|---|---|---|---|
| *Heliotropium abbreviatun* | 2.5–6 | 1–2.5 | 20–20 |
| *Heliotropium amplexicaule* | 1.5–9 | 0.3–2.5 | 20–60 |
| *Heliotropium angiospermum* | 0.8–15 | 0.4–5 | 15–150 |
| *Heliotropium curassavicum* | 0.5–7 | 0.1–1.5 | 5–50 |
| *Heliotropium elongatum* | 1.5–12.5 | 0.5–7.8 | 10–100 |
| *Heliotropium indicum* | 2–17 | 0.8–13 | 10–150 |
| *Heliotropium kurtzii* | 1.5–2.4 | 0.1–0.15 | 15–25 |
| *Heliotropium microstachyum* | 0.6–4.5 | 0.2–1.5 | 5–25 |
| *Heliotropium nicoteanaefolium* | 2–11 | 1–5 | 20–60 |
| *Heliotropium paronychioides* | 0.8–2.5 | 0.1–0.3 | 3–15 |
| *Heliotropium patagonicum* | 0.3–1.2 | 0.3–1.5 | 5–25 |
| *Heliotropium phylicoides* | 0.5–2.5 | 0.1–1.5 | 40–62 |
| *Heliotropium pinnatisectum* | 0.8–2 | 0.2–0.5 | 3–4 |
| *Heliotropium transalpinum* | 1.5–17 | 0.3–7.9 | 40–200 |
| *Heliotropium veronicifolium* | 0.5–5 | 0.3–3.5 | 10–70 |
| *Tournefortia argentea* | 10–23 | 3–8 | 100–1000 |
| *Tournefortia bicolour* | 5–15 | 1.3–9 | 100–700 |
| *Tournefortia buchtienii* | 7–14 | 3–5.5 | 200–400 |
| *Tournefortia chinchensis* | 3–7 | 0.8–3 | 200–200 |
| *Tournefortia glabra* | 5–23 | 2.5–12 | 500–1000 |
| *Tournefortia gnaphalodes* | 2.5–10 | 0.2–0.6 | 30–300 |
| *Tournefortia hirsutissima* | 6–20 | 2.5–8 | 300–500 |
| *Tournefortia luzonica* | 1–13 | 1.2–7 | ? |
| *Tournefortia microcalyx* | 4–10 | 1–3.5 | 100–200 |
| *Tournefortia polystachya* | 6–25 | 2–20 | 200–800 |
| *Tournefortia rollotii* | 8–15 | 5–10 | 100–100 |
| *Tournefortia ternifolia* | 8–16 | 2–7.5 | 50–200 |
| *Heliotropium chenopodiaceum* | 0.25–1.25 | 0.05–0.7 | 30–85 |
| *Heliotropium eremogenum* | 0.2–0.65 | 0.1–0.2 | 30–30 |
| *Heliotropium filifolium* | 0.2–1.1 | 0.05–0.15 | 48–92 |
| *Heliotropium floridum* | 0.65–3 | 0.1–0.95 | 15–77 |
| *Heliotropium glutinosum* | 0.8–2.3 | 0.15–0.6 | 34–78 |
| *Heliotropium huascoense* | 1–4.1 | 0.1–0.3 | 30–140 |
| *Heliotropium inconspicuum* | 0.4–1 | 0.07–0.2 | 57–100 |
| *Heliotropium jaffuelii* | 0.4–0.95 | 0.07–0.1 | ? |
| *Heliotropium krauseanum* | 1.1–6 | 0.2–1.1 | 100–150 |
| *Heliotropium linariifolium* | 0.85–3.7 | 0.1–0.55 | 15–60 |
| *Heliotropium longistylum* | 1.2–6.2 | 0.1–0.6 | 73–108 |
| *Heliotropium megalanthum* | 1.3–4.4 | 0.35–1.05 | 14–24 |
| *Heliotropium myosotifolium* | 0.5–1.35 | 0.07–0.25 | 20–30 |
| *Heliotropium philippianum* | 0.9–2.9 | 0.15–0.55 | 60–150 |
| *Heliotropium pycnophyllum* | 0.35–6.55 | 0.07–0.45 | 35–150 |

| **Species** | **Leaf length** | **Leaf width** | **Plant height** |
|---|---|---|---|
| *Heliotropium sinuatum* | 1.5–5 | 0.1–0.5 | 78–260 |
| *Heliotropium stenophyllum* | 0.95–3.2 | 0.07–0.2 | 100–200 |
| *Heliotropium taltalense* | 1.25–4.4 | 0.1–0.55 | 98–200 |
| *Ceballosia fruticosa* | 8–10 | 1–1.5 | 100–400 |
| *Heliotropium arbainense* | ? | ? | 20–40 |
| *Heliotropium erosum* | ? | ? | 20–40 |
| *Heliotropium europaeum* | 2–6.5 | 1–4 | 5–60 |
| *Heliotropium giessii* | 3.5–12 | 1–3.5 | 40–100 |
| *Heliotropium zeylanicum* | 0.8–9 | 0.2–1.4 | 25–80 |
| *Heliotropium adenogynum* | 2–5 | 0.5–3 | 50–50 |
| *Heliotropium arborescens* | 3.5–8 | 2–4.5 | 100–200 |
| *Heliotropium corymbosum* | 4–8 | 2–4 | 50–220 |
| *Heliotropium incanum* | 4–6 | 2–3 | 100–180 |
| *Heliotropium mandonii* | 7–14 | 2.5–6 | 90–200 |
| *Heliotropium rufipilum* | 4–14 | 2–4.5 | 100–200 |
| *Heliotropium submolle* | 7.8–30.5 | 2.5–15.2 | 61–300 |
| *Euploca procumbens* | 0.5–5 | 0.5–2.8 | 10–100 |
| *Myriopus salzmannii* | 2.5–9 | 1.5–5 | 200–600 |
| *Tournefortia rubicunda* | 2–8 | 1–3.5 | 100–400 |
| *Ixorhea tschudiana* | 4.5–4.5 | 1.5–1.5 | 100–250 |

## B.6 Eigenvalues for each PCO axis and coordinates of the species in the PCO axes

### All characters

| | | Axis 1 | Axis 2 | Axis 3 | Axis 4 | Axis 5 | Axis 6 | Axis 7 | Axis 8 | Axis 9 | Axis 10 | Axis 11 | Axis 12 | Axis 13 | Axis 14 | Axis 15 | Axis 16 | Axis 17 | Axis 18 | Axis 19 | Axis 20 | Axis 21 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Eigenvalues | 3.88661149 | 2.55375076 | 1.40003248 | 1.04799385 | 0.80746055 | 0.70370988 | 0.58132185 | 0.51496550 | 0.41798599 | 0.32163666 | 0.30460106 | 0.25694181 | 0.22110902 | 0.17938846 | 0.15183222 | 0.12812281 | 0.12557230 | 0.11839901 | 0.11580851 | 0.11160418 | 0.10694658 |
| | Percentage | 24.47514509 | 16.08172579 | 8.81641968 | 6.59952805 | 5.08481849 | 4.43146981 | 3.66075607 | 3.24289048 | 2.63218170 | 2.02544145 | 1.91816321 | 1.61803880 | 1.39238909 | 1.12966230 | 0.95613249 | 0.80682735 | 0.79076599 | 0.74559367 | 0.72928051 | 0.70280463 | 0.67347433 |
| | Cumulative percentage | 24.47514509 | 40.55687088 | 49.37329057 | 55.97281862 | 61.05763711 | 65.48910692 | 69.14986299 | 72.39275346 | 75.02493516 | 77.05037662 | 78.96853982 | 80.58657862 | 81.97896771 | 83.10863001 | 84.06476250 | 84.87158985 | 85.66235583 | 86.40794950 | 87.13723001 | 87.84003464 | 88.51350897 |
| Clade | Species | | | | | | | | | | | | | | | | | | | | | |
| Cochranea | *H. chenopodiaceum* | 0.12830973 | -0.29643740 | -0.11096465 | -0.10359812 | 0.02454033 | 0.12942487 | 0.12156549 | -0.18930778 | 0.09752481 | 0.07405716 | 0.07993827 | -0.04085216 | 0.06691473 | -0.03144428 | -0.01510847 | -0.04978092 | 0.03575446 | 0.00900638 | 0.01490038 | -0.01816889 | 0.05524137 |
| Cochranea | *H. eremogenum* | 0.38427701 | -0.02217435 | 0.10474766 | -0.15422008 | -0.05749666 | 0.05236921 | -0.30624811 | -0.02070935 | 0.07940543 | 0.13736747 | -0.06164775 | -0.05661582 | 0.02679055 | -0.04473810 | -0.03494177 | -0.00487813 | 0.05787273 | 0.04779309 | 0.12702034 | -0.03828801 | -0.01068731 |
| Cochranea | *H. filifolium* | 0.11107402 | -0.39814982 | -0.09061875 | -0.02626866 | 0.06873579 | -0.06850430 | 0.19916910 | -0.15407986 | -0.07817300 | 0.02557526 | -0.18071450 | -0.10060696 | 0.01324659 | 0.02393793 | 0.05282014 | 0.00394042 | -0.03344333 | -0.00600783 | 0.05641430 | -0.02056538 | 0.01993868 |
| Cochranea | *H. floridum* | 0.23127183 | -0.11189735 | -0.11243140 | -0.25752421 | -0.11803896 | 0.10645710 | 0.01513890 | 0.05732620 | -0.12321419 | 0.05747956 | 0.09461159 | -0.04981339 | 0.07212492 | -0.03311503 | -0.02042543 | -0.04297944 | -0.01336262 | 0.03954221 | -0.06164471 | 0.03571975 | -0.01968503 |
| Cochranea | *H. glutinosum* | 0.03584778 | -0.17244207 | -0.23259151 | -0.02332957 | 0.06628739 | 0.07177001 | 0.12664738 | -0.18636074 | 0.00592889 | 0.03580399 | -0.10078672 | 0.06083204 | -0.04541812 | 0.06777538 | 0.04013842 | 0.10841843 | 0.04192114 | -0.03067920 | -0.07780073 | 0.02223719 | -0.04180589 |
| Cochranea | *H. huascoense* | 0.15039962 | -0.34045214 | 0.04464253 | 0.02289714 | 0.20934682 | 0.10713466 | -0.10318781 | -0.11322002 | 0.02105381 | -0.02007495 | 0.11244017 | 0.11405778 | 0.00533530 | 0.02816351 | 0.03220972 | 0.06384894 | 0.05499883 | -0.07320643 | 0.03820087 | 0.03199050 | 0.00420495 |
| Cochranea | *H. inconspicuum* | -0.00213517 | -0.32632624 | 0.26223301 | -0.08044297 | 0.09527143 | -0.19896058 | -0.04964908 | 0.15704663 | 0.05511169 | 0.23238998 | -0.04068834 | -0.05621526 | 0.02338197 | 0.01626338 | 0.10710065 | -0.05277970 | -0.04715670 | 0.02371154 | -0.00643701 | 0.00653407 | 0.00610323 |
| Cochranea | *H. krauseanum* | -0.31041825 | -0.03813021 | -0.03811195 | 0.09547559 | -0.13494435 | -0.09042300 | -0.07124266 | 0.07013535 | -0.00030233 | 0.01879296 | 0.05393363 | 0.06817256 | 0.01481718 | 0.05922632 | 0.11518012 | 0.12023579 | 0.02651864 | 0.07173656 | 0.03041944 | 0.08988751 | 0.04057342 |
| Cochranea | *H. linariifolium* | 0.37720011 | -0.05974553 | -0.08033481 | -0.24939501 | -0.21211606 | -0.05357516 | -0.13964179 | -0.07621382 | 0.00135796 | -0.07692950 | 0.01626731 | 0.00348283 | 0.00821442 | -0.00606028 | 0.04653898 | -0.01640715 | 0.01326721 | -0.08844573 | -0.01105173 | -0.03525216 | -0.02597705 |
| Cochranea | *H. longistylum* | 0.13663180 | -0.27411052 | -0.12440842 | -0.15046889 | -0.00122013 | 0.00774784 | 0.03645406 | 0.11621936 | 0.04290803 | -0.14096033 | 0.12060489 | 0.06115162 | -0.00578226 | 0.02073714 | 0.03225793 | -0.02093946 | -0.06279379 | -0.06159643 | 0.00296464 | -0.03951718 | 0.08474332 |
| Cochranea | *H. megalanthum* | 0.26446118 | -0.13390830 | -0.08295809 | -0.15897292 | -0.16703184 | -0.02652485 | -0.02263949 | -0.01717179 | 0.29508187 | -0.07295044 | -0.01368200 | 0.02714477 | -0.06181228 | 0.03651903 | -0.05390506 | 0.00319802 | -0.04029644 | 0.08416644 | -0.02332218 | 0.01600432 | -0.02031273 |
| Cochranea | *H. myosotifolium* | 0.20400333 | -0.35466685 | -0.01527742 | -0.12695303 | -0.05084774 | -0.12465488 | 0.17872756 | 0.13593409 | 0.00883393 | 0.00086362 | -0.10734908 | -0.14602612 | 0.02981666 | -0.01259695 | -0.06474465 | 0.01757666 | 0.02382826 | 0.03010252 | 0.04721783 | 0.06531101 | 0.01590201 |
| Cochranea | *H. philippianum* | 0.23126312 | -0.12093492 | 0.07156469 | -0.14299299 | 0.04905100 | 0.13221348 | -0.17890381 | 0.13036955 | -0.14600961 | 0.09439220 | 0.09385772 | -0.00447277 | 0.06019510 | -0.05551892 | 0.07958687 | 0.12274437 | -0.01008493 | -0.02114556 | -0.07436013 | 0.01692175 | 0.03453285 |
| Cochranea | *H. pycnophyllum* | 0.14612278 | -0.29189020 | -0.12771835 | -0.14400625 | 0.01987236 | -0.00404811 | 0.01193027 | 0.10727238 | 0.02711621 | -0.16926894 | 0.13918828 | 0.08553146 | -0.01237646 | 0.01845941 | -0.01184409 | -0.04732190 | -0.00175998 | 0.01556991 | -0.00220710 | -0.00347857 | -0.08163922 |
| Cochranea | *H. sinuatum* | -0.26429603 | -0.15197592 | 0.03971323 | -0.01556817 | 0.09822042 | -0.35829859 | 0.02482993 | 0.07643565 | -0.10872294 | -0.05164899 | -0.07378326 | 0.09932120 | -0.00486901 | -0.07378495 | -0.05285078 | 0.00223112 | 0.00088825 | -0.02288224 | -0.05006608 | 0.00874335 | -0.01605630 |
| Cochranea | *H. stenophyllum* | 0.16752026 | -0.45699290 | 0.16932345 | 0.08685180 | 0.24364042 | -0.03006938 | -0.03677630 | -0.10181644 | -0.09305818 | -0.05915582 | -0.03118063 | 0.00575905 | -0.01302123 | -0.05679876 | -0.06392712 | -0.00997894 | 0.00494972 | 0.05590392 | -0.00845653 | -0.03419152 | -0.01684567 |
| Cochranea | *H. taltalense* | -0.30965829 | -0.14877329 | 0.06872117 | 0.16355821 | -0.11641355 | -0.28218415 | 0.00000001 | 0.07643545 | -0.12686684 | -0.05122222 | -0.05975902 | -0.01400029 | 0.00983687 | 0.00454910 | 0.02544018 | 0.02992993 | 0.04378133 | -0.06428096 | -0.00916952 | -0.03923869 | -0.00607688 |
| Heliothmanus | *H. adenogynum* | -0.31760761 | 0.00924505 | -0.03564588 | 0.09328851 | -0.14207060 | -0.02698567 | -0.03981887 | 0.06523569 | 0.05484177 | 0.08568466 | 0.01476880 | 0.03685321 | 0.05700100 | 0.06664618 | -0.04716995 | -0.07904148 | 0.12720179 | -0.03315792 | 0.01389048 | 0.12700568 | 0.02025705 |
| Heliothmanus | *H. arborescens* | -0.36163613 | 0.01322513 | -0.02484955 | 0.09625417 | -0.11154919 | -0.00481618 | -0.05047617 | 0.07008434 | 0.04440282 | 0.04578704 | 0.03500218 | 0.00352291 | 0.01815897 | -0.00322052 | -0.04881545 | -0.03037767 | -0.01589443 | -0.02480991 | -0.05443284 | -0.09283174 | 0.02438018 |
| Heliothmanus | *H. corymbosum* | -0.35845049 | 0.01190100 | -0.02694266 | 0.09539330 | -0.11368878 | -0.00531705 | -0.05084218 | 0.07115002 | 0.04489800 | 0.04904393 | 0.03503806 | 0.00621811 | 0.02138298 | 0.00681044 | -0.04235833 | -0.01838544 | -0.01451665 | -0.02336346 | -0.02881419 | -0.07973813 | 0.02202016 |
| Heliothmanus | *H. incanum* | -0.35061560 | -0.06603291 | -0.02001245 | 0.15871391 | -0.05754628 | 0.03712271 | -0.00673716 | -0.19766072 | 0.00955873 | 0.08135088 | 0.03961499 | 0.03397698 | 0.03186418 | 0.02530552 | -0.01587025 | -0.00110187 | 0.03130525 | 0.01885172 | -0.04291175 | -0.06744542 | 0.10703398 |
| Heliothmanus | *H. mandonii* | -0.36632336 | -0.05822061 | -0.02124594 | 0.15722163 | -0.04605803 | 0.05069275 | -0.00739533 | -0.19539514 | 0.01351744 | 0.06578943 | 0.04417244 | -0.00201324 | -0.00088704 | -0.01943813 | 0.00473942 | 0.02047415 | -0.05220013 | 0.00648814 | 0.05110058 | -0.02353980 | -0.05853992 |
| Heliothmanus | *H. rufipilum* | -0.36376200 | 0.01181816 | -0.02913111 | 0.09426650 | -0.11178982 | -0.00537465 | -0.05566231 | 0.07250190 | 0.03586326 | 0.03541183 | 0.03686548 | -0.00961472 | -0.00559983 | -0.00852479 | -0.02752399 | 0.01579796 | -0.06617940 | 0.03072050 | 0.03933885 | -0.05518015 | -0.07306312 |
| Heliothmanus | *H. submolle* | -0.38141139 | -0.05515139 | -0.01969213 | 0.15876737 | -0.04108160 | 0.06054595 | -0.00532747 | -0.20148256 | 0.02358210 | 0.06018667 | 0.04671177 | -0.01577828 | -0.02909056 | -0.06360830 | 0.03408814 | -0.04187263 | -0.02376733 | -0.03763427 | 0.01329128 | 0.06821699 | -0.08556223 |
| Tournefortia | *H. amplexicaule* | 0.02969116 | 0.03624013 | -0.20338982 | 0.02886717 | -0.26041649 | 0.15864057 | -0.02081111 | 0.05154228 | -0.19550490 | 0.00555763 | -0.07160512 | -0.05206062 | -0.01764146 | 0.13624986 | -0.01127085 | -0.07218061 | -0.01819399 | -0.03849958 | -0.01932692 | 0.00844882 | -0.02642865 |
| Tournefortia | *H. angiospermum* | 0.05011762 | 0.19887582 | 0.10662619 | -0.11974509 | 0.15651642 | 0.22892690 | -0.03526134 | 0.06101850 | -0.16963141 | -0.01073707 | -0.09170772 | -0.02251438 | -0.06319442 | 0.13849246 | -0.01157637 | 0.04064702 | -0.01842992 | -0.00785207 | 0.02383512 | -0.03383389 | -0.01734520 |
| Tournefortia | *H. curassavicum* | 0.49105730 | 0.16388477 | 0.53973827 | 0.27565982 | -0.28286890 | 0.03219378 | 0.11933634 | 0.01708752 | 0.00066217 | -0.05076736 | 0.06979202 | -0.03181993 | -0.04603943 | 0.09289912 | 0.04642552 | 0.02113443 | -0.02777183 | 0.01202697 | 0.03581686 | 0.02385646 | 0.00367657 |
| Tournefortia | *H. elongatum* | 0.04582684 | 0.46752027 | -0.08564551 | 0.06985208 | 0.19771444 | 0.02125498 | 0.15296049 | 0.00873776 | -0.11043418 | -0.06633256 | 0.15922556 | -0.16212151 | 0.12914033 | 0.02388821 | -0.07298384 | 0.01684023 | 0.05137620 | 0.02523204 | 0.03933114 | 0.02241233 | 0.02801762 |
| Tournefortia | *H. indicum* | 0.10025602 | 0.17200639 | -0.16479856 | 0.27006935 | 0.33158521 | 0.07863001 | 0.04029547 | 0.17450683 | 0.13522113 | 0.09487835 | 0.06028501 | -0.09208867 | -0.03012767 | -0.02591001 | 0.05171263 | -0.03192531 | -0.10694162 | -0.04145945 | -0.03980129 | 0.00764271 | 0.01332786 |
| Tournefortia | *H. kurtzii* | 0.47279846 | 0.26820044 | -0.14475497 | 0.25343117 | 0.21430971 | -0.19432207 | -0.27673298 | -0.00787843 | -0.04870477 | -0.02482024 | 0.02558784 | 0.06579378 | -0.04558785 | 0.01249735 | -0.04821119 | -0.01563802 | 0.04206983 | 0.05400755 | 0.03769096 | 0.02619866 | -0.02722148 |
| Tournefortia | *H. microstachyum* | 0.25816433 | 0.19848769 | -0.23589505 | 0.01591304 | -0.10867147 | 0.07675385 | 0.28255415 | 0.09141289 | -0.15812782 | 0.15326822 | -0.00100459 | 0.27118432 | -0.06997890 | -0.11167625 | -0.01900985 | -0.02089783 | -0.03375367 | 0.06247076 | 0.07833147 | 0.01293332 | 0.02209179 |
| Tournefortia | *H. nicoteanaefolium* | -0.00179388 | -0.02252367 | -0.05240966 | 0.01836613 | 0.14975515 | 0.16922495 | -0.05384415 | 0.14996216 | 0.08359472 | 0.08640666 | -0.14747865 | 0.05280952 | -0.06016636 | 0.04717458 | -0.14317440 | 0.00880691 | 0.00804238 | -0.08605272 | -0.00604877 | 0.00814182 | 0.00855833 |
| Tournefortia | *H. paronychioides* | 0.44958209 | 0.28281457 | -0.35222324 | 0.08614515 | -0.02197998 | -0.23929662 | -0.00933816 | -0.06746434 | 0.00394151 | -0.04632737 | 0.01175303 | -0.03957280 | -0.00739087 | 0.00641738 | 0.05710091 | -0.03142069 | 0.00610785 | -0.08982164 | 0.09300720 | -0.05917196 | 0.06950996 |
| Tournefortia | *H. patagonicum* | 0.60767358 | 0.20521894 | 0.53856503 | 0.06468950 | -0.06220229 | -0.02918975 | 0.20402565 | -0.02203985 | 0.08048951 | 0.05325426 | 0.04021382 | 0.03245192 | -0.01436618 | -0.08644135 | -0.06598289 | 0.04467985 | 0.05250595 | -0.08425572 | -0.05377297 | -0.04238546 | -0.02770247 |
| Tournefortia | *H. pinnatisectum* | 0.43286965 | 0.32945869 | -0.35147786 | 0.06960335 | -0.05701801 | -0.17149997 | 0.01636496 | -0.07660707 | 0.06525665 | 0.05227933 | -0.00601898 | -0.09092856 | -0.00883355 | 0.00974115 | -0.00147823 | 0.06452787 | -0.01843207 | 0.06310613 | -0.14058919 | 0.01663020 | -0.06917918 |
| Tournefortia | *H. transalpinum* | -0.20273337 | 0.01200394 | -0.07168257 | 0.15771913 | -0.09331334 | 0.17118907 | -0.02227234 | 0.08297450 | 0.05892621 | -0.17099389 | -0.12301736 | -0.00184703 | 0.24726379 | -0.13962773 | -0.02963645 | 0.08926558 | -0.03666226 | -0.00492916 | 0.02863306 | 0.01794839 | -0.01370228 |
| Tournefortia | *H. veronicifolium* | 0.28308909 | 0.41700830 | 0.13629551 | 0.05508184 | 0.06552302 | 0.11280377 | -0.05158328 | -0.04711616 | 0.07129483 | -0.08674521 | -0.23416944 | 0.13040178 | 0.14285913 | 0.00528449 | 0.12655608 | -0.10962326 | -0.00729393 | 0.03244601 | -0.05473814 | 0.00100124 | 0.02206018 |
| Tournefortia | *T. argentea* | -0.16746844 | -0.03866608 | -0.10733915 | 0.13725300 | -0.08447390 | 0.21934903 | -0.03159869 | 0.12041777 | 0.03096625 | -0.11860415 | -0.06964150 | -0.12708296 | -0.24124226 | -0.13621243 | 0.06357777 | 0.02709198 | 0.11092010 | 0.02337340 | 0.00121297 | -0.03122703 | 0.02300340 |
| Tournefortia | *T. bicolor* | -0.28311778 | 0.27590631 | 0.10168597 | -0.20784663 | 0.04790620 | 0.01595673 | 0.00562662 | -0.02348329 | -0.15058986 | 0.01418710 | 0.04300179 | -0.02344518 | 0.01479774 | -0.05932724 | 0.06706640 | -0.07693647 | 0.08234544 | 0.03344522 | -0.02360304 | -0.07375425 | -0.09772915 |
| Tournefortia | *T. glabra* | -0.35303685 | 0.14945572 | 0.08685086 | -0.14137526 | 0.11923978 | -0.00244410 | 0.08743351 | 0.01508765 | 0.08803453 | -0.06760658 | 0.01062923 | -0.02013131 | -0.07524352 | -0.04418435 | 0.05141061 | -0.06772773 | 0.08740980 | 0.03486207 | -0.04270461 | 0.06696428 | 0.06126884 |
| Tournefortia | *T. gnaphalodes* | 0.07270577 | -0.43460136 | 0.19695748 | 0.27653587 | 0.02567009 | 0.06814655 | -0.07334890 | -0.07868918 | -0.12189115 | -0.12133038 | 0.03093760 | -0.02049169 | -0.02882602 | 0.03434408 | -0.05295397 | -0.08814838 | -0.06804769 | 0.05952782 | -0.04764057 | 0.04939005 | 0.02328029 |
| Tournefortia | *T. hirsutissima* | -0.26176379 | 0.35434095 | 0.13825011 | -0.24348094 | -0.01501933 | -0.05236087 | -0.09891711 | -0.13567239 | -0.05466338 | -0.04905200 | -0.00863951 | -0.03645283 | -0.10189639 | -0.09450207 | 0.00162794 | 0.00942767 | -0.14628582 | -0.01974738 | 0.03337815 | 0.07170030 | 0.06877246 |
| Tournefortia | *T. luzonica* | -0.25490514 | 0.38777585 | 0.11736401 | -0.26407662 | -0.03907897 | -0.06887440 | -0.09100644 | -0.13743597 | -0.02918010 | 0.00449338 | -0.03197269 | -0.00562659 | -0.02892390 | 0.01010052 | -0.11769849 | 0.03631267 | -0.02985246 | -0.02250122 | -0.03825215 | 0.04585970 | 0.06219044 |
| Tournefortia | *T. microcalyx* | -0.30666634 | 0.12482561 | 0.07876276 | -0.12935273 | 0.09586263 | -0.04167301 | 0.08078265 | 0.02215452 | 0.05679996 | -0.03869057 | 0.00834617 | 0.04695176 | 0.00919658 | 0.11309553 | -0.00451167 | 0.05351859 | 0.01872944 | 0.12172602 | -0.00046049 | -0.11089916 | 0.05541693 |
| Tournefortia | *T. rollotii* | -0.32255848 | 0.14546132 | 0.08125905 | -0.13172976 | 0.11733932 | -0.01004966 | 0.09776009 | 0.02528153 | 0.09847970 | -0.03085150 | 0.01689743 | 0.00498023 | 0.01239215 | 0.04849456 | 0.02383018 | -0.02332638 | 0.00636369 | -0.09150270 | 0.03135166 | 0.04401926 | -0.06826567 |
| Tournefortia | *T. ternifolia* | -0.32185610 | 0.13852897 | 0.07925049 | -0.13052682 | 0.11054832 | -0.01910175 | 0.08766040 | 0.02347436 | 0.08042076 | -0.03923151 | 0.01516179 | 0.01159519 | 0.00358445 | 0.05365783 | 0.01856491 | 0.03302082 | -0.03503728 | 0.01801467 | 0.08026507 | -0.01301223 | -0.09228042 |
| | Centroids | | | | | | | | | | | | | | | | | | | | | |
| | Cochranea | 0.11465268 | -0.22661985 | -0.02498565 | -0.08331636 | 0.00406354 | -0.02452017 | -0.00343725 | 0.00274671 | 0.00158131 | -0.00222243 | 0.00869986 | 0.00320589 | 0.01128342 | -0.00115360 | 0.01138942 | 0.01103208 | 0.00377953 | -0.00021485 | -0.00098904 | 0.00374788 | 0.00212649 |
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## All characters (continued)

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
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| -0.02626077 | 0.02739400 | -0.00497484 | 0.00248543 | -0.10413675 | 0.00710716 | 0.02983661 | -0.01744262 | 0.03810200 | -0.08909392 | -0.02272066 | 0.02203960 | -0.01863688 | 0.08644240 | -0.03968343 | -0.00160421 | 0.07814463 | -0.04588770 | -0.01176271 | -0.05470658 | 0.01424781 | 0.03140511 | 0.00039429 |
| -0.00567103 | -0.03655930 | 0.01551073 | 0.11692703 | 0.08253987 | -0.05378729 | -0.02485018 | 0.07891745 | 0.02133091 | -0.05421105 | -0.03990045 | -0.02069473 | 0.01971399 | -0.01189319 | -0.01878503 | -0.04456855 | -0.01344158 | 0.00881635 | -0.04727026 | 0.01546135 | 0.02057833 | 0.03656828 | 0.01000243 |
| -0.06434535 | 0.05317471 | 0.16933022 | -0.01122311 | -0.06739872 | -0.06626710 | -0.08788177 | 0.00548244 | 0.01703011 | 0.04102834 | 0.02017898 | 0.00747071 | -0.03849568 | -0.02855705 | -0.00545003 | 0.03042507 | -0.01497234 | 0.00112238 | -0.02272048 | 0.03482185 | 0.01637250 | 0.02654654 | 0.01596385 |
| 0.00255148 | -0.03479785 | -0.02228038 | -0.11634011 | 0.06607612 | 0.09050630 | 0.12539967 | -0.10302268 | 0.01184190 | -0.04960934 | -0.01559184 | 0.00129340 | -0.01910614 | 0.00168698 | -0.00717032 | 0.02053313 | -0.03841951 | 0.00173051 | -0.03005017 | 0.01935831 | 0.01380479 | 0.02672739 | 0.01348290 |
| | | | | | | | | | | | | | | | | | | | | | | |
| -0.00083020 | -0.00083909 | -0.00021631 | 0.00046671 | 0.00107706 | -0.00050416 | 0.00076746 | 0.00031673 | 0.00121061 | 0.00336738 | 0.00261797 | 0.00215500 | -0.00443979 | 0.00243279 | -0.00076317 | 0.00300532 | 0.00026284 | -0.00450344 | 0.00530844 | -0.00143277 | -0.00160600 | -0.00134838 | -0.00353015 |
| 0.00100796 | -0.00678994 | -0.00358613 | 0.00451192 | 0.00072483 | 0.00053195 | -0.00352106 | -0.00028889 | -0.00331120 | 0.00109513 | -0.00471909 | 0.00685497 | 0.00988163 | -0.00058816 | 0.00461951 | 0.02000041 | 0.00125815 | 0.00951222 | -0.00942261 | -0.00368769 | -0.02072987 | -0.01627544 | 0.00567128 |
| 0.00013345 | 0.00276655 | 0.00075818 | -0.00167200 | -0.00083676 | 0.00038990 | 0.00028102 | -0.00021202 | -0.00004842 | -0.00247564 | -0.00172407 | -0.00322972 | 0.00027868 | -0.00268375 | -0.00171259 | -0.00838998 | 0.00017411 | 0.00044981 | -0.00051175 | 0.00166831 | 0.00748436 | 0.00469941 | 0.00166608 |

# Leaf morphology

| | | Axis 1 | Axis 2 | Axis 3 | Axis 4 | Axis 5 | Axis 6 | Axis 7 | Axis 8 | Axis 9 | Axis 10 | Axis 11 | Axis 12 | Axis 13 | Axis 14 | Axis 15 | Axis 16 | Axis 17 | Axis 18 | Axis 19 | Axis 20 | Axis 21 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Eigenvalues | 6.07787036 | 3.20290035 | 2.18899683 | 1.44654185 | 1.15428117 | 0.98713706 | 0.86276662 | 0.71099257 | 0.52994725 | 0.36138426 | 0.28456093 | 0.26260143 | 0.21105083 | 0.19943510 | 0.19062335 | 0.16521905 | 0.15977756 | 0.15406043 | 0.14115978 | 0.13985838 | 0.13859157 |
| | Percentage | 27.55120010 | 14.51885992 | 9.92279961 | 6.55722508 | 5.23239714 | 4.47472702 | 3.91095145 | 3.22295434 | 2.40226952 | 1.63816756 | 1.28992470 | 1.19038152 | 0.95670084 | 0.90404630 | 0.86410237 | 0.74894374 | 0.72427732 | 0.69836137 | 0.63988224 | 0.63398293 | 0.62824046 |
| | Cumulative percentage | 27.55120010 | 42.07006002 | 51.99285963 | 58.55008471 | 63.78248185 | 68.25720887 | 72.16816031 | 75.39111466 | 77.79338418 | 79.43155174 | 80.72147644 | 81.91185796 | 82.86855879 | 83.77260510 | 84.63670747 | 85.38565121 | 86.10992853 | 86.80828990 | 87.44817215 | 88.08215508 | 88.71039554 |
| Clade | Species | | | | | | | | | | | | | | | | | | | | | |
| Cochranea | *H. chenopodiaceum* | -0.36424334 | 0.19813401 | 0.14878581 | 0.06972507 | 0.16603649 | -0.33611511 | 0.02922375 | -0.15119776 | -0.04283629 | 0.04807450 | -0.02696987 | 0.07137559 | 0.01655925 | 0.02453457 | -0.12437860 | 0.02361671 | -0.03055843 | 0.00816018 | 0.03509184 | -0.07006691 | -0.00832267 |
| Cochranea | *H. eremogenum* | -0.45337475 | -0.22325763 | -0.09448592 | -0.05967990 | -0.00408560 | 0.09250988 | -0.20493488 | -0.25348312 | -0.17217476 | 0.10719789 | 0.11044827 | -0.01593119 | -0.04064130 | 0.12123942 | -0.11671872 | -0.06696210 | -0.02913733 | -0.13287749 | -0.02071043 | 0.04817694 | -0.00504108 |
| Cochranea | *H. filifolium* | -0.41755681 | 0.37180850 | 0.10661001 | 0.15815674 | 0.11255819 | -0.12930788 | 0.33196200 | 0.13929567 | -0.21205856 | 0.02985789 | 0.05581146 | -0.08971632 | -0.03705181 | 0.04326030 | 0.02225549 | 0.01965087 | -0.03152738 | -0.05097187 | 0.00397195 | 0.01649903 | -0.00085827 |
| Cochranea | *H. floridum* | -0.42892078 | -0.20276065 | 0.21398299 | 0.08529172 | -0.19400136 | -0.13053268 | -0.05491336 | -0.16381173 | 0.01613307 | 0.03561518 | 0.04871647 | -0.00459574 | 0.10490484 | -0.03620639 | 0.02521256 | -0.06551788 | 0.07945561 | 0.03387608 | -0.10024243 | 0.03966655 | 0.04222009 |
| Cochranea | *H. glutinosum* | -0.16495603 | 0.13998461 | 0.28908146 | 0.01654474 | 0.24558207 | -0.13557808 | 0.19801993 | 0.03928459 | -0.08705851 | -0.06945748 | -0.16784729 | 0.06816973 | -0.06411428 | 0.01105326 | 0.05383178 | -0.04612349 | 0.04713730 | 0.04523902 | -0.01434686 | 0.03413394 | 0.00843611 |
| Cochranea | *H. huascoense* | -0.42365613 | 0.24466279 | -0.12062294 | -0.04709977 | 0.31813267 | 0.02232974 | -0.04014369 | -0.18045334 | 0.17440675 | -0.01235363 | -0.08848496 | 0.04805603 | -0.10225319 | 0.01522999 | 0.03789185 | 0.05591226 | 0.05285685 | -0.05228579 | -0.04964400 | 0.05568925 | 0.01958755 |
| Cochranea | *H. inconspicuum* | -0.20557321 | 0.33162228 | -0.41592623 | 0.31510573 | -0.11077716 | 0.15984548 | -0.21517028 | -0.10651612 | -0.28467310 | 0.02506760 | -0.06264452 | -0.10377334 | 0.00022306 | -0.03398931 | -0.02912757 | 0.01398198 | 0.02842304 | 0.01070669 | 0.01101395 | -0.01285567 | -0.00622619 |
| Cochranea | *H. krauseanum* | 0.36404135 | 0.22672082 | 0.06667550 | -0.05249491 | -0.18920373 | 0.11080055 | -0.06112532 | -0.05550897 | 0.03603109 | -0.01409256 | -0.13402634 | -0.01483712 | -0.14602713 | 0.04604774 | 0.08190821 | -0.10577895 | -0.13521241 | 0.00413732 | 0.06906548 | -0.04755185 | -0.04288825 |
| Cochranea | *H. linariifolium* | -0.47122144 | -0.16229555 | 0.21517891 | 0.11710705 | -0.20677968 | -0.03959130 | -0.00148757 | -0.15920365 | 0.09860183 | 0.03677461 | 0.03820406 | -0.02666972 | -0.05505618 | -0.05889252 | 0.04466225 | 0.11346801 | -0.01981572 | 0.01328385 | 0.08071749 | 0.00880644 | -0.06175703 |
| Cochranea | *H. longistylum* | -0.39224175 | 0.13452376 | 0.18744760 | 0.16098189 | -0.04573701 | -0.05522387 | -0.16539722 | 0.07065435 | 0.23998909 | -0.03065933 | -0.03389460 | -0.00987808 | 0.02123697 | -0.02970666 | 0.01274235 | 0.09851158 | -0.00255813 | -0.17356676 | -0.09241187 | -0.02224121 | 0.08603016 |
| Cochranea | *H. megalanthum* | -0.33528675 | 0.07177666 | 0.18685416 | 0.11858530 | -0.05862347 | -0.20536770 | -0.23268976 | 0.06142140 | 0.04134793 | -0.02861576 | -0.04590659 | -0.04861214 | 0.03958638 | 0.02629225 | 0.08805800 | -0.06826675 | -0.05672706 | 0.02689728 | 0.04971482 | -0.00676543 | -0.00836459 |
| Cochranea | *H. myosotifolium* | -0.49190466 | 0.24586381 | 0.02295489 | 0.26000113 | -0.19015814 | -0.08974488 | -0.01519887 | 0.23792125 | -0.14663526 | 0.06033101 | 0.11984512 | -0.04543415 | -0.03556250 | 0.02406009 | -0.01541380 | -0.00566732 | -0.01206630 | 0.05798498 | -0.00685503 | -0.02001456 | 0.00777743 |
| Cochranea | *H. philippianum* | -0.45431351 | -0.20837382 | -0.08918556 | -0.05564112 | -0.04685692 | 0.14089294 | -0.18102111 | -0.22371446 | -0.01793344 | 0.03390375 | 0.01293721 | 0.01765846 | -0.08315548 | -0.03768262 | 0.20032701 | 0.05408798 | -0.04031282 | 0.12455671 | -0.01954307 | -0.00745378 | 0.03481171 |
| Cochranea | *H. pycnophyllum* | -0.41798873 | 0.15160526 | 0.18497282 | 0.16141704 | -0.02199219 | -0.01693262 | -0.14999294 | 0.05389487 | 0.30233473 | -0.03218824 | -0.02665176 | 0.00236675 | 0.04492915 | -0.00797138 | -0.11993471 | -0.06907368 | 0.05998055 | 0.09224047 | 0.05819073 | 0.02386826 | -0.06865030 |
| Cochranea | *H. sinuatum* | 0.24693278 | 0.32241738 | -0.08838035 | 0.36799086 | -0.06928472 | 0.34163910 | 0.14270912 | 0.13469166 | 0.06066290 | 0.02655252 | 0.01255620 | 0.10083025 | 0.09761788 | -0.03202357 | 0.10742628 | -0.02090568 | 0.03902788 | -0.06752574 | -0.03788897 | -0.09229079 | 0.02579724 |
| Cochranea | *H. stenophyllum* | -0.52834259 | 0.38830842 | -0.31167483 | 0.00870702 | 0.25767155 | 0.11118805 | 0.14448460 | -0.00877468 | 0.05924365 | 0.02912325 | 0.09523221 | -0.01509029 | 0.04952243 | 0.02135721 | -0.01817239 | -0.03905711 | 0.01172975 | 0.05135500 | 0.01296436 | -0.10585734 | 0.01231853 |
| Cochranea | *H. taltalense* | 0.31826658 | 0.40013891 | -0.09950901 | 0.04380582 | -0.29694491 | 0.24503108 | 0.16464219 | 0.10902664 | 0.01435373 | 0.01326138 | 0.01127739 | 0.02584511 | -0.06774006 | -0.01424925 | -0.02910898 | 0.06617643 | -0.00661373 | 0.04010308 | -0.02459587 | 0.17503552 | -0.00466832 |
| Heliothmanus | *H. adenogynum* | 0.42149678 | 0.18349987 | 0.05912783 | -0.09503244 | -0.14357251 | 0.03654481 | -0.09997271 | -0.04118493 | -0.02709456 | 0.01603628 | -0.08496684 | 0.05977371 | 0.07157175 | 0.04179154 | -0.06446542 | -0.04186974 | -0.11200251 | -0.02836607 | -0.06775705 | 0.04169786 | 0.14379815 |
| Heliothmanus | *H. arborescens* | 0.45225722 | 0.17238616 | 0.05662241 | -0.10541176 | -0.11552358 | 0.02027374 | -0.11995556 | -0.02681339 | -0.03071285 | -0.00236324 | 0.00622000 | 0.05485294 | 0.06640382 | 0.03472476 | -0.03866550 | 0.08711573 | 0.00534641 | 0.04535021 | 0.03473351 | -0.02781093 | -0.02840455 |
| Heliothmanus | *H. corymbosum* | 0.44998611 | 0.17425866 | 0.05825623 | -0.10477359 | -0.11761814 | 0.02210064 | -0.11898127 | -0.02938751 | -0.03030926 | -0.00463638 | 0.00321444 | 0.04552761 | 0.06081754 | 0.04421031 | -0.03540015 | 0.06903489 | 0.02656987 | 0.02670313 | -0.00746005 | -0.05212889 | -0.06671374 |
| Heliothmanus | *H. incanum* | 0.38968777 | 0.29339586 | 0.02601092 | -0.15310656 | 0.06641392 | -0.10742147 | 0.12436048 | -0.18802581 | -0.04101715 | 0.00543444 | -0.06557196 | 0.04216787 | 0.06895995 | 0.08440262 | 0.01869246 | 0.05393079 | -0.04227058 | 0.00452527 | -0.00252760 | 0.00279175 | 0.01719151 |
| Heliothmanus | *H. mandonii* | 0.41206346 | 0.28818070 | 0.02744514 | -0.15685497 | 0.08680423 | -0.11850969 | 0.11080050 | -0.17930797 | -0.03572473 | -0.01028368 | 0.03238648 | 0.00269138 | -0.01880512 | -0.03741754 | 0.04045241 | -0.02451513 | 0.09497542 | -0.04487135 | 0.14357034 | 0.02309983 | 0.08969925 |
| Heliothmanus | *H. rufipilum* | 0.45365441 | 0.17439792 | 0.06232453 | -0.10413947 | -0.11660504 | 0.02600999 | -0.12047736 | -0.02795814 | -0.02242453 | -0.01960968 | 0.05085537 | -0.00346810 | -0.00486192 | 0.01480452 | 0.00556366 | -0.02457904 | 0.13610588 | -0.02541909 | 0.02394836 | 0.03018639 | 0.00670062 |
| Heliothmanus | *H. submolle* | 0.42913862 | 0.28946741 | 0.02720474 | -0.16206780 | 0.10068512 | -0.13286314 | 0.10298557 | -0.17823177 | -0.03801276 | -0.01718416 | 0.05078297 | 0.01464452 | -0.04565324 | -0.14918744 | -0.01061690 | -0.02924919 | -0.03002842 | -0.00416526 | -0.14455881 | -0.04407855 | -0.13156370 |
| Tournefortia | *H. amplexicaule* | -0.03484479 | -0.15052056 | 0.33144538 | -0.31577027 | -0.25473868 | -0.02023166 | 0.11430854 | 0.03431247 | -0.04063648 | -0.08822561 | -0.02558553 | -0.11224002 | 0.07114398 | -0.00687943 | -0.06878679 | 0.05562667 | 0.03704237 | 0.04513520 | -0.01445639 | -0.08714339 | 0.06765187 |
| Tournefortia | *H. angiospermum* | -0.00750580 | -0.49275860 | -0.15032521 | -0.11916882 | 0.17057369 | 0.04225278 | 0.03361292 | 0.05978997 | -0.03226174 | -0.13813338 | 0.03396232 | -0.14699725 | -0.01337102 | 0.06130987 | 0.01886056 | 0.04432471 | 0.07815499 | 0.02167688 | -0.01828501 | 0.04922517 | -0.02761765 |
| Tournefortia | *H. curassavicum* | -0.31356045 | -0.16519832 | -0.59233135 | -0.32436326 | -0.37850993 | -0.18057793 | 0.09311770 | 0.10715934 | 0.05719301 | -0.13680295 | -0.08125231 | -0.03703829 | -0.08854929 | 0.02061121 | 0.01500575 | -0.04006817 | 0.02248102 | -0.08420829 | -0.00174981 | -0.12571858 | 0.00316813 |
| Tournefortia | *H. elongatum* | 0.19685047 | -0.45269979 | -0.01774087 | 0.00472958 | 0.06745255 | -0.08737993 | 0.12984551 | 0.06591272 | 0.12370554 | 0.04155364 | 0.22301871 | 0.08111084 | -0.02761620 | 0.14905286 | 0.06101771 | 0.00358328 | -0.11464716 | 0.02324953 | -0.02053338 | -0.01206057 | 0.06330292 |
| Tournefortia | *H. indicum* | -0.00512908 | -0.07861373 | 0.02543370 | -0.14298717 | 0.29475471 | 0.07929378 | -0.24896738 | 0.17284790 | -0.13480404 | -0.09079389 | 0.06735263 | 0.06309765 | 0.00641154 | -0.16331469 | 0.01682032 | 0.01132106 | -0.03723206 | -0.01183419 | 0.05719634 | -0.01230664 | 0.08047445 |
| Tournefortia | *H. kurtzii* | -0.27556833 | -0.21537720 | 0.04104203 | -0.13185238 | 0.16565755 | 0.52860343 | 0.08221270 | -0.05545070 | 0.08908437 | -0.04980615 | -0.01195681 | 0.03918432 | -0.01332586 | 0.03291062 | -0.11983064 | -0.09888146 | -0.01597900 | 0.01504860 | 0.03051300 | -0.04079534 | -0.01730947 |
| Tournefortia | *H. microstachyum* | -0.15650279 | -0.29191729 | 0.36697300 | -0.00608061 | -0.06251925 | 0.03192977 | 0.09181446 | 0.03792490 | -0.08567920 | -0.04945749 | -0.02554638 | 0.01186749 | 0.15639531 | -0.03926425 | 0.08905958 | -0.09774663 | -0.07193391 | -0.13016646 | 0.06430453 | 0.07112027 | -0.12410575 |
| Tournefortia | *H. nicoteanaefolium* | -0.02762235 | -0.06558941 | 0.03128951 | -0.13831518 | 0.26163208 | 0.10452866 | -0.23513637 | 0.16347416 | -0.13792785 | -0.08659959 | -0.00816589 | 0.05934742 | 0.07587111 | 0.07858111 | 0.07930474 | 0.08461390 | 0.03367470 | -0.01553484 | -0.02603170 | -0.03620606 | -0.07692925 |
| Tournefortia | *H. paronychioides* | -0.24461091 | -0.22117878 | 0.37521332 | 0.06789115 | -0.06238707 | 0.19525021 | 0.18514822 | 0.02864893 | 0.00247965 | -0.01792148 | -0.02353301 | 0.02318116 | -0.11404122 | -0.02033805 | -0.08533174 | 0.14425805 | -0.01257147 | -0.07027023 | 0.04118418 | -0.00798612 | -0.02983686 |
| Tournefortia | *H. patagonicum* | -0.43817650 | -0.33265834 | -0.63103123 | -0.01614547 | -0.14392730 | -0.19168454 | 0.06761710 | 0.09636059 | -0.05265911 | -0.03212238 | -0.04894175 | 0.29473540 | 0.04025183 | -0.04557759 | -0.04272836 | 0.00686901 | 0.01555012 | 0.01312486 | 0.02376314 | 0.08572013 | -0.03308774 |
| Tournefortia | *H. pinnatisectum* | -0.20557527 | -0.26820523 | 0.36930785 | 0.03711729 | -0.06858559 | 0.08585642 | 0.12564773 | 0.01584040 | -0.11928445 | -0.02293314 | -0.05262935 | 0.07603784 | -0.04374777 | 0.00078453 | -0.00445295 | -0.08833168 | 0.06042149 | 0.10914410 | -0.07254313 | -0.01765796 | 0.07893354 |
| Tournefortia | *H. transalpinum* | 0.23473276 | 0.07021576 | 0.10868601 | -0.31074024 | -0.01471189 | -0.05576655 | -0.07882473 | 0.20425647 | 0.07848282 | 0.38858659 | 0.06024170 | 0.05642849 | -0.06640463 | 0.00541503 | 0.03709224 | -0.03650046 | 0.09507596 | -0.01972119 | 0.01548325 | -0.02260814 | -0.05059652 |
| Tournefortia | *H. veronicifolium* | -0.02841209 | -0.46522098 | -0.16633783 | -0.15857276 | 0.16366724 | 0.04120660 | 0.05768424 | 0.13458116 | -0.01266539 | 0.30134235 | -0.23519528 | -0.14376852 | 0.06706930 | -0.07402779 | -0.02422624 | 0.03367318 | -0.03960536 | 0.01488152 | -0.01390032 | 0.01534140 | 0.02786512 |
| Tournefortia | *T. argentea* | 0.14031536 | 0.07905567 | 0.18678325 | -0.32362023 | -0.00341247 | -0.03784155 | -0.14358579 | 0.17214895 | -0.01317082 | -0.09853217 | 0.10298106 | -0.03907714 | -0.07897958 | -0.03846119 | -0.03798642 | -0.01447854 | -0.02197705 | 0.01194874 | -0.03441341 | 0.05704205 | 0.00187335 |
| Tournefortia | *T. bicolor* | 0.45068616 | -0.35607789 | -0.09885308 | 0.17000374 | -0.00986496 | -0.01550300 | 0.09426940 | -0.12734948 | 0.01892040 | 0.01095557 | 0.04763362 | -0.02505361 | 0.02944521 | -0.06288634 | -0.00247426 | 0.00575986 | 0.00829368 | -0.00328865 | 0.04549656 | -0.05456581 | 0.02686029 |
| Tournefortia | *T. glabra* | 0.46366852 | -0.09153660 | -0.09995133 | 0.22019638 | 0.12361281 | -0.10453400 | -0.07287008 | 0.07559590 | 0.04761288 | -0.03239572 | 0.00727789 | -0.02728987 | -0.04806328 | -0.06024027 | -0.06719540 | -0.00892953 | -0.07181905 | 0.02362049 | -0.08069593 | -0.04720876 | -0.07418221 |
| Tournefortia | *T. gnaphalodes* | -0.36252603 | 0.46473789 | -0.31000864 | -0.31685047 | 0.03862126 | 0.03448557 | 0.13035971 | -0.01814872 | 0.16556347 | -0.03464535 | 0.07868611 | -0.14152154 | 0.13645653 | -0.02877921 | 0.03028542 | -0.00944095 | -0.06976610 | 0.03782835 | 0.01200928 | 0.09055329 | -0.00521988 |
| Tournefortia | *T. hirsutissima* | 0.45022355 | -0.35390344 | -0.09528007 | 0.17118596 | -0.01036050 | -0.01094383 | 0.09318552 | -0.12658317 | 0.02234016 | -0.00639888 | 0.06417039 | -0.06544549 | -0.01885014 | -0.09581064 | 0.01570570 | -0.07133198 | 0.05597071 | -0.04191468 | -0.06641994 | 0.02208165 | -0.01994331 |
| Tournefortia | *T. luzonica* | 0.44078230 | -0.35605332 | -0.10072672 | 0.17143432 | -0.02044760 | -0.00853571 | 0.10061463 | -0.12900184 | 0.01823105 | 0.02010843 | 0.01323103 | -0.00372520 | 0.07947787 | 0.04202054 | 0.01277137 | 0.07545005 | -0.00510174 | 0.03737239 | 0.05376167 | -0.01414906 | -0.01869449 |
| Tournefortia | *T. microcalyx* | 0.41981620 | -0.07983272 | -0.09352098 | 0.23174275 | 0.08039921 | -0.06560124 | -0.04777259 | 0.06337872 | 0.05480611 | -0.04088690 | -0.09766274 | -0.07140029 | -0.00208873 | 0.19283591 | 0.02508232 | -0.00875684 | 0.04731488 | 0.01841061 | -0.06144819 | 0.04507738 | -0.04665616 |
| Tournefortia | *T. rollotii* | 0.46369010 | -0.09415096 | -0.10284953 | 0.21991529 | 0.12478723 | -0.10548970 | -0.07332404 | 0.07994072 | 0.04612469 | -0.02737828 | 0.00160995 | -0.01151724 | -0.03438818 | -0.06827784 | -0.07052260 | 0.01233090 | -0.09156278 | 0.04042800 | 0.02943526 | 0.03362789 | 0.05128197 |
| Tournefortia | *T. ternifolia* | 0.45132434 | -0.08898232 | -0.09696834 | 0.22313262 | 0.11218684 | -0.09129518 | -0.06668361 | 0.07174352 | 0.05010589 | -0.03529939 | -0.00121927 | -0.05586990 | -0.05450756 | 0.00465374 | -0.01449189 | -0.05126561 | 0.06543804 | -0.04000062 | 0.10288920 | 0.01808134 | 0.06185800 |
| | Centroids | | | | | | | | | | | | | | | | | | | | | |
| | Cochranea | -0.30834489 | 0.12987696 | 0.04474951 | 0.09878920 | -0.01262356 | -0.01907293 | -0.02986849 | -0.02664078 | 0.01483899 | 0.01318953 | -0.00523384 | -0.00350233 | -0.01193596 | 0.00443681 | 0.01045072 | -0.00124183 | -0.00145974 | 0.00164503 | -0.00242356 | -0.00002061 | 0.00230670 |
| | Heliothmanus | 0.43053170 | 0.22232909 | 0.04604266 | -0.12460318 | -0.03918885 | -0.03274414 | -0.02274672 | -0.09223446 | -0.03195232 | -0.00453981 | -0.00134816 | 0.03137955 | 0.02985162 | 0.00730247 | -0.01296268 | 0.01413051 | 0.01205694 | -0.00306410 | -0.00172555 | -0.00374213 | 0.00494681 |
| | Tournefortia-clade | 0.10707784 | -0.19664955 | -0.01431895 | -0.02221107 | 0.04036536 | 0.00767724 | 0.01285045 | 0.05160180 | 0.00364378 | -0.00976106 | 0.00825853 | -0.01134336 | 0.00166230 | -0.00260161 | -0.00395768 | -0.00054764 | -0.00173061 | 0.00068187 | 0.00186054 | 0.00057874 | -0.00182804 |

# Leaf morphology (continued)

| Axis 22 | Axis 23 | Axis 24 | Axis 25 | Axis 26 | Axis 27 | Axis 28 | Axis 29 | Axis 30 | Axis 31 | Axis 32 | Axis 33 | Axis 34 | Axis 35 | Axis 36 | Axis 37 | Axis 38 | Axis 39 | Axis 40 | Axis 41 | Axis 42 | Axis 43 | Axis 44 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.13705514 | 0.13362864 | 0.13302841 | 0.13247715 | 0.13089874 | 0.13035779 | 0.13022386 | 0.12923237 | 0.12874317 | 0.12583560 | 0.12193108 | 0.11900453 | 0.11768762 | 0.11287880 | 0.10865654 | 0.09771700 | 0.09599545 | 0.08997649 | 0.08539061 | 0.08125565 | 0.06413543 | 0.05460142 | 0.02980624 |
| 0.62127579 | 0.60574334 | 0.60302247 | 0.60052360 | 0.59336858 | 0.59091644 | 0.59030936 | 0.58581487 | 0.58359733 | 0.57041719 | 0.55271788 | 0.53945171 | 0.53348210 | 0.51168355 | 0.49254391 | 0.44295460 | 0.43515074 | 0.40786660 | 0.38707866 | 0.36833470 | 0.29072816 | 0.24751015 | 0.13511273 |
| 89.33167133 | 89.93741467 | 90.54043714 | 91.14096074 | 91.73432932 | 92.32524576 | 92.91555512 | 93.50136999 | 94.08496731 | 94.65538451 | 95.20810239 | 95.74755409 | 96.28103620 | 96.79271975 | 97.28526365 | 97.72821825 | 98.16336899 | 98.57123559 | 98.95831425 | 99.32664895 | 99.61737712 | 99.86488727 | 100.00000000 |
| | | | | | | | | | | | | | | | | | | | | | | |
| 0.05585354 | 0.02640772 | 0.08540360 | -0.03147267 | 0.00038276 | 0.00488991 | -0.00911726 | 0.01744616 | -0.04785648 | -0.02693047 | -0.04609426 | 0.08791980 | 0.02903403 | -0.08548300 | -0.03952598 | -0.03736374 | -0.03261074 | -0.02233462 | 0.06654807 | -0.03336459 | -0.04822191 | 0.08335834 | 0.03390770 |
| -0.04998863 | -0.03196833 | -0.04940990 | 0.03336866 | 0.00917415 | 0.00002968 | -0.00795673 | -0.00266913 | 0.01089898 | 0.00977304 | 0.03486490 | -0.01013541 | -0.01203304 | 0.04099501 | 0.01351203 | -0.04544349 | 0.01901414 | 0.00294273 | -0.08743561 | -0.03380367 | -0.06641455 | 0.02956963 | -0.02319781 |
| -0.03282434 | -0.01717298 | -0.05601527 | 0.01783551 | 0.00396625 | 0.00131100 | 0.00071225 | -0.01047626 | 0.02402798 | 0.00129435 | 0.02391546 | -0.01761640 | -0.00077978 | -0.02425958 | 0.12897166 | -0.03974378 | -0.06255659 | -0.02438687 | 0.06206945 | 0.05999334 | 0.07125753 | 0.01394332 | -0.03016533 |
| -0.00003009 | -0.01997473 | 0.12313271 | 0.02717750 | -0.00424512 | -0.01967940 | 0.03027699 | -0.03849985 | 0.11744262 | -0.00214666 | 0.03872836 | -0.03518110 | -0.00655300 | 0.05020227 | 0.04214316 | 0.06109623 | 0.05324384 | 0.02479793 | 0.10718220 | 0.04005460 | -0.03308071 | 0.00028391 | 0.00718310 |
| -0.01588882 | 0.00521572 | 0.00975986 | 0.01268435 | 0.00311435 | -0.00250701 | -0.00095966 | -0.00414184 | -0.00140014 | 0.01568181 | 0.00650941 | -0.01461810 | -0.01124985 | 0.19060257 | -0.07861644 | -0.08943370 | 0.06964097 | -0.04315832 | -0.03003573 | -0.01158846 | 0.01207869 | 0.03108145 | 0.00175546 |
| -0.04380295 | -0.01454881 | -0.10104203 | 0.02556024 | -0.00545027 | -0.00108377 | 0.02848656 | -0.03821342 | 0.10665705 | -0.00590262 | -0.02012282 | 0.00482154 | 0.01078307 | -0.04101932 | -0.07841049 | 0.08434500 | -0.08031793 | 0.03097863 | 0.05343954 | -0.03851963 | 0.01682308 | 0.00841522 | -0.02259556 |
| -0.01168833 | 0.00173431 | -0.00272753 | 0.00367382 | 0.00011329 | 0.00091614 | -0.00105452 | -0.00107013 | 0.00101892 | -0.00321012 | -0.00901292 | -0.00744283 | -0.00362235 | 0.00980256 | 0.00753815 | -0.00544850 | 0.00447986 | -0.03872311 | 0.02768945 | 0.03613871 | 0.03798847 | -0.01916035 | 0.06817073 |
| -0.03760992 | -0.03890171 | 0.07534010 | 0.03382744 | 0.01900517 | -0.00612748 | -0.02616627 | 0.00801579 | 0.01746861 | -0.02861945 | -0.04718504 | -0.07363811 | -0.08515066 | -0.01157602 | 0.05944394 | -0.00266604 | 0.00362651 | 0.05499645 | 0.05831913 | -0.08882218 | -0.00338845 | 0.00719521 | 0.00550875 |
| 0.00111802 | 0.01523748 | -0.15981108 | -0.02717324 | -0.00000458 | 0.01932369 | -0.02353185 | 0.03091506 | -0.12411577 | 0.00480653 | -0.02944171 | 0.00679220 | 0.00779894 | 0.07892889 | 0.00954103 | 0.03301351 | 0.07385882 | 0.05367719 | 0.07195323 | 0.03046078 | -0.03727164 | -0.00731499 | 0.00772731 |
| -0.03013250 | -0.03919881 | 0.09567714 | 0.06037963 | 0.04132923 | 0.00289189 | -0.07062996 | 0.04690409 | -0.09694386 | -0.00798695 | -0.02661947 | 0.00480804 | -0.00968042 | 0.02404145 | 0.03041928 | -0.01112763 | -0.00536907 | -0.02417689 | -0.04495109 | -0.01363145 | 0.05391735 | -0.02515576 | 0.01354162 |
| 0.00029263 | 0.02062581 | -0.03435989 | -0.02636757 | -0.00978551 | 0.00297921 | 0.00864900 | 0.00420257 | -0.03795163 | 0.06148320 | 0.21130756 | -0.07401303 | -0.00220980 | -0.05304988 | -0.08470342 | 0.04176832 | -0.05439462 | -0.01941328 | -0.04126508 | 0.00995425 | 0.01337688 | 0.01643337 | 0.02180828 |
| 0.00982419 | 0.00024360 | 0.01218510 | -0.00247022 | -0.00371912 | -0.00572795 | 0.00821413 | -0.00839870 | 0.04405060 | -0.02157594 | -0.13318176 | 0.00638429 | -0.02683826 | -0.01120370 | -0.14560938 | 0.07561201 | 0.03907111 | 0.01799663 | -0.05545753 | -0.04396270 | 0.02867293 | -0.03888644 | -0.01820814 |
| 0.06449343 | 0.03005271 | 0.06267485 | -0.02943797 | -0.00905827 | -0.00402998 | 0.01208040 | -0.00024873 | 0.01148008 | -0.00764181 | -0.05296346 | 0.04337131 | 0.02476309 | -0.01229350 | 0.03164637 | -0.06628702 | -0.07020646 | -0.04515383 | -0.06929530 | 0.05696208 | -0.00006863 | 0.01287095 | -0.03528966 |
| -0.00329070 | 0.01009044 | -0.07444084 | -0.01805647 | -0.01950409 | -0.00388494 | 0.04086787 | -0.03335455 | 0.09222810 | -0.02201458 | -0.03962318 | 0.02317702 | 0.01111711 | -0.01284249 | 0.10992313 | -0.07980845 | 0.00489905 | -0.01012419 | -0.06511736 | -0.03005933 | 0.03345416 | -0.02062128 | 0.02449056 |
| -0.03528519 | -0.00815622 | -0.06212853 | -0.01057761 | -0.00744863 | 0.00357750 | 0.01553132 | -0.01653538 | 0.03106112 | -0.00993417 | -0.01998792 | -0.03008116 | -0.00251067 | -0.03136474 | -0.03622951 | -0.06585920 | -0.00708602 | 0.04445828 | -0.01765523 | 0.03992816 | -0.08925882 | 0.05918862 | 0.02288157 |
| 0.03910702 | 0.02522117 | 0.07325271 | -0.05624908 | -0.01528463 | -0.00031536 | 0.00828812 | 0.01418473 | -0.07111616 | 0.02402884 | 0.06813900 | -0.00184976 | 0.04225092 | 0.08695941 | 0.04785479 | 0.02640894 | -0.03244661 | 0.11875608 | -0.01404210 | -0.05545343 | -0.00726102 | -0.04184474 | -0.03134281 |
| 0.04859753 | 0.01293003 | 0.03497340 | 0.02038544 | 0.00818824 | -0.00278569 | -0.00684210 | 0.00814753 | -0.00785591 | 0.01345349 | 0.08110495 | 0.08712451 | 0.05495083 | 0.04081474 | 0.03049892 | 0.06197543 | -0.03838041 | -0.03782801 | -0.01510201 | -0.07788193 | -0.03134874 | 0.03619177 | 0.02727202 |
| 0.10064231 | 0.12248719 | -0.07582966 | -0.05855525 | 0.00553933 | -0.00036036 | 0.04285120 | -0.08109627 | -0.04249379 | 0.01307789 | -0.04522695 | -0.06138387 | 0.06833014 | 0.00782188 | -0.00494118 | -0.03507895 | 0.01455055 | 0.01293778 | 0.04577587 | -0.00675547 | 0.03773910 | -0.02734146 | -0.01636707 |
| -0.05639191 | -0.12991165 | 0.00908908 | 0.02926815 | 0.14927034 | -0.06863978 | 0.18282496 | 0.04097829 | -0.02211186 | -0.00058826 | 0.02917293 | 0.02595140 | 0.02170146 | 0.02334352 | -0.04741214 | -0.05052416 | -0.02872865 | 0.00833050 | 0.03147835 | 0.01323478 | 0.01656771 | -0.02753463 | -0.02484121 |
| 0.07405158 | -0.09994794 | -0.01778940 | 0.00012265 | -0.03648780 | 0.07075235 | -0.21519425 | -0.06355955 | 0.07097655 | 0.06202809 | 0.03642651 | 0.03011371 | -0.00895256 | 0.02895399 | -0.04357406 | -0.05256951 | -0.02980354 | 0.01161264 | 0.03435001 | 0.00973016 | 0.01896573 | -0.02882032 | -0.02395456 |
| 0.00738270 | -0.03164833 | -0.01919085 | -0.03989214 | -0.07675942 | -0.00735018 | -0.01503455 | 0.20517761 | 0.08691605 | -0.04577509 | -0.01267403 | -0.04103437 | 0.05237986 | -0.01427544 | 0.03052013 | 0.05964685 | 0.05053155 | 0.01446249 | -0.07369606 | 0.03801222 | 0.00352168 | -0.02754954 | 0.02696557 |
| 0.02506636 | -0.02270573 | 0.02612166 | 0.03133926 | 0.05777587 | 0.14725395 | 0.03577071 | -0.12325592 | -0.02941309 | -0.01139902 | -0.01233534 | 0.01385636 | -0.03760802 | -0.02391464 | 0.01478346 | 0.03789956 | 0.00861742 | 0.00836169 | -0.06362281 | 0.03051057 | -0.01555703 | -0.04379464 | 0.02743536 |
| -0.11490383 | 0.15981312 | 0.02736267 | -0.01317422 | -0.12726781 | 0.00274999 | 0.00806928 | 0.08893515 | -0.03922154 | -0.04343137 | 0.02312695 | 0.06514554 | -0.08667843 | -0.00516854 | -0.03632446 | -0.05611587 | -0.03790687 | 0.00447086 | 0.05025880 | -0.00308494 | 0.01259755 | -0.03245034 | -0.02374526 |
| -0.03413857 | 0.03979344 | -0.02043972 | -0.00052855 | 0.00651182 | -0.14217204 | -0.01157318 | -0.07694794 | -0.04110713 | 0.05528066 | -0.00591151 | 0.00104315 | -0.02831981 | -0.02290941 | 0.00694372 | 0.01675633 | -0.00413893 | -0.01300320 | -0.04744131 | 0.00914079 | -0.00902273 | -0.04689522 | 0.02689226 |
| -0.02166742 | 0.00209168 | -0.04989464 | -0.02829204 | -0.00667539 | -0.00415993 | 0.00926239 | -0.00432796 | 0.00220942 | 0.01900794 | -0.05661608 | -0.05904774 | -0.08946226 | 0.04922453 | 0.03575040 | 0.06397472 | -0.11095890 | -0.04625674 | -0.03909170 | -0.02612777 | -0.04342601 | 0.04965798 | -0.00675097 |
| 0.01396000 | -0.00036152 | 0.02215309 | 0.02869733 | 0.00389575 | -0.00011566 | -0.01577910 | 0.00663281 | -0.02704977 | -0.01309039 | -0.04847983 | -0.12870032 | 0.10488322 | -0.01762384 | -0.03642385 | -0.07311530 | -0.05806572 | 0.02605272 | 0.03265657 | -0.04523509 | -0.03416750 | -0.04016330 | 0.05180630 |
| -0.01451570 | 0.00430665 | -0.01738045 | -0.02157135 | -0.01474648 | 0.00204956 | 0.02984645 | -0.02404661 | 0.04650247 | -0.00843851 | 0.03513646 | 0.08885448 | 0.09484186 | 0.00707084 | -0.00288330 | -0.00299255 | 0.05302827 | -0.03078907 | 0.00775109 | 0.01488267 | -0.00328747 | -0.00255592 | -0.00231847 |
| -0.01647036 | 0.00434257 | -0.03111692 | -0.00830914 | 0.00552843 | -0.00673900 | 0.00966604 | -0.01634313 | 0.04135546 | 0.00594007 | 0.01776089 | 0.06981105 | -0.08151450 | 0.03290931 | -0.00748626 | -0.02515184 | -0.01900411 | -0.02912026 | 0.02824937 | -0.00320403 | 0.00975819 | -0.04084361 | 0.06417371 |
| -0.04427122 | -0.03316842 | -0.01630130 | -0.02137149 | -0.04511194 | 0.01367431 | 0.01820674 | 0.05259779 | 0.04658101 | 0.16864042 | -0.02482759 | 0.02669160 | 0.02071284 | -0.00929353 | 0.04730674 | 0.01102757 | 0.04983680 | -0.02746140 | 0.03873345 | -0.06181302 | -0.01389593 | 0.00343842 | 0.00467852 |
| -0.00568431 | -0.00777446 | 0.02802991 | 0.00436844 | 0.00522355 | 0.00295477 | -0.01900515 | 0.01873686 | -0.04496597 | 0.00431776 | -0.01854903 | 0.00353896 | -0.00983593 | 0.02005148 | -0.05054081 | 0.07962467 | -0.00724910 | -0.06721546 | 0.03028496 | 0.09791112 | 0.05789022 | 0.01191925 | 0.01510850 |
| 0.01727316 | 0.00240705 | 0.02758010 | 0.00595637 | -0.01514031 | 0.00412805 | 0.01100189 | -0.00109078 | 0.01107359 | -0.01286966 | -0.06262430 | 0.07957386 | 0.07667470 | 0.01454476 | -0.02012110 | 0.02279799 | -0.07075790 | 0.00596884 | -0.00795488 | -0.00344577 | -0.00784128 | -0.03496248 | -0.01277562 |
| 0.06007806 | 0.04646122 | -0.02343689 | -0.01676247 | 0.03113695 | -0.01629865 | 0.00867942 | -0.06821768 | -0.01650736 | -0.16263290 | 0.04051873 | 0.01516916 | -0.05300731 | -0.00416321 | 0.06331803 | 0.06279789 | 0.07265353 | -0.02846868 | 0.00311837 | -0.04173420 | 0.00209441 | 0.02008333 | -0.00223327 |
| 0.05479109 | 0.04055103 | 0.09018417 | -0.06202966 | -0.04020728 | -0.01251337 | 0.06021698 | -0.03094516 | 0.06583943 | 0.03272289 | 0.07341556 | -0.06807962 | -0.03621182 | -0.08047006 | -0.02276741 | -0.04150174 | 0.06125105 | 0.00371087 | -0.01682594 | 0.01609307 | -0.01880569 | -0.04217974 | -0.01685813 |
| 0.00283649 | -0.00706708 | 0.00947420 | 0.01007217 | 0.00478070 | 0.00106598 | -0.02012624 | 0.02268479 | -0.04599325 | 0.01315647 | -0.02251856 | -0.08855128 | -0.09174540 | -0.01686594 | 0.02397418 | 0.00335983 | -0.04188641 | 0.02814246 | -0.01230083 | 0.01991848 | 0.01326346 | -0.00127463 | -0.00599684 |
| -0.04416405 | -0.04071627 | -0.06178863 | 0.06846612 | 0.05245209 | 0.01307794 | -0.07260148 | 0.03890626 | -0.07207175 | -0.03570436 | 0.04417191 | 0.04892986 | 0.04947251 | -0.13440215 | 0.02501630 | -0.00145386 | 0.03752111 | 0.01092809 | -0.00378908 | -0.02871957 | -0.01881909 | -0.04617532 | -0.01720079 |
| 0.00937243 | -0.00725570 | 0.01266723 | 0.00017682 | -0.01267479 | 0.00359899 | 0.00085387 | 0.00814264 | -0.02835923 | 0.00808975 | -0.02652339 | -0.09165534 | 0.08574662 | -0.00301171 | 0.01515590 | 0.01776708 | 0.00646075 | -0.06985179 | 0.01398012 | 0.00774048 | 0.00704467 | 0.01668964 | -0.00073757 |
| -0.01442405 | 0.00440143 | -0.00893368 | 0.00056602 | 0.00988538 | -0.00165886 | -0.00086378 | -0.00513982 | 0.02261066 | -0.00927897 | 0.02767232 | 0.08561622 | -0.07329293 | 0.00039465 | -0.01400176 | -0.01804081 | -0.00593828 | 0.06732902 | -0.01215639 | 0.00262505 | -0.00476032 | -0.01976168 | 0.01581009 |
| 0.01161997 | -0.00589120 | 0.01813462 | 0.01538544 | 0.00727989 | 0.00533614 | -0.00738804 | 0.00373394 | 0.00254605 | -0.02675502 | -0.00511482 | 0.02429653 | 0.01341686 | -0.01434077 | -0.01134772 | -0.01661269 | 0.01384062 | 0.16467319 | -0.03101163 | 0.09342169 | 0.04307494 | 0.08854980 | 0.01877690 |
| 0.11067841 | -0.03384288 | -0.03187536 | 0.19826502 | -0.14474120 | -0.06530895 | 0.05376533 | -0.00854092 | -0.02175285 | -0.02390936 | 0.02470625 | -0.00902030 | 0.00147954 | -0.00030300 | -0.01312095 | -0.00342602 | 0.01776477 | 0.00236717 | -0.01277524 | -0.04691991 | 0.06466885 | 0.04273901 | -0.01271854 |
| 0.03077366 | 0.09832345 | -0.00729259 | 0.10779937 | 0.06664119 | 0.18710559 | 0.04263946 | 0.08202273 | 0.04329135 | -0.00991198 | 0.01101106 | -0.01979985 | 0.00058918 | 0.03204038 | 0.00771894 | 0.01723184 | -0.01939493 | -0.03050836 | 0.00492882 | 0.03335671 | -0.04759795 | -0.01456557 | -0.02744725 |
| -0.00114874 | -0.01132821 | 0.00432853 | 0.04086423 | 0.02488875 | 0.00041415 | -0.03444849 | 0.01478489 | -0.01968628 | -0.00897470 | -0.00752665 | -0.02756427 | -0.05747830 | -0.07167635 | -0.04766335 | -0.05361742 | 0.09535809 | -0.07278783 | 0.02421967 | -0.00027877 | -0.02961978 | 0.01400447 | -0.03168596 |
| 0.05479736 | -0.08686943 | -0.01819198 | -0.20147961 | 0.05233246 | 0.06808332 | 0.01857314 | 0.06071861 | -0.01134513 | -0.03759425 | 0.01380990 | -0.00576723 | -0.03981344 | -0.01707842 | -0.01681693 | -0.01573221 | 0.01004961 | -0.01533429 | 0.00675226 | -0.06459618 | 0.06917817 | 0.03630211 | -0.01064745 |
| -0.16626047 | 0.12235537 | 0.04606112 | -0.00189922 | 0.08981393 | 0.00354748 | -0.06845672 | -0.05445511 | 0.03315248 | 0.05916558 | -0.01020202 | -0.01546987 | 0.07684925 | -0.01854853 | 0.00708499 | 0.02843923 | 0.04726236 | 0.01611667 | -0.03408260 | -0.02880287 | 0.06462041 | 0.05769566 | -0.01471698 |
| 0.01697105 | -0.05810690 | 0.02757996 | -0.02285223 | -0.07963685 | 0.01086834 | 0.06532131 | -0.03085095 | -0.09462905 | 0.14850463 | -0.06578882 | 0.04816649 | -0.03419747 | -0.04454478 | 0.04230460 | 0.04157740 | 0.03964736 | 0.00602433 | -0.00841243 | 0.04228214 | -0.02871860 | 0.01223186 | -0.02084521 |
| -0.12107629 | -0.09514054 | 0.03157272 | -0.06867747 | -0.10849794 | -0.02129934 | -0.02962635 | -0.08846065 | -0.03277470 | -0.14178946 | 0.01576339 | -0.02469640 | 0.06100911 | 0.03050987 | -0.00285735 | 0.02045278 | -0.01672620 | -0.03491803 | -0.00105538 | 0.03975336 | -0.04938324 | -0.01321113 | -0.02779079 |
| 0.10607741 | 0.04656465 | -0.01334140 | -0.00904030 | 0.12421758 | -0.17982223 | -0.09430015 | 0.05701813 | 0.04733414 | 0.00765265 | -0.00811105 | 0.01418929 | -0.02003911 | 0.01247046 | 0.01000801 | 0.02154129 | -0.01228018 | -0.00907901 | 0.00483451 | 0.04569973 | -0.04733709 | -0.00878023 | -0.02546304 |
| | | | | | | | | | | | | | | | | | | | | | | |
| -0.00217738 | -0.00077485 | 0.00120059 | 0.00144509 | 0.00058369 | -0.00044166 | 0.00021144 | -0.00103126 | 0.00269234 | 0.00012217 | 0.00272100 | 0.00003188 | 0.00138112 | 0.01223510 | 0.00033189 | -0.00323587 | -0.00643217 | 0.00300167 | -0.00101508 | -0.00777202 | 0.00030594 | 0.00721938 | 0.00422910 |
| 0.00020151 | 0.00454528 | -0.00998249 | -0.00731847 | -0.00305109 | 0.00130582 | 0.00366222 | -0.00046339 | -0.00193632 | 0.00404729 | 0.00258673 | 0.00561773 | -0.00266579 | 0.00004063 | -0.01270762 | -0.01339045 | -0.00474532 | 0.00699495 | -0.00099750 | 0.01262924 | 0.00989039 | -0.03317264 | -0.00229555 |
| 0.00214306 | -0.00040279 | 0.00125162 | 0.00060540 | 0.00044645 | 0.00009443 | -0.00118868 | 0.00100131 | -0.00169140 | -0.00127490 | -0.00290255 | -0.00051956 | 0.00108506 | -0.00901096 | 0.00236226 | 0.00634457 | 0.00472576 | -0.00383062 | 0.00088708 | 0.00099374 | -0.00065706 | 0.00375581 | -0.00141685 |

# Habit

| | | Axis 1 | Axis 2 | Axis 3 | Axis 4 | Axis 5 | Axis 6 | Axis 7 | Axis 8 | Axis 9 | Axis 10 | Axis 11 | Axis 12 | Axis 13 | Axis 14 | Axis 15 | Axis 16 | Axis 17 | Axis 18 | Axis 19 | Axis 20 | Axis 21 | Axis 22 | Axis 23 | Axis 24 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Eigenvalues | 7.81596775 | 2.66441231 | 2.10819354 | 0.97485702 | 0.72721384 | 0.56516548 | 0.48980413 | 0.44783154 | 0.40266672 | 0.38613056 | 0.34957821 | 0.34641919 | 0.33927122 | 0.33785403 | 0.33210155 | 0.32909302 | 0.32813717 | 0.32743349 | 0.32680005 | 0.32384495 | 0.32342624 | 0.32235748 | 0.32212897 | 0.32123745 |
| | Percentage | 26.65281380 | 9.08577000 | 7.18903810 | 3.32430780 | 2.47983303 | 1.92724058 | 1.67025489 | 1.52712640 | 1.37311224 | 1.31672320 | 1.19207797 | 1.18130555 | 1.15693065 | 1.15209795 | 1.13248175 | 1.12222251 | 1.11896301 | 1.11656343 | 1.11440338 | 1.10432635 | 1.10289854 | 1.09925402 | 1.09847478 | 1.09543464 |
| | Cumulative percentage | 26.65281380 | 35.73858381 | 42.92762191 | 46.25192970 | 48.73176274 | 50.65900332 | 52.32925822 | 53.85638462 | 55.22949686 | 56.54622006 | 57.73829803 | 58.91960358 | 60.07653423 | 61.22863219 | 62.36111393 | 63.48333644 | 64.60229945 | 65.71886288 | 66.83326627 | 67.93759261 | 69.04049116 | 70.13974518 | 71.23821996 | 72.33365460 |
| Clade | Species | | | | | | | | | | | | | | | | | | | | | | | | |
| Cochranea | *H. chenopodiaceum* | 0.16184826 | -0.02964610 | -0.01389298 | -0.13033999 | 0.07739411 | 0.07544342 | -0.10458978 | -0.01950843 | 0.01152410 | 0.03351012 | 0.09179281 | -0.05562078 | -0.12589033 | 0.12991280 | 0.01176370 | 0.08979231 | 0.01784234 | 0.02618733 | 0.00438373 | 0.20321089 | 0.03896997 | 0.08266335 | -0.10433553 | 0.04298949 |
| Cochranea | *H. eremogenum* | -0.21836530 | 0.53001833 | 0.01464260 | -0.19956126 | -0.04106485 | -0.08362085 | 0.00978512 | 0.02730436 | -0.05254450 | -0.02981260 | -0.06259864 | 0.08551273 | 0.00863549 | -0.00090958 | -0.03768148 | 0.29783350 | -0.04053241 | -0.00763252 | -0.03671610 | -0.04637636 | -0.01248945 | -0.00592468 | 0.00915408 | -0.00215380 |
| Cochranea | *H. filifolium* | 0.17555578 | -0.03476067 | -0.00601077 | -0.10401627 | 0.04087436 | 0.08708397 | -0.05756097 | -0.02192421 | 0.05474891 | -0.07719653 | 0.08238185 | 0.01679673 | -0.12188907 | 0.00624233 | -0.08587548 | 0.06224921 | 0.08681935 | -0.01411701 | 0.18178901 | 0.15817355 | 0.01742637 | -0.15543083 | 0.22702159 | -0.15357762 |
| Cochranea | *H. floridum* | 0.14662572 | -0.01934613 | -0.02591262 | -0.15311882 | 0.11191033 | 0.04503964 | -0.12078778 | -0.00621338 | -0.03130660 | 0.09535716 | 0.00615764 | -0.02706952 | 0.04238586 | -0.00738507 | 0.00949445 | -0.07210967 | -0.05599820 | -0.05501261 | -0.01599055 | -0.20418554 | -0.03267029 | -0.07178143 | 0.08792646 | -0.03760857 |
| Cochranea | *H. glutinosum* | 0.15997265 | -0.02893809 | -0.01493969 | -0.13356418 | 0.08200964 | 0.07339870 | -0.10995292 | -0.01895034 | 0.00551295 | 0.04762160 | 0.08851528 | -0.06229876 | -0.11722745 | 0.13635742 | 0.02359727 | 0.08101419 | 0.00587693 | 0.02734817 | -0.02022287 | 0.15653490 | 0.03100265 | 0.08622078 | -0.11107976 | 0.04980799 |
| Cochranea | *H. huascoense* | 0.18900661 | -0.03811278 | 0.00059626 | -0.07609244 | 0.00492660 | 0.08940386 | -0.00599242 | -0.01942502 | 0.08018386 | -0.15243874 | 0.03534939 | 0.05741337 | -0.03442171 | -0.06991947 | -0.05262606 | -0.01672006 | 0.00502090 | -0.01528211 | 0.00568096 | -0.08957121 | -0.01244780 | 0.07746876 | -0.11752356 | 0.07052992 |
| Cochranea | *H. inconspicuum* | 0.18338397 | -0.03763416 | -0.00139397 | -0.08759276 | 0.01894848 | 0.09145946 | -0.02787436 | -0.02219662 | 0.07560295 | -0.13397104 | 0.05921052 | 0.05500314 | -0.08094387 | -0.06795022 | -0.10187134 | 0.00869164 | 0.06993546 | -0.02756472 | 0.14771430 | -0.04601244 | -0.01618288 | -0.06233822 | 0.06364853 | 0.03540911 |
| Cochranea | *H. jaffuelii* | 0.31266761 | -0.00762637 | 0.01534957 | -0.08614728 | 0.09499494 | -0.24615250 | 0.00088611 | -0.02601061 | 0.15021552 | 0.04084454 | 0.00145907 | 0.03190200 | 0.00690464 | 0.02303204 | -0.00904288 | -0.00033508 | 0.00961482 | 0.00307425 | -0.00590040 | 0.00265101 | -0.02121113 | 0.00408176 | 0.00216900 | 0.00037509 |
| Cochranea | *H. krauseanum* | 0.21420193 | -0.03665044 | 0.00829107 | -0.01162409 | -0.05880604 | 0.04190529 | 0.09224108 | 0.00806881 | 0.01135402 | -0.02351545 | -0.09092698 | -0.07135899 | 0.11177793 | 0.11309224 | 0.09060973 | 0.03076744 | 0.04543020 | 0.00096514 | 0.15576512 | -0.03607624 | -0.02468598 | -0.01054119 | -0.05810701 | 0.09756735 |
| Cochranea | *H. linariifolium* | -0.20394840 | 0.52346474 | 0.02827023 | -0.19570489 | -0.07318092 | -0.03629545 | -0.03260404 | 0.08833702 | 0.00311055 | 0.01296991 | 0.02609772 | -0.00210037 | 0.05732806 | 0.00046252 | -0.03290636 | -0.06373007 | -0.16613675 | -0.20970200 | 0.07287987 | 0.07264249 | 0.03687220 | 0.01134761 | -0.02085609 | 0.00526080 |
| Cochranea | *H. longistylum* | 0.19337211 | -0.03804361 | 0.00186409 | -0.06649477 | -0.00586283 | 0.08491813 | 0.01166753 | -0.01585266 | 0.07710343 | -0.15168843 | 0.00994290 | 0.04417151 | 0.01305114 | -0.04302889 | 0.01692751 | -0.02581349 | -0.05954557 | 0.00681421 | -0.13354277 | -0.02391435 | 0.00820858 | 0.11480974 | -0.13161586 | -0.03647149 |
| Cochranea | *H. megalanthum* | -0.24267237 | 0.53533884 | -0.00232292 | -0.19797917 | 0.03840537 | -0.18629324 | 0.12415716 | -0.05142293 | -0.07987245 | -0.12675412 | 0.07904664 | -0.06564992 | -0.08956411 | 0.07082866 | 0.04332649 | -0.18159789 | 0.08069039 | 0.07667802 | -0.00768884 | -0.00971155 | -0.01182946 | -0.00143397 | 0.00437449 | -0.00080622 |
| Cochranea | *H. myosotifolium* | 0.10915306 | -0.00185908 | -0.05493629 | -0.17210400 | 0.18898589 | -0.07625909 | -0.02114827 | -0.14613279 | -0.15587813 | 0.01278036 | -0.15490975 | 0.09554916 | 0.03711449 | -0.11561409 | 0.01176334 | 0.09088766 | 0.21426576 | 0.25743681 | -0.06484865 | -0.01738132 | -0.02715019 | 0.00018873 | 0.00623284 | -0.00106418 |
| Cochranea | *H. philippianum* | 0.20322003 | -0.03756319 | 0.00484555 | -0.04190062 | -0.03094489 | 0.06785341 | 0.05150265 | -0.00528440 | 0.05305188 | -0.10851677 | -0.05027307 | -0.01150421 | 0.09944881 | 0.04837793 | 0.12865801 | -0.00574007 | -0.08085049 | 0.03296905 | -0.13746123 | 0.11314889 | 0.01525814 | -0.13034906 | 0.18491221 | -0.01212534 |
| Cochranea | *H. pycnophyllum* | 0.19486065 | -0.03799816 | 0.00230484 | -0.06301679 | -0.00960421 | 0.08290795 | 0.01773674 | -0.01444957 | 0.07485297 | -0.14854250 | 0.00067698 | 0.03755162 | 0.02881129 | -0.03086968 | 0.03964119 | -0.02601750 | -0.07457648 | 0.01360314 | -0.16282846 | 0.00410605 | 0.01351806 | 0.09516840 | -0.09711603 | -0.06002824 |
| Cochranea | *H. sinuatum* | 0.22968866 | -0.03320661 | 0.01359650 | 0.04023722 | -0.08654192 | -0.01597894 | 0.09199208 | 0.01905248 | -0.04668918 | 0.08784823 | 0.06799946 | 0.05703773 | -0.07605534 | -0.09229835 | 0.08584730 | 0.00232363 | -0.09029281 | 0.05661986 | 0.03745662 | 0.02320368 | -0.10504972 | -0.17533549 | -0.15460080 | -0.07131361 |
| Cochranea | *H. stenophyllum* | 0.22446058 | -0.03502245 | 0.01168921 | 0.02054514 | -0.08144689 | 0.00825671 | 0.11132110 | 0.01889212 | -0.03476851 | 0.07208838 | -0.02375999 | -0.03472040 | -0.04929811 | -0.01826165 | -0.11396562 | -0.01637339 | 0.00864482 | -0.01684165 | -0.07634200 | 0.01412025 | 0.01935603 | -0.00961485 | 0.04007894 | 0.10276637 |
| Cochranea | *H. taltalense* | 0.22411738 | -0.03509930 | 0.01157132 | 0.01938680 | -0.08082746 | 0.00956631 | 0.11133182 | 0.01864009 | -0.03340500 | 0.06942773 | -0.02784820 | -0.03805053 | -0.04387211 | -0.01233621 | -0.11278800 | -0.01510771 | 0.01347766 | -0.01857636 | -0.06940071 | 0.00955487 | 0.02229336 | 0.00633486 | 0.03918850 | 0.06637199 |
| Heliothmanus | *H. adenogynum* | 0.15234270 | -0.02364034 | -0.02117622 | -0.14596598 | 0.10046632 | 0.05862320 | -0.12042489 | -0.01237615 | -0.01693880 | 0.08282096 | 0.05020979 | -0.05373924 | -0.03621740 | 0.07853507 | 0.02890180 | -0.00693697 | -0.05518205 | -0.03060480 | -0.05292027 | -0.23115927 | -0.03601434 | -0.05214481 | 0.05770831 | -0.01142283 |
| Heliothmanus | *H. arborescens* | 0.22446058 | -0.03502245 | 0.01168921 | 0.02054514 | -0.08144689 | 0.00825671 | 0.11132110 | 0.01889212 | -0.03476851 | 0.07208838 | -0.02375999 | -0.03472040 | -0.04929811 | -0.01826165 | -0.11396562 | -0.01637339 | 0.00864482 | -0.01684165 | -0.07634200 | 0.01412025 | 0.01935603 | -0.00961485 | 0.04007894 | 0.10276637 |
| Heliothmanus | *H. corymbosum* | 0.21869019 | -0.03604673 | 0.00975592 | 0.00200713 | -0.06932494 | 0.02821295 | 0.10362214 | 0.01325347 | -0.00913111 | 0.01945610 | -0.07320890 | -0.06747522 | 0.05017982 | 0.07125119 | -0.01206639 | 0.01374145 | 0.05451037 | -0.01784350 | 0.08438745 | -0.04650028 | 0.01197063 | 0.11336169 | -0.04114276 | -0.27151643 |
| Heliothmanus | *H. incanum* | 0.22074826 | -0.03572764 | 0.01043655 | 0.00844300 | -0.07392624 | 0.02149517 | 0.10769961 | 0.01548175 | -0.01857149 | 0.03915062 | -0.05986448 | -0.06054571 | 0.01602096 | 0.04380265 | -0.05876059 | 0.00306797 | 0.04742432 | -0.02272518 | 0.03041405 | -0.03482850 | 0.02470203 | 0.11825909 | -0.01262813 | -0.27564919 |
| Heliothmanus | *H. mandonii* | 0.22267284 | -0.03538762 | 0.01108127 | 0.01462688 | -0.07798747 | 0.01483135 | 0.11032921 | 0.01738269 | -0.02721989 | 0.05696174 | -0.04306464 | -0.04944906 | -0.01849599 | 0.01276363 | -0.09525276 | -0.00779726 | 0.03103443 | -0.02251686 | -0.02870585 | -0.01157088 | 0.02784593 | 0.06897889 | 0.02095667 | -0.11283557 |
| Heliothmanus | *H. rufipilum* | 0.22446058 | -0.03502245 | 0.01168921 | 0.02054514 | -0.08144689 | 0.00825671 | 0.11132110 | 0.01889212 | -0.03476851 | 0.07208838 | -0.02375999 | -0.03472040 | -0.04929811 | -0.01826165 | -0.11396562 | -0.01637339 | 0.00864482 | -0.01684165 | -0.07634200 | 0.01412025 | 0.01935603 | -0.00961485 | 0.04007894 | 0.10276637 |
| Heliothmanus | *H. submolle* | 0.23235991 | -0.03210235 | 0.01459712 | 0.05069783 | -0.08786248 | -0.02896622 | 0.07748019 | 0.01810226 | -0.04944235 | 0.08759144 | 0.10521235 | 0.09550789 | -0.06612333 | -0.10239043 | 0.16183706 | 0.01227850 | -0.08683413 | 0.05883548 | 0.07820255 | -0.00037711 | -0.04514116 | 0.01292188 | -0.00979809 | -0.03721891 |
| Tournefortia | *H. abbreviatun* | -0.43437116 | -0.48634483 | -0.59906469 | 0.08175441 | 0.22356879 | -0.08797802 | 0.06390712 | 0.12903726 | -0.12660697 | -0.08776456 | -0.09150063 | 0.11362833 | -0.08848494 | 0.09015058 | 0.00149808 | 0.00631681 | -0.06615145 | -0.08073646 | 0.01539154 | 0.00647852 | 0.01314348 | 0.00099314 | -0.00566619 | 0.00183028 |
| Tournefortia | *H. amplexicaule* | 0.13688211 | -0.01207511 | -0.03372989 | -0.16316492 | 0.12884920 | 0.02075124 | -0.11555709 | 0.00450192 | -0.05227109 | 0.10481068 | -0.06932593 | 0.02549527 | 0.15772980 | -0.14836584 | -0.02852277 | -0.12836933 | -0.01235351 | -0.04848837 | 0.06063355 | 0.12112826 | 0.02108656 | 0.02585670 | -0.02976981 | 0.00913926 |
| Tournefortia | *H. angiospermum* | 0.18688346 | -0.03811649 | -0.00000785 | -0.08045608 | 0.01004482 | 0.09089792 | -0.01433843 | -0.02086200 | 0.07997981 | -0.14883709 | 0.04547059 | 0.06016191 | -0.05418471 | -0.07654323 | -0.07921786 | -0.00976653 | 0.03490807 | -0.02298663 | 0.07085011 | -0.09458701 | -0.01836424 | 0.02959244 | -0.06275013 | 0.08516883 |
| Tournefortia | *H. curassavicum* | -0.85974797 | 0.22140906 | -0.52470423 | 0.07300770 | -0.28308428 | 0.17464666 | -0.14436510 | -0.14379500 | -0.01445816 | 0.07362669 | -0.14131610 | 0.13511299 | -0.00359045 | 0.00295673 | -0.02003664 | 0.13541999 | -0.04521197 | -0.04031011 | -0.00385583 | -0.00471449 | 0.00676912 | -0.00082303 | -0.00175945 | 0.00049609 |
| Tournefortia | *H. elongatum* | -0.51005350 | -0.59727226 | 0.38298426 | 0.01616945 | -0.01365514 | 0.10804407 | -0.14960342 | -0.04712532 | -0.03538254 | 0.15488191 | 0.01236500 | -0.06784548 | -0.01069463 | 0.08055264 | 0.05347239 | 0.00143561 | 0.01399738 | 0.05264092 | -0.05353297 | 0.03621873 | 0.00127526 | 0.01891219 | -0.01770083 | -0.00260469 |
| Tournefortia | *H. indicum* | -0.48206651 | -0.61128978 | 0.40348442 | 0.09128631 | -0.10954242 | 0.12300090 | -0.01135529 | -0.04507530 | 0.06340535 | -0.09854496 | -0.02105473 | 0.05983975 | 0.01657996 | -0.09927226 | -0.04462764 | -0.02897765 | 0.02924030 | -0.00685885 | 0.04482287 | -0.03864929 | -0.00802808 | -0.01869361 | 0.01929384 | 0.00232256 |
| Tournefortia | *H. kurtzii* | -0.98908721 | 0.01131472 | 0.36990906 | -0.02003928 | -0.02380721 | -0.01138313 | -0.03224757 | 0.05930430 | -0.33743278 | -0.16449311 | -0.06021531 | 0.02846781 | -0.09540788 | 0.06643027 | 0.03055465 | -0.14337926 | -0.00283593 | -0.02229933 | 0.01752904 | 0.00799891 | 0.00574023 | -0.00073862 | -0.00000164 | -0.00063969 |
| Tournefortia | *H. microstachyum* | -0.44631861 | -0.48609737 | -0.60279617 | 0.08995809 | 0.26190872 | -0.13041533 | 0.12536169 | 0.05200371 | 0.03082576 | -0.02789751 | 0.10565762 | -0.09400429 | 0.06623550 | -0.04188717 | -0.02130727 | 0.05153185 | -0.03863748 | -0.03395716 | 0.00704924 | 0.00489329 | 0.00236677 | 0.00083684 | -0.00046198 | -0.00025863 |
| Tournefortia | *H. nicoteanaefolium* | 0.13688211 | -0.01207511 | -0.03372989 | -0.16316492 | 0.12884920 | 0.02075124 | -0.11555709 | 0.00450192 | -0.05227109 | 0.10481068 | -0.06932593 | 0.02549527 | 0.15772980 | -0.14836584 | -0.02852277 | -0.12836933 | -0.01235351 | -0.04848837 | 0.06063355 | 0.12112826 | 0.02108656 | 0.02585670 | -0.02976981 | 0.00913926 |
| Tournefortia | *H. paronychioides* | -1.01846249 | 0.02017130 | 0.38901746 | -0.00579803 | 0.06437321 | -0.09264624 | 0.07032224 | -0.03943071 | -0.04454459 | -0.04428686 | 0.16612671 | -0.21709979 | 0.14766209 | -0.15822699 | -0.03465208 | 0.22707728 | -0.04021541 | -0.03315484 | -0.01192641 | -0.00621039 | 0.00707887 | -0.00041611 | -0.00290068 | 0.00112097 |
| Tournefortia | *H. patagonicum* | -0.89484940 | 0.22882678 | -0.53989473 | 0.08336570 | -0.17939803 | 0.05053636 | 0.00008468 | -0.24693971 | 0.09949329 | 0.03735062 | 0.11864201 | -0.14084361 | 0.01516514 | -0.02908179 | 0.03233283 | -0.17985678 | 0.08920178 | 0.08369120 | -0.00265620 | 0.00158325 | -0.01215496 | -0.00019110 | 0.00432186 | -0.00126754 |
| Tournefortia | *H. phylicoides* | 0.15367664 | -0.02464803 | -0.02003734 | -0.14400532 | 0.09746147 | 0.06156986 | -0.11951449 | -0.01372853 | -0.01328809 | 0.07841960 | 0.05881106 | -0.05786386 | -0.05290281 | 0.09433348 | 0.03113605 | 0.00926309 | -0.04870816 | -0.02106972 | -0.05477997 | -0.19263421 | -0.02928783 | -0.03404354 | 0.03487644 | -0.00130321 |
| Tournefortia | *H. pinnatisectum* | -1.03960339 | 0.03355738 | 0.42059912 | 0.00490383 | 0.15137617 | -0.15162107 | 0.13937456 | -0.09417218 | 0.29089480 | 0.14362160 | -0.10588731 | 0.19664528 | -0.05991029 | 0.11641112 | -0.00693444 | -0.05390705 | -0.03457055 | -0.03188069 | 0.01248027 | 0.00594095 | 0.00023107 | 0.00127021 | -0.00063228 | 0.00003446 |
| Tournefortia | *H. transalpinum* | 0.21168289 | -0.03689418 | 0.00749186 | -0.01876734 | -0.05252574 | 0.04834506 | 0.08360428 | 0.00501600 | 0.02157947 | -0.04463518 | -0.08645450 | -0.06132593 | 0.11920400 | 0.10793796 | 0.11435924 | 0.02659131 | 0.01932174 | 0.01046472 | 0.10974402 | -0.00163787 | -0.02287588 | -0.06506316 | -0.00211368 | 0.15597461 |
| Tournefortia | *H. veronicifolium* | -0.66014446 | 0.21529289 | -0.07231874 | 0.01703965 | -0.06735477 | 0.07412864 | -0.10646471 | 0.53426049 | 0.15581450 | 0.04549472 | -0.00054122 | -0.01914166 | 0.00714905 | -0.04571474 | 0.02124822 | -0.02160837 | 0.14007810 | 0.16209505 | -0.03807292 | -0.01953590 | -0.02137339 | -0.00194507 | 0.00743751 | -0.00161891 |
| Tournefortia | *T. argentea* | 0.27115632 | -0.01512410 | 0.02824431 | 0.18339052 | -0.07959768 | -0.21349627 | -0.17859666 | -0.01367402 | 0.03145324 | -0.05616180 | -0.06145137 | -0.06161819 | -0.01420258 | 0.00598264 | -0.06824013 | -0.01227131 | -0.14066341 | 0.15350452 | 0.06827908 | -0.03818136 | 0.20570927 | -0.03957964 | -0.02556727 | -0.00261996 |
| Tournefortia | *T. bicolor* | 0.26134318 | -0.01730655 | 0.02576127 | 0.16620467 | -0.08058937 | -0.16415506 | -0.12603161 | -0.00567230 | -0.02190214 | -0.02814897 | 0.11363858 | 0.10228058 | 0.14951079 | 0.12857101 | -0.12336533 | -0.01284785 | 0.03701568 | -0.00667872 | -0.04299115 | 0.06425231 | -0.39207446 | 0.08948705 | 0.05923037 | 0.00581954 |
| Tournefortia | *T. buchtienii* | 0.25129343 | -0.02281232 | 0.02187096 | 0.12673489 | -0.08611515 | -0.12101267 | -0.05533608 | 0.00354029 | -0.03835210 | 0.01919009 | 0.18376578 | 0.17806956 | 0.13901425 | 0.07808433 | 0.05132187 | 0.01114805 | 0.26426396 | -0.17052257 | -0.10696442 | -0.03433906 | 0.24410366 | -0.14481194 | -0.09954241 | -0.01963025 |
| Tournefortia | *T. chinchensis* | 0.23633443 | -0.03029558 | 0.01610756 | 0.06653293 | -0.08859761 | -0.04849518 | 0.05212517 | 0.01576677 | -0.05015128 | 0.07939429 | 0.14300680 | 0.13512676 | -0.03189498 | -0.08702091 | 0.21133114 | 0.02116666 | -0.03024859 | 0.02512481 | 0.08877394 | -0.03675102 | 0.09704913 | 0.28903056 | 0.22962017 | 0.08175219 |
| Tournefortia | *T. glabra* | 0.27959401 | -0.01276329 | 0.03018286 | 0.19151268 | -0.07233871 | -0.23515633 | -0.19809441 | -0.01844587 | 0.07447092 | -0.05854052 | -0.19238912 | -0.17493793 | -0.18727320 | -0.15328218 | 0.17929003 | 0.03018066 | 0.11447622 | -0.22369198 | -0.05277115 | 0.02474688 | -0.09252857 | 0.01491263 | 0.00712264 | 0.00084911 |
| Tournefortia | *T. gnaphalodes* | 0.22867322 | -0.03358793 | 0.01322172 | 0.03634451 | -0.08575879 | -0.01116210 | 0.09651172 | 0.01918893 | -0.04490073 | 0.08611411 | 0.05141240 | 0.04020534 | -0.07463144 | -0.08208026 | 0.04966173 | -0.00159139 | -0.07912547 | 0.04746000 | 0.01671221 | 0.02632710 | -0.10031295 | -0.18917821 | -0.15655609 | -0.05426269 |
| Tournefortia | *T. hirsutissima* | 0.14515052 | 0.40841101 | 0.11147495 | 0.56150682 | 0.17523080 | 0.19558925 | -0.04572822 | -0.00513624 | -0.11117497 | -0.03528793 | 0.04221609 | 0.01856654 | 0.02925577 | 0.03566377 | -0.02347796 | 0.00188745 | -0.02773673 | -0.02879638 | 0.00396951 | 0.00794192 | -0.01819342 | 0.00511470 | 0.00092975 | 0.00052903 |
| Tournefortia | *T. luzonica* | 0.17519580 | 0.51859461 | 0.11283592 | 0.33579341 | 0.40584189 | 0.15353045 | 0.06228530 | -0.04201789 | 0.06731836 | 0.04613110 | -0.05425158 | -0.01903079 | -0.02910256 | -0.04206533 | 0.02390250 | -0.00183434 | 0.02107486 | 0.02176420 | -0.00114085 | -0.00644599 | 0.02166922 | -0.00522414 | -0.00176505 | -0.00039833 |
| Tournefortia | *T. microcalyx* | 0.22446058 | -0.03502245 | 0.01168921 | 0.02054514 | -0.08144689 | 0.00825671 | 0.11132110 | 0.01889212 | -0.03476851 | 0.07208838 | -0.02375999 | -0.03472040 | -0.04929811 | -0.01826165 | -0.11396562 | -0.01637339 | 0.00864482 | -0.01684165 | -0.07634200 | 0.01412025 | 0.01935603 | -0.00961485 | 0.04007894 | 0.10276637 |
| Tournefortia | *T. polystachya* | 0.26836039 | -0.01580723 | 0.02756118 | 0.17932427 | -0.08069460 | -0.20196294 | -0.16671564 | -0.01162621 | 0.01620419 | -0.05074292 | -0.01031127 | -0.01459438 | 0.04269841 | 0.05321036 | -0.11727305 | -0.01917293 | -0.14199115 | 0.17932730 | 0.06253414 | -0.02181583 | 0.09060905 | -0.00723947 | -0.00222729 | 0.00061985 |
| Tournefortia | *T. rollotii* | 0.20004968 | -0.03775989 | 0.00387123 | -0.05016594 | -0.02283295 | 0.07418400 | 0.03890756 | -0.00893342 | 0.06275526 | -0.12724706 | -0.03247844 | 0.00786754 | 0.07880264 | 0.01961955 | 0.10782547 | -0.01608223 | -0.09477830 | 0.03129515 | -0.18355527 | 0.10089801 | 0.02134187 | -0.07144084 | 0.12965416 | -0.06334470 |
| Tournefortia | *T. ternifolia* | 0.21420193 | -0.03665044 | 0.00829107 | -0.01162409 | -0.05880604 | 0.04190529 | 0.09224108 | 0.00806881 | 0.01135402 | -0.02351545 | -0.09092698 | -0.07135899 | 0.11177793 | 0.11309224 | 0.09060973 | 0.03076744 | 0.04543020 | 0.00096514 | 0.15576512 | -0.03607624 | -0.02468598 | -0.01054119 | -0.05810701 | 0.09756735 |
| | Centroids | | | | | | | | | | | | | | | | | | | | | | | | |
| | Cochranea | 0.14370349 | 0.03904486 | -0.00093328 | -0.08574626 | 0.01247636 | 0.01186685 | 0.00603919 | -0.01178959 | 0.01290909 | -0.02608175 | 0.00781170 | 0.00627000 | -0.01908552 | 0.00326246 | -0.00463556 | 0.01313907 | 0.00103978 | 0.00958820 | -0.00758282 | 0.01654476 | -0.00355873 | -0.00814426 | -0.00741255 | 0.00544857 |
| | Heliothmanus | 0.21438640 | -0.03339924 | 0.00719392 | -0.00254158 | -0.05488010 | 0.01539006 | 0.07396448 | 0.01310180 | -0.02734416 | 0.06113792 | -0.01074210 | -0.02928847 | -0.02163198 | 0.00902828 | -0.03022393 | -0.00261663 | 0.00206671 | -0.00969613 | -0.00555737 | -0.04008185 | 0.00374971 | 0.03569053 | 0.01314043 | -0.07262771 |
| | Tournefortia-clade | -0.03377151 | -0.03092728 | 0.00180983 | 0.05403275 | 0.00184270 | -0.01173291 | -0.02739506 | 0.00560521 | 0.00005847 | 0.00174997 | -0.00221856 | 0.00458330 | 0.02252472 | -0.00578539 | 0.01290815 | -0.01002827 | -0.00013918 | -0.00304959 | 0.00764744 | 0.00050153 | 0.00160721 | -0.00450357 | 0.00160596 | 0.01859830 |

# Habit (continued)

| Axis 25 | Axis 26 | Axis 27 | Axis 28 | Axis 29 | Axis 30 | Axis 31 | Axis 32 | Axis 33 | Axis 34 | Axis 35 | Axis 36 | Axis 37 | Axis 38 | Axis 39 | Axis 40 | Axis 41 | Axis 42 | Axis 43 | Axis 44 | Axis 45 | Axis 46 | Axis 47 | Axis 48 | Axis 49 | Axis 50 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.32078561 | 0.32015525 | 0.32010681 | 0.31958548 | 0.31937811 | 0.31919180 | 0.31892375 | 0.31888087 | 0.31885086 | 0.31852043 | 0.31847318 | 0.31842704 | 0.31839647 | 0.31833015 | 0.31831158 | 0.31805586 | 0.31779199 | 0.31779199 | 0.31779199 | 0.31779199 | 0.31779199 | 0.31703358 | 0.31252599 | 0.30992883 | 0.28569138 | 0.19467404 |
| 1.09389388 | 1.09174432 | 1.09157913 | 1.08980136 | 1.08909421 | 1.08845890 | 1.08754481 | 1.08739860 | 1.08729628 | 1.08616948 | 1.08600838 | 1.08585102 | 1.08574679 | 1.08552062 | 1.08545732 | 1.08458529 | 1.08368548 | 1.08368548 | 1.08368548 | 1.08368548 | 1.08368548 | 1.08109926 | 1.06572818 | 1.05687174 | 0.97422091 | 0.66384752 |
| 73.42754848 | 74.51929279 | 75.61087192 | 76.70067328 | 77.78976750 | 78.87822640 | 79.96577121 | 81.05316982 | 82.14046609 | 83.22663557 | 84.31264395 | 85.39849497 | 86.48424177 | 87.56976239 | 88.65521970 | 89.73980499 | 90.82349047 | 91.90717595 | 92.99086142 | 94.07454690 | 95.15823238 | 96.23933164 | 97.30505983 | 98.36193157 | 99.33615248 | 100.00000000 |
| 0.06142729 | 0.10236860 | 0.00209823 | 0.00022085 | -0.02514894 | 0.00348390 | 0.00052633 | 0.00030228 | -0.00058966 | 0.38678325 | 0.02927220 | 0.00000562 | 0.00000009 | -0.00141081 | 0.04855834 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | -0.00490926 | 0.00400702 | 0.10059057 | 0.00000806 | -0.00980188 |
| -0.00365650 | 0.02718397 | -0.00341579 | 0.00012818 | 0.00066742 | -0.00014512 | -0.00012367 | -0.00038363 | -0.30508612 | -0.00323058 | -0.00044471 | -0.00000424 | -0.00000583 | 0.00005385 | -0.00018965 | 0.00000010 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.07005875 | -0.14299528 | -0.00821290 | -0.00254181 | -0.03975269 |
| -0.26745623 | -0.04296456 | -0.00078026 | -0.00123042 | 0.14749808 | -0.02423110 | -0.00729522 | -0.00588588 | 0.00065807 | -0.02574559 | -0.01898429 | -0.00000607 | -0.00000025 | 0.00242492 | -0.00248349 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | -0.00008569 | -0.00009859 | -0.02968877 | 0.00338777 | -0.00639540 |
| -0.06512073 | 0.44749942 | 0.00558523 | 0.00002124 | -0.00183433 | 0.00012900 | 0.00003480 | 0.00004914 | 0.01747336 | -0.01972862 | -0.00135645 | -0.00000010 | 0.00000019 | 0.00006408 | 0.04940657 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00824545 | 0.00710216 | 0.03109494 | -0.00292587 | -0.01656612 |
| 0.07339607 | 0.05386813 | 0.00106328 | 0.00022242 | -0.02344811 | 0.00329955 | 0.00084704 | 0.00069796 | 0.00019607 | -0.39168806 | -0.03173118 | -0.00000670 | -0.00000011 | 0.00219101 | -0.09135359 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | -0.01584697 | 0.00576468 | 0.13818487 | -0.00044943 | -0.01040023 |
| 0.07685441 | 0.01636030 | 0.00004641 | -0.00175602 | 0.30176053 | -0.06345689 | -0.02075215 | -0.01569527 | 0.00033561 | -0.02612187 | 0.31744575 | 0.00016240 | 0.00000896 | -0.15699819 | 0.00008289 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00022384 | -0.00124228 | -0.07182669 | 0.00457349 | -0.00376584 |
| 0.14927321 | -0.00385002 | -0.00015119 | 0.00259509 | -0.38511910 | 0.07748954 | 0.03203902 | 0.02731564 | -0.00236996 | -0.02542747 | 0.14266291 | 0.00005219 | 0.00000239 | -0.02602131 | 0.00032589 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00120834 | -0.00255191 | -0.13131735 | 0.00605281 | -0.00485865 |
| 0.00022550 | 0.00035825 | -0.00205217 | 0.00004206 | -0.00006738 | 0.00000552 | 0.00000380 | 0.00001381 | 0.00951281 | -0.00071552 | -0.00003900 | -0.00000031 | -0.00000057 | -0.00000097 | 0.00002091 | 0.00000002 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.02396246 | -0.01140389 | -0.00859872 | -0.25895249 | 0.32139763 |
| -0.07752769 | -0.00258186 | -0.00004155 | 0.00050685 | -0.04424578 | -0.18662316 | -0.03865736 | 0.11132370 | -0.00010811 | 0.00004582 | -0.00040514 | -0.01953937 | -0.00168446 | -0.00021746 | 0.00000005 | -0.00009885 | -0.21393523 | 0.12452066 | -0.05693442 | -0.28669653 | -0.11038973 | 0.00001960 | -0.00002198 | -0.00099685 | 0.00119315 | -0.00095297 |
| 0.00764519 | -0.03068430 | 0.00420957 | -0.00012035 | -0.00060410 | 0.00011416 | 0.00008982 | 0.00027445 | 0.21789947 | 0.00157712 | 0.00029821 | 0.00000351 | 0.00000499 | -0.00004577 | 0.00001982 | -0.00000011 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | -0.27662227 | -0.10108487 | -0.02168816 | -0.00116931 | -0.01990493 |
| -0.21416542 | -0.01066279 | -0.00005460 | -0.00135992 | -0.03872051 | 0.06886188 | 0.07825875 | 0.07424497 | -0.00007487 | -0.00458420 | 0.08760819 | -0.00011044 | -0.00001135 | 0.38766038 | -0.00009709 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00004965 | -0.00049645 | -0.03314565 | 0.00321872 | -0.00304376 |
| -0.00092513 | 0.00351834 | -0.00020918 | -0.00000609 | -0.00036685 | 0.00005861 | 0.00003124 | 0.00008465 | 0.06270873 | -0.00135731 | -0.00007755 | 0.00000031 | 0.00000031 | 0.00000129 | 0.00014584 | 0.00000001 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.18122140 | 0.24156475 | -0.00249204 | -0.02237887 | -0.07352483 |
| -0.00107070 | -0.01490939 | -0.00128832 | -0.00001916 | 0.00014070 | 0.00002473 | 0.00005800 | 0.00020039 | 0.16849689 | 0.00540552 | 0.00053151 | 0.00000350 | 0.00000491 | -0.00004742 | 0.00004082 | -0.00000011 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | -0.20200712 | -0.05593384 | 0.01256335 | -0.05092012 | -0.05869555 |
| 0.19947650 | 0.00928114 | 0.00005604 | 0.00019002 | 0.09257412 | 0.04872071 | 0.23656222 | 0.25824405 | -0.00024471 | 0.00138657 | -0.01545987 | -0.00100761 | -0.00007361 | -0.01601891 | 0.00000340 | -0.00000048 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00004573 | -0.00009419 | -0.00696663 | 0.00173375 | -0.00185803 |
| -0.22271324 | -0.01422446 | -0.00005862 | -0.00023708 | -0.12571915 | 0.05110375 | 0.02297309 | 0.01704810 | -0.00010145 | 0.01109768 | -0.15954896 | 0.00002029 | 0.00000595 | -0.35798375 | 0.00008291 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00003524 | -0.00035544 | -0.02513567 | 0.00287545 | -0.00282901 |
| 0.01364732 | 0.00010822 | 0.00114441 | 0.10785674 | 0.00223586 | 0.00849613 | -0.01331565 | 0.00999581 | 0.00002592 | 0.00000079 | -0.00001635 | 0.04805853 | -0.40867754 | -0.00000096 | -0.00000001 | 0.00166347 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00002844 | -0.00002190 | 0.00007537 | 0.00656885 | -0.00049107 |
| -0.02954182 | -0.00044165 | -0.00019028 | -0.01513476 | -0.00543709 | -0.02799577 | 0.05308954 | -0.04034622 | 0.00003688 | -0.00000239 | 0.00003024 | -0.04072223 | -0.01325979 | -0.00000262 | 0.00000000 | 0.10309702 | -0.32218657 | -0.26328027 | -0.11898404 | 0.06654399 | 0.21595833 | 0.00000813 | -0.00000788 | -0.00003332 | 0.00234632 | -0.00048916 |
| -0.01649053 | -0.00017538 | -0.00019356 | -0.01873338 | -0.00054189 | 0.00139582 | -0.01745057 | 0.01554320 | -0.00000904 | 0.00000268 | -0.00003896 | 0.06103963 | -0.00553408 | 0.00000486 | 0.00000001 | -0.51030324 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000942 | -0.00000820 | -0.00004611 | 0.00223889 | -0.00049790 |
| -0.00399040 | -0.18475728 | -0.00214144 | -0.00004151 | 0.00258916 | -0.00022034 | -0.00007445 | -0.00007813 | -0.00075489 | 0.10299920 | 0.00776789 | 0.00000154 | 0.00000009 | -0.00049772 | -0.39122004 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | -0.00092201 | 0.00395623 | 0.06085188 | -0.00168461 | -0.01339674 |
| -0.02954182 | -0.00044165 | -0.00019028 | -0.01513476 | -0.00543709 | -0.02799577 | 0.05308954 | -0.04034622 | 0.00003688 | -0.00000239 | 0.00003024 | -0.04072223 | -0.01325979 | -0.00000262 | 0.00000000 | 0.10309702 | 0.01832378 | 0.32433402 | 0.29050262 | -0.01502787 | 0.21954058 | 0.00000813 | -0.00000788 | -0.00003332 | 0.00234632 | -0.00048916 |
| 0.07610030 | 0.00081093 | 0.00024144 | 0.02172329 | -0.00708347 | -0.07752650 | 0.27662480 | -0.22459122 | 0.00021069 | -0.00000553 | -0.00002043 | 0.21011722 | 0.01943484 | 0.00005578 | 0.00000004 | 0.00311694 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00002671 | -0.00001652 | -0.00039307 | 0.00141866 | -0.00070753 |
| 0.09376888 | 0.00167224 | 0.00015106 | 0.00557734 | 0.02012655 | 0.09369685 | -0.10252306 | 0.06234846 | -0.00001353 | -0.00001338 | 0.00022603 | -0.39628260 | -0.04005606 | -0.00003900 | 0.00000001 | -0.02088697 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00001988 | -0.00001309 | -0.00021797 | 0.00161810 | -0.00061485 |
| 0.04551189 | 0.00102774 | -0.00007144 | -0.01648561 | 0.01992531 | 0.11935636 | -0.27949661 | 0.21983689 | -0.00016973 | 0.00001735 | -0.00022805 | 0.31962901 | 0.04069815 | 0.00002068 | 0.00000003 | 0.12098503 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00001544 | -0.00001032 | -0.00010814 | 0.00191406 | -0.00054245 |
| -0.02954182 | -0.00044165 | -0.00019028 | -0.01513476 | -0.00543709 | -0.02799577 | 0.05308954 | -0.04034622 | 0.00003688 | -0.00000239 | 0.00003024 | -0.04072223 | -0.01325979 | -0.00000262 | 0.00000000 | 0.10309702 | 0.02133101 | 0.18388720 | -0.23306703 | 0.23005018 | -0.31117705 | 0.00000813 | -0.00000788 | -0.00003332 | 0.00234632 | -0.00048916 |
| 0.01128315 | 0.00023611 | -0.00237333 | -0.45560179 | -0.00388589 | -0.00899670 | 0.00802876 | -0.00554637 | -0.00000818 | -0.00000056 | 0.00000401 | -0.01082290 | 0.08592650 | 0.00000019 | 0.00000005 | -0.00012648 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00005018 | -0.00003473 | 0.00018537 | 0.01023045 | -0.00055207 |
| 0.00309734 | -0.00407053 | 0.00351559 | -0.00009016 | -0.00105022 | 0.00015516 | 0.00008274 | 0.00022732 | 0.16851400 | -0.00388653 | -0.00018673 | 0.00000094 | 0.00000113 | -0.00000651 | 0.00024204 | 0.00000001 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.20765042 | -0.19990307 | 0.00001645 | 0.01892624 | -0.01277381 |
| 0.01305079 | -0.06511819 | -0.00148956 | 0.00002781 | 0.00034967 | -0.00004997 | -0.00003714 | -0.00011166 | -0.08858505 | -0.00054421 | -0.00011613 | -0.00000158 | -0.00000225 | 0.00001741 | -0.00161179 | 0.00000005 | 0.14463101 | 0.09607698 | -0.27807509 | -0.09095492 | 0.20772224 | 0.11323834 | 0.02363231 | 0.01403813 | -0.00578304 | -0.02307819 |
| 0.16988384 | 0.01694778 | 0.00005979 | -0.00020801 | 0.12642899 | -0.04605276 | -0.03537184 | -0.03295265 | 0.00000580 | 0.02722817 | -0.39968327 | -0.00016127 | -0.00000766 | 0.10111375 | -0.00011426 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00077243 | -0.00201070 | -0.10644745 | 0.00546951 | -0.00417120 |
| 0.00099439 | -0.00283093 | 0.00183964 | -0.00004986 | -0.00037873 | 0.00006263 | 0.00004177 | 0.00012259 | 0.09458545 | -0.00054824 | 0.00002623 | 0.00000102 | 0.00000138 | -0.00001214 | 0.00010677 | -0.00000002 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.03788710 | 0.26009309 | -0.00645605 | 0.00926011 | 0.08103625 |
| -0.01448101 | -0.00051400 | -0.00077657 | -0.00011501 | 0.01483136 | -0.00214685 | -0.00036184 | -0.00023270 | 0.00099253 | -0.01339849 | 0.00149160 | 0.00000088 | 0.00000002 | -0.00065064 | 0.00004503 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.01872276 | -0.01093564 | -0.34060122 | 0.00333616 | 0.00436567 |
| 0.01403376 | 0.00083874 | 0.00021684 | 0.00012371 | -0.01476289 | 0.00213798 | 0.00036105 | 0.00023449 | 0.00116828 | 0.01341361 | -0.00148189 | -0.00000091 | -0.00000011 | 0.00064827 | -0.00003657 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | -0.00152777 | 0.00579420 | 0.33869191 | -0.02678183 | 0.00713422 |
| -0.00123459 | 0.00377629 | -0.00083623 | 0.00004088 | 0.00061512 | -0.00010460 | -0.00006849 | -0.00019767 | -0.15214484 | 0.00168984 | 0.00001467 | -0.00000175 | -0.00000235 | 0.00001776 | -0.00019498 | 0.00000003 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | -0.12871516 | -0.00385213 | 0.00195311 | 0.03510705 | 0.13451421 |
| -0.00097109 | 0.00351853 | -0.00233497 | 0.00007470 | 0.00091097 | -0.00014525 | -0.00008477 | -0.00024044 | -0.18123098 | 0.00199306 | 0.00005928 | -0.00000113 | -0.00000134 | 0.00000879 | -0.00026057 | -0.00000001 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | -0.23732054 | 0.20054292 | -0.02049893 | -0.00269503 | -0.03322648 |
| 0.01305079 | -0.06511819 | -0.00148956 | 0.00002781 | 0.00034967 | -0.00004997 | -0.00003714 | -0.00011166 | -0.08858505 | -0.00054421 | -0.00011613 | -0.00000158 | -0.00000225 | 0.00001741 | -0.00161179 | 0.00000005 | -0.14463101 | -0.09607698 | 0.27807509 | 0.09095492 | -0.20772224 | 0.11323834 | 0.02363231 | 0.01403813 | -0.00578304 | -0.02307819 |
| 0.00214633 | -0.00479683 | 0.00295961 | -0.00008201 | -0.00086241 | 0.00013401 | 0.00007752 | 0.00021924 | 0.16558166 | -0.00200334 | -0.00005082 | 0.00000130 | 0.00000167 | -0.00001218 | 0.00020634 | -0.00000001 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.13033795 | -0.00475723 | 0.00156298 | 0.01211474 | 0.01771907 |
| -0.00202357 | 0.00291060 | -0.00202791 | 0.00004990 | 0.00042796 | -0.00006532 | -0.00003944 | -0.00011167 | -0.08523783 | 0.00146778 | 0.00003394 | -0.00000105 | -0.00000148 | 0.00001174 | -0.00009013 | 0.00000002 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | -0.00679024 | -0.26595433 | 0.02003784 | -0.01032325 | 0.00904281 |
| 0.01209612 | -0.24293288 | -0.00288742 | -0.00002920 | 0.00171881 | -0.00011806 | -0.00002298 | -0.00002389 | -0.00421789 | -0.03421608 | -0.00348187 | -0.00000093 | -0.00000011 | 0.00045703 | 0.39000290 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | -0.00457237 | 0.00409679 | 0.07702308 | -0.00145286 | -0.01277744 |
| -0.00029029 | 0.00055994 | -0.00096472 | 0.00002220 | 0.00036054 | -0.00005005 | -0.00001597 | -0.00003615 | -0.02388829 | -0.00007041 | 0.00002472 | 0.00000026 | 0.00000043 | -0.00000946 | -0.00002850 | -0.00000002 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | -0.01964482 | 0.01087003 | -0.00534052 | -0.01145655 | -0.12725788 |
| -0.03339114 | 0.00091744 | -0.00010311 | -0.01211777 | 0.07135808 | 0.40221980 | -0.04020162 | -0.20643073 | 0.00028231 | -0.00023207 | 0.00227565 | 0.00789623 | 0.00063065 | 0.00159777 | -0.00000025 | 0.00001255 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00004054 | -0.00003621 | -0.00193465 | 0.00125079 | -0.00113339 |
| -0.00215292 | 0.00067987 | -0.00169232 | 0.00002267 | 0.00012642 | -0.00000577 | 0.00000597 | 0.00002444 | 0.02219290 | 0.00178241 | 0.00013494 | 0.00000056 | 0.00000075 | -0.00000595 | 0.00002221 | -0.00000002 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00438142 | 0.00877450 | 0.01157767 | -0.01988556 | 0.00065130 |
| 0.00060233 | 0.00468989 | -0.37318322 | 0.00055753 | -0.00009023 | 0.00001053 | 0.00000122 | 0.00000294 | 0.00169812 | 0.00002671 | -0.00000013 | 0.00000000 | -0.00000008 | 0.00000035 | 0.00000068 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | -0.00030969 | 0.00085645 | 0.00063289 | 0.04070320 | -0.02713296 |
| -0.00105173 | 0.00030791 | -0.10193048 | 0.00282358 | -0.00043933 | 0.00008694 | 0.00000821 | 0.00003364 | 0.01796909 | 0.00122914 | 0.00002580 | 0.00000150 | -0.00000994 | 0.00001460 | 0.00001015 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | -0.00180002 | 0.00001500 | 0.01156470 | 0.12470385 | -0.00383891 |
| 0.00299290 | -0.00003755 | 0.01817421 | -0.01983903 | -0.00007263 | -0.00020500 | 0.00010277 | -0.00006708 | -0.00107107 | -0.00005653 | -0.00000136 | -0.00003660 | 0.00026046 | -0.00000040 | -0.00000010 | -0.00000007 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00010161 | -0.00008051 | 0.00309527 | 0.06133325 | -0.00206863 |
| -0.01537258 | -0.00017563 | -0.00160061 | 0.21469734 | 0.00150451 | 0.00291815 | -0.00194901 | 0.00128077 | 0.00021665 | 0.00000212 | -0.00000070 | 0.00129807 | -0.00973851 | 0.00000006 | 0.00000018 | 0.00000579 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00012562 | -0.00006290 | 0.00049124 | 0.01786792 | -0.00072007 |
| -0.00007833 | -0.00042990 | 0.05267334 | -0.00004048 | 0.00023037 | -0.00003249 | -0.00000948 | -0.00002031 | -0.01320511 | -0.00027873 | 0.00000455 | 0.00000014 | 0.00000023 | -0.00000677 | -0.00001526 | -0.00000001 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | -0.01131283 | 0.00582445 | -0.00436100 | 0.00571073 | -0.05643839 |
| 0.00801977 | -0.00000374 | 0.00172143 | 0.22728733 | 0.00245681 | 0.00622317 | -0.00433769 | 0.00258644 | 0.00003223 | -0.00000025 | 0.00001033 | -0.03821765 | 0.37352689 | 0.00000119 | 0.00000008 | -0.00665699 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00002886 | -0.00001917 | 0.00004784 | 0.00552642 | -0.00048022 |
| 0.00014471 | 0.00054351 | -0.00281203 | 0.00005926 | 0.00026814 | -0.00004131 | -0.00001086 | -0.00001911 | -0.01203173 | -0.00088100 | -0.00001878 | -0.00000001 | -0.00000009 | -0.00001075 | -0.00000740 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00169564 | -0.00000496 | -0.01658067 | -0.32263022 | -0.10060305 |
| 0.00005789 | -0.00076936 | 0.00307474 | -0.00006427 | -0.00028075 | 0.00004244 | 0.00001073 | 0.00001793 | 0.01086770 | 0.00072045 | 0.00000712 | -0.00000001 | 0.00000007 | 0.00001117 | 0.00000581 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | -0.00109326 | -0.00264463 | 0.01464340 | 0.28821995 | 0.14664720 |
| -0.02954182 | -0.00044165 | -0.00019028 | -0.01513476 | -0.00543709 | -0.02799577 | 0.05308954 | -0.04034622 | 0.00003688 | -0.00000239 | 0.00003024 | -0.04072223 | -0.01325979 | -0.00000262 | 0.00000000 | 0.10309702 | 0.28253178 | -0.24494095 | 0.06154846 | -0.28156629 | -0.12432187 | 0.00000813 | -0.00000788 | -0.00003332 | 0.00234632 | -0.00048916 |
| -0.00032534 | -0.00497923 | 0.40888523 | -0.00101938 | 0.00012751 | -0.00001793 | -0.00000125 | -0.00000442 | -0.00228718 | -0.00008691 | -0.00000172 | -0.00000009 | 0.00000054 | -0.00000068 | -0.00000041 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | -0.00004982 | 0.00032234 | 0.00260266 | 0.05861220 | -0.01947741 |
| 0.09140345 | 0.00095160 | 0.00004674 | 0.00437988 | -0.06886581 | -0.18133594 | -0.26823222 | -0.25947147 | 0.00035152 | -0.00353985 | 0.04384911 | 0.00033853 | 0.00002205 | 0.06383136 | -0.00001393 | 0.00000005 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00000000 | 0.00003621 | -0.00015076 | -0.01137830 | 0.00206114 | -0.00219003 |
| -0.07752769 | -0.00258186 | -0.00004155 | 0.00050685 | -0.04424578 | -0.18662316 | -0.03865736 | 0.11132370 | -0.00010811 | 0.00004582 | -0.00040514 | -0.01953937 | -0.00168446 | -0.00021746 | 0.00000005 | -0.00009885 | 0.21393523 | -0.12452066 | 0.05693442 | 0.28669653 | 0.11038973 | 0.00001960 | -0.00002198 | -0.00099685 | 0.00119315 | -0.00095297 |
| -0.01865620 | 0.03152143 | 0.00032518 | 0.00414081 | -0.00625141 | -0.00214814 | 0.01921646 | 0.02656264 | 0.00991593 | -0.00537873 | 0.02068040 | 0.00271530 | -0.02442896 | -0.00980776 | 0.00024519 | -0.02332481 | -0.03094801 | -0.00789146 | -0.01014628 | -0.01283949 | 0.00599352 | -0.01182604 | -0.00349222 | -0.00297899 | -0.01786808 | 0.00718391 |
| 0.02371805 | -0.02409918 | -0.00063131 | -0.06781215 | 0.00299803 | 0.01025962 | 0.00112696 | -0.00405250 | -0.00008674 | 0.01366495 | 0.00103671 | 0.00596383 | 0.01131747 | -0.00006135 | -0.05190710 | 0.04487022 | 0.00575209 | 0.07371960 | 0.00833127 | 0.03118988 | -0.01329225 | -0.00010384 | 0.00051189 | 0.00798645 | 0.00263349 | -0.00226825 |
| 0.00707573 | -0.01632883 | -0.00007407 | 0.01814558 | 0.00392999 | -0.00144116 | -0.01542811 | -0.01947014 | -0.00775111 | -0.00048626 | -0.01644529 | -0.00405145 | 0.01584783 | 0.00766784 | 0.01768149 | 0.00438372 | 0.02263877 | -0.01683787 | 0.00540440 | 0.00031174 | -0.00060347 | 0.00969944 | 0.00256146 | -0.00018313 | 0.01215622 | -0.00427429 |

## B.7 Aridity index for the spatial median of the distribution of the species

Latitude and Longitude of the spatial median is indicated along with the value of the Aridity index (AI). Water balance (WB) is indicated as P (positive) and N (negative).

| **Species** | **Latitude** | **Longitude** | **AI** | **WB** |
|---|---|---|---|---|
| Euploca procumbens (Mill.) Diane & Hilger | 10.231 | -84.908 | 1.619 | P |
| Heliotropium abbreviatum Rusby | -17.38 | -66.15 | 0.361 | N |
| Heliotropium adenogynum I.M.Johnst. | -11.93 | -76.7 | 0.094 | N |
| Heliotropium amplexicaule Vahl | -31.176 | -59.573 | 0.867 | N |
| Heliotropium angiospermum Murray | 14.002 | -87.212 | 0.831 | N |
| Heliotropium arborescens L. | -8.205 | -78.493 | 0.456 | N |
| Heliotropium chenopodiaceum (A.DC.) Clos | -28.613 | -70.476 | 0.062 | N |
| Heliotropium corymbosum Ruiz & Pav. | -12.043 | -76.668 | 0.044 | N |
| Heliotropium curassavicum L. | 7.83 | -85.554 | 1.101 | P |
| Heliotropium elongatum (Lehm.) I.M.Johnst. | -24.078 | -57.915 | 0.73 | N |
| Heliotropium eremogenum I.M.Johnst. | -23.542 | -70.447 | 0.008 | N |
| Heliotropium filifolium (Miers) I.M.Johnst. | -28.12 | -71.07 | 0.061 | N |
| Heliotropium floridum (A.DC.) Clos | -27.128 | -70.836 | 0.103 | N |
| Heliotropium glutinosum Phil. | -26.4 | -69.53 | 0.016 | N |
| Heliotropium huascoense I.M.Johnst. | -29.448 | -71.244 | 0.083 | N |
| Heliotropium incanum Ruiz & Pav. | -12.186 | -74.775 | 0.466 | N |
| Heliotropium inconspicuum Reiche | -25.43 | -70.45 | 0.009 | N |
| Heliotropium indicum L. | 10.163 | -84.347 | 1.547 | P |
| Heliotropium jaffuelii I.M.Johnst. | -22.065 | -70.19 | 0.005 | N |
| Heliotropium krauseanum Fedde | -15.832 | -74.162 | 0.005 | N |
| Heliotropium kurtzii Gangui | -38.24 | -70.56 | 0.571 | N |
| Heliotropium linariifolium Phil. | -25.443 | -70.473 | 0.009 | N |
| Heliotropium lippioides K.Krause | -5.84 | -79.49 | 0.498 | N |
| Heliotropium longistylum Phil. | -28.075 | -71.132 | 0.061 | N |
| Heliotropium mandonii I.M.Johnston | -15.725 | -68.684 | 0.511 | N |
| Heliotropium megalanthum I.M.Johnst. | -28.164 | -71.003 | 0.061 | N |
| Heliotropium microstachyum Ruiz & Pav. | -15.656 | -69.689 | 0.663 | N |
| Heliotropium myosotifolium (A.DC.) Reiche | -28.065 | -70.681 | 0.045 | N |
| Heliotropium nicotianifolium Poir. | -17.74 | -63.2 | 0.711 | N |
| Heliotropium paronychioides A.DC | -36.543 | -71.078 | 0.955 | N |
| Heliotropium patagonicum (Speg.) I.M.Johnst. | -44.39 | -70.59 | 0.423 | N |
| Heliotropium philippianum I.M.Johnst. | -24.78 | -70.52 | 0.008 | N |
| Heliotropium phylicoides Cham. | -30.365 | -57.536 | 1.014 | P |
| Heliotropium pilosum Ruiz & Pav. | -15.779 | -74.351 | 0.001 | N |
| Heliotropium pinnatisectum R.L. PÚrez-Mor. | -39.6 | -70.58 | 0.749 | N |
| Heliotropium pycnophyllum Phil. | -25.4 | -70.48 | 0.009 | N |
| Heliotropium rufipilum (Benth.) I.M.Johnst. | -2.028 | -79.883 | 0.717 | N |
| Heliotropium sclerocarpum Phil. | -28.38 | -70.72 | 0.037 | N |
| Heliotropium sinuatum (Miers) I.M.Johnst. | -28.382 | -70.935 | 0.043 | N |
| Heliotropium stenophyllum Hook. & Arn. | -30.273 | -71.35 | 0.116 | N |
| Heliotropium submolle Klotzsch | -2.432 | -78.969 | 0.691 | N |
| Heliotropium taltalense (Phil.) I.M.Johnst. | -25.027 | -70.444 | 0.008 | N |
| Heliotropium transalpinum Vell. | -25.339 | -57.179 | 1.062 | P |
| Heliotropium veronicifolium Griseb. | -28.45 | -62.85 | 0.545 | N |
| Ixorhea tschudiana Fenzl | 25.98 | -65.917 | 0.332 | N |
| Myriopus salzmannii (DC.) Diane & Hilger | -25.26 | -57.455 | 1.193 | P |
| Tournefortia argentea L. f. | -15.95 | 50.22 | 1.857 | P |
| Tournefortia bicolour Sw. | 9 | -81.913 | 1.822 | P |
| Tournefortia buchtienii Killip | -15.48 | -68.59 | 0.686 | N |

| **Species** | **Latitude** | **Longitude** | **AI** | **WB** |
|---|---|---|---|---|
| Tournefortia chinchensis Killip | -12.33 | -74.82 | 0.466 | N |
| Tournefortia glabra L. | 10.161 | -84.287 | 2.127 | P |
| Tournefortia gnaphalodes (L.) R. Br. ex Roem. & Schult. | 20.22 | -87.526 | 0.905 | N |
| Tournefortia hirsutissima L. | 10.141 | -84.412 | 1.547 | P |
| Tournefortia microcalyx (Ruiz & Pav.) I.M.Johnst. | -4.165 | -78.828 | 1.123 | P |
| Tournefortia paniculata Cham. | -32.3 | -64.5 | 0.532 | N |
| Tournefortia polystachya Ruiz & Pav. | 2.095 | -76.526 | 1.736 | P |
| Tournefortia rollotii Killip | 5.15 | -73.68 | 1.351 | P |
| Tournefortia rubicunda Salzm. | -25.656 | -56.805 | 1.233 | P |

# Appendix C: Supplementary data to Chapter 4

## C.1 Plant material included in the phylogenetic study of South American *Heliotropium*

Information is given in the following order: Species; Voucher specimen or reference; *rps*16 GenBank accession; *trnL-trnF* GenBank accession; *trnS-trnG* GenBank accession.

**Heliotropiaceae**: *Ceballosia fruticosa* (L.f.) Kunkel ex Förther; *Weigend & Weigend* 8703 (B); HQ286259; HQ286165; HQ286099. *Euploca procumbens* (Mill.) Diane & Hilger; *Nee & Wen 53873*(US); EF688959; EF688803; HQ286100. *Heliotropium abbreviatum* Rusby; *de la Barra 286* (BSB); HQ286240; HQ286147; HQ286075. *H. adenogynum* I.M.Johnst.; *Cano 10058* (USM); HQ286232; HQ286139; HQ286065. *H. amplexicaule* Vahl; *Hilger et al. 95/70* (BSB); HQ286238; HQ286145; HQ286072. *H. angiospermum* Murray; *Gillis 8155* (FTG); HQ286244; HQ286151; HQ286081. *H. arbainense* Fresen.; *Förther 4049* (BSB); HQ286256; HQ286162; HQ286096. *H. arborescens* L.; *Schwerdtfeger 2443* (cult. BGBM) (B); HQ286233; HQ286140; HQ286066. *H. chenopodiaceum* (A.DC.) Clos; *Luebert & García 2501/895* (SGO); EF688975; EF688819; HQ286046. *H. curassavicum* L.; *Luebert & García 2521* (SGO); EF688999; EF688843; HQ286080. *H. elongatum* (Lehm.) I.M.Johnst.; *Nee & Wen 53844* (US); EF688958; EF688802; HQ286082. *H. eremogenum* I.M.Johnst.; *Luebert & García 2575/969* (SGO); EF688968; EF688812; HQ286047. *H. erosum* Lehm.; *Zippel 00/69* (BSB); HQ286257; HQ286163; HQ286097. *H. europaeum* L.; *Hilger 97/06* (BSB); HQ286254; HQ286160; HQ286094. *H. filifolium* (Miers) I.M.Johnst.; *Luebert & Torres 1973* (SGO); EF688985; EF688829; HQ286048. *H. floridum* (A.DC.) Clos; *Luebert & Torres 1974* (SGO); EF688987; EF688831; HQ286049. *H. giessii* Friedr.-Holz; *Hilger 93/03* (BSB); HQ286255; HQ286161; HQ286095. *H. glutinosum* Phil.; *Luebert & Torres 1970* (SGO); EF688988; EF688832; HQ286050. *H. incanum* Ruiz & Pav.; *Weigend et al. 00/162* (NY); HQ286234; HQ286141; HQ286067. *H. inconspicuum* Reiche; *Luebert et al. 2081* (SGO); EF688994; EF688838; HQ286051. *H. indicum* L.; *Hilger* 1584 (BSB); HQ286245; -; HQ286083. *H. krauseanum* Fedde; *Dillon 8779* (F); EF688997; EF688841; HQ286052. *H. kurtzii* Gangui; *Weigend et al. 5914* (BSB); HQ286242; HQ286149; HQ286077. *H. linariifolium* Phil.; *Luebert et al. 2054* (SGO); EF688995; EF688839; HQ286053. *H.* cf. *lippioides* Krause; *Weigend et al. 8545* (M); HQ286235; HQ286142; HQ286068. *H. longistylum* Phil.; *Luebert & Torres 1971* (SGO); EF688986; EF688830; HQ286054. *H. mandonii* I.M.Johnst.; *Hilger K04/02* (B); HQ286236; HQ286143; HQ286069. *H. megalanthum* I.M.Johnst.; *Luebert & Becker 2165* (SGO); EF688979; EF688823; HQ286055. *H. microstachyum* Ruiz & Pav.; *Weigend et al. 97/320* (BSB); HQ286241; HQ286148; HQ286076. *H. molle* (Torr.) I.M.Johnst.; *Turner 25-139* (TEX); HQ286246; HQ286153; HQ286085. *H. myosotifolium* (A.DC.) Reiche; *Luebert et al. 2011* (SGO); HQ286228; HQ286135; HQ286056. *H. nicotianifolium* Poir.; *Nee & Wen 53843* (US); EF688957; EF688801; HQ286073. *H. paronychioides* A.DC.; *Luebert & Teillier 2241*(SGO); EF688998; EF688842; HQ286078. *H. patagonicum* (Speg.) I.M.Johnst.; *Weigend et al. 6012* (BSB); HQ286229; HQ286136; HQ286062. *H. philippianum* I.M.Johnst.; *Luebert et al. 2124* (SGO); EF688990; EF688834; HQ286057. *H. phylicoides* Cham.; *Hilger et al. 95/09* (BSB); HQ286239; HQ286146; HQ286074. *H. pinnatisectum* Pérez-Mor.; *Weigend et al. 5901* (BSB); HQ286243; HQ286150; HQ286079. *H. pycnophyllum* Phil.; *Luebert & García 2813/1207* (SGO); EF688971; EF688815; HQ286058. *H. sinuatum* (Miers) I.M.Johnst.; *Luebert & Torres 1972* (SGO); EF688984; EF688828; HQ286059. *H. stenophyllum* Hook. et Arn.; *Luebert*

*& Becker 1990* (SGO); EF689001; EF688847; HQ286060. *H. taltalense* (Phil.) I.M.Johnst.; *Luebert et al. 2083* (SGO); EF688992; EF688836; HQ286061. *H. transalpinum* Vell.; *Hilger et al. 95/23* (BSB); HQ286231; HQ286138; HQ286064. *H. veronicifolium* Griseb.; *Hilger et al. 95/29* (BSB); HQ286230; HQ286137; HQ286063. *H. zeylanicum* (Burm.f.) Lam.; *Hilger 94/04* (BSB); HQ286258; HQ286164; HQ286098. *Ixorhea tschudiana* Fenzl; *Hilger et al. 95/65* (BSB); HQ286260; HQ286166; HQ286101. *Myriopus salzmannii* (DC.) Diane & Hilger; *Nee & Wen 53848* (US); EF688956; EF688800; HQ286102. *Tournefortia argentea* L.f.; *Tillich 3555* (MSB); HQ286247; HQ286154; HQ286086. *T.* cf. *buchtienii* Killip; *Nee & Wen 53944* (US); EF688961; EF688805; HQ286087. *T. chinchensis* Killip; *Weigend et al. 5809* (BSB); HQ286248; HQ286155; HQ286088. *T. gnaphalodes* (L.) Kunth; *Hilger 99/34* (BSB); HQ286249; HQ286156; HQ286089. *T. microcalyx* (Ruiz & Pav.) I.M.Johnst.; *Weigend & Dostert 97/5* (MSB); HQ286251; HQ286157; HQ286091. *T. polystachya* Ruiz & Pav.; *Weigend 3869* (BSB); HQ286252; HQ286158; HQ286092. *T. rubicunda* Salzm.; *Nee & Wen 53846* (US); EF688955; EF688799; HQ286103. *T. ternifolia* Kunth; *Weigend et al. 5675* (BSB); HQ286253; HQ286159; HQ286093. **Ehretiaceae**: *Ehretia aquatica* (Lour.) Gottschling & Hilger; *Jongkind 2517* (MO); HQ286264; EU599923+EU600011; HQ286274. *E. cymosa* Thonn.; *de Wilde 4230* (B); HQ286265; EU599924+EU600012; HQ286275. *E. tinifolia* L.; *Gottschling CUB52* (BSB); HQ286266; HQ286270; HQ286276. *Tiquilia paronychioides* (Phil.) A.T. Richardson; *Dillon 8798* (F); EF688963; EF688807; HQ286104. **Cordiaceae**: *Cordia decandra* Hook. & Arn.; *Luebert & Kritzner 1873* (SGO); EF689005; EF688851; HQ286105. *C. dentata* Poir.; *Narvaez & Seymour 2527* (B); HQ286263; EU599918+EU600006; HQ286273. *C. myxa* L.; *HB Berlin-Dahlem* (BSB); HQ286262; EU599916+EU600004; HQ286272. *C. nodosa* Lam.; *Weigend et al. 5742* (BSB); HQ286261; HQ286269; HQ286271. **Hydrophyllaceae**: *Wigandia urens* Urb.; *Wen 8671* (US); EF689000; EF688846; HQ286106. **Boraginaceae**: *Lithospermum macbridei* I.M. Johnst.; *Weigend et al. 5073* (BSB); HQ286268; FJ763273; FJ763320. *Ulugbekia tschinganica* (B.Fedtsch.) Zak.; *Orazowa & Fissjun 5785* (B); HQ286267; FJ763279; FJ763323. **Solanaceae**: *Nicotiana tabacum* L.; Wakasugi et al. (1998); Z00044; Z00044; Z00044.

## C.2 Dispersal transition matrices used in the DEC analysis

Areas A-G as defined in Section 4.2.4: A, Andes; B, Eastern South America; C, Mesoamerica and the Caribbean, D, North America; E, Africa; F, Eurasia; G, Indo-Pacific.

0 – 10 Ma

$$\begin{array}{cc} & \begin{array}{ccccccc} A & B & C & D & E & F & G \end{array} \\ \begin{array}{c} A \\ B \\ C \\ D \\ E \\ F \\ G \end{array} & \begin{bmatrix} - & 1.0 & 1.0 & 0.5 & 0.1 & 0.1 & 0.1 \\ & - & 1.0 & 0.6 & 0.2 & 0.1 & 0.1 \\ & & - & 1.0 & 0.2 & 0.1 & 0.1 \\ & & & - & 0.1 & 0.5 & 0.1 \\ & & & & - & 1.0 & 0.8 \\ & & & & & - & 1.0 \\ & & & & & & - \end{bmatrix} \end{array}$$

11 – 30 Ma

$$\begin{array}{cc} & \begin{array}{ccccccc} A & B & C & D & E & F & G \end{array} \\ \begin{array}{c} A \\ B \\ C \\ D \\ E \\ F \\ G \end{array} & \begin{bmatrix} - & 1.0 & 1.0 & 0.5 & 0.1 & 0.1 & 0.3 \\ & - & 1.0 & 0.6 & 0.3 & 0.1 & 0.3 \\ & & - & 0.8 & 0.2 & 0.1 & 0.1 \\ & & & - & 0.1 & 0.8 & 0.1 \\ & & & & - & 1.0 & 0.8 \\ & & & & & - & 1.0 \\ & & & & & & - \end{bmatrix} \end{array}$$

31 – 60 Ma

$$\begin{array}{cc} & \begin{array}{ccccccc} A & B & C & D & E & F & G \end{array} \\ \begin{array}{c} A \\ B \\ C \\ D \\ E \\ F \\ G \end{array} & \begin{bmatrix} - & 1.0 & 1.0 & 0.5 & 0.1 & 0.1 & 0.5 \\ & - & 1.0 & 0.6 & 0.5 & 0.1 & 0.5 \\ & & - & 0.8 & 0.2 & 0.1 & 0.1 \\ & & & - & 0.3 & 1.0 & 0.1 \\ & & & & - & 0.8 & 0.7 \\ & & & & & - & 1.0 \\ & & & & & & - \end{bmatrix} \end{array}$$

# Appendix D: Supplementary data to Chapter 5

## D.1 Correlation matrices of bioclimatic and monthly variables

### D.1.1 Correlation matrix of bioclimatic variables

| BIO1 | BIO2 | BIO3 | BIO4 | BIO5 | BIO6 | BIO7 | BIO8 | BIO9 | BIO10 | BIO11 | BIO12 | BIO13 | BIO14 | BIO15 | BIO16 | BIO17 | BIO18 | BIO19 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | -0.08 | 0.00 | -0.24 | 0.74 | 0.78 | -0.14 | 0.81 | 0.84 | 0.96 | 0.97 | -0.43 | -0.46 | 0.02 | -0.48 | -0.45 | -0.02 | -0.22 | -0.36 | BIO1 |
| | | 0.80 | -0.24 | 0.45 | -0.55 | 0.90 | 0.05 | -0.12 | -0.16 | -0.05 | 0.03 | 0.02 | -0.03 | -0.16 | 0.02 | 0.00 | 0.05 | -0.01 | BIO2 |
| | | | -0.59 | 0.29 | -0.23 | 0.47 | 0.22 | -0.19 | -0.18 | 0.11 | -0.17 | -0.18 | -0.03 | -0.13 | -0.17 | -0.02 | 0.21 | -0.28 | BIO3 |
| | | | | 0.00 | -0.10 | 0.10 | -0.56 | 0.13 | 0.04 | -0.45 | 0.48 | 0.49 | 0.02 | 0.30 | 0.48 | 0.04 | -0.32 | 0.65 | BIO4 |
| | | | | | 0.38 | 0.46 | 0.53 | 0.68 | 0.76 | 0.67 | -0.17 | -0.21 | 0.10 | -0.38 | -0.20 | 0.09 | -0.21 | -0.10 | BIO5 |
| | | | | | | -0.65 | 0.57 | 0.64 | 0.77 | 0.75 | -0.38 | -0.40 | 0.08 | -0.19 | -0.39 | 0.04 | -0.12 | -0.34 | BIO6 |
| | | | | | | | -0.11 | -0.05 | -0.11 | -0.17 | 0.22 | 0.21 | 0.00 | -0.13 | 0.21 | 0.04 | -0.06 | 0.25 | BIO7 |
| | | | | | | | | 0.48 | 0.66 | 0.88 | -0.50 | -0.55 | 0.11 | -0.62 | -0.53 | 0.08 | 0.08 | -0.58 | BIO8 |
| | | | | | | | | | 0.90 | 0.73 | -0.25 | -0.27 | -0.13 | -0.46 | -0.27 | -0.16 | -0.52 | -0.04 | BIO9 |
| | | | | | | | | | | 0.87 | -0.29 | -0.32 | 0.03 | -0.41 | -0.32 | -0.01 | -0.33 | -0.16 | BIO10 |
| | | | | | | | | | | | -0.50 | -0.53 | 0.03 | -0.52 | -0.52 | -0.02 | -0.12 | -0.48 | BIO11 |
| | | | | | | | | | | | | 0.98 | 0.26 | 0.37 | 0.99 | 0.36 | 0.32 | 0.89 | BIO12 |
| | | | | | | | | | | | | | 0.15 | 0.46 | 0.99 | 0.23 | 0.27 | 0.91 | BIO13 |
| | | | | | | | | | | | | | | -0.09 | 0.18 | 0.94 | 0.35 | 0.06 | BIO14 |
| | | | | | | | | | | | | | | | 0.43 | -0.08 | 0.18 | 0.35 | BIO15 |
| | | | | | | | | | | | | | | | | 0.27 | 0.31 | 0.90 | BIO16 |
| | | | | | | | | | | | | | | | | | 0.44 | 0.11 | BIO17 |
| | | | | | | | | | | | | | | | | | | -0.14 | BIO18 |
| | | | | | | | | | | | | | | | | | | | BIO19 |

### D.1.2 Correlation matrix of monthly variables

| | P9 | P10 | P11 | P12 | P1 | P2 | P3 | P4 | P5 | P6 | P7 | P8 | T9 | T10 | T11 | T12 | T1 | T2 | T3 | T4 | T5 | T6 | T7 | T8 | M9 | M10 | M11 | M12 | M1 | M2 | M3 | M4 | M5 | M6 | M7 | M8 | m9 | m10 | m11 | m12 | m1 | m2 | m3 | m4 | m5 | m6 | m7 | m8 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P9 | | 0.81 | 0.57 | 0.22 | 0.11 | 0.12 | 0.26 | 0.87 | 0.89 | 0.86 | 0.84 | 0.90 | -0.37 | -0.31 | -0.23 | -0.16 | -0.14 | -0.16 | -0.29 | -0.22 | -0.36 | -0.38 | -0.38 | -0.40 | -0.28 | -0.14 | -0.14 | -0.06 | -0.04 | -0.09 | -0.13 | -0.22 | -0.32 | -0.32 | -0.35 | -0.32 | -0.27 | -0.25 | -0.23 | -0.24 | -0.25 | -0.26 | -0.26 | -0.24 | -0.25 | -0.30 | -0.30 | -0.32 |
| P10 | | | 0.92 | 0.65 | 0.45 | 0.46 | 0.61 | 0.92 | 0.60 | 0.53 | 0.51 | 0.59 | -0.31 | -0.29 | -0.26 | -0.22 | -0.19 | -0.18 | -0.21 | -0.19 | -0.26 | -0.28 | -0.27 | -0.31 | -0.17 | -0.09 | -0.12 | -0.09 | -0.08 | -0.11 | -0.10 | -0.12 | -0.18 | -0.14 | -0.18 | -0.18 | -0.16 | -0.14 | -0.14 | -0.18 | -0.17 | -0.16 | -0.13 | -0.10 | -0.11 | -0.23 | -0.22 | -0.25 |
| P11 | | | | 0.85 | 0.67 | 0.67 | 0.80 | 0.81 | 0.31 | 0.25 | 0.22 | 0.29 | -0.23 | -0.24 | -0.25 | -0.25 | -0.22 | -0.19 | -0.14 | -0.16 | -0.16 | -0.18 | -0.17 | -0.22 | -0.06 | -0.03 | -0.08 | -0.10 | -0.11 | -0.12 | -0.07 | -0.04 | -0.06 | 0.00 | -0.04 | -0.05 | -0.10 | -0.08 | -0.11 | -0.16 | -0.14 | -0.11 | -0.07 | -0.02 | -0.04 | -0.17 | -0.16 | -0.19 |
| P12 | | | | | 0.90 | 0.90 | 0.96 | 0.55 | -0.03 | -0.10 | -0.11 | -0.06 | -0.19 | -0.23 | -0.30 | -0.33 | -0.31 | -0.26 | -0.12 | -0.20 | -0.11 | -0.10 | -0.10 | -0.16 | -0.01 | -0.03 | -0.10 | -0.18 | -0.22 | -0.21 | -0.11 | -0.02 | 0.01 | 0.07 | 0.05 | 0.02 | -0.07 | -0.07 | -0.12 | -0.18 | -0.15 | -0.10 | -0.04 | 0.01 | 0.00 | -0.12 | -0.12 | -0.15 |
| P1 | | | | | | 0.99 | 0.94 | 0.37 | -0.12 | -0.18 | -0.19 | -0.14 | -0.16 | -0.21 | -0.30 | -0.35 | -0.35 | -0.29 | -0.11 | -0.21 | -0.07 | -0.07 | -0.07 | -0.13 | 0.03 | 0.00 | -0.08 | -0.19 | -0.25 | -0.23 | -0.12 | 0.00 | 0.06 | 0.11 | 0.10 | 0.06 | -0.08 | -0.10 | -0.16 | -0.21 | -0.20 | -0.13 | -0.06 | 0.00 | 0.00 | -0.09 | -0.09 | -0.14 |
| P2 | | | | | | | 0.94 | 0.39 | -0.10 | -0.16 | -0.18 | -0.12 | -0.19 | -0.24 | -0.33 | -0.37 | -0.37 | -0.31 | -0.13 | -0.23 | -0.10 | -0.10 | -0.10 | -0.16 | 0.00 | -0.03 | -0.11 | -0.22 | -0.28 | -0.26 | -0.14 | -0.03 | 0.03 | 0.07 | 0.06 | 0.03 | -0.11 | -0.13 | -0.18 | -0.22 | -0.21 | -0.15 | -0.08 | -0.03 | -0.03 | -0.11 | -0.11 | -0.16 |
| P3 | | | | | | | | 0.57 | 0.04 | -0.02 | -0.04 | 0.01 | -0.26 | -0.31 | -0.37 | -0.40 | -0.39 | -0.34 | -0.20 | -0.27 | -0.18 | -0.18 | -0.18 | -0.24 | -0.07 | -0.07 | -0.15 | -0.24 | -0.28 | -0.27 | -0.18 | -0.09 | -0.05 | 0.00 | -0.02 | -0.04 | -0.15 | -0.15 | -0.20 | -0.25 | -0.23 | -0.18 | -0.12 | -0.06 | -0.07 | -0.16 | -0.17 | -0.21 |
| P4 | | | | | | | | | 0.76 | 0.71 | 0.69 | 0.75 | -0.44 | -0.41 | -0.36 | -0.32 | -0.30 | -0.30 | -0.37 | -0.33 | -0.42 | -0.44 | -0.43 | -0.46 | -0.25 | -0.13 | -0.16 | -0.12 | -0.13 | -0.17 | -0.19 | -0.25 | -0.30 | -0.27 | -0.31 | -0.28 | -0.35 | -0.32 | -0.31 | -0.34 | -0.34 | -0.34 | -0.32 | -0.28 | -0.30 | -0.37 | -0.38 | -0.40 |
| P5 | | | | | | | | | | 0.97 | 0.96 | 0.98 | -0.41 | -0.33 | -0.23 | -0.15 | -0.14 | -0.19 | -0.38 | -0.27 | -0.45 | -0.47 | -0.46 | -0.45 | -0.31 | -0.15 | -0.14 | -0.04 | -0.03 | -0.09 | -0.18 | -0.31 | -0.40 | -0.40 | -0.43 | -0.37 | -0.35 | -0.32 | -0.27 | -0.27 | -0.30 | -0.34 | -0.35 | -0.34 | -0.35 | -0.35 | -0.36 | -0.36 |
| P6 | | | | | | | | | | | 0.98 | 0.98 | -0.42 | -0.34 | -0.23 | -0.15 | -0.13 | -0.18 | -0.39 | -0.28 | -0.46 | -0.49 | -0.47 | -0.47 | -0.36 | -0.20 | -0.18 | -0.08 | -0.06 | -0.12 | -0.22 | -0.36 | -0.45 | -0.44 | -0.47 | -0.41 | -0.35 | -0.31 | -0.26 | -0.25 | -0.28 | -0.33 | -0.34 | -0.33 | -0.35 | -0.33 | -0.35 | -0.35 |
| P7 | | | | | | | | | | | | 0.97 | -0.43 | -0.35 | -0.23 | -0.15 | -0.14 | -0.19 | -0.40 | -0.29 | -0.47 | -0.50 | -0.48 | -0.47 | -0.36 | -0.20 | -0.18 | -0.08 | -0.07 | -0.12 | -0.23 | -0.38 | -0.46 | -0.45 | -0.49 | -0.42 | -0.36 | -0.32 | -0.26 | -0.25 | -0.28 | -0.33 | -0.35 | -0.35 | -0.36 | -0.34 | -0.36 | -0.36 |
| P8 | | | | | | | | | | | | | -0.41 | -0.33 | -0.22 | -0.13 | -0.12 | -0.17 | -0.37 | -0.26 | -0.44 | -0.47 | -0.45 | -0.45 | -0.35 | -0.18 | -0.16 | -0.06 | -0.04 | -0.10 | -0.19 | -0.33 | -0.42 | -0.43 | -0.46 | -0.40 | -0.34 | -0.31 | -0.26 | -0.25 | -0.28 | -0.32 | -0.33 | -0.33 | -0.34 | -0.34 | -0.35 | -0.36 |
| T9 | | | | | | | | | | | | | | 0.99 | 0.94 | 0.90 | 0.85 | 0.85 | 0.91 | 0.87 | 0.94 | 0.95 | 0.96 | 0.99 | 0.68 | 0.61 | 0.66 | 0.71 | 0.72 | 0.74 | 0.77 | 0.81 | 0.79 | 0.73 | 0.74 | 0.71 | 0.74 | 0.72 | 0.68 | 0.71 | 0.73 | 0.74 | 0.71 | 0.70 | 0.71 | 0.63 | 0.67 | 0.70 |
| T10 | | | | | | | | | | | | | | | 0.98 | 0.95 | 0.90 | 0.89 | 0.92 | 0.90 | 0.93 | 0.93 | 0.94 | 0.97 | 0.67 | 0.62 | 0.68 | 0.75 | 0.77 | 0.79 | 0.79 | 0.81 | 0.77 | 0.70 | 0.72 | 0.69 | 0.76 | 0.74 | 0.71 | 0.75 | 0.76 | 0.75 | 0.72 | 0.70 | 0.71 | 0.64 | 0.69 | 0.72 |
| T11 | | | | | | | | | | | | | | | | 0.99 | 0.95 | 0.94 | 0.92 | 0.92 | 0.91 | 0.90 | 0.90 | 0.92 | 0.60 | 0.57 | 0.65 | 0.75 | 0.79 | 0.80 | 0.78 | 0.77 | 0.70 | 0.63 | 0.64 | 0.61 | 0.78 | 0.78 | 0.76 | 0.80 | 0.80 | 0.78 | 0.75 | 0.72 | 0.73 | 0.66 | 0.71 | 0.75 |
| T12 | | | | | | | | | | | | | | | | | 0.98 | 0.97 | 0.91 | 0.95 | 0.89 | 0.87 | 0.86 | 0.88 | 0.53 | 0.52 | 0.60 | 0.73 | 0.78 | 0.80 | 0.76 | 0.72 | 0.63 | 0.55 | 0.55 | 0.53 | 0.80 | 0.80 | 0.80 | 0.84 | 0.84 | 0.82 | 0.78 | 0.75 | 0.76 | 0.67 | 0.72 | 0.75 |
| T1 | | | | | | | | | | | | | | | | | | 0.99 | 0.92 | 0.97 | 0.88 | 0.85 | 0.84 | 0.84 | 0.45 | 0.43 | 0.52 | 0.66 | 0.74 | 0.77 | 0.73 | 0.68 | 0.56 | 0.49 | 0.48 | 0.45 | 0.85 | 0.86 | 0.86 | 0.90 | 0.91 | 0.88 | 0.85 | 0.82 | 0.82 | 0.72 | 0.76 | 0.79 |
| T2 | | | | | | | | | | | | | | | | | | | 0.95 | 0.99 | 0.91 | 0.88 | 0.87 | 0.85 | 0.45 | 0.43 | 0.50 | 0.64 | 0.72 | 0.76 | 0.73 | 0.70 | 0.58 | 0.51 | 0.50 | 0.46 | 0.88 | 0.89 | 0.88 | 0.92 | 0.93 | 0.92 | 0.89 | 0.87 | 0.87 | 0.76 | 0.80 | 0.81 |
| T3 | | | | | | | | | | | | | | | | | | | | 0.98 | 0.99 | 0.97 | 0.95 | 0.93 | 0.54 | 0.48 | 0.53 | 0.62 | 0.68 | 0.73 | 0.75 | 0.78 | 0.70 | 0.63 | 0.62 | 0.57 | 0.90 | 0.89 | 0.85 | 0.88 | 0.90 | 0.92 | 0.91 | 0.90 | 0.90 | 0.80 | 0.83 | 0.84 |
| T4 | | | | | | | | | | | | | | | | | | | | | 0.95 | 0.92 | 0.90 | 0.88 | 0.48 | 0.44 | 0.50 | 0.62 | 0.70 | 0.74 | 0.74 | 0.74 | 0.63 | 0.56 | 0.54 | 0.49 | 0.91 | 0.91 | 0.89 | 0.92 | 0.94 | 0.94 | 0.92 | 0.90 | 0.91 | 0.80 | 0.83 | 0.84 |
| T5 | | | | | | | | | | | | | | | | | | | | | | 0.99 | 0.98 | 0.96 | 0.55 | 0.47 | 0.51 | 0.58 | 0.63 | 0.68 | 0.71 | 0.77 | 0.71 | 0.64 | 0.65 | 0.58 | 0.89 | 0.87 | 0.82 | 0.84 | 0.86 | 0.88 | 0.88 | 0.87 | 0.88 | 0.81 | 0.84 | 0.84 |
| T6 | | | | | | | | | | | | | | | | | | | | | | | 0.99 | 0.97 | 0.55 | 0.47 | 0.52 | 0.58 | 0.62 | 0.66 | 0.70 | 0.77 | 0.72 | 0.65 | 0.66 | 0.60 | 0.84 | 0.82 | 0.77 | 0.79 | 0.82 | 0.84 | 0.83 | 0.82 | 0.84 | 0.78 | 0.80 | 0.81 |
| T7 | | | | | | | | | | | | | | | | | | | | | | | | 0.99 | 0.57 | 0.49 | 0.53 | 0.59 | 0.62 | 0.66 | 0.70 | 0.76 | 0.73 | 0.65 | 0.67 | 0.61 | 0.82 | 0.80 | 0.75 | 0.77 | 0.80 | 0.82 | 0.81 | 0.80 | 0.81 | 0.75 | 0.78 | 0.79 |
| T8 | | | | | | | | | | | | | | | | | | | | | | | | | 0.63 | 0.56 | 0.60 | 0.65 | 0.67 | 0.70 | 0.73 | 0.78 | 0.76 | 0.70 | 0.71 | 0.67 | 0.76 | 0.74 | 0.70 | 0.73 | 0.75 | 0.76 | 0.74 | 0.73 | 0.74 | 0.68 | 0.71 | 0.73 |
| M9 | | | | | | | | | | | | | | | | | | | | | | | | | | 0.97 | 0.96 | 0.89 | 0.83 | 0.83 | 0.87 | 0.90 | 0.95 | 0.97 | 0.97 | 0.99 | 0.34 | 0.33 | 0.29 | 0.30 | 0.32 | 0.33 | 0.33 | 0.32 | 0.32 | 0.12 | 0.21 | 0.25 |
| M10 | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.98 | 0.92 | 0.87 | 0.85 | 0.88 | 0.87 | 0.90 | 0.91 | 0.90 | 0.94 | 0.26 | 0.27 | 0.24 | 0.25 | 0.26 | 0.26 | 0.26 | 0.25 | 0.25 | 0.04 | 0.13 | 0.17 |
| M11 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.97 | 0.92 | 0.91 | 0.92 | 0.90 | 0.91 | 0.90 | 0.90 | 0.94 | 0.31 | 0.32 | 0.29 | 0.31 | 0.32 | 0.32 | 0.31 | 0.29 | 0.29 | 0.09 | 0.19 | 0.23 |
| M12 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.98 | 0.97 | 0.95 | 0.90 | 0.87 | 0.84 | 0.83 | 0.86 | 0.41 | 0.42 | 0.41 | 0.43 | 0.45 | 0.43 | 0.41 | 0.39 | 0.38 | 0.20 | 0.28 | 0.33 |
| M1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.99 | 0.97 | 0.90 | 0.83 | 0.79 | 0.77 | 0.80 | 0.49 | 0.51 | 0.50 | 0.53 | 0.55 | 0.53 | 0.50 | 0.47 | 0.47 | 0.28 | 0.36 | 0.40 |
| M2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.98 | 0.92 | 0.85 | 0.81 | 0.79 | 0.80 | 0.54 | 0.56 | 0.54 | 0.57 | 0.60 | 0.58 | 0.56 | 0.53 | 0.53 | 0.35 | 0.42 | 0.46 |
| M3 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.97 | 0.91 | 0.87 | 0.85 | 0.85 | 0.55 | 0.57 | 0.54 | 0.56 | 0.59 | 0.59 | 0.58 | 0.56 | 0.55 | 0.37 | 0.44 | 0.46 |
| M4 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.97 | 0.92 | 0.92 | 0.91 | 0.57 | 0.57 | 0.52 | 0.53 | 0.57 | 0.59 | 0.59 | 0.58 | 0.58 | 0.40 | 0.47 | 0.49 |
| M5 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.97 | 0.98 | 0.97 | 0.49 | 0.48 | 0.41 | 0.43 | 0.46 | 0.48 | 0.49 | 0.48 | 0.49 | 0.32 | 0.40 | 0.43 |
| M6 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.98 | 0.98 | 0.45 | 0.45 | 0.39 | 0.39 | 0.42 | 0.44 | 0.45 | 0.45 | 0.45 | 0.25 | 0.33 | 0.37 |
| M7 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.99 | 0.45 | 0.43 | 0.38 | 0.37 | 0.40 | 0.42 | 0.43 | 0.43 | 0.44 | 0.25 | 0.34 | 0.38 |
| M8 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.36 | 0.35 | 0.30 | 0.30 | 0.33 | 0.34 | 0.35 | 0.34 | 0.35 | 0.15 | 0.24 | 0.28 |
| m9 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.99 | 0.98 | 0.97 | 0.96 | 0.97 | 0.97 | 0.97 | 0.98 | 0.91 | 0.95 | 0.96 |
| m10 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.99 | 0.99 | 0.98 | 0.98 | 0.98 | 0.98 | 0.98 | 0.88 | 0.92 | 0.93 |
| m11 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.99 | 0.97 | 0.96 | 0.96 | 0.95 | 0.95 | 0.87 | 0.91 | 0.92 |
| m12 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.99 | 0.98 | 0.97 | 0.95 | 0.95 | 0.86 | 0.90 | 0.91 |
| m1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.99 | 0.98 | 0.97 | 0.96 | 0.85 | 0.88 | 0.89 |
| m2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.99 | 0.98 | 0.98 | 0.86 | 0.89 | 0.89 |
| m3 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1.00 | 0.99 | 0.87 | 0.90 | 0.89 |
| m4 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1.00 | 0.87 | 0.90 | 0.89 |
| m5 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.89 | 0.92 | 0.91 |
| m6 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.98 | 0.97 |
| m7 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.99 |
| m8 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

## D.2 Eingenvectors and eigenvalues of the Principal Components Analysis

| Principal components: | PCA1 | PCA2 | PCA3 | PCA4 | PCA5 | PCA6 | PCA7 | PCA8 | PCA9 | PCA10 | PCA11 | PCA12 | PCA13 | PCA14 | PCA15 | PCA16 | PCA17 | PCA18 | PCA19 | PCA20 | PCA21 | PCA22 | PCA23 | PCA24 | PCA25 | PCA26 | PCA27 | PCA28 | PCA29 | PCA30 | PCA31 | PCA32 | PCA33 | PCA34 | PCA35 | PCA36 | PCA37 | PCA38 | PCA39 | PCA40 | PCA41 | PCA42 | PCA43 | PCA44 | PCA45 | PCA46 | PCA47 | PCA48 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Eigen values: | 27.37 | 6.87 | 5.70 | 5.22 | 0.96 | 0.50 | 0.39 | 0.25 | 0.22 | 0.11 | 0.06 | 0.05 | 0.05 | 0.04 | 0.03 | 0.02 | 0.02 | 0.02 | 0.02 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Percentage of total variance explained: | 57.03 | 14.32 | 11.88 | 10.88 | 2.00 | 1.05 | 0.82 | 0.53 | 0.46 | 0.23 | 0.12 | 0.11 | 0.10 | 0.08 | 0.06 | 0.05 | 0.05 | 0.04 | 0.04 | 0.03 | 0.03 | 0.02 | 0.02 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Cumulated percentage of total variance explained: | 57.03 | 71.35 | 83.22 | 94.10 | 96.10 | 97.15 | 97.97 | 98.50 | 98.96 | 99.18 | 99.30 | 99.41 | 99.51 | 99.59 | 99.65 | 99.70 | 99.74 | 99.78 | 99.82 | 99.85 | 99.87 | 99.89 | 99.91 | 99.93 | 99.94 | 99.95 | 99.96 | 99.97 | 99.97 | 99.98 | 99.98 | 99.99 | 99.99 | 99.99 | 99.99 | 99.99 | 100.00 | 100.00 | 100.00 | 100.00 | 100.00 | 100.00 | 100.00 | 100.00 | 100.00 | 100.00 | 100.00 | 100.00 |
| Eigenvectors : | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| P1 | 0.03 | -0.09 | 0.09 | -0.38 | 0.07 | -0.30 | -0.27 | 0.03 | -0.04 | -0.25 | -0.08 | -0.13 | -0.09 | 0.04 | -0.17 | 0.13 | -0.09 | -0.07 | -0.04 | 0.09 | 0.00 | -0.26 | 0.10 | 0.14 | 0.30 | -0.25 | -0.08 | -0.28 | 0.38 | 0.00 | 0.08 | 0.06 | 0.04 | 0.02 | 0.01 | 0.04 | 0.00 | 0.02 | 0.03 | 0.02 | -0.04 | -0.02 | -0.01 | 0.02 | 0.01 | -0.01 | 0.00 | 0.00 |
| P2 | 0.04 | -0.08 | 0.10 | -0.38 | 0.07 | -0.30 | -0.29 | 0.04 | -0.01 | -0.23 | -0.14 | -0.15 | -0.07 | 0.08 | -0.12 | -0.08 | -0.03 | 0.15 | 0.04 | -0.20 | -0.03 | 0.05 | 0.05 | 0.06 | -0.28 | 0.29 | 0.07 | 0.31 | -0.40 | 0.05 | -0.09 | -0.11 | -0.02 | 0.00 | -0.01 | -0.04 | -0.01 | -0.02 | -0.02 | -0.03 | 0.04 | 0.04 | -0.02 | -0.03 | -0.01 | 0.01 | 0.00 | 0.00 |
| P3 | 0.05 | -0.08 | 0.16 | -0.36 | 0.03 | -0.11 | -0.19 | -0.03 | 0.16 | 0.25 | 0.19 | 0.12 | 0.11 | -0.06 | 0.30 | -0.29 | 0.40 | 0.21 | 0.10 | 0.03 | 0.23 | 0.28 | -0.13 | -0.20 | 0.01 | -0.10 | -0.08 | -0.12 | 0.10 | -0.04 | 0.05 | 0.08 | 0.02 | -0.02 | -0.02 | 0.00 | 0.00 | 0.02 | 0.00 | 0.01 | 0.00 | -0.02 | 0.01 | 0.02 | 0.01 | 0.00 | 0.00 | 0.00 |
| P4 | 0.09 | -0.09 | 0.34 | -0.05 | 0.05 | 0.13 | 0.13 | 0.04 | 0.11 | 0.29 | 0.16 | 0.41 | -0.27 | 0.03 | -0.41 | -0.05 | 0.06 | 0.15 | -0.08 | -0.39 | -0.05 | -0.16 | 0.09 | 0.17 | 0.12 | -0.01 | 0.00 | 0.01 | 0.01 | 0.02 | -0.02 | -0.12 | 0.03 | 0.07 | -0.01 | 0.00 | 0.01 | 0.01 | 0.02 | 0.00 | 0.01 | 0.00 | 0.02 | -0.01 | -0.01 | 0.00 | -0.01 | 0.00 |
| P5 | 0.08 | -0.03 | 0.31 | 0.20 | 0.03 | -0.21 | 0.01 | -0.02 | -0.08 | 0.08 | 0.15 | 0.08 | 0.34 | 0.49 | 0.13 | -0.18 | -0.24 | -0.16 | 0.14 | 0.08 | 0.18 | 0.07 | 0.32 | 0.25 | 0.11 | -0.05 | -0.03 | 0.04 | -0.13 | 0.10 | 0.03 | 0.06 | -0.01 | -0.03 | -0.01 | -0.04 | -0.03 | 0.00 | -0.01 | -0.02 | -0.02 | 0.01 | -0.02 | -0.01 | 0.01 | -0.01 | 0.00 | 0.00 |
| P6 | 0.08 | -0.01 | 0.29 | 0.23 | 0.02 | -0.23 | -0.03 | -0.09 | -0.07 | 0.21 | 0.05 | -0.40 | -0.07 | -0.14 | -0.14 | -0.16 | 0.10 | -0.24 | -0.41 | 0.03 | -0.11 | 0.16 | -0.28 | 0.21 | -0.21 | 0.00 | -0.21 | 0.02 | 0.12 | 0.05 | 0.04 | -0.03 | -0.05 | -0.02 | 0.03 | 0.03 | 0.01 | -0.06 | -0.01 | 0.01 | 0.01 | -0.02 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 |
| P7 | 0.09 | -0.01 | 0.28 | 0.23 | 0.01 | -0.23 | -0.08 | -0.13 | -0.07 | 0.21 | -0.14 | -0.03 | -0.10 | -0.30 | 0.28 | 0.52 | -0.05 | 0.35 | 0.23 | -0.01 | 0.00 | -0.01 | 0.15 | 0.11 | -0.12 | -0.09 | 0.01 | -0.10 | -0.06 | -0.04 | -0.05 | -0.01 | 0.01 | 0.04 | 0.04 | 0.01 | -0.01 | -0.02 | -0.01 | 0.00 | 0.02 | -0.01 | -0.01 | 0.00 | 0.01 | -0.03 | 0.01 | 0.00 |
| P8 | 0.08 | -0.02 | 0.31 | 0.21 | 0.05 | -0.18 | -0.05 | 0.00 | -0.12 | -0.01 | 0.04 | -0.05 | 0.11 | 0.22 | -0.19 | 0.06 | -0.04 | 0.06 | 0.10 | 0.02 | -0.07 | -0.21 | -0.33 | -0.65 | 0.08 | 0.11 | 0.23 | 0.04 | 0.10 | -0.09 | -0.05 | 0.01 | 0.08 | -0.01 | -0.04 | 0.03 | 0.01 | 0.02 | 0.00 | -0.01 | 0.00 | 0.01 | 0.00 | 0.00 | -0.01 | 0.01 | -0.01 | -0.01 |
| P9 | 0.07 | -0.05 | 0.36 | 0.09 | 0.07 | -0.02 | 0.13 | 0.22 | -0.22 | -0.48 | -0.07 | 0.28 | -0.01 | -0.51 | 0.18 | -0.23 | 0.00 | -0.24 | 0.00 | -0.07 | 0.09 | 0.03 | 0.02 | -0.06 | 0.09 | -0.01 | 0.01 | 0.03 | -0.04 | 0.02 | 0.00 | 0.03 | -0.03 | -0.03 | -0.01 | -0.02 | 0.01 | 0.01 | 0.00 | -0.01 | -0.01 | 0.00 | -0.01 | 0.01 | 0.00 | 0.01 | 0.00 | -0.01 |
| P10 | 0.06 | -0.07 | 0.35 | -0.12 | 0.02 | 0.34 | 0.30 | -0.01 | -0.04 | -0.23 | -0.18 | -0.15 | 0.07 | 0.21 | -0.01 | -0.08 | 0.22 | 0.34 | -0.01 | 0.33 | -0.41 | 0.05 | 0.11 | 0.07 | -0.11 | -0.07 | -0.06 | -0.07 | 0.00 | 0.00 | 0.01 | 0.06 | 0.03 | 0.03 | 0.01 | -0.01 | -0.01 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | -0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| P11 | 0.04 | -0.09 | 0.28 | -0.25 | 0.02 | 0.36 | 0.24 | -0.10 | 0.11 | 0.02 | -0.12 | -0.35 | -0.18 | 0.13 | 0.12 | 0.25 | -0.10 | -0.27 | 0.06 | -0.15 | 0.50 | 0.03 | -0.08 | -0.07 | 0.01 | 0.06 | 0.01 | 0.05 | 0.02 | 0.00 | 0.01 | 0.00 | 0.00 | -0.05 | 0.00 | -0.01 | -0.01 | 0.01 | -0.01 | 0.01 | 0.00 | 0.00 | -0.02 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 |
| P12 | 0.04 | -0.08 | 0.16 | -0.37 | 0.03 | 0.12 | -0.06 | -0.13 | 0.19 | 0.23 | 0.16 | 0.17 | 0.25 | -0.24 | 0.10 | 0.14 | -0.39 | -0.30 | -0.06 | 0.23 | -0.39 | -0.07 | -0.07 | -0.05 | -0.06 | 0.06 | 0.09 | 0.06 | -0.08 | 0.02 | -0.04 | 0.00 | -0.07 | 0.00 | 0.02 | 0.02 | 0.00 | -0.03 | 0.00 | -0.01 | 0.01 | 0.01 | 0.01 | -0.01 | -0.01 | 0.01 | 0.00 | 0.00 |
| T1 | -0.17 | 0.06 | 0.09 | 0.11 | 0.08 | 0.13 | -0.16 | -0.06 | 0.12 | -0.11 | 0.21 | -0.10 | -0.09 | -0.04 | 0.06 | -0.12 | -0.02 | 0.02 | 0.13 | 0.02 | 0.00 | -0.05 | 0.14 | 0.08 | -0.12 | 0.19 | 0.17 | 0.04 | 0.19 | -0.06 | 0.03 | -0.08 | 0.05 | -0.09 | 0.10 | 0.47 | -0.21 | 0.12 | 0.28 | -0.10 | 0.01 | -0.13 | 0.35 | 0.12 | -0.10 | 0.03 | 0.23 | -0.06 |
| T2 | -0.18 | 0.07 | 0.09 | 0.07 | 0.06 | 0.11 | -0.18 | 0.04 | 0.02 | -0.03 | 0.19 | -0.05 | -0.19 | 0.00 | 0.04 | -0.01 | 0.02 | -0.01 | 0.11 | 0.05 | -0.08 | 0.02 | 0.07 | 0.03 | -0.03 | 0.12 | 0.05 | -0.01 | 0.18 | 0.07 | 0.03 | 0.00 | -0.16 | -0.24 | -0.05 | 0.00 | 0.16 | 0.27 | -0.17 | -0.18 | 0.10 | 0.40 | -0.18 | -0.33 | 0.38 | -0.04 | -0.15 | 0.09 |
| T3 | -0.19 | 0.04 | 0.04 | -0.02 | 0.12 | 0.05 | -0.07 | 0.19 | -0.11 | -0.05 | 0.13 | 0.09 | -0.16 | 0.15 | 0.10 | 0.08 | -0.10 | -0.01 | -0.07 | 0.03 | 0.00 | 0.02 | -0.14 | -0.01 | -0.16 | -0.09 | -0.07 | -0.21 | -0.13 | -0.04 | -0.07 | -0.08 | 0.06 | 0.02 | -0.28 | -0.02 | -0.17 | -0.29 | -0.14 | 0.05 | -0.22 | 0.00 | 0.39 | -0.01 | 0.22 | -0.39 | -0.11 | -0.13 |
| T4 | -0.18 | 0.07 | 0.08 | 0.03 | 0.06 | 0.09 | -0.13 | 0.15 | -0.05 | -0.03 | 0.18 | 0.02 | -0.18 | 0.08 | 0.10 | -0.03 | -0.13 | 0.02 | 0.04 | 0.05 | 0.01 | -0.03 | -0.13 | 0.10 | -0.17 | 0.04 | 0.03 | -0.23 | 0.05 | -0.02 | -0.15 | 0.06 | 0.00 | 0.05 | -0.21 | -0.33 | -0.07 | 0.09 | -0.04 | 0.18 | 0.40 | -0.12 | -0.12 | -0.01 | -0.42 | 0.30 | -0.01 | -0.03 |
| T5 | -0.18 | 0.04 | 0.01 | -0.05 | 0.20 | -0.01 | 0.02 | 0.12 | -0.11 | -0.02 | 0.02 | 0.14 | -0.05 | 0.12 | -0.07 | 0.15 | 0.04 | -0.07 | -0.02 | 0.05 | 0.02 | 0.20 | -0.03 | -0.09 | -0.12 | -0.21 | 0.07 | -0.08 | -0.05 | 0.06 | 0.21 | -0.23 | 0.04 | -0.13 | 0.41 | 0.08 | -0.01 | -0.43 | 0.15 | -0.27 | 0.19 | 0.12 | -0.21 | -0.04 | -0.15 | 0.04 | 0.03 | 0.07 |
| T6 | -0.18 | 0.03 | -0.01 | -0.05 | 0.27 | 0.00 | 0.05 | 0.15 | -0.11 | 0.13 | -0.03 | 0.06 | 0.02 | -0.10 | -0.32 | 0.06 | -0.09 | -0.02 | 0.16 | 0.13 | 0.12 | 0.13 | 0.02 | -0.02 | -0.26 | -0.02 | -0.10 | 0.02 | 0.05 | 0.15 | -0.17 | 0.40 | 0.26 | -0.06 | 0.12 | -0.08 | 0.10 | 0.19 | -0.02 | -0.06 | -0.39 | -0.02 | 0.02 | 0.10 | 0.02 | 0.18 | 0.07 | -0.01 |
| T7 | -0.18 | 0.02 | -0.01 | -0.05 | 0.31 | -0.02 | 0.06 | 0.03 | -0.14 | 0.14 | -0.24 | 0.02 | 0.14 | -0.03 | -0.19 | 0.04 | 0.04 | -0.08 | 0.26 | -0.03 | -0.06 | 0.16 | -0.08 | 0.01 | 0.16 | 0.05 | -0.20 | 0.03 | -0.06 | -0.15 | 0.27 | 0.00 | -0.34 | 0.13 | -0.09 | 0.21 | -0.18 | 0.15 | -0.29 | 0.07 | 0.21 | -0.02 | 0.18 | -0.08 | -0.08 | 0.05 | 0.00 | -0.02 |
| T8 | -0.18 | -0.01 | -0.03 | -0.01 | 0.34 | 0.02 | 0.05 | -0.07 | -0.07 | 0.17 | -0.30 | -0.02 | 0.15 | -0.04 | 0.04 | -0.19 | -0.09 | 0.06 | -0.08 | -0.05 | 0.06 | -0.17 | -0.03 | -0.02 | 0.02 | -0.01 | -0.07 | -0.17 | -0.09 | 0.01 | -0.22 | -0.12 | 0.02 | -0.13 | -0.12 | 0.02 | -0.02 | 0.12 | 0.51 | 0.04 | 0.12 | -0.16 | -0.20 | -0.20 | 0.18 | -0.19 | -0.02 | 0.02 |
| T9 | -0.18 | -0.04 | -0.02 | 0.01 | 0.32 | 0.00 | 0.03 | -0.16 | -0.03 | 0.09 | -0.17 | -0.02 | 0.08 | 0.01 | 0.24 | -0.11 | 0.03 | 0.07 | -0.26 | -0.17 | -0.01 | -0.18 | 0.13 | -0.03 | -0.04 | 0.02 | 0.28 | 0.02 | 0.17 | 0.24 | 0.10 | -0.02 | 0.00 | 0.06 | -0.02 | 0.01 | 0.00 | -0.13 | -0.17 | 0.29 | -0.18 | 0.41 | 0.05 | 0.10 | -0.16 | 0.14 | -0.01 | 0.00 |
| T10 | -0.18 | -0.04 | 0.00 | 0.05 | 0.29 | -0.02 | 0.00 | -0.20 | 0.10 | -0.07 | -0.03 | 0.03 | 0.07 | 0.02 | 0.10 | 0.02 | 0.07 | 0.02 | -0.23 | -0.03 | 0.01 | -0.08 | 0.03 | 0.06 | 0.08 | 0.00 | 0.13 | 0.08 | 0.02 | -0.16 | -0.04 | -0.09 | 0.16 | -0.09 | 0.11 | -0.20 | 0.17 | 0.13 | -0.41 | -0.37 | 0.12 | -0.42 | 0.07 | 0.18 | 0.08 | -0.05 | -0.07 | 0.00 |
| T11 | -0.18 | -0.01 | 0.04 | 0.09 | 0.23 | 0.01 | -0.05 | -0.20 | 0.18 | -0.17 | 0.18 | -0.01 | -0.03 | -0.02 | -0.05 | 0.13 | 0.05 | 0.05 | -0.02 | 0.05 | 0.01 | 0.07 | -0.05 | 0.01 | 0.20 | -0.15 | -0.17 | 0.31 | -0.11 | -0.07 | -0.02 | 0.26 | -0.04 | 0.16 | -0.27 | -0.08 | 0.30 | -0.15 | 0.28 | -0.03 | 0.17 | 0.24 | 0.05 | 0.16 | -0.03 | -0.09 | 0.16 | -0.07 |
| T12 | -0.18 | 0.02 | 0.07 | 0.12 | 0.17 | 0.05 | -0.13 | -0.13 | 0.17 | -0.15 | 0.19 | -0.04 | -0.15 | 0.03 | 0.04 | 0.01 | 0.05 | -0.01 | 0.05 | 0.04 | -0.07 | 0.05 | -0.05 | -0.01 | 0.17 | 0.06 | -0.06 | -0.01 | -0.18 | -0.11 | 0.07 | -0.09 | -0.16 | 0.20 | 0.19 | -0.03 | -0.13 | -0.03 | 0.02 | 0.27 | -0.48 | -0.25 | -0.34 | -0.09 | 0.02 | 0.11 | -0.12 | 0.14 |
| M1 | -0.15 | -0.19 | 0.07 | 0.13 | -0.11 | 0.07 | -0.12 | 0.13 | 0.25 | 0.06 | -0.16 | -0.09 | 0.16 | -0.14 | -0.17 | -0.07 | 0.07 | 0.03 | -0.04 | 0.06 | 0.13 | -0.09 | 0.07 | 0.07 | 0.08 | 0.27 | 0.17 | -0.24 | -0.05 | -0.10 | -0.02 | 0.32 | -0.17 | 0.12 | 0.08 | -0.23 | -0.29 | -0.30 | 0.03 | -0.26 | 0.03 | 0.11 | 0.01 | 0.01 | 0.07 | -0.02 | 0.00 | 0.02 |
| M2 | -0.15 | -0.17 | 0.07 | 0.11 | -0.14 | 0.07 | -0.13 | 0.21 | 0.23 | 0.05 | -0.12 | -0.09 | 0.03 | -0.08 | -0.04 | -0.14 | -0.08 | 0.06 | 0.07 | 0.15 | 0.14 | -0.25 | -0.12 | -0.04 | -0.15 | -0.49 | 0.02 | 0.16 | -0.16 | 0.17 | 0.26 | -0.28 | -0.07 | 0.13 | -0.03 | -0.12 | 0.03 | 0.23 | 0.01 | -0.10 | -0.08 | 0.02 | 0.10 | 0.00 | -0.02 | 0.07 | 0.01 | -0.01 |
| M3 | -0.16 | -0.18 | 0.05 | 0.05 | -0.13 | 0.05 | -0.08 | 0.33 | 0.11 | 0.02 | -0.13 | 0.00 | 0.09 | 0.10 | 0.12 | -0.02 | -0.13 | 0.08 | -0.02 | -0.23 | -0.09 | 0.02 | -0.23 | 0.19 | -0.02 | -0.11 | 0.12 | 0.05 | 0.00 | -0.23 | 0.02 | 0.31 | 0.01 | -0.18 | 0.11 | 0.35 | 0.32 | -0.09 | -0.09 | 0.23 | 0.02 | -0.10 | -0.15 | 0.04 | 0.02 | -0.08 | -0.03 | 0.00 |
| M4 | -0.16 | -0.19 | 0.01 | -0.01 | -0.04 | 0.01 | 0.03 | 0.34 | -0.05 | -0.04 | 0.13 | -0.08 | 0.29 | 0.05 | 0.16 | 0.22 | -0.06 | 0.09 | -0.18 | -0.25 | -0.07 | 0.16 | 0.03 | -0.06 | 0.06 | 0.20 | -0.27 | 0.03 | 0.23 | -0.02 | -0.10 | -0.22 | 0.06 | 0.37 | 0.13 | -0.08 | 0.05 | 0.19 | 0.15 | -0.13 | -0.06 | 0.09 | 0.07 | -0.05 | -0.05 | 0.00 | -0.04 | 0.00 |
| M5 | -0.15 | -0.22 | -0.04 | -0.04 | -0.02 | -0.08 | 0.14 | 0.14 | -0.09 | 0.02 | 0.21 | -0.03 | 0.10 | -0.04 | 0.01 | 0.19 | 0.20 | 0.08 | -0.05 | 0.05 | 0.01 | -0.13 | -0.02 | 0.06 | 0.12 | -0.12 | -0.03 | 0.42 | 0.08 | 0.15 | -0.21 | 0.03 | -0.10 | -0.38 | -0.06 | -0.02 | -0.47 | -0.07 | -0.05 | 0.10 | 0.04 | -0.09 | -0.10 | 0.00 | 0.06 | 0.06 | 0.04 | -0.02 |
| M6 | -0.14 | -0.23 | -0.04 | -0.06 | -0.11 | -0.05 | 0.15 | -0.10 | -0.22 | 0.06 | 0.11 | -0.10 | -0.21 | -0.14 | -0.05 | -0.20 | -0.49 | 0.41 | -0.13 | 0.18 | 0.11 | 0.26 | -0.04 | -0.04 | 0.30 | 0.11 | 0.08 | 0.01 | -0.03 | 0.02 | 0.18 | -0.03 | 0.04 | -0.08 | 0.02 | -0.01 | 0.01 | -0.02 | -0.01 | -0.01 | 0.01 | -0.01 | 0.04 | 0.01 | 0.00 | 0.01 | -0.02 | 0.00 |
| M7 | -0.14 | -0.23 | -0.06 | -0.06 | -0.06 | -0.08 | 0.22 | -0.14 | -0.18 | -0.02 | 0.19 | -0.10 | 0.07 | -0.05 | -0.09 | -0.09 | 0.11 | -0.05 | 0.34 | 0.01 | 0.03 | -0.09 | -0.10 | 0.14 | -0.07 | -0.02 | 0.19 | -0.17 | 0.06 | 0.09 | -0.36 | -0.20 | -0.37 | 0.13 | 0.08 | 0.02 | 0.34 | -0.12 | -0.04 | -0.01 | -0.06 | -0.02 | 0.05 | 0.10 | -0.02 | -0.06 | 0.04 | 0.00 |
| M8 | -0.13 | -0.26 | -0.06 | -0.03 | -0.05 | -0.06 | 0.13 | -0.16 | -0.15 | 0.02 | 0.18 | -0.12 | 0.00 | -0.06 | 0.03 | -0.08 | 0.12 | -0.17 | 0.18 | -0.10 | -0.11 | -0.21 | -0.05 | 0.08 | -0.01 | -0.06 | -0.05 | -0.12 | -0.27 | -0.36 | 0.11 | 0.02 | 0.49 | 0.02 | 0.11 | -0.04 | -0.16 | 0.14 | -0.01 | 0.03 | 0.06 | 0.30 | -0.03 | 0.02 | 0.02 | 0.00 | -0.02 | 0.02 |
| M9 | -0.13 | -0.27 | -0.05 | -0.01 | -0.11 | -0.07 | 0.07 | -0.18 | -0.11 | -0.02 | 0.05 | 0.00 | -0.14 | 0.07 | 0.10 | -0.03 | -0.04 | -0.10 | 0.02 | -0.33 | -0.20 | -0.04 | 0.26 | -0.27 | -0.29 | -0.09 | -0.11 | -0.03 | 0.09 | 0.07 | 0.30 | 0.31 | -0.22 | -0.04 | -0.12 | -0.10 | 0.00 | -0.05 | 0.13 | -0.15 | -0.03 | -0.26 | 0.02 | -0.08 | 0.02 | 0.04 | -0.03 | 0.00 |
| M10 | -0.12 | -0.29 | 0.00 | 0.04 | -0.12 | -0.10 | -0.02 | -0.14 | -0.02 | 0.02 | -0.32 | 0.42 | -0.26 | 0.21 | 0.15 | 0.00 | 0.05 | -0.10 | 0.04 | 0.33 | 0.07 | -0.09 | -0.20 | 0.12 | -0.11 | 0.27 | -0.18 | 0.21 | 0.23 | -0.06 | 0.00 | -0.05 | 0.02 | 0.09 | 0.06 | -0.01 | 0.00 | -0.01 | 0.07 | -0.01 | -0.02 | 0.05 | -0.01 | 0.03 | 0.02 | -0.01 | -0.01 | 0.01 |
| M11 | -0.13 | -0.27 | 0.00 | 0.07 | -0.10 | -0.07 | -0.04 | -0.09 | 0.10 | -0.03 | -0.11 | 0.05 | -0.10 | 0.04 | -0.07 | 0.10 | 0.12 | -0.19 | -0.12 | 0.04 | -0.05 | 0.36 | 0.09 | -0.06 | 0.10 | -0.15 | 0.29 | -0.10 | -0.11 | 0.21 | -0.24 | 0.00 | 0.22 | 0.22 | -0.26 | 0.30 | -0.07 | 0.12 | -0.10 | -0.07 | 0.02 | -0.05 | -0.10 | -0.26 | -0.07 | 0.03 | 0.07 | -0.04 |
| M12 | -0.14 | -0.23 | 0.05 | 0.12 | -0.08 | 0.00 | -0.09 | 0.02 | 0.23 | -0.03 | -0.05 | 0.00 | 0.06 | -0.07 | -0.20 | 0.08 | 0.08 | -0.10 | 0.01 | 0.08 | -0.01 | 0.11 | 0.31 | -0.22 | 0.01 | 0.17 | -0.24 | -0.19 | -0.06 | 0.05 | 0.02 | -0.26 | 0.07 | -0.40 | -0.01 | -0.09 | 0.20 | -0.03 | -0.05 | 0.37 | 0.08 | 0.00 | 0.10 | 0.19 | -0.04 | -0.04 | -0.01 | 0.01 |
| m1 | -0.17 | 0.14 | 0.08 | -0.01 | -0.14 | 0.13 | -0.13 | -0.07 | -0.06 | 0.09 | -0.07 | -0.11 | 0.06 | -0.13 | -0.02 | -0.13 | 0.01 | -0.01 | 0.25 | -0.05 | -0.07 | -0.08 | 0.04 | 0.02 | 0.12 | 0.08 | -0.16 | 0.18 | 0.14 | 0.16 | 0.00 | -0.03 | 0.22 | -0.04 | -0.14 | 0.04 | 0.02 | -0.18 | -0.10 | -0.19 | -0.13 | -0.05 | -0.20 | -0.06 | -0.45 | -0.35 | -0.27 | -0.10 |
| m2 | -0.17 | 0.14 | 0.08 | -0.04 | -0.13 | 0.12 | -0.13 | 0.02 | -0.15 | 0.09 | -0.06 | -0.06 | 0.00 | -0.03 | 0.02 | -0.09 | 0.00 | -0.06 | 0.17 | -0.07 | -0.10 | 0.02 | 0.05 | -0.03 | 0.07 | 0.03 | 0.00 | 0.07 | 0.08 | 0.20 | 0.06 | -0.10 | 0.20 | 0.25 | -0.02 | -0.01 | -0.02 | -0.21 | -0.04 | 0.12 | 0.19 | -0.15 | -0.17 | 0.28 | 0.52 | 0.22 | 0.12 | -0.24 |
| m3 | -0.17 | 0.14 | 0.08 | -0.07 | -0.17 | 0.06 | -0.10 | 0.05 | -0.19 | 0.10 | -0.06 | 0.00 | -0.05 | 0.05 | 0.09 | 0.01 | 0.05 | -0.04 | -0.06 | -0.03 | -0.06 | -0.07 | -0.01 | -0.04 | 0.14 | 0.02 | -0.07 | -0.03 | -0.13 | 0.07 | -0.05 | 0.03 | -0.01 | -0.02 | -0.11 | 0.02 | 0.03 | 0.02 | -0.04 | -0.09 | -0.05 | -0.01 | 0.06 | 0.17 | -0.03 | -0.03 | 0.34 | 0.77 |
| m4 | -0.16 | 0.13 | 0.09 | -0.09 | -0.17 | 0.01 | -0.06 | 0.06 | -0.24 | 0.14 | -0.02 | 0.03 | -0.04 | 0.04 | 0.05 | 0.08 | 0.16 | -0.05 | -0.23 | 0.09 | 0.03 | -0.11 | 0.10 | -0.04 | 0.10 | 0.08 | 0.02 | -0.06 | -0.19 | -0.19 | 0.06 | -0.03 | -0.18 | -0.12 | -0.01 | -0.04 | 0.14 | 0.13 | -0.01 | -0.08 | -0.22 | 0.04 | -0.13 | -0.07 | -0.13 | 0.00 | 0.43 | -0.49 |
| m5 | -0.17 | 0.14 | 0.08 | -0.09 | -0.14 | -0.02 | -0.01 | 0.05 | -0.22 | 0.09 | 0.09 | 0.02 | -0.01 | -0.01 | -0.05 | 0.13 | 0.20 | -0.06 | -0.22 | 0.19 | 0.14 | -0.10 | 0.17 | -0.03 | -0.02 | 0.03 | 0.17 | 0.06 | -0.18 | 0.01 | 0.06 | 0.14 | -0.08 | 0.14 | 0.07 | 0.16 | 0.09 | 0.15 | 0.19 | 0.10 | 0.13 | -0.05 | 0.09 | 0.18 | 0.01 | -0.01 | -0.60 | 0.05 |
| m6 | -0.14 | 0.21 | 0.04 | -0.06 | -0.01 | -0.29 | 0.29 | 0.24 | 0.24 | 0.18 | -0.12 | -0.14 | -0.28 | 0.00 | 0.08 | -0.20 | -0.08 | -0.12 | 0.08 | 0.07 | -0.14 | 0.08 | 0.30 | -0.17 | 0.03 | -0.14 | 0.09 | 0.18 | 0.14 | -0.34 | -0.23 | -0.04 | -0.04 | 0.09 | 0.05 | -0.10 | -0.03 | -0.05 | 0.00 | 0.04 | 0.01 | 0.05 | 0.02 | 0.02 | -0.01 | -0.06 | -0.01 | 0.03 |
| m7 | -0.15 | 0.18 | 0.04 | -0.06 | -0.06 | -0.28 | 0.30 | 0.10 | 0.22 | -0.02 | -0.06 | 0.01 | 0.02 | 0.04 | 0.08 | 0.13 | 0.13 | -0.05 | 0.15 | -0.08 | -0.18 | 0.09 | -0.26 | 0.22 | 0.17 | 0.19 | 0.22 | -0.11 | -0.04 | 0.22 | 0.29 | -0.04 | 0.10 | -0.19 | -0.18 | -0.17 | 0.07 | 0.06 | 0.23 | -0.06 | -0.13 | -0.05 | 0.12 | 0.01 | 0.01 | 0.12 | -0.07 | -0.04 |
| m8 | -0.16 | 0.17 | 0.03 | -0.04 | -0.07 | -0.25 | 0.32 | -0.01 | 0.28 | -0.12 | 0.13 | 0.03 | 0.01 | -0.02 | 0.04 | -0.03 | -0.08 | 0.13 | -0.11 | 0.06 | 0.14 | -0.30 | -0.03 | -0.11 | -0.12 | 0.13 | -0.34 | -0.17 | -0.14 | 0.23 | -0.01 | 0.10 | 0.02 | 0.12 | 0.04 | 0.34 | 0.00 | -0.04 | -0.23 | -0.06 | 0.13 | 0.01 | -0.15 | -0.05 | 0.02 | 0.02 | 0.08 | -0.04 |
| m9 | -0.17 | 0.14 | 0.07 | -0.06 | -0.13 | -0.07 | 0.10 | -0.13 | 0.01 | -0.13 | 0.08 | 0.10 | 0.23 | -0.07 | -0.22 | 0.09 | -0.01 | 0.05 | -0.05 | 0.02 | 0.17 | 0.11 | 0.02 | 0.07 | -0.29 | 0.00 | 0.24 | 0.08 | 0.24 | -0.11 | 0.24 | -0.03 | 0.06 | 0.14 | -0.04 | -0.16 | -0.08 | 0.11 | -0.03 | 0.27 | 0.06 | -0.06 | -0.18 | -0.09 | 0.05 | -0.41 | 0.22 | 0.12 |
| m10 | -0.17 | 0.14 | 0.08 | -0.05 | -0.17 | 0.02 | -0.01 | -0.17 | -0.04 | -0.05 | -0.04 | 0.03 | 0.20 | -0.06 | -0.08 | 0.00 | 0.01 | 0.05 | -0.04 | -0.01 | 0.13 | -0.06 | 0.04 | 0.04 | -0.04 | -0.06 | -0.07 | 0.10 | 0.06 | -0.25 | -0.08 | -0.08 | 0.12 | -0.06 | -0.09 | 0.01 | 0.15 | -0.30 | 0.00 | 0.04 | -0.06 | -0.06 | 0.28 | -0.51 | 0.06 | 0.45 | -0.08 | 0.10 |
| m11 | -0.16 | 0.15 | 0.09 | -0.02 | -0.22 | -0.01 | -0.01 | -0.27 | 0.05 | -0.15 | -0.13 | 0.13 | 0.12 | 0.06 | -0.08 | -0.01 | -0.16 | 0.06 | -0.06 | -0.20 | 0.00 | 0.19 | -0.11 | 0.00 | -0.09 | -0.19 | -0.08 | -0.12 | 0.04 | -0.18 | -0.19 | -0.10 | -0.17 | -0.16 | -0.12 | 0.07 | -0.23 | 0.14 | 0.02 | -0.17 | -0.12 | 0.22 | -0.14 | 0.40 | 0.01 | 0.15 | -0.18 | -0.06 |
| m12 | -0.17 | 0.15 | 0.08 | 0.00 | -0.17 | 0.02 | -0.09 | -0.21 | 0.02 | -0.07 | -0.10 | 0.04 | -0.06 | 0.06 | 0.04 | -0.04 | -0.02 | -0.01 | 0.01 | -0.15 | -0.09 | 0.07 | -0.14 | -0.06 | 0.16 | -0.14 | -0.05 | 0.00 | -0.07 | 0.27 | -0.20 | 0.19 | -0.03 | -0.02 | 0.53 | -0.20 | -0.09 | 0.14 | 0.00 | 0.18 | 0.14 | 0.03 | 0.31 | -0.18 | -0.02 | -0.17 | 0.05 | -0.11 |

## D.3 Area of potential distribution of present and future projections, under different sets of climatic variables, thresholds, and scenarios of climate change

Values given in km$^2$. MCP: Area calculated from Minimum Convex Polygons; 4km$^2$: Area calculated from buffers of 4km$^2$ around occurrence data; Mc, Mr, B, Bc,Br, PC are sets of climatic variables; A2 and B2 are climate change scenarios; '0.5' indicate 50% threshold; otherwise threshold was optimized. See text for details.

| **Species** | MCP | 4km$^2$ | Mc | Mc 0.5 | Mc B2 | Mc B2 0.5 | Mc A2 | Mc A2 0.5 | Mr | Mr 0.5 | Mr B2 | Mr B2 0.5 | Mr A2 | Mr A2 0.5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Heliotropium chenopodiaceum* | 45604 | 3293 | 19453 | 13651 | 33749 | 26392 | 21445 | 17544 | 5416 | 1897 | 5982 | 338 | 18556 | 4761 |
| *Heliotropium filifolium* | 1185 | 529 | 683 | 1844 | 0 | 0 | 0 | 0 | 1764 | 1742 | 59 | 58 | 128 | 123 |
| *Heliotropium floridum* | 6009 | 1527 | 2528 | 3285 | 3821 | 4195 | 606 | 671 | 3857 | 5288 | 3448 | 2125 | 1201 | 3438 |
| *Heliotropium inconspicuum* | 1081 | 406 | 828 | 226 | 9144 | 5753 | 13587 | 9180 | 1921 | 1501 | 4442 | 2199 | 2611 | 1011 |
| *Heliotropium krauseanum* | 99008 | 599 | 3379 | 1794 | 1523 | 1328 | 31046 | 9932 | 3868 | 5874 | 11 | 12 | 0 | 0 |
| *Heliotropium linariifolium* | 4207 | 1760 | 6963 | 5677 | 33435 | 13759 | 55987 | 22179 | 4603 | 7541 | 45320 | 116290 | 34546 | 101568 |
| *Heliotropium longistylum* | 393 | 453 | 142 | 192 | 0 | 0 | 0 | 0 | 223 | 938 | 0 | 0 | 0 | 0 |
| *Heliotropium megalanthum* | 3912 | 855 | 7669 | 8929 | 2697 | 3037 | 5825 | 6343 | 707 | 7656 | 17 | 2312 | 0 | 1531 |
| *Heliotropium myosotifolium* | 9070 | 1318 | 10300 | 9739 | 0 | 0 | 0 | 0 | 1213 | 13249 | 389 | 2712 | 1043 | 4439 |
| *Heliotropium pycnophyllum* | 9327 | 2331 | 2948 | 3959 | 40379 | 61451 | 53194 | 78083 | 3701 | 3267 | 2061 | 1743 | 11662 | 9474 |
| *Heliotropium sinuatum* | 14182 | 2439 | 4385 | 4385 | 0 | 0 | 0 | 0 | 16108 | 12501 | 16878 | 13246 | 13041 | 10829 |
| *Heliotropium stenophyllum* | 33348 | 2972 | 5147 | 5147 | 16794 | 16794 | 13291 | 13291 | 4623 | 5856 | 8467 | 9131 | 7530 | 8215 |
| *Heliotropium taltalense* | 814 | 669 | 613 | 493 | 1414 | 219 | 1190 | 190 | 465 | 629 | 130 | 2195 | 1571 | 4061 |

| **Species** | MCP | 4km$^2$ | B | B 0.5 | B B2 | B B2 0.5 | B A2 | B A2 0.5 | Bc | Bc 0.5 | Bc B2 | Bc B2 0.5 | Bc A2 | Bc A2 0.5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Heliotropium chenopodiaceum* | 45604 | 3293 | 4519 | 2498 | 15881 | 7809 | 22501 | 16299 | 5482 | 2291 | 34591 | 27381 | 11769 | 6294 |
| *Heliotropium filifolium* | 1185 | 529 | 682 | 1142 | 0 | 0 | 0 | 0 | 1469 | 1298 | 0 | 0 | 12 | 9 |
| *Heliotropium floridum* | 6009 | 1527 | 1227 | 3004 | 0 | 1291 | 0 | 13 | 3446 | 3446 | 123 | 123 | 2518 | 2518 |
| *Heliotropium inconspicuum* | 1081 | 406 | 146 | 1716 | 287 | 3985 | 162 | 2487 | 1188 | 1279 | 3574 | 4334 | 7 | 17 |
| *Heliotropium krauseanum* | 99008 | 599 | 4992 | 280 | 11861 | 5483 | 100351 | 3368 | 4275 | 377 | 29358 | 61 | 89862 | 4896 |
| *Heliotropium linariifolium* | 4207 | 1760 | 5225 | 3607 | 13996 | 9103 | 6443 | 2366 | 1464 | 5377 | 7117 | 12733 | 1004 | 3320 |
| *Heliotropium longistylum* | 393 | 453 | 143 | 417 | 0 | 0 | 0 | 0 | 171 | 217 | 0 | 0 | 0 | 0 |
| *Heliotropium megalanthum* | 3912 | 855 | 977 | 3775 | 1 | 860 | 2 | 77 | 7373 | 5851 | 1300 | 1133 | 666 | 556 |
| *Heliotropium myosotifolium* | 9070 | 1318 | 4429 | 14829 | 79 | 2339 | 1099 | 18977 | 5636 | 8222 | 1646 | 3429 | 6695 | 8800 |
| *Heliotropium pycnophyllum* | 9327 | 2331 | 4660 | 5511 | 4498 | 7762 | 112 | 200 | 3091 | 5984 | 4618 | 6786 | 649 | 1962 |
| *Heliotropium sinuatum* | 14182 | 2439 | 1828 | 9952 | 202 | 4121 | 146 | 413 | 4080 | 11824 | 625 | 4416 | 146 | 1624 |
| *Heliotropium stenophyllum* | 33348 | 2972 | 9097 | 14904 | 19210 | 21957 | 2 | 65 | 1543 | 2779 | 6838 | 9696 | 968 | 1951 |
| *Heliotropium taltalense* | 814 | 669 | 873 | 586 | 127 | 3 | 618 | 187 | 469 | 936 | 2 | 192 | 0 | 40 |

| **Species** | MCP | 4km$^2$ | Br | Br 0.5 | Br B2 | Br B2 0.5 | Br A2 | Br A2 0.5 | PC | PC 0.5 | PC B2 | PC B2 0.5 | PC A2 | PC A2 0.5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Heliotropium chenopodiaceum* | 45604 | 3293 | 10006 | 2878 | 23289 | 6717 | 32773 | 13392 | 9520 | 3319 | 9517 | 8636 | 654 | 6 |
| *Heliotropium filifolium* | 1185 | 529 | 250 | 2195 | 0 | 0 | 0 | 0 | 1758 | 2272 | 10 | 2146 | 8 | 104 |
| *Heliotropium floridum* | 6009 | 1527 | 1069 | 2757 | 65 | 149 | 433 | 1265 | 1248 | 2952 | 0 | 101 | 0 | 1 |
| *Heliotropium inconspicuum* | 1081 | 406 | 164 | 474 | 0 | 0 | 0 | 0 | 335 | 0 | 0 | 0 | 0 | 4 |
| *Heliotropium krauseanum* | 99008 | 599 | 951 | 227 | 8915 | 76 | 7859 | 1 | 20186 | 2572 | 16904 | 2800 | 1284 | 0 |
| *Heliotropium linariifolium* | 4207 | 1760 | 3419 | 1697 | 17696 | 13398 | 9182 | 6692 | 4010 | 3433 | 0 | 0 | 0 | 0 |
| *Heliotropium longistylum* | 393 | 453 | 2763 | 585 | 704 | 0 | 732 | 0 | 120 | 680 | 0 | 0 | 0 | 0 |
| *Heliotropium megalanthum* | 3912 | 855 | 7925 | 6016 | 4335 | 1814 | 1722 | 453 | 7381 | 2401 | 4523 | 1723 | 2693 | 0 |
| *Heliotropium myosotifolium* | 9070 | 1318 | 1072 | 14686 | 7 | 6425 | 479 | 15061 | 928 | 6325 | 104 | 2911 | 2 | 4608 |
| *Heliotropium pycnophyllum* | 9327 | 2331 | 8298 | 3737 | 5737 | 1623 | 2384 | 1091 | 1782 | 8520 | 0 | 0 | 0 | 0 |
| *Heliotropium sinuatum* | 14182 | 2439 | 6554 | 10907 | 3129 | 5979 | 2448 | 6286 | 2163 | 11585 | 1388 | 5385 | 227 | 2707 |
| *Heliotropium stenophyllum* | 33348 | 2972 | 3401 | 4743 | 7305 | 8635 | 7784 | 9332 | 16114 | 13464 | 4832 | 4469 | 4834 | 1218 |
| *Heliotropium taltalense* | 814 | 669 | 895 | 834 | 2 | 2 | 58 | 0 | 1652 | 0 | 0 | 0 | 1 | 0 |

## D.4 Extinction risk of modelled species under the IUCN criteria of Extent of Occurrence (B1) and Area of Occupancy (B2)

IUCN (2001) extinction risk categories are given: EX, Extinct; CR, Critically endangered; EN, Endangered; VU, Vulnerable; LC, Least concern. MCP: Extinction risk calculated for Minimum Convex Polygon; 4km$^2$: Extinction risk calculated for buffers of 4km$^2$ around occurrence data; Mc, Mr, B, Bc,Br, PC are sets of climatic variables; '0.5' indicate 50% threshold; otherwise threshold was optimized. See text for details.

**Extent of Occurrence**

| **Species** | **MCP** | **Mc** | **Mc 0.5** | **Mr** | **Mr 0.5** | **B** | **B 0.5** |
|---|---|---|---|---|---|---|---|
| *Heliotropium chenopodiaceum* | LC | VU | VU | VU | EN | EN | EN |
| *Heliotropium filifolium* | EN | EN | EN | EN | EN | EN | EN |
| *Heliotropium floridum* | VU | EN | EN | EN | VU | EN | EN |
| *Heliotropium inconspicuum* | EN | EN | EN | EN | EN | EN | EN |
| *Heliotropium krauseanum* | LC | EN | EN | EN | VU | EN | EN |
| *Heliotropium linariifolium* | EN | VU | VU | EN | VU | VU | EN |
| *Heliotropium longistylum* | EN | EN | EN | EN | EN | EN | EN |
| *Heliotropium megalanthum* | EN | VU | VU | EN | VU | EN | EN |
| *Heliotropium myosotifolium* | VU | VU | VU | EN | VU | EN | VU |
| *Heliotropium pycnophyllum* | VU | EN | EN | EN | EN | EN | VU |
| *Heliotropium sinuatum* | VU | EN | EN | VU | VU | EN | VU |
| *Heliotropium stenophyllum* | LC | VU | VU | EN | VU | VU | VU |
| *Heliotropium taltalense* | EN | EN | EN | EN | EN | EN | EN |

| **Species** | **MCP** | **Bc** | **Bc 0.5** | **Br** | **Br 0.5** | **PC** | **PC 0.5** |
|---|---|---|---|---|---|---|---|
| *Heliotropium chenopodiaceum* | LC | VU | EN | VU | EN | VU | EN |
| *Heliotropium filifolium* | EN | EN | EN | EN | EN | EN | EN |
| *Heliotropium floridum* | VU | EN | EN | EN | EN | EN | EN |
| *Heliotropium inconspicuum* | EN | EN | EN | EN | EN | EN | EX |
| *Heliotropium krauseanum* | LC | EN | EN | EN | EN | LC | EN |
| *Heliotropium linariifolium* | EN | EN | VU | EN | EN | EN | EN |
| *Heliotropium longistylum* | EN | EN | EN | EN | EN | EN | EN |
| *Heliotropium megalanthum* | EN | VU | VU | VU | VU | VU | EN |
| *Heliotropium myosotifolium* | VU | VU | VU | EN | VU | EN | VU |
| *Heliotropium pycnophyllum* | VU | EN | VU | VU | EN | EN | VU |
| *Heliotropium sinuatum* | VU | EN | VU | VU | VU | EN | VU |
| *Heliotropium stenophyllum* | LC | EN | EN | EN | EN | VU | VU |
| *Heliotropium taltalense* | EN | EN | EN | EN | EN | EN | EX |

**Area of Occupancy**

| **Species** | **4km2** | **Mc** | **Mc 0.5** | **Mr** | **Mr 0.5** | **B** | **B 0.5** |
|---|---|---|---|---|---|---|---|
| *Heliotropium chenopodiaceum* | LC | LC | LC | LC | VU | LC | LC |
| *Heliotropium filifolium* | VU | VU | VU | VU | VU | VU | VU |
| *Heliotropium floridum* | VU | LC | LC | LC | LC | VU | LC |
| *Heliotropium inconspicuum* | EN | VU | EN | VU | VU | EN | VU |
| *Heliotropium krauseanum* | VU | LC | VU | LC | LC | LC | EN |
| *Heliotropium linariifolium* | VU | LC | LC | LC | LC | LC | LC |
| *Heliotropium longistylum* | EN | EN | EN | EN | VU | EN | EN |
| *Heliotropium megalanthum* | VU | LC | LC | VU | LC | VU | LC |
| *Heliotropium myosotifolium* | VU | LC | LC | VU | LC | LC | LC |
| *Heliotropium pycnophyllum* | LC | LC | LC | LC | LC | LC | LC |
| *Heliotropium sinuatum* | LC | LC | LC | LC | LC | VU | LC |
| *Heliotropium stenophyllum* | LC | LC | LC | LC | LC | LC | LC |
| *Heliotropium taltalense* | VU | VU | EN | EN | VU | VU | VU |

| **Species** | **4km2** | **Bc** | **Bc 0.5** | **Br** | **Br 0.5** | **PC** | **PC 0.5** |
|---|---|---|---|---|---|---|---|
| *Heliotropium chenopodiaceum* | LC | LC | LC | LC | LC | LC | LC |
| *Heliotropium filifolium* | VU | VU | VU | EN | LC | VU | LC |
| *Heliotropium floridum* | VU | LC | LC | VU | LC | VU | LC |
| *Heliotropium inconspicuum* | EN | VU | VU | EN | EN | EN | EX |
| *Heliotropium krauseanum* | VU | LC | EN | VU | EN | LC | LC |
| *Heliotropium linariifolium* | VU | VU | LC | LC | VU | LC | LC |
| *Heliotropium longistylum* | EN | EN | EN | LC | VU | EN | VU |
| *Heliotropium megalanthum* | VU | LC | LC | LC | LC | LC | LC |
| *Heliotropium myosotifolium* | VU | LC | LC | VU | LC | VU | LC |
| *Heliotropium pycnophyllum* | LC | LC | LC | LC | LC | VU | LC |
| *Heliotropium sinuatum* | LC | LC | LC | LC | LC | LC | LC |
| *Heliotropium stenophyllum* | LC | VU | LC | LC | LC | LC | LC |
| *Heliotropium taltalense* | VU | EN | VU | VU | VU | VU | EX |

## D.5 Extinction risk of modelled species under the IUCN criterion of projected change in area (A3)

IUCN (2001) extinction risk categories are given: EX, Extinct; CR, Critically endangered; EN, Endangered; VU, Vulnerable; LC, Least concern. Mc, Mr, B, Bc,Br, PC are sets of climatic variables; A2 and B2 are climate change scenarios;'0.5' indicate 50% threshold; otherwise threshold was optimized. See text for details.

| **Species** | **Mc B2** | **Mc B2 0.5** | **Mc A2** | **Mc A2 0.5** | **Mr B2** | **Mr B2 0.5** | **Mr A2** | **Mr A2 0.5** |
|---|---|---|---|---|---|---|---|---|
| *Heliotropium chenopodiaceum* | LC | LC | LC | LC | LC | CR | LC | LC |
| *Heliotropium filifolium* | CR | CR | CR | CR | CR | CR | CR | CR |
| *Heliotropium floridum* | LC | LC | EN | EN | LC | EN | EN | VU |
| *Heliotropium inconspicuum* | LC | LC | LC | LC | LC | LC | LC | VU |
| *Heliotropium krauseanum* | EN | LC | LC | LC | CR | CR | CR | CR |
| *Heliotropium linariifolium* | LC | LC | LC | LC | LC | LC | LC | LC |
| *Heliotropium longistylum* | CR | CR | CR | CR | CR | CR | CR | CR |
| *Heliotropium megalanthum* | EN | EN | LC | LC | CR | EN | CR | CR |
| *Heliotropium myosotifolium* | CR | CR | CR | CR | EN | EN | LC | EN |
| *Heliotropium pycnophyllum* | LC | LC | LC | LC | VU | VU | LC | LC |
| *Heliotropium sinuatum* | CR | CR | CR | CR | LC | LC | LC | LC |
| *Heliotropium stenophyllum* | LC | LC | LC | LC | LC | LC | LC | LC |
| *Heliotropium taltalense* | LC | EN | LC | EN | EN | LC | LC | LC |

| **Species** | **B B2** | **B B2 0.5** | **B A2** | **B A2 0.5** | **Bc B2** | **Bc B2 0.5** | **Bc A2** | **Bc A2 0.5** |
|---|---|---|---|---|---|---|---|---|
| *Heliotropium chenopodiaceum* | LC | LC | LC | LC | LC | LC | LC | LC |
| *Heliotropium filifolium* | CR | CR | CR | CR | CR | CR | CR | CR |
| *Heliotropium floridum* | CR | EN | CR | CR | CR | CR | LC | LC |
| *Heliotropium inconspicuum* | LC | LC | LC | LC | LC | LC | CR | CR |
| *Heliotropium krauseanum* | LC | LC | LC | LC | LC | CR | LC | LC |
| *Heliotropium linariifolium* | LC | LC | LC | VU | LC | LC | VU | VU |
| *Heliotropium longistylum* | CR | CR | CR | CR | CR | CR | CR | CR |
| *Heliotropium megalanthum* | CR | EN | CR | CR | CR | CR | CR | CR |
| *Heliotropium myosotifolium* | CR | CR | EN | LC | EN | EN | LC | LC |
| *Heliotropium pycnophyllum* | LC | LC | CR | CR | LC | LC | EN | EN |
| *Heliotropium sinuatum* | CR | EN | CR | CR | CR | EN | CR | CR |
| *Heliotropium stenophyllum* | LC | LC | CR | CR | LC | LC | VU | LC |
| *Heliotropium taltalense* | CR | CR | LC | EN | CR | EN | CR | CR |

| **Species** | **Br B2** | **Br B2 0.5** | **Br A2** | **Br A2 0.5** | **PC B2** | **PC B2 0.5** | **PC A2** | **PC A2 0.5** |
|---|---|---|---|---|---|---|---|---|
| *Heliotropium chenopodiaceum* | LC | LC | LC | LC | LC | LC | CR | CR |
| *Heliotropium filifolium* | CR | CR | CR | CR | CR | LC | CR | CR |
| *Heliotropium floridum* | CR | CR | EN | EN | CR | CR | CR | CR |
| *Heliotropium inconspicuum* | CR | CR | CR | CR | CR | - | CR | - |
| *Heliotropium krauseanum* | LC | EN | LC | CR | LC | LC | CR | CR |
| *Heliotropium linariifolium* | LC | LC | LC | LC | CR | CR | CR | CR |
| *Heliotropium longistylum* | EN | CR | EN | CR | CR | CR | CR | CR |
| *Heliotropium megalanthum* | VU | EN | EN | CR | VU | LC | EN | CR |
| *Heliotropium myosotifolium* | CR | EN | EN | LC | CR | EN | CR | LC |
| *Heliotropium pycnophyllum* | VU | EN | EN | EN | CR | CR | CR | CR |
| *Heliotropium sinuatum* | EN | VU | EN | VU | VU | EN | CR | EN |
| *Heliotropium stenophyllum* | LC | LC | LC | LC | EN | EN | EN | CR |
| *Heliotropium taltalense* | CR | CR | CR | CR | CR | - | CR | - |

# Appendix E: Supplementary data to Chapter 6

## Specimens examined for the revision of *Heliotropium* sect. *Cochranea*

**1. *Heliotropium pycnophyllum* Phil.**
**CHILE**. Región de Antofagasta, Prov. Antofagasta: Cerro Moreno, 500 m, 15 Sept. 1969, *O. Zoellner* 3497 (CONC); Cerro Moreno, 930 m, 19 Oct. 1994, *M. Richter* 94/11 (M); Foot of Cerro Moreno, 22 Oct. 1965, *Ricardi, Marticotena & Matthei* 1423 (CONC); Cerro Moreno, 23 July 1974, *O. Zoellner* 7802 (CONC); Cerro Moreno, 26 Sept. 1941, *E. Barros* 6295 (GH); Cerro Moreno, 31 July 1973, *O. Zoellner* 7095 (CONC); Cerro Moreno, 1 May 1959, *B. Araya* 154 (SGO); Cerro Moreno, 18 Aug. 1963, *W. Hermosilla* s.n. (SGO 77389); Cerro Moreno, 23°28'25.7''S, 70°35'56.3''W, 340 m, 2 Oct. 2005, *F. Luebert & N. García* 2607/1001 (BSB); Quebrada Bolsico, 53 m, 30 Nov. 2001, *C. Aedo* 7025 (CONC, MA); Cerro Moreno, 23°30'53.7''S, 70°32'27''W, 500 m, 21 Sept. 2004, *F. Luebert, C. Becker & N. García* 2145 (SGO); Cerro Moreno, 23°30'S, 70°34'W, 25 Oct. 2005, *N. Schulz* 4 (ULS); Morro Moreno, 10 Nov. 2002, *R. Pinto* 567 (SGO); Morro Moreno, foothills, near Juan López, 50 m, 30 Oct. 1985, *F. Schlegel* 7784 (CONC, SGO); Ravine W of Juan López, 23°30'42.7''S, 70°32'2.1''W, 140 m, 21 Sept. 2004, *F. Luebert, C. Becker & N. García* 2149 (BSB); Ravine opposite Juan López, 150 m, 13 Nov. 1996, *R. Rodriguez* 3080 (CONC); Peninsula Moreno, hills O Juan López, 23°30'S, 70°33'W, 250 m, 15 Oct. 1992, *G. Baumann* 18 (CONC, SGO, ULS); Juan López, 150 m, 19 July 2003, *M. Antonissen* 2 (BSB); Peninsula Moreno, hills opposite Juan López, 300 m, 29 Sept. 1991, *M. Quezada & E. Ruiz* 62 (CONC, M); In flats over Juan López, Peninsula, 200 m, 12 Nov. 1995, *K. Gengler* 89 (SGO); Quebrada La Chimba, 16 km N of Antofagasta, 500 m, 16 Dec. 1943, *C. Muñoz* 3641 (SGO); Antofagasta, Aug. 1959, *F. Schlegel* s.n. (SGO 73213); Caleta Coloso, Quebrada Paralela, 400 m, 1 April 1992, *J. Anabalón* s.n. (SGO 126921); 5 km of Antofagasta, Cerro Coloso/Cerro Jarón area, Quebrada del Buey, 3 km W of the coast on mining road towards Pozo Lombriz, 23°47'S, 70°27'W, 180 m, 17 Feb. 1997, *U. Eggli, B. E. Leuenberger & S. Arroyo Leuenberger* 2691 (B, CONC); Cerro Coloso, 8 Dec. 2002, *R. Pinto* 700 (SGO); Cerro Jarón, 8 Dec. 2002, *R. Pinto* 688 (SGO); Cerro Jarón, 21 Oct. 2000, *R. Pinto* 665 (SGO); Cerro Jarón, 650 m, 21 Oct. 2000, *R. Pinto* 672 (SGO); Quebrada Caleta El Cobre, 300 m, 2 Oct. 1991, *M. Quezada & E. Ruiz* 131 (CONC); Road to Caleta El Cobre, 24°15'43.2''S, 70°31'0.2''W, 315 m, 4 Oct. 2005, *F. Luebert & N. García* 2614/1008 (BSB); Road to Caleta El Cobre, 24°15'S, 70°30'W, 1 Oct. 1987, *S. Teillier* 478 (CONC, SGO); Road to Caleta El Cobre, 24°15'S, 70°33'W, 200 m, 1 Oct. 1987, *S. Teillier* 500 (NY); Road to Caleta El Cobre, 600–660 m, 4 Oct. 1988, *M. O. Dillon & D. Dillon* 5623 (F); 15 km E of Caleta El Cobre, below the Mirador, 600–660 m, 4 Oct. 1988, *M. O. Dillon & D. Dillon* 5623 (MSB); Quebrada Remiendos, 24°21'S, 70°32'W, 100 m, 12 Feb. 1998, *G. Arancio & F. Squeo* 11159 (ULS); Morro Pintado, 24°22'S, 70°31'W, 350 m, 12 Feb. 1998, *G. Arancio & F. Squeo* 11171 (ULS); Quebrada Blanco Encalada, 50–250 m, 11 Dec. 1949, *W. Biese* 3133 (SGO); Quebrada Blanco Encalada, 150 m, 11 Dec. 1949, *W. Biese* 3137 (SGO); Blanco Encalada, 180–250 m, 17 Oct. 1990, *E. Bayer, J. Grau, A. Marticorena & R. Rodríguez* BY4889 (NY); Caleta Botija, 24°30'5.8''S, 70°33'26.4''W, 80 m, 4 Oct. 2005, *F. Luebert & N. García* 2620/1014 (BSB, SGO); Quebrada Botija, 500–800 m, 26 Nov. 1996, *C. Ehrhart & E. Sonderegger* 96/990 (MSB); Near Quebrada Botija, ca. 11 km N of Miguel Diaz; ca. 60 km N of Paposo, 24°31'S, 70°33'W, 18 Dec. 1987, *M. O. Dillon* 5355 (F); Quebrada Izcuña, 50 km N of Paposo, 24°36'S, 70°33'W, 1 Oct. 1987, *S. Teillier* 509 (CONC, SGO); Punta Colorada N of Paposo, 4 Dec. 1925, *I. M. Johnston* 5242 (GH); Panul, 24°47'27.1''S, 70°32'32.8''W, 200 m, 7 Oct. 2005, *F. Luebert & N. García* 2677/1071 (BSB); Aguada

Panulcito, 24°47'52.5''S, 70°32'16.2''W, 165 m, 19 Sept. 2004, *F. Luebert, C. Becker & N. García* 2128 (BSB); Paposo, Quebrada El Médano, 4 Nov. 1973, *H. Niemeyer* s.n. (CONC 121917); Alluvium front of Cerro Carnero, N of Paposo, 24°56'18.4''S, 70°28'33.5''W, 200–300 m, 23 Oct. 2009, *F. Luebert & A. Moreira* 2997 (BSB, SGO); ca. 7 km N of Paposo along road to El Cobre, 24°57'S, 70°29'W, 40–40 m, 14 Dec. 1987, *M. O. Dillon & S. Teillier* 5269 (F); Paposo, 25°0'S, 70°30'W, 20 m, 17 Oct. 1994, *M. Richter* 94/13 (M); N of Paposo, aprox. 1 km after cemetery, 27 Oct. 1987, *M. Muñoz-Schick. & I. Meza* 2297 (SGO); Paposo, 10 Oct. 1983, *M. Elgueta* 25 (SGO); Paposo, 18 Sept. 1968, *O. Zoellner* 2881 (CONC); Cuesta Paposo, 800 m, 9 Nov. 1969, *C. Jiles* 5407 (M); Paposo, near the beach, 15 Nov. 1959, *A. Torres* 108 (SGO); Quebrada Paposo, 700 m, 7 Oct. 1966, *C. Jiles* 4963 (CONC, M); Cachinal, beach, 20 m, 14 Sept. 1994, *Loyola* 94-15 (CONC); Playa Cachinales, N of Taltal, 25°10'S, 70°27'W, 20 m, 25 Nov. 1997, *M. O. Dillon* 8096 (F); Between Paposo and Taltal, 20 Oct. 1990, *E. Bayer, J. Grau, A. Marticorena & R. Rodríguez* BY5006 (NY); Taltal-Paposo, Sept. 1909, *K. Reiche* s.n. (SGO 61444); Cachinalcito N of Taltal, 20 m, 11 Sept. 1936, *G. Montero* 2984 (CONC, GH); 25 km N of Taltal, 25°15'S, 70°26'W, 2 Oct. 1987, *S. Teillier* 589 (NY); Quebrada Cascabeles, N of Taltal, 10 m, 16 Sept. 1941, *C. Muñoz & G. T. Johnson* 2841 (SGO); Road Taltal-Paposo, 0 m, Nov. 1996, *R. Rodriguez* 3109 (CONC); Between Taltal and Paposo, km 6, 26 July 1960, *Hartmann* s.n. (CONC 35776); Taltal, Quebrada Peralito, 16 Sept. 1953, *M. Ricardi* 2452 (CONC); Quebrada San Ramón, 6 Oct. 1988, *G. Arancio* 88265 (ULS); Quebrada de San Ramón, N of Taltal, 26 Nov. 1925, *I. M. Johnston* 5155 (GH); 3 km N Taltal, Quebrada San Ramón, 50–100 m, 29 Nov. 1996, *C. Ehrhart & E. Sonderegger* 96/1000 (MSB); Coast N of Taltal, Oct. 1940, *C. Grandjot & G. Grandjot* 4574 (SGO); Coast N of Taltal, 18 Sept. 1948, *W. Biese* 2469 (SGO); Hueso Parado, Oct. 1887, *A. Borchers* (lectotype of *Heliotropium brevifolium* SGO 54372); Taltal, 1 Nov. 1930, *F. Jaffuel* 957 (GH); Taltal, 7 Oct. 1983, *M. Elgueta* 20 (SGO); Taltal, 17 Sept. 1968, *O. Zoellner* 2714 (CONC); Taltal, 26 Sept. 1940, *E. Barros* 6228 (GH); Taltal, 26 Sept. 1940, *E. Barros* 6229 (GH); Taltal, 100 m, Oct. 1925, *E. Werdermann* 849 (B, BM, CONC, F, GH, K, M, MSB, NY, US); Taltal, July 1976, *O. Zoellner* 8909 (CONC); 15 km S of crossroad to Taltal, 25°24'S, 70°29'W, 130 m, 2 Sept. 1991, *G. Arancio* 91227 (ULS); Taltal, Quebrada Los Changos, 25°26'55.9''S, 70°29'16.54''W, 292 m, 15 Nov. 2005, *M. Acosta, P. Guerrero & M. Rosas* 3093 (K); Quebrada de Taltal, km 9.96, 25°26'S, 70°29'W, 400 m, 14 Sept. 1992, *S. Teillier, P. Rundel & P. García* 2643 (SGO); Lomas de Taltal, near road from Taltal to the Panamaericana, 25°27'50''S, 70°26'42''W, 360 m, 24 Oct. 2002, *M. Ackermann* 471 (B, CONC, F); Quebrada de Taltal, 4 Dec. 1944, *W. Biese* 528 (A); Quebrada de Taltal, 9 Sept. 1936, *G. Montero* 2870 (GH); ca. 16 km SE of Taltal, 2-5 km NE of Breas, 25°29'S, 70°22'W, 590–610 m, 29 Oct. 1988, *M. O. Dillon & D. Dillon* 5792 (F, MSB); Breas, 1888, *A. Larrañaga* s.n. (holotype of *Heliotropium breanum* SGO 54371; isotypes GH, SGO 54373, SGO 54369 [lectoparatype of *H. brevifolium*]); Breas, 25°29'55.8''S, 70°24'2.9''W, 570 m, 10 Oct. 2005, *F. Luebert & N. García* 2732/1126 (BSB, SGO); Along the road from Rte 5 to Taltal, at its intersection with the road to Cifuncho and for 2 km along this road toward Cifuncho, 25°30'27''S, 70°24'55''W, 600 m, 13 April 1994, *C. M. Taylor & A. Pool* 11586 (CONC, SGO); Road to Cifuncho, 12 km after crossroad from road Taltal-Panamericana , 380 m, 30 Nov. 1996, *C. Ehrhart & E. Sonderegger* 96/1008 (MSB); Crossroad Taltal-Cifuncho, 25°30'33.7''S, 70°24'55''W, 595 m, 16 Sept. 2004, *F. Luebert, C. Becker & N. García* 2068 (BSB); Road Taltal-Panamericana, 9 Nov. 1990, *O. F. Clarke* 17-jun (CONC); Taltal, Chepica, 17 Sept. 1954, *M. Ricardi* 3082 (CONC); Quebrada Breas, conjunction Quebrada El Ají, 8 km E of Taltal, 650 m, 29 April 1955, *R. Wagenknecht* 644 (CONC, G); Quebrada Los Zanjones, 5 km SW on road to Cifuncho, 15 km SW of Taltal, 25°31'S, 70°25'W, 610–620 m, 25 Sept. 1988, *M. O. Dillon, D. Dillon & V. Poblete* 5499 (F, MSB); Taltal, Quebrada Setiembre, 6 Oct. 1954, *M. Ricardi* 3134 (CONC); Las Tórtolas, Sierra de San Pedro, 25°33'30.3''S, 70°35'44.5''W, 170 m, 12 Oct. 2005, *F. Luebert & N. García* 2759/1153 (BSB); Quebrada to Bahia Tórtolas, S side of Cerro San Pedro, ca. 22 km (air) SW of Taltal, ca. 13 km N of Cifuncho, 25°33'S, 70°37'W, 20–70 m, 12 Oct. 1988, *M. O. Dillon & D. Dillon* 5673 (F); Cifuncho, right hand side of the mouth of the Quebrada, ca. 0.5 km inland from the coast, 25°39'0''S, 70°38'16''W, 40 m, 14 Dec. 1994, *U. Eggli & B. E. Leuenberger* 2642 (B, CONC, SGO); Cifuncho, on rocks above the town, 25°39'9.3''S, 70°38'40.5''W, 50–100 m, 24 Oct. 2009, *F. Luebert, A. Moreira & M. O. Dillon* 3004 (BSB, SGO); Cifuncho, 25°39'10.9''S, 70°38'26.6''W, 9 m, 16 Sept. 2004, *F. Luebert, C. Becker & N. García* 2061 (BSB); Quebrada Tigrillo, 25°46'S, 70°33'W, 520 m, 9 Feb. 1998, *G. Arancio & F. Squeo* 10953 (ULS); Road to Bahía Cifuncho, 6 Sept. 1991, *C. von Bohlen* 1281 (SGO); Sierra Esmeralda, 25°53'15.3''S, 70°39'7.7''W, 290 m, 13 Oct. 2005, *F. Luebert & N. García* 2810/1204 (BSB); Sierra Esmeralda, Road to Esmeralda, 25°53'31.8''S, 70°33'33.2''W, 520 m, 12 Oct. 2005, *F. Luebert & N. García* 2779/1173 (BSB); Aguada Cachina (Cachinal de La Costa), 400 m, 13 Dec. 1949, *W. Biese* 3257 (SGO); Quebrada Cachina, Road to Esmeralda, 14 Sept. 1958, *M. Ricardi & C. Marticorena* 4623/1008 (CONC); Cifuncho on road to Panamericana, crossroad to Esmeralda, Pampa Cachina, Quebrada Cachina, 25°54'S, 70°36'W, 360 m, 8 Dec. 2002, *C. Ehrhart* 2002/236 (M); Quebrada

Cachina, 340 m, 16 Oct. 1980, *J. Grau* 2157 (M); 60 km S of Taltal, near mouth of Quebrada La Cachina, 26°0’S, 70°37’W, 50–100 m, 28 Nov. 1988, *M. O. Dillon & D. Dillon* 6041 (F, MSB). Región de Atacama, Prov. Chañaral: Cachinal de la Costa, Dec. 1853, *R. A. Philippi* s.n. (holotype SGO 54374); Vicinity of Aguada Grande (‘Cachinal de la Costa’ of Philippi), 26°4’2.1’’S, 70°31’39.1’’W, 330 m, 16–18 Dec. 1925, *I. M. Johnston* 5809 (G, GH); Quinchihue (Cachinal de La Costa), 26°5’S, 70°37’W, 500 m, 14 Oct. 2005, *F. Luebert & N. García* 2813/1207 (BSB, SGO); Sierra Las Tipias, N.P. Pan de Azúcar, 26°6’54.9’’S, 70°34’66.7’’W, 210 m, 30 Sept. 2005, *N. Schulz* 15 (ULS); Pan de Azúcar, 30 m, 15 Sept. 2004, *F. Luebert, C. Becker & N. García* 2059 (BSB); Pan de Azúcar, 13 Oct. 1994, *M. Richter* 94/12 (M); Pan de Azúcar, N of Chañaral, 26°7’S, 70°25’W, 21 Sept. 1979, *O. Zoellner* 10500 (CONC); N.P. Pan de Azúcar, 26°7’S, 70°38’W, 125 m, 15 Sept. 1992, *S. Teillier, P. Rundel & P. García* 2726 (F, SGO); N.P. Pan de Azúcar, 26°9’S, 70°39’W, 160–200 m, 19 Jan. 2004, *F. Luebert & R. Torres* 1966 (BSB); Between Chañaral and Pan de Azúcar, coastal road km 10, 19 Jan. 2004, *F. Luebert & R. Torres* 1961 (BSB); 12 km from road coastal access to N.P. Pan de Azúcar, 31 Oct. 1991, *M. Muñoz-Schick, S. Teillier & I. Meza* 2823 (SGO); N.P. Pan de Azúcar, Quebrada Coquimbo, 26°8’S, 70°38’W, 50 m, 5 Dec. 1987, *M. O. Dillon & S. Teillier* 5099 (F, MSB); Chañaral, Falda Verde, 140 m, 27 Sept. 1952, *M. Ricardi* 2263 (CONC); Port of Chañaral, 27 Oct. 1941, *E. Pisano & R. Bravo* 526 (CONC); Chañaral, 13 Sept. 1965, *A. Kohler* 110 (CONC); Chañaral, 50 m, 20 Sept. 1941, *E. Barros* 6231 (GH); Barquito harbor near Chañaral, 18 Nov. 1935, *J. West* 3875 (GH, M); Vicinity of Puerto de Chañaral, hills back of El Barquito, 10 m, 28–29 Nov. 1925, *I. M. Johnston* 4807 (GH, K, US); Chañaral-Caldera, km 15, Caleta Pedregal, 26°30’55.8’’S, 70°41’54.2’’W, 0 m, 9 Feb. 1988, *C. Marticorena, T. Stuessy & C. Baeza* 9906 (CONC); Villa Alegre, 17 Sept. 2003, *F. Luebert & L. Kritzner* 1851 (BSB); Panamericana, ca. 17 km S of Chañaral, 26°34’S, 70°41’W, 20 m, 19 Sept. 1966, *E. Kausel* 5066 (SGO); Dunes behind Caleta Flamenco, 26°34’S, 70°41’W, 20 m, 14 Oct. 1991, *S. Teillier, L. Villarroel & R. Torres* 2590 (SGO); Dunes behind Caleta Flamenco, 26°35’43.8’’S, 70°40’9.2’’W, 100 m, 14 Oct. 1991, *S. Teillier, L. Villarroel & R. Torres* 2594 (SGO); Caleta Flamenco, garbage dump, 26°37’30.5’’S, 70°39’27.4’’W, 262 m, 17 Sept. 2003, *F. Luebert & L. Kritzner* 1850 (BSB); Quebrada Flamenco, E of Caleta Flamenco, 17 Sept. 2003, *F. Luebert & L. Kritzner* 1843 (BSB). Región de Atacama, Prov. Copiapó: Road Caldera to Chañaral, km 30, 24 Oct. 1971, *C. Marticorena, R. Rodríguez & E. Weldt* 1887 (CONC); Caldera, 0–930 m, 26 Dec. 1974, *O. Zoellner* 8056 (CONC); Indefinite: s. loc., *s. col.* (SGO 61445).

### 2. ***Heliotropum filifolium*** **(Miers) I.M.Johnst.**

**CHILE**. Región de Atacama, Prov. Copiapó: Road to Totoral, 19 Sept. 1989, *G. Arancio* 89550 (ULS); Totoral, 27°53’41.8’’S, 70°57’54.7’’W, 116 m, 13 Sept. 2004, *F. Luebert, C. Becker & N. García* 2015 (BSB, SGO); Road between Totoral and Bahía Totoral, 6 km, 110 m, 8 Sept. 1991, *C. von Bohlen* 1380 (SGO). Región de Atacama, Prov. Huasco: Between Canto de Agua and Totoral, 27°56’48.5’’S, 70°53’40’’W, 274 m, 15 Sept. 2003, *F. Luebert & L. Kritzner* 1825 (BSB); 47 km N of Vallenar y and 136 km SO, 530 m, 23 Sept. 1941, *C. Muñoz & G. T. Johnson* 1956 (SGO); Carrizal Bajo, 10 Dec. 1989, *G. Colon* s.n. (ULS 1517); Carrizal Bajo, 10 Dec. 1989, *X. Duarte* 68 (ULS); Carrizal Bajo, 28°4’S, 71°8’W, 12 Oct. 1994, *S. Teillier & R. Torres* 3904 (SGO); Carrizal Bajo, 30 Sept. 1952, *M. Ricardi* 2281 (CONC); Carrizal Bajo, 28°5’S, 71°9’W, 25 m, 30 Sept. 1989, *G. Arancio* 89617 (ULS); Valle Carrizal, near the coast, 28°6’26.4’’S, 71°6’15.7’’W, 55 m, 26 Sept. 2004, *F. Luebert & C. Becker* 2166 (BSB); Valle Carrizal Sept. 1885 *s. col.* [*F. Philippi*?] (holotype of *Cochranea kingi* SGO 54430 [fragm. GH], isotype B†, possible isotype K); Quebrada Carrizal, 28°6’8.9’’S, 71°9’0.6’’W, 47 m, 15 Sept. 2003, *F. Luebert & L. Kritzner* 1818 (BSB); Quebrada Carrizal, 28°6’45.2’’S, 71°6’57.4’’W, 26 m, 15 Sept. 2003, *F. Luebert & L. Kritzner* 1820 (BSB); Quebrada Carrizal, 28°6’45.2’’S, 71°6’57.4’’W, 30 m, 21 Jan. 2004, *F. Luebert & R. Torres* 1973 (SGO, BSB); Quebrada Carrizal, 28°6’S, 71°7’W, 325 m, 13 Oct. 1991, *S. Teillier, L. Villarroel & R. Torres* 2564 (CONC, SGO); Quebrada Carrizal, 28°6’S, 71°7’W, 350 m, 13 Oct. 1991, *S. Teillier, L. Villarroel & R. Torres* 2565 (SGO); Carrizal Alto, Cerro Azúcar, 28°7’S, 70°57’W, 5 Sept. 2004, *S. Teillier* s.n. (BSB); Quebrada Carrizal, 28°7’47’’S, 71°5’1.1’’W, 100 m, 21 Jan. 2004, *F. Luebert & R. Torres* 1977 (BSB); Carrizal Bajo, coastal cliff, 28°8’S, 71°5’W, 4 Nov. 1987, *K. H. Rechinger & W. Rechinger* 63396 (B, M); Carrizal Bajo (Road to), near Canto de Agua, 30 Oct. 1987, *M. Muñoz-Schick & I. Meza* 2348 (SGO); Canto de Agua, 23 Sept. 1972, *O. Zoellner* 6433 (CONC); Ravine ca. 10 km W of Canto de Agua, 25 Oct. 1997, *C. Ehrhart & J. Grau* 97/1278 (M); Vallenar, road to Carrizal Bajo, 28°9’S, 71°3’W, 9 Oct. 1987, *S. Teillier* 960 (CONC, SGO); Road from highway toward Carrizal Bajo, Llano de La Jaula front of Sierra Los Nichos, 2 Nov. 1991, *M. Muñoz-Schick, S. Teillier & I. Meza* 2910 (SGO); 19-20 km N of the southern (main) road to Carrizal Alto and Canto de Agua, 28°15’19’’S, 70°41’46’’W, 400 m, 15 April 1994, *C. M. Taylor & A. Pool* 11619 (SGO); Road Carrizal Bajo–Huasco, 28°15’57’’S, 71°9’47.6’’W, 20 m, 19 Oct. 2005, *F. Luebert & C. Becker* 2901 (BSB); 15 km N of Vallenar, along the highway, 28°35’S, 70°16’W, 4 Oct. 1987, *K. H. Rechinger & W. Rechinger* 63308 (B, K, M, NY); Vallenar, Sept. 1900, *K. Reiche* s.n. (BM). Región de Atacama, Indefinite: dry valleys and hills between Huasco and Copiapó, [Sept. 1841], *T. Bridges* 1343 (lectotype BM [fragm.GH], duplicates A, E, G, K, P [fragm. F 515812], W).

**3. *Heliotropium jaffuelii* I.M.Johnst.**
**CHILE**. Región de Antofagasta, Prov. Tocopilla: Road from Tocopilla to Quebrada Mamilla, 21 Oct. 1964, *M. Ricardi, C. Marticorena & O. Matthei* 1065 (CONC); Tocopilla, Nov. 1931, *F. Jaffuel* 2524 (holotype GH, isotypes CONC, G).

**4. *Heliotropium glutinosum* Phil.**
**CHILE**. Región de Atacama, Prov. Chañaral: Vicinity of Potrerillos, Rio Sal station, 1670 m, 27 Oct. 1925, *I. M. Johnston* 4749 (US); Quebrada Potrerillos, 26°23’13.6”S, 69°38’34.8”W, 1638 m, 18 Sept. 2003, *F. Luebert & L. Kritzner* 1857 (BSB); Quebrada Potrerillos, Encanche, 26°23’59.3”S, 69°32’59.5”W, 1938 m, 18 Sept. 2003, *F. Luebert & L. Kritzner* 1852 (BSB); Potrerillos, quebrada El Asiento, 26°23’52”S, 69°33’33”W, 2007 m, 18 April 2006, *M. Acosta & M. Rosas* 3672 (K); Quebrada Potrerillos, 1900 m, 20 Jan. 2004, *F. Luebert & R. Torres* 1970 (BSB, SGO); Potrerillos, 23 Sept. 1976, *O. Zoellner* 9324 (CONC); Quebrada Potrerillos, along the road between Encanche and the town of Potrerillos, 2025–2200 m, 22 Oct. 1925, *I. M. Johnston* 3698 (K, US); Quebrada Salado, Desertum Atacama, *F. San Román* s.n. (SGO 42215 42239 54386 54388); Road down from Potrerillos, at abandoned station Encanche, 2030 m, 30 Oct. 1991, *M. Muñoz-Schick, S. Teillier & I. Meza* 2772, 2778 (SGO); Agua Dulce in Deserto Atacama, 1920 m, 21 Feb. 1854, *R. A. Philippi* s.n. (holotype SGO 54387, isotype GH); Road to La Finca de Chañaral, 26°35’59”S, 69°51’41.9”W, 1390 m, 25 Sept. 2004, *F. Luebert & C. Becker* 2161 (BSB, SGO); Inca de Oro, km 6 on road to La Finca, 26°42’28.9”S, 69°51’58.6”W, 1639 m, 18 Sept. 2003, *F. Luebert & L. Kritzner* 1858 (BSB); Inca de Oro, 9 Oct. 1965, *Galleguillos* (CONC); Quebrada San Andrés, road to Salar de Maricunga, 27°10’49.6”S, 69°54’2.8”W, 1195 m, 18 Sept. 2005, *F. Luebert & N. García* 2508/902 (EIF). Región de Atacama, Indefinite: Atacama, 1883, *s.col.* (BM).

**5. *Heliotropium sinuatum* (Miers) I.M.Johnst.**
**CHILE**. Región de Arica y Parinacota, Prov. Arica: Valle del Vitor, 4 July 1970, *O. Zöllner* 4472 (CONC). Región de Atacama, Prov. Copiapó: Road Totoral–Caldera, 27°40’45.6”S, 70°56’59.2”W, 30 m, 16 Sept. 2003, *F. Luebert & L. Kritzner* 1831 (SGO); Estancia Castilla, 27°43’40.5”S, 71°0’2.4”W, 92 m, 16 Sept. 2003, *F. Luebert & L. Kritzner* 1828 (BSB); Road Bahia Salada–Totoral, 27°46’44.7”S, 70°48’17.5”W, 240 m, 18 Oct. 2005, *F. Luebert & C. Becker* 2897 (BSB); 7 Km W of Totoral on gravel road towards Totoral Bajo (=48 km W of Panamericana), 27°52’34”S, 71°0’25”W, 250 m, 9 Dec. 1994, *U. Eggli & B.E. Leuenberger* 2606 (B, CONC, SGO); Quebrada de Totoral (Boquerones), 180 m, 24 Nov. 1941, *E. Pisano & R. Bravo* 805 (CONC); Coastal road Carrizal Bajo–Totoral, at milestone on km 51 of the mining road southwards, 0 m, 5 Sept. 2000, *M. Muñoz-Schick* 4104 (SGO); Between Canto de Agua and Totoral, 27°56’48.5”S, 70°53’40”W, 274 m, 15 Sept. 2003, *F. Luebert & L. Kritzner* 1824 (BSB); Road to Yerbas Buenas, near Panamericana, 28°1’7.5”S, 70°33’11.3”W, 521 m, 20 Sept. 2003, *F. Luebert & L. Kritzner* 1868 (BSB); Sierra Los Sapos, 28°2’30.5”S, 70°25’5.3”W, 840 m, 17 Sept. 2005, *F. Luebert & N. García* 2492/886 (BSB, SGO); Quebrada de Los Sapos, Dec. 1887, *G. Geisse* s.n. (CONC 121883, SGO 72724, 72728 ); Panamericana, 70 km N of Vallenar, 18 Sept. 1966, *G. Kausel* 5095 (SGO). Región de Atacama, Prov. Huasco: Crossroad Totoral–Canto de Agua, 28°4’38.7”S, 70°42’41.7”W, 300 m, 13 Sept. 2004, *F. Luebert, C. Becker & N. García* 2008 (BSB); Carrizal Bajo, 10 Dec. 1989, *X. Duarte* s.n. (ULS 1518); Carrizal Bajo, 28°5’27.7”S, 71°8’43”W, 0–20 m, 15 Oct. 2009, *F. Luebert & E. Daniłowicz* 2983 (SGO); Carrizal Bajo, 25 m, Sept. 1885, *F. Philippi* s.n. (SGO 42230, 54376); Carrizal Bajo, 30 Sept. 1952, *M. Ricardi* 2299 (CONC); Valle Carrizal, near the coast, 28°6’26.4”S, 71°6’15.7”W, 55 m, 26 Sept. 2004, *F. Luebert & C. Becker* 2167 (BSB); Road to Mina Oriente, 28°6’51.1”S, 71°5’49.8”W, 30 m, 19 Oct. 2005, *F. Luebert & C. Becker* 2899 (BSB); Quebrada Carrizal, 28°6’45.2”S, 71°6’57.4”W, 26 m, 15 Sept. 2003, *F. Luebert & L. Kritzner* 1821 (BSB); Quebrada Carrizal, 28°6’45.2”S, 71°6’57.4”W, 30 m, 21 Jan. 2004, *F. Luebert & R. Torres* 1972 (BSB, SGO); Road to Carrizal Bajo, near Mina Oriente, 30 Oct. 1987, *M. Muñoz-Schick & I. Meza* 2349 (SGO); Ravine E of Carrizal Bajo, 28°7’47”S, 71°5’1.1”W, 37 m, 14 Sept. 2003, *F. Luebert & L. Kritzner* 1815 (BSB); Carrizal Alto, Cerro Azúcar, 5 Sept. 2004, *S. Teillier* s.n. (BSB); Carrizal Bajo, valley 5 Km from the town, 300–320 m, 14 Nov. 1985, *F. Schlegel*

8033 (CONC, SGO); Chañarcito near Carrizal, 26 Sept. 1885, *[F. Philippi]* s.n. (lectotype of *Heliotropium izagae* SGO 42231 [fragm.: GH], duplicates B†, BM, SGO 54378, possible isotype: K); ca. 10 km W of Canto de Agua, 25 Oct. 1997, *C. Ehrhart & J. Grau* 97/1277 (M); Carrizal, road to Canto de Agua, 23 Sept. 1977, *M. Muñoz Schick, I. Meza & E. Barrera* 1111 (SGO); 3 Km from Canto de Agua on road to Carrizal Bajo , 26 Oct. 1965, *M. Ricardi, C. Marticorena & O. Matthei* 1518 (CONC); Quebrada de Carrizal, 28°9’S, 71°3’W, 9 Oct. 1987, *S. Teillier* 987 (CONC, SGO); Road to El Bolsico, 28°13’2.7’’S, 70°32’46.6’’W, 622 m, 20 Sept. 2003, *F. Luebert & L. Kritzner* 1872 (BSB); Road Carrizal Bajo–Huasco, 50 m, 13 Oct. 1991, *S. Teillier, L. Villarroel & R. Torres* 2571 (SGO); 19–20 km N of the southern (main) road to Carrizal Alto and Canto de Agua, 28°15’19’’S, 70°41’46’’W, 400 m, 15 April 1994, *C.M. Taylor & A. Pool* 11612 (CONC, SGO); Longitudinal highway, 5 Km N of crossroad to Carrizal Bajo, 26 Oct. 1987, *M. Muñoz-Schick & I. Meza* 2234 (SGO); Panamericana, km 695 from Santiago, 20 Sept. 1967, *G. Kausel* 5315 (SGO); North of Playa de Luna, 28°19’23.2’’S, 71°9’6’’W, 38 m, 14 Sept. 2003, *F. Luebert & L. Kritzner* 1809 (BSB); N of Vallenar, crossroad to Mina Los Colorados 7–10 km, 2 Nov. 1991, *M. Muñoz Schick, S. Teillier & I. Meza* 2897 (SGO); Quebrada Baratillo, 28°21’56.7’’S, 71°7’21’’W, 150 m, 14 Sept. 2003, *F. Luebert & L. Kritzner* 1802 (BSB); La Arena, 28°28’40.7’’S, 71°8’57.2’’W, 0 m, 14 Sept. 2003, *F. Luebert & L. Kritzner* 1800 (BSB); Huasco, 2 Nov. 1930, *F. Jaffuel* 1178 (CONC); Huasco, 24 Sept. 1977, *O. Zoellner* 9811 (CONC); Huasco, Oct. 1866, *R.A. Philippi* s.n. (holotype of *Heliotropium rosmarinifolium* SGO 42229 [fragm.: GH], isotype: B†); Huasco, 10 Km al Este, 28°28’S, 71°12’W, 8 Oct. 1987, *S. Teillier* 918 (CONC, SGO); Valley of río Huasco near Freirina, 21 Sept. 1962, *K. Kubitzki* 291 (CONC, M); Freirina, 27 Jan. 1950, *A. Pfister* s.n. (CONC); Freirina, 19 Sept. 1962, *P. Weisser* s.n. (CONC 105393); 20–30 km S of Freirina, road to Quebradita, 300–500 m, 9 Sept. 1949, *W. Biese* 2594 (SGO); Road Vallenar–Huasco, 20 km from Vallenar, 20 Sept. 1966, *E. Kausel* 5117 (SGO); Panamericana, 8 km N of Vallenar, 400 m, 13 Oct. 1991, *S. Teillier, L. Villarroel & R. Torres* 2563 (SGO); Panamericana, 2 km N of Vallenar, 19 Feb. 1970, *Rodriguez & Rivera* 59 (CONC); Vallenar, 18 Nov. 1974, *P.L. Meserve* s.n. (SGO 134956); Vallenar, Sept. 1885, *[F. Philippi]* s.n. (K); Ravine S of Vallenar, 19 Sept. 1952, *C. Jiles* 2212 (CONC); Vallenar, Quebrada del Jilgero, 11 Nov. 1956, *M. Ricardi & C. Marticorena* 3882 (CONC); 5 km S of Vallenar, 9 Oct. 1958, *M. Ricardi & C. Marticorena* 4872/1257 (CONC); Vallenar–La Serena, km 9, Quebrada Romero, 560 m, 10 Feb. 1988, *C. Marticorena, T. Stuessy & C. Baeza* 9938 (CONC); Freirina, Quebrada Agua del Medio on road to Maitenes, 4 Sept. 2004, *S. Teillier* s.n. (BSB); Vallenar, S exit, 28°40’59.4’’S, 70°45’56.6’’W, 627 m, 20 Sept. 2003, *F. Luebert & L. Kritzner* 1875 (BSB); Panamericana, 10 km S of Vallenar, 520 m, 3 Dec. 1996, *C. Ehrhart & E. Sonderegger* 96/1014 (MSB); 14 km S of Vallenar, 26 Oct. 1964, *M. Ricardi, C. Marticorena & O. Matthei* 1123 (CONC); Vallenar, road to Alto del Carmen, 16 Oct. 1992, *M. Muñoz-Schick* 3116 (SGO); Road to Mina Algarrobo, 18 Sept. 1965, *J. Saa* s.n. (CONC, 121880); Vallenar, Mina Algarrobo, 1000 m, Nov. 1923, *E. Werdermann* 145 (BM, F, K, M, MSB); Vallenar–Alto del Carmen, km 22, 900 m, 12 Oct. 1991, *S. Teillier, L. Villarroel & R. Torres* 2559 (SGO); Río El Transito, 1500 m, 8 Aug. 1985, *R. Callejas* s.n. (SGO 104963); San Félix, 1250 m, 9 Nov. 1956, *M. Ricardi & C. Marticorena* 3840 (CONC); Quebrada El Morado, 23 Oct. 1971, *C. Marticorena, R. Rodríguez & E. Weldt* 1792 (CONC); Domeyko, 778 m, 21 July 1973, *O. Zoellner* 6853 (CONC); Cuesta Pajonales, 17 July 1970, *O. Zoellner* 4168 (CONC); 92 km N of La Serena, 29°10’S, 71°3’W, 1000 m, 19 March 1988, *F. Squeo* 88196 (ULS); Cuesta Pajonales, exit to Los Cristales, 29°11’22.1’’S, 71°1’22.3’’W, 870 m, 20 Sept. 2003, *F. Luebert & L. Kritzner* 1877 (BSB). Región de Atacama, Indefinite: Bandurrias, *G. Geisse* s.n. (SGO 42243, 54375); Dry valleys and hills between Huasco and Copiapó, Sept. 1841, *T. Bridges* 1342 (holotype of *Heliophytum floridum* var. *bridgesii* G-DC, isotypes BM, G, K [lectoparatype of *Cochranea sinuata*]); Prov. Coquimbo, *T. Bridges* s.n. (lectotype BM, possible duplicate BM). Región de Coquimbo, Prov. Elqui: Valle Choros Bajos, 350 m, 13 June 1968, *O. Zalensky* XVIII-989 (EIF); Los Choros, 300 m, 21 Nov. 1976, *H. Valenzuela* ene-17 (EIF); Los Choros, 11 July 1976, *O. Zoellner* 8975 (CONC); Mineral Los Plomos 16 km E of Tres Cruces, 1150 m, 3 Nov. 1949, *W. Biese* 2987 (SGO); Road to Los Morros, 29°23’S, 70°50’W, 1230 m, 21 Sept. 1999, *G. Arancio* 11980 (ULS); La Higuera, road to Mina El Tofo, 29°27’13.3’’S, 71°12’34.1’’W, 370 m, 17 Sept. 2005, *F. Luebert & N. García* 2488/882 (BSB); Desert in front of El Tofo, 9 Feb. 1968, *M. Ricardi* 5463 (CONC); Near La Higuera., 18 Sept. 1958, *E. Bailey* s.n. (SGO 132568); La Higuera, 650 m, 7 Oct. 2000, *F. Luebert* 1289 (EIF); Road from Almirante Latorre to Condoriaco, km 2, 1000 m, 18 Oct. 1971, *C. Marticorena, R. Rodríguez & E. Weldt* 1535 (B, CONC); Región de Coquimbo, Indefinite: Coquimbo, N Chile, *R. Pearce* s.n. (K). Indefinite: N Chile, *W. Lobb* 442 (holotype of *Cochranea conferta* var. *auriculata* K, isotype BM); s.loc., *s.col.* (BM); s.loc., *s.col.* (SGO 54377); s.loc., *s.col.* (SGO 54379).

**6. *Heliotropium taltalense* (Phil.) I.M.Johnst.**

**CHILE**. Región de Antofagasta, Prov. Antofagasta: Quebrada Botija, 300–500 m, 25 Nov. 1996, *C. Ehrhart & E. Sonderegger* 96/984 (MSB); Quebrada Botija, 24°31'S, 70°33'W, 90 m, 12 Feb. 1998, *G. Arancio & F. Squeo* 11134 (ULS); Between Blanco Encalada and Miguel Díaz, 160 m, 15 Nov. 1996, *R. Rodríguez* 3139 (CONC); Miguel Díaz, 24°33'5.3''S, 70°32'21.2''W, 890 m, 5 Oct. 2005, *F. Luebert & N. García* 2650/1044 (BSB, SGO); Miguel Díaz, 600 m, 17 Oct. 1994, *M. Richter* 94/2 (M); Vicinity of Aguada Miguel Díaz, 1–4 Dec. 1925, *I.M. Johnston* 5414 (GH); Quebrada Rancho Monte, 24°45'S, 70°33'W, 300 m, 11 Feb. 1998, *G. Arancio & F. Squeo* 11062 (ULS); Vicinity of Aguada Cardón, 30 Nov. 1925, *I.M. Johnston* 5293 (GH, K, US); Aguada Panulcito, 24°47'55.7''S, 70°31'36.6''W, 345 m, 19 Sept. 2004, *F. Luebert, C. Becker & N. García* 2123 (BSB); Aguada Panulcito: along trail of the old Andacolla mine on slope above the waterhole, 5 Dec. 1925, *I.M. Johnston* 5476 (GH); Aguada Panulcito, 24°48'2.2''S, 70°31'32.6''W, 375 m, 19 Sept. 2004, *F. Luebert, C. Becker & N. García* 2122 (BSB); 20 km N of Paposo, Quebrada El Médano, April 1985, *H. Niemeyer* s.n. (SGO 104088); Alluvium front of cerro Carnero, N of Paposo, 24°56'14.5''S, 70°28'29.9''W, 200–300 m, 23 Oct. 2009, *F. Luebert & A. Moreira* 2998 (BSB, G, SGO); El Rincón, just north of Paposo, along traild to old Parañas mine, 7 Dec. 1925, *I.M. Johnston* 5544 (GH); Quebrada La Rinconada, N of Taltal, 200 m, 14 Jan. 1994, *Loyola* 94-9 (CONC); El Rincón, 5 Oct. 1955, *M. Ricardi* 3565 (CONC); Rinconada de Paposo, 125 m, 1 Dec. 1989, *O.Gálvez, A.Cornejo & M.Villarroel* 8 (SGO); Portezuelo Quebrada Yumbe, 25°0'S, 70°26'W, 1060 m, 14 Feb. 1998, *G. Arancio & F. Squeo* 11316 (ULS); Cuesta de Paposo, Quebrada Despoblado, 500–800 m, 17 Dec. 1993, *A. Chapin, M. Grehan & J.J. Lazare* AC 23646 (G); Paposo, 1000 m, 10 Nov. 1987, *A. Hoffmann & X. Rodríguez* 94 (CONC); Paposo, Oct. 1984, *Morales* 21 (CONC); Paposo, Dec. 1853, *R.A. Philippi* s.n. (holotype SGO 54381 [fragm. GH]); Paposo, Sept. 1909, *K. Reiche* s.n. (SGO 61442); Paposo, 10 Oct. 1983, *M. Elgueta* 26 (SGO); Paposo, road to Mina Liverpool, Quebrada Paposo, 25°1'15''S, 70°26'51.6''W, 450 m, 12 Dec. 2006, *M. Ackermann* 685 (BSB, M); Paposo, "El Gaucho" sector, 50 m, 18 Sept. 1992, *S. Teillier, P. Rundel & P.García* 2923 (SGO); Paposo, 25 Aug. 1963, *W. Hermosilla* s.n. (SGO 77388); Quebrada de Paposo, 25°1'S, 70°25'W, 350–950 m, 28 Sept. 1988, *M.O. Dillon, D. Dillon & V. Poblete* 5583 (F, MSB); Quebrada de Paposo, ca 5-6 km E of Caleta Paposo, 25°1'S, 70°25'W, 500–620 m, 10 Dec. 1987, *M.O. Dillon & S. Teillier* 5233 (F, MSB); Quebrada de Paposo, E of Caleta Paposo, Quebrada Los Yales, 25°1'S, 70°27'W, 550 m, 15 Nov. 1997, *M.O. Dillon & C. Trujillo* 8044 (CONC, F, MSB, SGO); Quebrada Los Yales, Paposo, 25 Aug. 1992, *J.C. Torres-Mura* s.n. (SGO 128786); Quebrada Portezuelo, 520 m, 4 Oct. 1991, *M. Quezada & E. Ruiz* 224 (CONC, M); Quebrada Portezuelo, 550 m, Feb. 1997, *M.León* 18 (CONC); Quebrada Portezuelo, 25°1'S, 70°27'W, 550 m, 2 July 1997, *M.León* 18 (ULS); Perales, Quebrada Guanillos, E of Paposo, 500 m, 18 Sept. 1941, *C. Muñoz & G.T. Johnson* 2950 (SGO); Paposo, Quebrada Peralito, 25°2'S, 70°26'W, 601 m, 16 Nov. 2005, *P. Guerrero & M. Rosas* 3103 (K); Quebrada de Paposo, 500 m, 4 Oct. 1991, *M. Quezada & E. Ruiz* 211 (CONC); Quebrada de Paposo, Sept. 1952, *L.E. Peña* s.n. (CONC 121867); Quebrada Peralito, 200 m, 8 Oct. 1991, *M. Quezada & E. Ruiz* 371 (CONC, M, SGO); Between Paposo and Punta Grande, 25°3'S, 70°30'W, 2 Oct. 1987, *S. Teillier* 564 (CONC, SGO); Quebrada de Paposo, Agua Perales, 24 Sept. 1953, *M. Ricardi* 2614 (CONC); Quebrada de Paposo, Quebrada Guanillos, 25°3'S, 70°30'W, 610 m, 16 Sept. 1992, *S. Teillier, P. Rundel & P.García* 2823 (F); Quebrada Destiladora, 25°5'48.6''S, 70°26'34.3''W, 550 m, 8 Oct. 2005, *F. Luebert & N. García* 2694/1088 (BSB); Quebrada Matancilla, 160 m, 6 Nov. 1985, *F. Schlegel* 7903 (CONC, SGO); Quebrada Matancilla, 25°6'44.7''S, 70°27'28.7''W, 400 m, 8 Oct. 2005, *F. Luebert & N. García* 2723/1117 (BSB); Quebrada Matancilla, 25°6'59.6''S, 70°27'31''W, 220 m, 18 Sept. 2004, *F. Luebert, C. Becker & N. García* 2101 (BSB, SGO); Taltal, Quebrada Peralito, 16 Sept. 1953, *M. Ricardi* 2462 (CONC); Hills southeast of Taltal, 25 Nov. 1925, *I.M. Johnston* 5118 (GH); Taltal, 26 Sept. 1940, *E. Barros* 6227 (GH); Taltal, 200 m, Oct. 1925, *E. Werdermann* 837 (B, CONC, F, GH, K, MSB, NY, US); Cerro Perales, 25°25'S, 70°25'W, 245 m, 16 Oct. 2005, *N. Schulz* 21F25 (ULS); Cerro Perales, ca. 5 km E of Taltal, 25°25'S, 70°25'W, 950 m, 21 Nov. 1998, *M.O. Dillon & D. Dillon* 5998 (F, MSB); Summit Cerro Perales, 25°25'11.3''S, 70°25'32.4''W, 1019 m, 17 Sept. 2004, *F. Luebert, C. Becker & N. García* 2083 (BSB, SGO); Quebrada Las Tipias, 25°26'54.1''S, 70°26'9.1''W, 275 m, 17 Sept. 2004, *F. Luebert, C. Becker & N. García* 2076 (BSB); Lomas de Taltal, near road from Taltal to the Panamaericana, 25°28'19''S, 70°26'44''W, 430 m, 25 Oct. 2002, *M. Ackermann* 501 (B, CONC); Taltal, Quebrada El Nueve, 3 Oct. 1953, *M. Ricardi* 2726 (CONC); Quebrada de Taltal, 100–200 m, 9 Sept. 1936, *G. Montero* 2881 (CONC, GH); Taltal region in Quebradas, Oct. 1889, *L. Darapsky* 30 (holotype SGO 54432 [fragm. GH]); Breas, 1888, *A. Larrañaga* s.n. (SGO 54380, 54382).

**7. *Heliotropium krauseanum* Fedde** subsp. ***krauseanum***

**PERU**. Depto. Lima, Prov. Yauyos: Road from Yauyos to Imperial, km. 25.7 after Yauyos, 12°37'18''S, 75°58'4''W, 1700 m, 8 Oct. 2002, *M. Weigend, A. Ackermann. A. Cano & M.I. La Torre* 7316 (BSB, F, K, M, MA); Road from Huancayo to San Vicente de Cañete, 161 km. from Huancayo, 12°38'39''S, 75°58'33''W, 1734 m, 22 Sept. 2001, *M. Weigend & J. Skrabal* 5887 (BSB, NY); Road from Pacaran to Yauyos, km. 26 after Pacaran, 12°48'25''S, 75°53'40''W, 1280 m, 6 Oct. 2002, *M. Weigend, A. Ackermann. A. Cano & M.I. La Torre* 7202 (BSB, F, K, M, MA). Depto. Arequipa, Prov. Caravelí: Caravelí, Lomas ca. 3 km. E of km. 655 Panamericana Sur, 350–960 m, 4 Oct. 1997, *M. Weigend & H. Förther* 97/743 (B, F, MSB); Between Atiquipa and the port of Chala, 280 m, Nov. 1915, *A. Weberbauer* 7188 (GH, MSB); Lomas de Atiquipa, near Chala, 28 July 1944, *C.A. Ridoutt* 14499 (MSB); Atiquipa, near Chala, 350–400 m, 25 Oct. 1976, *R. Ferreyra* 18681 (MSB); Lomas de Atiquipa, 300–400 m, 5 Sept. 1984, *R. Ferreyra* 20321 (MSB); Lomas de Atiquipa, 280–300 m, 9 Nov. 1952, *R. Ferreyra* 8813 (M); Lomas de Atiquipa, 300–450 m, 2 May 1983, *R. Ferreyra, E. Cerrate & M. Chanco* 8627 (MSB); Atiquipa, near Chala, 300–450 m, 2 May 1983, *R. Ferreyra, E. Cerrate & M. Chanco* 19840 (MSB); Atiquipa, 200–970 m, 6 Dec. 1997, *F.L.S.P* 468 (US); 7-8 km. N of Atiquipa, 100–120 m, 20 Sept. 1938, *C.R. Worth & J.L. Morrison* 15647 (F, G, GH, K); Nazca and Chala, km. 524, 17 Oct. 1946, *R. Ferreyra* 1387 (GH); km. 545 from Lima, 23 Aug. 1948, *R. Scolnik* 1031 (GH); km. 585 Panamericana Sur, 250 m, 3 Oct. 1997, *M. Weigend & H. Förther* 97/727 (B, F, MSB); A few km. S of km. 588, N of Atiquipa, 360 m, 19 Feb. 1994, *Anderson et al.* 7887 (F); Lomas de Okopa, between Nazca and Chala, 300–400 m, 11 Oct. 1955, *R. Ferreyra* 11485 (MSB); 628 km. from Lima (Panamerican Highway) N of Puerto Chala, 250 m, July 1956, *M. Køie* s.n. (B); Lomas de Capacc, near Chala, 200–260 m, 10 Oct. 1956, *R. Ferreyra* 11925 (MSB); Quebrada Honda, ca. 6 km. SE of Puerto Chala, at km. 655 Panamericana, 120 m, 14 Jan. 1963, *H.H. Iltis, C.M. Iltis, D. Ugent & V. Ugent* 1565 (K); 1.5 km. N of Atico (=km. 695.5 Panamericana Sur), 50 m, 4 Oct. 1997, *M. Weigend & H. Förther* 97/751 (B, F, MSB); Atico, 200 m, 16 Nov. 1957, *O. Tovar* 2679 (MSB); Atico, 100–150 m, 8 Dec. 1956, *R. Ferreyra* 12004 (MSB); Lomas de Atico, between Chala and Camaná, 5–15 m, 10 Nov. 1949, *R. Ferreyra* 6360 (MSB). Depto. Arequipa, Prov. Islay: Lomas de Cachendo (km. 1028 Panamericana Sur), 775 m, 14 Oct. 1997, *M. Weigend & H. Förther* 97/859 (B, BSB, F, MSB); Lomas de Cachendo, 900 m, 9 Feb. 1983, *M.O. Dillon, U. Molau & P.A. Matekaitis* 3295 (F); Mollendo, 2 Oct. 1931, *F. Jaffuel* 2145 (GH); Mollendo, directly back of the port, 16 Oct. 1925, *I.M. Johnston* 3533 (F); Mollendo, beach at Sta. Catarindo, 17°0'S, 72°1'W, 3 m, 3 Dec. 2006, *M. Ackermann & F. Cáceres* 630 (BSB, M); Playa Catarindo, 17°0'S, 72°1'W, 71 m, 5 to 16 Feb. 2003, *N. Dostert & F. Cáceres* 1025 (BSB); Playa Catarindo, Mollendo, 30–100 m, 14 Oct. 1997, *M. Weigend & H. Förther* 97/868 (B, MSB); Mejía, south of Mollendo, 183 m, 18 Sept. 1937, *D. Stafford* 898 (BM, K). Depto. Moquegua: Prov. Ilo: Lomas de Mostazal, ca. 10 km. S Ilo (km. 140 on coastal road Tacna-Ilo), 100–200 m, 12 Oct. 1997, *M. Weigend & H. Förther* 97/826 (BSB, F, MSB); Beach 10 km. N of Ilo, 30–40 m, 30 Nov. 1955, *R. Ferreyra* 11627 (MSB); N of Ilo, 0 m, 22 Sept. 1937, *D. Stafford* 913 (BM, K); Ilo, 150–200 m, 3 Dec. 1997, *F.L.S.P* 366 (NY); Playa Huaca Luna, 17°49'12''S, 71°8'31''W, 20 m, 3 April 2005, *C. Aedo & A. Galán de Mera* 11337 (MA). Indefinite: southern Lomas, 50 m, 16 Feb. 1974, *J. Bogner* 888 (K). **CHILE**. Región de Tarapacá, Prov. Tamarugal: Punta Pichalo Sur, 22 Sept. 2002, *R. Pinto* 171 (SGO). **INDEFINITE**. Cobija, Iquiqui et Arica, Peruvia meridionalis, 1931, *H. Cuming* 955 (BM, GH, K [ex Herb. Bentham]); Lima, *H. Cuming* 955 (K [ex Herb. Hooker]).

**7a. *Heliotropium krauseanum* Fedde** subsp. ***jahuay* Luebert**

**PERU**. Depto. Arequipa, Prov. Caravelí: Cerro Los Cerrillos, W of Panam. Highway, 52 km. S of Nazca, 15°14'S, 74°57'W, 650 m, 26 Aug. 1957, *K. Rahn* 116 (M); Lomas de Jahuay, ca. 52 km S Nazca, near border with Depto. Ica, 365–380 m, 1 Nov. 1983, *M.O. Dillon & D. Dillon* 3766 (holotype F, isotype MSB); Lomas de Jahuay, ca. 15 km NW of Chaviña, 300 m, 7 Feb. 1983, *M.O. Dillon, U. Molau & P.A. Matekaitis* 3224 (F, K); Haway entre Nazca y Chala, 17 Nov. 1957, *O. Tovar* 2740 (MSB); Near Jahuay, highway Lima-Chala, between Nazca and Atiquipa, km 545-546 highway Lima -Arequipa, 300–400 m, 7 Nov. 1947, *R. Ferreyra* 2511 (F, MSB); Jahuay, between Nazca and Chala, 400 m, 9 Nov. 1952, *R. Ferreyra* 8802 (MSB); Lomas de Jahuay, 20 Dec. 1959, *R. Ferreyra* 14011 (MSB); Jahuay, between Nazca and Chala, 300–400 m, 28 April 1983, *R. Ferreyra, E. Cerrate & M. Chanco* 19775 (MSB); Lomas de Jahuay, between Nazca and Chala, 300–400 m, 5 Nov. 1984, *R. Ferreyra* 20311 (MSB). Depto. Arequipa, Indefinite: Chala region, 457 m, April 1943, *C. Sandeman* 4019 (K).

**8. *Heliotropium inconspicuum* Reiche**

**CHILE**. Región de Antofagasta, Prov. Antofagasta: Quebrada Destiladora, 25°5’50.8’’S, 70°26’32.9’’W, 525 m, 8 Oct. 2005, *F. Luebert & N. García* 2690/1084 (BSB); Between Quebrada Destiladora and Matancilla, 25°5’33.5’’S, 70°26’13.3’’W, 685 m, 8 Oct. 2005, *F. Luebert & N. García* 2707/1101 (BSB); End of Quebrada Destiladora, 25°5’54.3’’S, 70°27’4.5’’W, 780 m, 18 Sept. 2004, *F. Luebert, C. Becker & N. García* 2093 (BSB); Quebrada Destiladora, 25°6’0.4’’S, 70°26’47.1’’W, 605 m, 18 Sept. 2004, *F. Luebert, C. Becker & N. García* 2094 (BSB); Quebrada Destiladora, 25°6’0.8’’S, 70°26’41.9’’W, 570 m, 18 Sept. 2004, *F. Luebert, C. Becker & N. García* 2095 (BSB, SGO); Quebrada Destiladora, 25°6’5.8’’S, 70°26’39.1’’W, 530 m, 18 Sept. 2004, *F. Luebert, C. Becker & N. García* 2099 (BSB); Quebrada Matancilla, 25°6’59.6’’S, 70°27’31’’W, 220 m, 18 Sept. 2004, *F. Luebert, C. Becker & N. García* 2100 (BSB); Quebrada Matancilla., 25°23’S, 70°23’W, 185 m, 18 Sept. 1992, *S. Teillier, P. Rundel & P.García* 2944 (SGO, F); Cerro Perales, hillsides of Quebrada Las Tipias, 25°25’29.3’’S, 70°26’1.2’’W, 600–700 m, 24 Oct. 2009, *F. Luebert, A. Moreira & M.O. Dillon* 3006 (SGO); Cerro Perales, Aguada Lora, 25°25’40.6’’S, 70°26’7.8’’W, 535 m, 17 Sept. 2004, *F. Luebert, C. Becker & N. García* 2081 (BSB, SGO); ca. 10 km E of Taltal, Quebrada de Taltal, 100 m, 12 Oct. 1938, *C.R. Worth & J.L. Morrison* 15788 (K); Quebrada de Taltal, 25°26’S, 70°29’W, 410 m, 17 Sept. 1992, *S. Teillier, P. Rundel & P.García* 2851 (SGO, F); Breas, 1888, *A. Larrañaga* s.n. (holotype SGO 54431, isotype GH); Taltal, Quebrada Setiembre, 6 Oct. 1954, *M. Ricardi* 3122 (CONC); Quebrada El Vetado, between Taltal and caleta Cifuncho, 600 m, 29 Sept. 1941, *E. Pisano & R. Bravo* 316 (SGO); Sierra Esmeralda, 25°52’40’’S, 70°39’8.2’’W, 600 m, 13 Oct. 2005, *F. Luebert & N. García* 2805/1199 (BSB); Sierra Esmeralda, road to Caleta Guanillos, 25°53’24.2’’S, 70°39’11.2’’W, 200 m, 13 Oct. 2005, *F. Luebert & N. García* 2783/1177 (BSB, SGO). Región de Atacama, Prov. Chañaral: Near Aguada Grande, 1925, *I.M. Johnston* 5810 (GH); Sierra Las Tipias, Pan de Azúcar National Park, 26°5’S, 70°37’W, 500 m, 30 Sept. 2005, *N. Schulz* 14 (ULS); Mirador Pan de Azúcar, 26°6’29.3’’S, 70°38’46.7’’W, 330 m, 14 Oct. 2005, *F. Luebert & N. García* 2827/1221 (BSB); Pan de Azúcar National Park, Quebrada El Castillo, 26°8’S, 70°39’W, 100–400 m, 18 Nov. 2005, *N. Schulz* PA98 (BSB). Indefinite: Coast of the prov. Atacama, Sept. 1909, *K. Reiche* s.n. (SGO 61443).

**9. *Heliotropium megalanthum* I.M.Johnst.**

**CHILE**. Región de Atacama, Prov. Copiapó: Huasco-Copiapó, 20-25 km N of Totoral, Oct. 1991, *Taylor et al.* 10802 (CONC); S of Caleta Pajonales, 27°47’30’’S, 71°1’16’’W, 18 Sept. 2002, *s.col.* (SGO 150350); Road to Caleta Pajonales, 27°50’10.6’’S, 71°0’29.1’’W, 215 m, 13 Sept. 2004, *F. Luebert, C. Becker & N. García* 2019 (BSB); Estancia Castilla, 380 m, Sept. 1965, *G. Gleisner* 54 (CONC); On road between Totoral and Bahía Totoral., 400 m, 8 Sept. 1991, *C. von Bohlen* 1374 (SGO). Región de Atacama, Prov. Huasco: Road from Totoral to Carrizal Bajo, 27°57’S, 71°8’W, 50 m, 20 Sept. 1991, *G. Arancio* 91557 (ULS); 8 km N of Carrizal Bajo, Hacienda Higueras, 20 m, 14 Nov. 1985, *Schlegel F.* 8021 (SGO); Carrizal Bajo, 25 m, Oct. 1965, *A. Garaventa* 4736 (CONC); Carrizal Bajo, 30 Sept. 1989, *J. Armesto* 89619 (ULS); Carrizal Bajo, 25 m, Sept. 1952, *M. Ricardi* 2300 (CONC); Valle Carrizal, near the coast, 28°6’26.4’’S, 71°6’15.7’’W, 55 m, 26 Sept. 2004, *F. Luebert & C. Becker* 2165 (BSB, SGO); Road to Carrizal Bajo, near Mina Oriente, 28°6’S, 71°6’W, 30 Oct. 1987, *M. Muñoz-Schick. & I. Meza* 2350 (SGO); Quebrada de Carrizal., 28°6’S, 71°7’W, 350 m, 13 Oct. 1991, *S. Teillier, L. Villarroel & R. Torres* 2567 (SGO); Carrizal Alto, Cerro Azúcar, 28°7’S, 70°57’W, 5 Sept. 2004, *S. Teillier* s.n. (BSB); Quebrada Carrizal, km 42 from Panamericana, 17 Sept. 1991, *C. Fernández & H. Niemeyer* (91)166 (SGO); Between Canto de Agua and Totoral, 28°8’25.3’’S, 70°52’37.4’’W, 295 m, 15 Sept. 2003, *F. Luebert & L. Kritzner* 1823 (BSB); Carrizal Bajo, coast, 28°8’S, 71°5’W, 4 Nov. 1987, *K.H. Rechinger & W. Rechinger* 63403 (B); ca. 10 km W of Canto de Agua, 25 Oct. 1997, *C. Ehrhart & J. Grau* 97/1280 (M); ca. 1 km W of Canto de Agua, 25 Oct. 1997, *C. Ehrhart & J. Grau* 97/1294 (M); Chañarcito near Carrizal, Oct. 1885, *F. Philippi* s.n. (BM, GH, SGO 42219, SGO 54368, SGO 54370, US 942361); Carrizal Bajo, 8 km towards Canto del Agua, 30 Sept. 1997, *M. Muñoz-Schick.* 3825 (SGO); Canto del Agua, 5 km towards Carrizal, 170 m, 23 Sept. 1977, *M. Muñoz Schick, I. Meza, E. Barrera* 1076 (SGO); Road to Carrizal Bajo, near Canto del Agua, 250 m, 2 Nov. 1991, *M. Muñoz Schick, S. Teillier, I. Meza* 2920 (SGO); Road to Carrizal Bajo near Canto del Agua, 250 m, 2 Nov. 1991, *M. Muñoz Schick, S. Teillier, I. Meza* 2921 (SGO); Chañarcito in prov. Atacama *s.col.* (K); Near Huasco, 30 m, Oct. 1966, *C. Jiles* 4987 (CONC); Huasco Bajo, 28°28’S, 71°11’W, 10 m, 30 Sept. 1989, *G. Arancio* 89614 (ULS); Huasco, Lomas, 30 m, Sept. 1978, *G. Montero* 11021 (CONC); Huasco, Sept. 1900, *K. Reiche* s.n. (SGO 54367); Lomas in front of Las Lozas, 30 m, Nov. 1956, *M. Ricardi & C. Marticorena* 3933 (CONC); Huasco, 10 m, Sept. 1977, *O. Zoellner* 9840 (CONC); 10 km E of Huasco, 28°28’S, 71°12’W, 0 m, 8 Oct. 1987, *S. Teillier* 913 (CONC, SGO); Vallenar, Estancia La Totora, 620 m, Sept. 1919, *F. Behn* s.n. (CONC 8972); Freirina, Las Totoras, Sept. 1952, *M. Ricardi*

2194 (CONC); Freirina–Cuesta La Totora, 4 km S of Freirina, 280 m, 23 Oct. 1997, *C. Ehrhart & J. Grau* 97/1225 (M); Vallenar, 15 Oct. 1980, *X. León* s.n. (ULS 605); Road to El Algarrobo mine on the west side of the hill, 2.5 km from Route 5, 28°36'36.5''S, 70°46'56.1''W, 515 m, 2 Dec. 2005, *M. Acosta, P. Guerrero & M. Rosas* 3169 (K); Freirina, Quebrada Agua del Medio on road to Maitenes, 28°38'S, 71°2'W, 4 Sept. 2004, *S. Teillier* s.n. (SGO); 'Huasco', Oct. 1866, *R.A. Philippi* s.n. (lectotype of *Heliotropium crassifolium* Phil. SGO 54364, duplicates GH, SGO 54365, possible duplicate GH [Herb. Philippi N°3]); Coquimbo [dry valleys and hills between Huasco and Copiapó], 1841, *T. Bridges* 1341 (lectotype BM, duplicate K). Región de Coquimbo, Prov. Limarí: Fray Jorge, 300 m, Sept. 1958, *J. Kummerow* s.n. (CONC 41313). Indefinite: N. Chile, *R. Pearce* 40 (K).

**10. *Heliotropium chenopodiaceum* (A.DC.) Clos**

**CHILE**. Región de Atacama, Prov. Chañaral: Atacama: km 1000, 6 Oct. 1966, *C. Jiles* 4943 (CONC); Aguada Chañarcito, S of Diego de Almagro, 810 m, 16 Oct. 1980, *J. Grau* 2169 (M); Mineral de Coipa, Dec. 1887, *E. Gigoux* s.n. (GH). Región de Atacama, Prov. Copiapó: Caldera, Sept. 1876, *P. Ortega* s.n. (SGO 54400); Road to Salar de Maricunga, km 56, 1780 m, 31 Jan. 1963, *M. Ricardi, C. Marticorena & O. Matthei* 540 (CONC); Road to Salar de Maricunga, km 56, 2250 m, 31 Jan. 1963, *M. Ricardi, C. Marticorena & O. Matthei* 545 (B, CONC); Road to Salar de Maricunga, near Puquios, 31 Jan. 1963, *M. Ricardi, C. Marticorena & O. Matthei* 517 (CONC); Puquios station, road to Maricunga, 1300 m, 20 Jan. 2004, *F. Luebert & R. Torres* 1968 (BSB); La Puerta, 1800 m, 1 Feb. 1963, *M. Ricardi, C. Marticorena & O. Matthei* 622 (CONC); La Puerta, 1000 m, 28 Oct. 1956, *M. Ricardi & C. Marticorena* 3664 (CONC); Puquios, 27°9'35.5''S, 69°53'10.8''W, 1290 m, 18 Sept. 2005, *F. Luebert & N. García* 2501/895 (BSB, SGO); Puquios, road to Tinogasta, 20 Dec. 1963, *C. Castro* s.n. (CONC); Puquios, Quebrada Paipote, 19 Nov. 1995, *K. Gengler* 117 (SGO); Quebrada de Puquios, Jan. 1885, *F. Philippi* s.n. (SGO 54401, posible type of *Eritrichium glabratum*); Quebrada de Puquios, Desert Atacama, 1865, *F. Geisse f.* s.n. (SGO 54402); Quebrada Puquíos- Garín, 800 m, 13 Oct. 1949, *W. Biese* 2651 (SGO); Road between Copiapó and Inca de Oro, 27°10'21.4''S, 70°0'52.5''W, 1430 m, 19 Sept. 2005, *F. Luebert & N. García* 2512/906 (BSB); Quebrada San Andrés, road to Salar de Maricunga, 27°10'49.6''S, 69°54'2.8''W, 1195 m, 18 Sept. 2005, *F. Luebert & N. García* 2509/903 (BSB); Road Copiapó-Tinogasta, 1200 m, 6 Feb. 1988, *C. Marticorena, T. Stuessy & C. Baeza* 9815 (CONC); Quebrada Paipote, Ladrillos , 13 Oct. 1949, *W. Biese* 2664 (SGO); Quebrada Paipote, Jan. 1885, *F. Philippi* s.n. (SGO 42266); Quebrada Paipote, 27°12'S, 69°56'W, 900 m, 5 Dec. 2002, *C. Ehrhart* 2002/117 (M); 15 km N Copiapó, road to Adrianitas off Panamrican Highway, 500 m, 18 Sept. 1987, *C. Hannington* 24 (K, SGO); road to Tinogasta, 9 km before Puquios, 1090 m, 25 Oct. 1964, *M. Ricardi, C. Marticorena & O. Matthei* 1106 (CONC, G); Road to Tinogasta, Quebrada Cruz de Cañas, 1100 m, 6 Jan. 1973, *C. Marticorena, O. Matthei & M. Quezada* 479 (CONC); Quebrada Garín, 30 km E of Chulo, 2000 m, 13 Oct. 1949, *W. Biese* 2641 (SGO); Unidad 121 ducto CMP, 27°15'S, 70°23'W, 489 m, 25 Sept. 2004, *G. Arancio* 15166 (ULS); Quebrada San Andrés, road to Salar de Maricunga, 27°16'27.8''S, 70°1'57.5''W, 885 m, 18 Sept. 2005, *F. Luebert & N. García* 2510/904 (BSB); Road to Maricunga, 870 m, 20 Jan. 2004, *F. Luebert & R. Torres* 1969 (BSB); Piedra Colgada, 250 m, 10 Sept. 1954, *C. Jiles* 2595 (CONC, M); Piedra Colgada, Sept. 1885, *F. Philippi* s.n. (lectotype of Cochranea sentis SGO 54434, duplicates BM, GH [fragm.], SGO 42226); 4 km N of cross to Negro Francisco on road to Inca de Oro, 860 m, 29 Oct. 1991, *M. Muñoz-Schick, S. Teillier, I. Meza* 2718 (SGO); Panamericana, 6 km N of Paipote, 24 Oct. 1965, *M. Ricardi, C. Marticorena & O. Matthei* 1469 (CONC); 1st km of road from Copiapó to Inca de Oro, 600 m, 29 Oct. 1991, *M. Muñoz-Schick, S. Teillier, I. Meza* 2704 (SGO); 1st km of road from Copiapó to Inca de Oro, 600 m, 29 Oct. 1991, *M. Muñoz-Schick, S. Teillier, I. Meza* 2706 (SGO); Mountains NE of Copiapó, 300 m, 14 Sept. 1936, *G. Montero* 3000 (CONC, GH); Coquimbo [mountains near the Andes valleys of Copiapó], 1841, *T. Bridges* 1339 (lectotype of Cochranea ercoidea BM, duplicates F, GH, K); Vicinity of Copiapó, 900 m, 17 Nov. 1925, *I.M. Johnston* 5027 (US); Totoralillo, E side Copiapó valley, 700–800 m, 13 Oct. 1949, *W. Biese* 2678 (SGO); Paipote, 440 m, 31 Jan. 1973, *O. Zoellner* 6997 (CONC); Between Paipote and Tierra Amarilla, 27°25'49.1''S, 70°16'5.3''W, 458 m, 19 Sept. 2003, *F. Luebert & L. Kritzner* 1859 (BSB); S of Copiapó, 27°27'36.9''S, 70°22'37.2''W, 850 m, 19 Sept. 2003, *F. Luebert & L. Kritzner* 1860 (BSB); Copiapó-Vallenar, km 10, Quebrada Cardones, 760 m, 9 Feb. 1988, *C. Marticorena, T. Stuessy & C. Baeza* 9919 (CONC); Tierra Amarilla, 500 m, Sept. 1924, *E. Werdermann* 399 (BM, CONC, F, G, GH, K, M, NY); Tierra Amarilla–Las Juntas, Quebrada Molle Alto 3 km after cross to Mina Tres Marías, 970 m, 29 Oct. 1997, *C. Ehrhart & J. Grau* 97/1356 (M); Panamericana km 723, S of Copiapó, 480 m, 26 Nov. 1980, *J. Grau* 2528 (M); Travesia, 5 Nov. 1969, *C. Jiles* 5274 (CONC); Travesia, 18 Sept. 1965, *J. Saa* s.n. (CONC 121860); Quebrada Cerrillos, 15 km E of Estación Checo, 700–900 m, 14 Oct. 1949, *W.*

*Biese* 2744 (SGO); Road to Nantoco, 27°36’48.2”S, 70°27’45.8”W, 704 m, 19 Sept. 2003, *F. Luebert & L. Kritzner* 1865 (BSB); Road to Nantoco, 27°36’30.6”S, 70°19’30.1”W, 921 m, 19 Sept. 2003, *F. Luebert & L. Kritzner* 1866 (BSB); Quebrada de Serna, 1885, *F. San Roman* s.n. (SGO 54403); Quebrada La Rosa, 620 m, 8 Jan. 1973, *C. Marticorena, O. Matthei & M. Quezada* 601 (CONC); Chanarcillo, Sept. 1885, *F. Philippi* s.n. (SGO 42237, 54399); Chañarcillo, 27°48’12.8”S, 70°24’37.1”W, 946 m, 20 Sept. 2003, *F. Luebert & L. Kritzner* 1867 (BSB); Chañarcillo, *s.col.* (BM); Between Vallenar and Copiapó, 30 Jan. 1963, *M. Ricardi, C. Marticorena & O. Matthei* 509 (CONC); Bandurrias, 22 Sept. 1977, *O. Zoellner* 9780 (CONC); 74 km S of Copiapó, Panamericana, 1 Nov. 1990, *O.F. Clarke* 2204 (CONC). Región de Atacama, Prov. Huasco: Yerba Buena, *Ph. King* s.n. (SGO 42238); Yerba Buena, Oct. 1871, *T. King* 10 (SGO, K); Yerba Buena, 19 May 1875, *E.C. Reed* s.n. (BM); Yerba Buena, *s.col.* (BM); Yerba Buena, near Carrizal, *[A. Borchers]* s.n. (GH, SGO 42233, SGO 54356); Chañarcito, 26 Sept. 1885, *A. Borchers* 54 (BM); Road Copiapó to Vallenar, km 33, 26 Oct. 1964, *M. Ricardi, C. Marticorena & O. Matthei* 1120 (CONC); Panamericana, N of Vallenar, near Chacritas, 19 Sept. 1966, *E. Kausel* s.n. (SGO 109222, 109223); Llano Chacritas, ca. 16 km N of Vallenar, 28°25’S, 70°43’W, 700 m, 2 Dec. 1987, *M.O. Dillon & S. Teillier* 5031 (F, MSB); 15 km N of Vallenar, 28°26’S, 70°43’W, 12 Oct. 1994, *S. Teillier & R.Torres* 3903 (SGO); Huasco, 19 Sept. 1963, *Monypenny* 47 (CONC); Huasco, Oct. 1866, *R.A. Philippi* s.n. (lectotype of *Heliotropium sclerocarpum* SGO 54348, duplicates GH [fragm.], SGO 42241); 1 km N of Vallenar, 28°32’51.4”S, 70°45’22.2”W, 490 m, 19 Oct. 2005, *F. Luebert & C. Becker* 2907 (BSB, SGO); Vallenar, 27 Oct. 1951, *C. Jiles* 2074 (CONC); Vallenar, faldeo del aeródromo, 24 Oct. 1951, *C. Jiles* 2074 (M); 5 km S of Vallenar, 9 Oct. 1958, *M. Ricardi & C. Marticorena* 4876/1261 (CONC); 5 km S of Vallenar, 0 m, Oct. 1987, *S. Teillier* 733 (CONC); Freirina, Quebrada Agua del Medio on road to Maitenes, 4 Sept. 2004, *S. Teillier* s.n. (BSB, SGO); Road La Totora-El Morro, km 2 from Chanchoquín, 28°45’S, 70°14’W, Feb. 2004, *S. Teillier* 5553 (BSB); El Transito valley, 900 m, 13 Dec. 1941, *E. Pisano & R. Bravo* 1042 (CONC); 5 km N of Algarrobo, road between Vallenar and Algarrobo, 17 Sept. 1957, *G. Looser* 5783 (A, G); ca. 20 km S of Vallenar, road from Vallenar to Algarrobo, 17 Sept. 1957, *G. Looser* 5782 (G); Road to Mina Algarrobo, Sept. 1965, *J. Saa* s.n. (CONC 121864); Algarrobo, Sept. 1957, *J. Martinez* s.n. (CONC 121865); 30 km from Vallenar to La Serena, 1000 m, 13 Nov. 1987, *K.H. Rechinger & W. Rechinger* 63659 (B); Llano Palacios, 28°50’31.6”S, 70°49’5.9”W, 1006 m, 20 Sept. 2003, *F. Luebert & L. Kritzner* 1876 (BSB); El Transito, E of Vallenar, 1200 m, 1 Jan. 1926, *I.M. Johnston* 5884 (K); Rio Conay, 2000 m, 8 Aug. 1985, *R. Callejas* s.n. (SGO 104964); Rio Conay, 1700 m, 13 Oct. 1983, *C. Marticorena* 9544 (CONC, G); Domeyko, Quebrada de Algarrobal, 600 m, 16 Nov. 1956, *M. Ricardi & C. Marticorena* 3994 (CONC); Road El Tránsito–Conay., 1300 m, 12 Oct. 1991, *S. Teillier, L. Villarroel & R. Torres* 2555 (SGO); Rio Conay, bteween Junta Valeriano and Quebrada Albaricoque, 1600 m, 14 Feb. 1981, *M.T. Kalin* 81667 (CONC); Rio Chollay, 28°59’S, 70°9’W, 1500 m, 16 Jan. 1994, *G. Arancio, F. Squeo & M. León* 94065 (CONC, ULS); Road Domeyko–Carrizalillo, 9 km after the cross, 21 Oct. 1997, *C. Ehrhart & J. Grau* 97/1170 (M); Road Domeyko–Carrizalillo, after the cross, 21 Oct. 1997, *C. Ehrhart & J. Grau* 97/1179 (M); Road to Las Campanas observatory, 15 km to the E after the cross, 16 Oct. 1992, *M. Muñoz-Schick* 3135 (SGO); 33 km S drom San Felix, on road to Campamento El Colorado on the Proyecto Pascua (=16 km below the Campamento), 29°9’79”S, 70°21’23”W, 1850 m, 21 Oct. 1997, *U. Eggli & B.E. Leuenberger* 2988 (B, CONC, SGO); Cuesta de Pajonales, 29°7’S, 71°1’W, 10 Oct. 1987, *S. Teillier* 1021 (SGO); Cuesta Pajonales, 30 Oct. 1991, *G. Arancio* 91724 (ULS); Cuesta Pajonales, 2 km N of mina Monte Cristo, 29°9’S, 70°59’W, 1220 m, 2 Dec. 1987, *M.O. Dillon & S. Teillier* 5015 (F); Between Mineral Los Cristales and La Laja, 1300 m, 22 Oct. 1971, *C. Marticorena, R. Rodriguez & E. Weldt* 1743 (CONC); Incahuasi, 16 Sept. 1957, *M. Ricardi & C. Marticorena* 4370/755 (CONC); S of Incahuasi, road Vallenar-La Serena, 16 Feb. 1968, *M. Ricardi* 5547 (CONC). Región de Coquimbo, Prov. Elqui: Road Panamericana to Choros Bajos, km 3, 200 m, 21 Oct. 1971, *C. Marticorena, R. Rodriguez & E. Weldt* 1655 (CONC); Quebrada Honda, 11 Oct. 1965, *V. Rojas* s.n. (CONC 121866); Road Condoriaco- Almirante Latorre, km 4, 1250 m, 18 Oct. 1971, *C. Marticorena, R. Rodriguez & E. Weldt* 1532 (B, CONC); Quebrada Calvario, 29°44’S, 70°29’W, 1730 m, 17 Jan. 2000, *G. Arancio & F. Squeo* 12734 (ULS); Cross to La Silla observatory, 850 m, 8 Oct. 1991, *G. Arancio* 91615 (ULS); Cross to La Silla observatory, 29°45’S, 70°54’W, 850 m, 30 Oct. 1991, *G. Arancio* 91731 (ULS); Cuesta La Viñita, E of Marquesa, road to Mineral de Arqueros., 20 Sept. 1957, *C. Muñoz* 4225 (SGO); Road Marquesa-Condoriaco, Cuesta La Viñita, 950 m, 18 Oct. 1971, *C. Marticorena, R. Rodríguez & E. Weldt* 1524 (CONC); Cuesta de La Viñita, 1250 m, 21 Sept. 1957, *M. Ricardi & C. Marticorena* 4531/916 (CONC); Arqueros, 16 Oct. 1963, *C. Marticorena & O. Matthei* 317 (CONC); Arenales de Huanta, 25 km E of Rivadavia, along Rio Turbio, 1100 m, 19 Nov. 1940, *R. Wagenknecht* 18111 (CONC 50221, G, US); Estero de Guanta, 1500 m, 17-18 Jan. 1926, *I.M. Johnston* 6232 (US); Between Huanta and Las Juntas, 1700–2000 m, 6 April 1975, *J Grau & G. Grau* 1642 (M); Quebrada Huanta, 1300 m, 6 Nov.

1991, *G. Arancio* 91804 (ULS); Huanta, 6 Dec. 1989, *M. Ponce* s.n. (ULS); Road Juntas-Rivadavia, Rio Turbio, 1700 m, 11 Dec. 1979, *C. Villagran, M.T. Kalin, J. Armesto & [P.] Moreno* 1967 (CONC); Chapilca, Rio Turbio, 20 Sept. 1974, *O. Zoellner* 7857 (CONC); Rio Turbio, 30 Dec. 1978, *O. Zoellner* 10434 (CONC); Río Turbio, 15 June 2003, *N. García* s.n. (BSB); Río Turbio, 22 km E of Rivadavia, Oct. 1940, *R. Wagenkneckt* 4487 (G, GH, MSB); Río Turbio, en el camino a Hunata, 1000 m, 19 Nov. 1940, *R. Wagenknecht* 5779 (A, G); Road from La Pelicana to Arqueros, km 7, 16 Oct. 1963, *C. Marticorena & O. Matthei* 296 (CONC); Road from Vicuña to Embalse La Laguna, 29°54'S, 70°18'W, 1400 m, 27 Nov. 2002, *C. Ehrhart* 2002/68 (M); Ruta 41 to Paso Agua Negra, km 148 after Junta de Toro, 29°55'S, 70°10'W, 2050 m, 3 Dec. 1988, *G. Arancio* 88382 (ULS); Rivadavia, Jan. 1904, *K. Reiche* 5 (GH, SGO 54355); 15 km E of Rivadavia, 25 Dec. 1971, *K. Beckett, M. Cheese & J. Watson* 4672 (SGO); El Molle, 5 Oct. 1966, *C. Jiles* 4922 (CONC); El Molle, 5 Oct. 1966, *C. Jiles* 4923 (CONC); La Serena, Puerto Aereo El Pan de Azúcar, 26 Sept. 1953, *R.A. Philippi* s.n. (SGO 69524); Road from Vicuña to Embalse La Laguna, km 44, Río Turbio, 1110 m, 5 Dec. 1996, *C. Ehrhart & E. Sonderegger* 96/1053 (MSB); Road from de Rivadavia to Paihuano, 800 m, 23 Sept. 1948, *A. Pfister* s.n. (CONC); Road Paihuano-Rivadavia, 28 Sept. 1948, *F. Behn* s.n. (CONC); Paihuano, 400 m, , *E. Sepúlveda* s.n. (ULS); Paihuano, 22 Oct. 1983, *M.T. Jofré* s.n. (ULS); Paihuano, 22 Oct. 1983, *P. Tejo* s.n. (ULS); Paihuano, 950 m, 18 Sept. 1948, *A. Pfister* s.n. (CONC); Paihuano, 18 Oct. 1937, *Gajardo* s.n. (CONC 50173); Quebrada San Carlos, 16 Oct. 1974, *R. Osorio, R. Torres, C. Villagrán & G. Gómez* s.n. (SGO 132054); Quebrada San Carlos, 16-17 Oct. 1974, *R. Torres, C. Villagrán & C. Gómez* s.n. (CONC 121858); Elqui valley E of Vicuña, ca. 5 km below Monte Grande, 1000 m, 2 Aug. 2000, *L. Landrum & S. Landrum* 9848 (SGO); Puente San Guillermo along Río Claro, between Rivadavia and Monte Grande, 880 m, 14 Oct. 1940, *G. Looser* 4292 (CONC, G); Cerro Los Mantos, 670 m, 12 Oct. 1985, *M. Mahu* s.n. (SGO 102946); Tres Cruces, 1650 m, Oct. 1878, *F. Philippi* s.n. (SGO 42238, 54354). Región de Coquimbo, Prov. Limarí: Seron, 30 Aug. 1957, *C. Jiles* 3152 (CONC); Corral Quemado, 30 Oct. 1956, *C. Jiles* 3118 (CONC); Corral Quemado, Llano Los Pingos, 600–1000 m, 30 Oct. 1956, *C. Jiles* 3058 (CONC, M); Road between Fundina and Serón, 30°22'31.3''S, 70°48'22.9''W, 829 m, 15 Sept. 2005, *F. Luebert & N. García* 2462/856 (BSB, SGO); Colliguay, 30 Sept. 1994, *L. Olivares* s.n. (ULS); Los Molles, 8 Dec. 1957, *C. Jiles* 3348 (CONC, M); Rio Molles, 1600 m, 11 Oct. 1959, *C. Jiles* 3681 (CONC); Fray Jorge, 800–900 m, 26 Nov. 1983, *E. Sepúlveda* s.n. (ULS). Región de Coquimbo, Prov. Choapa: Aucó, El Bolsico, 1100 m, 5 July 2003, *F. Luebert* 1736 (BSB); Aucó, Quebrada El Cuyano, 840 m, 6 July 2003, *F. Luebert* 1740 (BSB). Región de Coquimbo, Indefinite: Coquimbo, 1885, *F. Philippi* s.n. (US 942630); Coquimbo, *R. Pearce* s.n. (holotype of *Heliotropium pearcei* SGO 42236); Coquimbo, *s.col.* (K); Prov. Coquimbo, 1839, *C. Gay* s.n. (lectotype G-DC, possible duplicates BM, F515900 [fragm.], G, GH, K); Saturno, Serena, etc., Oct. 1936, *C. Gay* 1075 (SGO [photo MSB]). Indefinite: Desert of Atacama, Sept. – Oct. 1890, *T. Morong* 1342 (K); Chile, *[J.] Lindley* s.n. (NY); s.loc., *s.col.* (BM); s.loc., *s.col.* (GH); s.loc., *s.col.* (K); s.loc., *s.col.* (SGO 54405).

### 11. *Heliotropium myosotifolium* (A.DC.) Reiche

**CHILE**. Región de Atacama, Prov. Copiapó: Caldera, *s.col.* (K); Bandurrias, 265 m, Sept. 1976, *O. Zoellner* 9075 (CONC); Bandurrias, 265 m, 25 Sept. 1976, *O. Zoellner* 9270 (CONC); 2 km Caseron, 10 Oct. 1965, *M.E. Alfaro* s.n. (CONC 121876); Vicinity of Copiapó, 900 m, 17 Nov. 1925, *I.M. Johnston* 5027 (K); Panamericana km 790, S of Copiapó, 17 Oct. 1980, *J. Grau* 2199 (BM); Panamericana km 790, S of Copiapó, 17 Oct. 1980, *J. Grau* 2129 (M); Panamericana km 723, S of Copiapó, 480 m, 26 Nov. 1980, *J. Grau* 2528 (BM); La Travesia, between Vallenar and Copiapó, 27 Oct. 1961, *A. Garaventa* 4396 (CONC); La Travesia, between Vallenar and Copiapó, 17 Oct. 1961, *A. Garaventa* s.n. (CONC 48602); Travesia, 5 Nov. 1969, *C. Jiles* 5274 (M); Quebrada Los Lirios, 27°33'S, 70°23'W, 450 m, 6 Sept. 1991, *G. Arancio* 91412 (ULS); Quebrada Los Lirios, 2 Oct. 1997, *M. Muñoz-Schick* 3827 (SGO); Road between Copiapó and Vallenar, 19 Sept. 1952, *C. Jiles* 2175 (CONC, M); Llano de Churque, S of Copiapó, 7 Oct. 1987, *S. Teillier* 838 (CONC, SGO); Llano de Churque, S of Copiapó, 7 Oct. 1987, *S. Teillier* 839 (CONC); Barros Luco, 8 Nov. 1956, *M. Ricardi & C. Marticorena* 3812 (CONC); Barros Luco, 8 Nov. 1956, *M. Ricardi & C. Marticorena* 3813 (CONC); Pabellan near Copiapó, 1885, *F. San Roman* s.n. (SGO 54404); Panamericana S of crossroad to Nantoco, 27°40'13.6''S, 70°28'15.4''W, 680 m, 25 Sept. 2004, *F. Luebert & C. Becker* 2162 (BSB, SGO); Panamericana Copiapó-Vallenar, km 38, 26 Oct. 1965, *M. Ricardi, C. Marticorena & O. Matthei* 1505 (CONC); Sierra Atacama, 39 km S of Copiapó., 175 m, 22 Sept. 1941, *C. Muñoz P. & G.T. Johnson* 1946 (SGO); 50 km before Copiapó, Vallenar-Copiapó, 25 Sept. 1952, *M. Ricardi* 2220 (CONC); Estancia Castilla, 28 Oct. 1965, *F. Behn* s.n. (CONC 35807); Estancia Castilla, 17 Sept. 1965, *G. Gleisner* 46 (CONC). Región de Atacama, Prov. Huasco: Yerba

Buena, 28 Sept. 1885, *[A. Borchers]* s.n. (lectotype of *Heliotropium canum* SGO 54347, isotypes BM, GH, K, SGO 42222, US 942362); Yerba Buena, 1885, *R. Godoi de Collao* s.n. (GH, SGO 54398); Canto de Agua–Totoral, 28°4’45.2”S, 70°44’40.2”W, 330 m, 13 Sept. 2004, *F. Luebert, C. Becker & N. García* 2011 (BSB, SGO); Cross Totoral-Canto de Agua, 28°4’38.7”S, 70°42’41.7”W, 300 m, 13 Sept. 2004, *F. Luebert, C. Becker & N. García* 2009 (BSB); Carrizal Bajo, 10 Oct. 1965, *A. Garaventa* 4734 (B, CONC); Quebrada Chuschampis, 480 m, 8 Jan. 1973, *C. Marticorena, O. Matthei & M. Quezada* 604 (CONC); Carrizal, 450 m, 11 Nov. 1969, *C. Jiles* 5526 (CONC); Quebrada de Carrizal, 250 m, 13 Oct. 1991, *S. Teillier, L. Villarroel & R. Torres* 2568 (CONC, SGO); Carrizal Alto, Cerro Azucar, 5 Sept. 2004, *S. Teillier* s.n. (BSB); 5 km N of crossroad to Carrizal Bajo, 26 Oct. 1987, *M. Muñoz-Schick & I. Meza* 2227 (SGO); El Algarrobal, 19 Sept. 1952, *C. Jiles* 2179 (CONC, M); ca. 1 km W of Canto de Agua, 25 Oct. 1997, *C. Ehrhart & J. Grau* 97/1291 (M); Canto del Agua, 5 km towards Carrizal, 170 m, 23 Sept. 1977, *M. Muñoz Schick, I. Meza & E. Barrera* 1094 (SGO); Chañarcito near Carrizal, Sept. 1885, *F. Philippi* s.n. (BM, GH [fragm.], K, SGO 42225, 54346 [photo F, GH, MSB, NY, US]); Valle Carrizal, Sept. 1885, *F. Philippi* s.n. (GH); Valle de Carrizal o del Huasco, 26 Sept. 1885, *[F. Philippi]* s.n. (holotype of *H. hipidulum* SGO 54345); 3 km from crossroad to Los Colorados on road to Carrizal Bajo, 290 m, 23 Sept. 1977, *M. Muñoz Schick, I. Meza, E. Barrera* 1047 (SGO); Vallenar, road to Carrizal Bajo., 1 Oct. 1992, *M. Muñoz-Schick* 2995 (SGO); Copiapó, 1 hour towards Vallenar, Quebrada on the left, 21 Sept. 1977, *M. Muñoz Schick, I. Meza, E. Barrera* 1023 (SGO); 36 km N of Vallenar, near Chacritas, Sept. 1968, *E. Kausel* 5101 (SGO); 30 km N of Vallenar, 17 Sept. 1957, *M. Ricardi & C. Marticorena* 4393/778 (CONC); 30 km N of Vallenar, 17 Sept. 1957, *A.L. Cabrera* 12637 (K); In front of Cerro Yunque, roadside, 24 Oct. 1984, *M. Muñoz-Schick* 1956 (SGO); N of Vallenar, crossroad to Mina Los Colorados, 7-10 km, 2 Nov. 1991, *M. Muñoz Schick, S. Teillier, I. Meza* 2890 (SGO); Quebrada del Pretil, 14 Nov. 1956, *M. Ricardi & C. Marticorena* 3971 (CONC); 20 km N of Vallenar, 28°30’S, 70°47’W, 7 Oct. 1987, *S. Teillier* 907 (SGO); Mina Lapingo, 28°31’S, 70°36’W, 1500 m, 31 Oct. 1991, *G. Arancio* 91692 (ULS); Freirina, Las Totoras, 24 Sept. 1952, *M. Ricardi* 2195 (CONC, M); Freirina–Cuesta La Totora, 4 km S of Freirina, 280 m, 23 Oct. 1997, *C. Ehrhart & J. Grau* 97/1219 (M); 15 km N of Vallenar, along the highway, 28°35’S, 70°16’W, 4 Nov. 1987, *K.H. Rechinger & W. Rechinger* 63313 (B, NY); 8 km N of Vallenar, 430 m, 13 Oct. 1991, *S. Teillier, L. Villarroel & R. Torres* 2562 (SGO); Vallenar, Sept. 1952, *Peña* s.n. (CONC 121856, 121875); Vallenar, 17 May 1952, *Peña* s.n. (CONC 121873); Quebrada El Morado, 23 Oct. 1971, *C. Marticorena, R. Rodríguez & E. Weldt* 1789 (CONC); Cuesta Pajonales, km 755, 11 Nov. 1969, *C. Jiles* 5507 (CONC). Región de Atacama, Indefinite: Road between Copiapó and Vallenar, 610 m, 7 Sept. 1991, *C. von Bohlen* 1324 (SGO); Coquimbo [barren and stony hills between Huasco and Copiapó], 1841, *T. Bridges* 1338 (holotype G-DC, isotypes BM, G, GH, K). Indefinite: Coquimbo, *T. Bridges* s.n. (holotype of *Cochranea hebecula* BM, possible isotypes BM, F 515813 [fragm.]); N Chile, *W. Lobb* 440 (holotype of *Cochranea hispidula* K, isotype BM); Quinteros, Jan. 1890, *F. Albert* s.n. (GH [fragm.], SGO 54433, 42248 [photo F, GH, MSB, NY]); s.loc., *s.col.* (GH).

**12. *Heliotropium stenophyllum* Hook. & Arn.**

**CHILE**. Región de Atacama, Prov. Huasco: Huasco, 19 Sept. 1963, *Monypenny* 46 (CONC); Huasco, 1920, *R.E. López* s.n. (holotype of Heliotropium huascoense GH); Punta del Huasco, 28°28’7.9”S, 71°14’73.1”W, 20 m, 19 Oct. 2005, *F. Luebert & C. Becker* 2902 (BSB, SGO); Punta del Huasco, 1889, *F. Vidal* s.n. (SGO 54366); Between La Serena and Vallenar, 16 Oct. 1971, *A. Garaventa* 4237 (CONC); Panamericana, Domeyko to Vallenar, 9 Oct. 1971, *E. Kausel* 5488 (SGO); Isla Chañaral, 115 m, 17 Nov. 2002, *G. Arancio* 15054 (CONC); Isla Chañaral, 29°1’S, 71°37’W, 7 March 1991, *J. Capella* 91029a (ULS); Chañaral de Aceituna, 23 Oct. 1971, *C. Marticorena, R. Rodríguez & E. Weldt* 1835 (CONC); Chañar de Aceitunas, 60 km W of Domeyko, 300–500 m, 8 Sept. 1949, *W. Biese* 2564 (SGO). Región de Coquimbo, Prov. Elqui: Isla Damas, 29°14’S, 71°31’W, 30 m, 31 Aug. 2002, *G. Arancio* 14849 (CONC, ULS); Isla Damas, 29°14’S, 71°31’W, 30 m, 31 Aug. 2002, *G. Arancio* 14876 (CONC, ULS); Isla Choros, 29°15’S, 71°32’W, 70 m, 19 Oct. 2002, *G. Arancio* 14911 (ULS); Punta Choros, 29°14’S, 71°31’W, 30 m, 30 April 2000, *G. Arancio & F. Squeo* 14475 (ULS); Los Choros, Quebrada 6 km from the beach, 150 m, 10 Oct. 1975, *M. Silva* s.n. (CONC 44047); Los Choros, 20 Sept. 1952, *C. Jiles* 2234 (CONC, M); Los Choros, 10 m, 10 Oct. 1975, *M. Silva* s.n. (CONC 44046); E of Los Choros, 29°19’6.4”S, 71°14’49.2”W, 222 m, 13 Sept. 2003, *F. Luebert & L. Kritzner* 1780 (BSB); Road to Punta Choros, 29°21’37.5”S, 71°8’22”W, 280 m, 20 Oct. 2005, *F. Luebert & C. Becker* 2908 (BSB); Cerros del Tofo, ca. 68 km N of La Serena, 200 m, 1 Nov. 1938, *C.R. Worth & J.L. Morrison* 16298 (GH, K); Panamericana in front of El Tofo, 29°26’S, 71°14’W, 10 Oct. 1987, *S. Teillier* 1056 (CONC, NY); Panamericana in front of El Tofo, 9 Oct. 1971, *E. Kausel* 5463 (SGO); Panamericana frente a El Tofo, 29°28’39”S, 71°12’51.3”W, 460 m, 26 Sept.

2004, *F. Luebert & C. Becker* 2168 (BSB, SGO); From Panamericana to Tembaldor, 24 March 1991, *C. Fernández & H. Niemeyer* (91)38 (SGO); El Tofo, 11 Sept. 1926, *E. Barros* 1378 (CONC); El Tofo, 20 Sept. 1961, *F. Schlegel* 3898 (CONC); El Tofo, 29°27'S, 71°14'W, 700 m, 7 Oct. 2005, *N. Schulz* 36 (ULS); El Tofo, 29°27'S, 71°14'W, 700 m, 7 Oct. 2005, *N. Schulz* 96 (ULS); La Higuera, road to Mina El Tofo, 29°27'13.3''S, 71°12'34.1''W, 370 m, 17 Sept. 2005, *F. Luebert & N. García* 2487/881 (BSB); Totoralillo, 150 m, 6 Dec. 1953, *E. Kausel* 3748 (F); about 45 km N of La Serena, along coast and ca 3 km NW of Panamerican on road to Totoralillo, 100 m, 21 Sept. 1991, *L.R. Landrum & S.S Landrum* 7510 (SGO); Cuesta Buenos Aires, 3 Dec. 1996, *C. Ehrhart & E. Sonderegger* 19/1017 (MSB); Cuesta Buenos Aires, 4 Oct. 1979, *E. Araya* s.n. (ULS 470); Cuesta Buenos Aires, 29°33'32.3''S, 71°15'3''W, 515 m, 20 Oct. 2005, *F. Luebert & C. Becker* 2909 (BSB, SGO); Cuesta Buenos Aires, 29°33'S, 71°15'W, 562 m, 17 Oct. 1989, *J. Castro* 25 (ULS); Cuesta Buenos Aires, 4 Oct. 1979, *S. Gómez* s.n. (ULS); Cuesta Buenos Aires, 29°34'S, 71°14'W, 600 m, 13 Nov. 1987, *K.H. Rechinger & W. Rechinger* 63688 (NY); Cuesta Buenos Aires, 23 Sept. 1952, *M. Ricardi* s.n. (CONC 12828); Cuesta Buenos Aires, 500 m, 20 Sept. 1961, *F. Schlegel* 3909 (CONC); Cuesta Buenos Aires, 350 m, 10 Oct. 1975, *M. Silva* s.n. (CONC 44045); Cuesta Buenos Aires, 550 Oct. 1971, *C. Marticorena, R. Rodríguez & E. Weldt* 1608 (CONC); S of Cuesta Buenos Aires, 27 Oct. 1991, *M. Muñoz-Schick, S. Teillier, I. Meza* 2621 (SGO); Yerba Buena, 19 May 1875, *E.C. Reed* s.n. (BM); Yerba Buena, *s.col.* (K); 40 km N of La Serena, Quebrada Honda, 20 Nov. 1996, *C. Ehrhart & E. Sonderegger* 96/956 (M); 19 km of N La Serena, 500 m, 1 Nov. 1981, *R.T. Schuh & N.I. Platnick* 6 (US); Caleta Hornos, 29°37'S, 71°17'W, 250 m, 7 Sept. 1989, *J. Armesto* 89554 (ULS); ca. 1 km S of Caleta Hornos, on road to La Serena, 29°38'19.4''S, 71°17'43''W, 100–200 m, 16 Oct. 2009, *F. Luebert & E. Daniłowicz* 2985 (BSB, G, K, SGO); 27 km from La Serena on Panamericana towards Vallenar, 29°40'14''S, 71°18'42''W, 120 m, 5 Dec. 1994, *U. Eggli & B.E. Leuenberger* 2580 (B, CONC); Between Punta Arrayán and Punta Hornos, 14 km S of bridge Juan Soldado, 29°40'S, 71°18'W, 40–120 m, 5 Dec. 1994, *U. Eggli & B.E. Leuenberger* 2580 (SGO); Quebrada Honda, Falda Occidental del Cerro Juan Soldado, 200–300 m, 4 Nov. 1949, *W. Biese* 3040 (SGO); La Serena, ca. 10.1 km N of road to El Romeral, ca. 1/2 km W of highway, 150 m, 1 Aug. 2000, *L. Landrum & S. Landrum* 9828 (SGO); Cuesta de Porotitos, 26 km N of La Serena, 140 m, 29 Oct. 1990, *T. Lammers, M. Baeza & P. Peñailillo* 7596 (CONC, F, NY); Cuesta Porotitos, 17 Oct. 1992, *C. Becerra* 9 (ULS); Cuesta Porotitos, 29°45'S, 71°17'W, 250 m, 17 Oct. 1992, *F. Fuica* 3 (ULS); Punta Teatinos, 7 Dec. 1953, *E. Kausel* 3760 (F); Punta Teatinos, 30 m, 23 Oct. 1948, *F. Behn* s.n. (CONC 8284, 22282); Punta Teatinos, 100 m, 7 Aug. 1942, *H. Larraguibel* 34 (SGO); Punta Teatinos, Oct. 1987, *L. Rodríguez* s.n. (ULS 750); Punta Teatinos, 3 km N of La Serena, 10–50 m, 7 Aug. 1942, *C. Muñoz & E. Pisano* 3263 (SGO); Punta Teatinos, 10 km N of La Serena, 50 m, 15 Oct. 1940, *G. Looser* 4272 (G, GH); km 490, hacia Los Roqueríos, 21 Oct. 1984, *M. Muñoz-Schick* 1915 (SGO); Panamericana, N of La Serena, km 490, 19 Sept. 1965, *G. Gleisner* 87 (CONC); Quebrada La Gracia, 5 km from Estacion Lambert, 28 Oct. 1974, *D. Contreras & E. Caviedes* 15 (SGO); Quebrada Santa Gracia, 200 m, 2 Aug. 1942, *H. Larraguibel* 2 (SGO); Quebrada El Jardín, La Serena, 10 June 1990, *P. Pladiur* 39 (ULS); La Serena, cerro Los Loros, 27 June 1940, *R. Santesson* 798 (NY); La Serena, cerro Los Loros, 27 April 1940, *R. Santesson* 799 (K); La Serena (Compañía Baja), 17-20 Sept. 1933, *G. Looser* 2901 (CONC, G, GH, M); Vicinity of La Serena, 1 Oct. 1953, *A.L. Cabrera* 11408 (M, SGO); Vicinity of La Serena, 50 m, 23 April 1959, *A. Consigny* s.n. (CONC 41310); La Serena, Oct. 1836, *C. Gay* 1076 (SGO); La Serena, Feb. 1930, *B. Claude-Joseph* 5477 (US); La Serena, Nov. 1936, *López* s.n. (CONC 121898); La Serena, 20 Sept. 1957, *M. Quezada* s.n. (CONC 24126); La Serena, 14 Oct. 1989, *M.Granada* s.n. (ULS 1512); La Serena, 7 Oct. 1989, *V. San Martín* s.n. (ULS 1513); La Serena, 29°54'S, 71°14'W, 80 m, 24 June 1957, *F. Schlegel* 1327 (CONC, F); 1 km S of La Serena, 10 m, 15 Sept. 1957, *M. Ricardi & C. Marticorena* 4332/717 (CONC); 10 km N of Coquimbo, 1 July 1970, *E. Weldt* 466 (CONC); Cuesta de La Pelicana, 15 Oct. 1963, *C. Marticorena & O. Matthei* 272 (CONC); Lomas de Peñuela, 6 km S of La Serena on road to Ovalle, 3 Oct. 1959, *O. Solbrig* 3034 (GH); Road from La Pelicana to Arqueros, km 7, 350 m, 16 Oct. 1963, *C. Marticorena & O. Matthei* 299 (CONC); Cerro Grande, Coquimbo, 250 m, 20 Aug. 1942, *H. Larraguibel* 2 (SGO); Cerro Grande, between La Serena and Coquimbo, Camino Longitudinal., 9 Sept. 1942, *C. Muñoz P. & E. Pisano* 3311 (SGO); La Serena (Cerro Grande), 17-20 Sept. 1933, *G. Looser* 2895 (G, GH); Coquimbo, *A. Caldcleugh* s.n. (F 1546957); Coquimbo, 61–91 m, 7 Oct. 1927, *C. Elliot* 36 (K); Coquimbo, 1831-1833, *C. Gaudichaud* 64 (F, G-DC, K); Coquimbo, 7 Jan. 1906, *C.S. Sargent* s.n. (A); Coquimbo, 100 m, Nov. 1923, *E. Werdermann* 120 (BM, F, GH); Coquimbo, 28 Feb. 1892, *O. Kuntze* s.n. (F 294542, NY, US 701107); Coquimbo, *Philippi* s.n. (US 944663); Coquimbo, July – Aug. 1856, *V.H. Harvey* s.n. (GH, K); Coquimbo, 15 m, Oct. 1878, *F. Philippi* s.n. (SGO 42232, 54391); Coquimbo, 15 m, Sept. 1885, *F. Philippi* s.n. (SGO 42244, 54394); Coquimbo, 15 m, Sept. 1853, *P. Germain* s.n. (SGO 42235); Coquimbo, 15 m, Oct. 1878, *P. Ortega* s.n. (SGO 54391); Coquimbo, Dec. 1902, *A.W. Hill* 329 (K); Coquimbo, Sept. 1885, *F. Philippi* 107

(BM); Coquimbo, Feb. 1882, *H.M.S. Alert* s.n. (K); Coquimbo, 1825, *J. Macrae* s.n. (K); Coquimbo, Nov. 1897, *Philippi* s.n. (SGO 54396); Coquimbo, 13 Oct. 1898, *Prizessin Therese von Bayern* 265 (M); Coquimbo, 1861, *R.A. Philippi* s.n. (G); Coquimbo, *s.col.* (K); Coquimbo, *s.col.* (K); Coquimbo, north Chile, *R. Pearce* s.n. (K); Coquimbo (Pampilla), 50 m, 20 Sept. 1957, *G. Looser* 5785 (A, G); Coquimbo, La Pampilla, Sept. 1989, *A.M. Mora* s.n. (SGO 131748); Ex arenosis et rupestribus chilesibus juxta Coquimbo, May 1882, *J . Ball* s.n. (GH, K, NY); Coquimbo, Playa, 80 m, 26 Sept. 1934, *G. Montero* 1875 (CONC); Vicinity of Coquimbo, Sept. 1931, *F. Jaffuel* 2686 (CONC, GH); El Faro, Port of Coquimbo, 20–50 m, 14 Sept. 1941, *C. Muñoz & G.T.Johnson* 2769 (SGO); El Faro, 14 Sept. 1978, *G. Montero* 11032 (CONC); El Faro, 30 m, 15 Sept. 1980, *G. Montero* 11953 (CONC); Panamericana S of Coquimbo, 30°2'24.8''S, 71°22'35.8''W, 120 m, 20 Oct. 2005, *F. Luebert & C. Becker* 2910 (neotype SGO, duplicate BSB); Las Tacas, 12 Oct. 1984, *A. Sánchez* s.n. (ULS); Las Tacas, Sept. 1987, *M. Muñoz* s.n. (ULS); E of Huachalalume, 29°59'S, 71°11'W, 450 m, 27 Sept. 1999, *G. Arancio* 12075 (ULS); Rocky point between Coquimbo and la Herradura Bay, 100 m, 19 Nov. 1935, *J. West* 3886 (GH); La Herradura, 18 Sept. 1972, *Niemeyer* s.n. (CONC 121886); Coquimbo, La Herradura, 9 Aug. 1917, *C. Skottsberg & I. Skottsberg* 721 (GH, NY); Coquimbo, La Herradura, 9 Aug. 1917, *C. Skottsberg & I. Skottsberg* s.n. (F 737186); 4 km S of Coquimbo, 2 May 1985, *B.J. Wallace* 323 (SGO); Between Vicuña and La Serena, 15 Oct. 1940, *G. Looser* 4303 (G, GH); Vicuña, Oct. 1926, *B. Claude-Joseph* 4452 (US); 17 km S of Coquimbo, 20 m, 12 Aug. 1993, *M. Hermann & A. Contreras* 1257 (SGO); Totoralillo bay, 30°5'S, 71°23'W, 50 m, 15 Jan. 2001, *G. Arancio* 14611 (ULS); Totoralillo bay, 30°5'S, 71°23'W, 50 m, 15 Jan. 2001, *G. Arancio* 14619 (ULS); Panamericana, 20 km S of La Herradura, 400 m, 27 Jan. 1991, *De Vore* 1542A (CONC); Playa Las Estacas, road Coquimbo-Guanaqueros, 10 m, 29 Sept. 1984, *Landero* 508 (CONC); Lagunillas, 26 Sept. 1987, *J. Galindo* s.n. (ULS 1399); Lagunillas, 30°6'S, 71°21'W, 50 m, 26 Sept. 1987, *N. Cisterna* s.n. (ULS 748); Lagunillas, 26 Sept. 1987, *R. Ramírez* s.n. (ULS 1401); Between Socos and Coquimbo, km 66, Los Morrillos, 150 m, 11 Feb. 1988, *C. Marticorena, T. Stuessy & C. Baeza* 9970 (CONC); Tongoy, Guanaqueros, 23 Sept. 1967, *G. Gleisner* s.n. (M); Guanaqueros, *O. Zoellner* 6811 (CONC); Quebrada Tongoicillo, 260 m, 19 Sept. 1948, *C. Jiles* 875 (CONC); 30 km S of Coquimbo, 28 July 1960, *Hartmann* s.n. (CONC 29135); Andacollo, 11 Oct. 1958, *M. Ricardi & C. Marticorena* 4955/1340 (CONC); Quebrada El Romeral, 6 Oct. 1990, *M.T. Guerrero* s.n. (ULS); Tongoy, 13 Oct. 1961, *A. Garaventa* 4305 (CONC); Tongoy, July 1963, *Bravo* s.n. (CONC 121890); Tongoy, 8 Sept. 1948, *C. Jiles* 782 (M); Tongoy, Sept. 1971, *P. Muñoz* s.n. (CONC 121899); Tongoy, 15 July 1956, *Mancinelli* s.n. (CONC 24253); Monte Redondo, 400 m, 1 Oct. 1947, *C. Jiles* 369 (M); Panamericana norte, 4 km from the junction to Tongoy, 30°19'8''S, 71°24'44''W, 125 m, 21 Nov. 2001, *L. Faúndez, P. León-Lobos & M.P. Way* INIA-KEW 006 (K); Las Cardas, 9 Oct. 1949, *C. Jiles* 1507 (CONC); Cuesta Las Cardas., 14 Sept. 1957, *C. Muñoz* 4165 (SGO); Between Ovalle and La Serena, 5 km N of Cuesta Las Cardas, 22 Dec. 1994, *C. Ehrhart & E. Sonderegger* 94/694 (MSB); 30 km S of Totoralillo and 58 km S of La Serena (km 421), 30°20'S, 71°24'W, 120 m, 29 Nov. 1987, *M.O. Dillon & S. Teillier* 4977 (F, MSB); ca. 10 mi S of Tongoy, 30°30'S, 71°30'W, 30 Oct. 1991, *C. Taylor, C. von Bohlen & A. Marticorena* 10634 (CONC, F). Región de Coquimbo, Prov. Limarí: Estancia Camarones, 11 Oct. 1968, *C. Jiles* 5198 (CONC, M); Corral Quemado, 700 m, 30 Oct. 1956, *C. Jiles* 3116 (CONC); Samo Alto, 689 m, 25 May 2004, *L. Kritzner* s.n. (BSB); La Silleta, near Ovalle., 10 Sept. 1942, *C. Muñoz P. & E. Pisano* 3446 (SGO); Cerro La Silleta, 28 Oct. 1965, *M. Ricardi, C. Marticorena & O. Matthei* 1533 (CONC); Ovalle, Sept. 1949, *B. Collantes* s.n. (CONC 121889); Ovalle, Nov. 1928, *E. Barros* s.n. (CONC 121893); E of Fray Jorge, 30°38'2''S, 71°35'44.4''W, 220 m, 21 Oct. 2005, *F. Luebert & C. Becker* 2911 (BSB, SGO); Valle del Encanto, 30°38'S, 71°23'W, 200 m, 24 June 1989, *G. Arancio* 89201 (ULS); Fray Jorge forest, 18 Sept. 1947, *B. Collantes* s.n. (CONC 121896); Fray Jorge forest, 480 m, 30 Nov. 1940, *C. Munoz & A. Coronel* 1408 (SGO); Fray Jorge forest, 300 m, 22 Sept. 1960, *F. Schlegel* 2837 (CONC); Fray Jorge, 450 m, 25 Sept. 1935, *C. Muñoz* 155 (SGO); Fray Jorge, 23 Sept. 1917, *Baeza* s.n. (CONC 121895); Fray Jorge, 450 m, 1 Sept. 1934, *C. Grandjot* 405 (SGO); Fray Jorge, 9 Aug. 1948, *C. Jiles* 674 (CONC); Fray Jorge, 16 Sept. 1963, *G. Gleisner* 113 (CONC); Fray Jorge, 300 m, Sept. 1958, *J. Kummerow* s.n. (CONC 41311-41315, F 1811871); Fray Jorge, 20 Sept. 1960, *J. Saa* s.n. (CONC 121892); Fray Jorge, 250 m, 16 Oct. 1961, *K. Kubitzki* 73 (M); Fray Jorge, 275 m, 20 May 1986, *R. Gajardo* s.n. (EIF 8111); Fray Jorge, 150 m, 7 July 1938, *Andreas* 849 (B); Fray Jorge, 15 Sept. 1947, *Ibañez, Kuschel & Muñoz* s.n. (SGO 130635, CONC 145074); Fray Jorge, 275 m, 6 April 1954, *A. Consigni* s.n. (EIF 5081); Fray Jorge, Quebrada El Mineral, 350 m, 12 May 1941, *G. Schwabe* 250 (SGO); Fray Jorge E side, 25 Sept. 1935, *C. Muñoz* B-155 (GH); Fray Jorge National Park, 1 Feb. 1979, *M. Morales & A. Córdoba* s.n. (SGO 138613); Fray Jorge National Park, 450 m, 21 June 1968, *O'Brien* s.n. (CONC 38409); Fray Jorge National Park, 1 Oct. 1973, *P.L. Meserve* 46 (SGO); Road to Fray Jorge, 8 Oct. 1994, *C. Ponce* 16 (ULS); Near Fray Jorge National Park, 30°41'S, 71°40'W, 240–250 m, 22 Sept. 1988, *M.O. Dillon, D. Dillon & V. Poblete* 5428 (F, MSB); 33 km SW of Ovalle, 15 Dec. 1967, *O'Brien* 139 (SGO); El Reloj, 5 Sept. 1949, *C. Jiles* 1305 (CONC); Potrerillo Alto, 300 m, 21 Dec. 1976, *H. Valenzuela* 41-21 (EIF); Potrerillo Alto, 300 m, 12 Nov. 1976, *H. Valenzuela* s.n. (EIF 5852); Caleta El Toro, 30°43'53.3''S, 71°41'50.2''W, 0 m, 22 Oct. 2005, *F. Luebert & C. Becker* 2918 (BSB); Panamericana, 8 km N of Quebrada del Teniente, 13 Oct. 1963, *C. Marticorena & O. Matthei* 162 (CONC); Zorrilla, July 1947, *C. Jiles* 215 (CONC); Cuesta de Punitaqui, 13 Sept. 1948, *F. Behn* s.n. (CONC 8284); Talinay, 18 Sept. 1975, *O. Zöllner* 8352 (NY); Amolanas, Panamericana, 89 km N of Los Vilos, 13 Oct. 1963, *C. Marticorena & O. Matthei* 128 (CONC); Corral de Julio, 300 m, 8 Sept. 1972, *A. Newnswander* s.n. (EIF 5452); Corral de Julio, El Silencio, 225 m, 7 Nov. 1976, *M. Muñoz-Schick* 951 (F, SGO). Región de Coquimbo, Prov. Choapa: 3 km N of Puerto Oscuro, 16 Oct. 1971, *C. Marticorena, R. Rodríguez & E. Weldt* 1420 (B, CONC); Panamericana, km 296, 2 km N of cross to El Totoral, N of Puerto Oscuro, 100–200 m, 13 Oct. 2009, *F. Luebert & E. Danilowicz* 2976 (BSB, K, SGO); 5 km from Canela Baja on road to Canela Alta, , 360 m, 10 March 1987, *O. Matthei & R. Rodriguez* 34 (CONC); Caleta Oscuro, 50 m, 2 Nov. 1974, *C. Marticorena, O. Matthei & R. Rodríguez* 265 (CONC); Puerto Oscuro, 9 Aug. 1974, *D. Contreras & T. Caviedes* 208 (SGO); 2 km E of Canela Alta, 1200 m, 30 Sept. 1967, *O'Brien* 52 (SGO); Panamericana, ca. 50 km N of Los Vilos near Puerto Oscuro, 15 m, 16 Sept. 1966, *E. Kausel* 5187 (SGO); Aucó, 580 m, 6 July 2003, *F. Luebert* 1752 (BSB); Aucó, El Bolsico, 720 m, 5 July 2003, *F. Luebert* 1732 (BSB); Aucó, El Bolsico, 990 m, 5 July 2003, *F. Luebert* 1735 (BSB); Rio Choapa, 9 Oct. 1965, *G. Montero* 7252 (CONC); Huentelauquen, 1 Oct. 1957, *G. Monsalve* 5 (SGO); Illapel, 340 m, 18 Sept. 1935, *G. Montero* 2379 (CONC); Illapel, 18 Sept. 1952, *M. Ricardi* 2030 (CONC); Illapel, 310 m, *R.A. Philippi* s.n. (SGO 42234); Illapel, 310 m, Dec. 1862, *L. Landbeck* s.n. (SGO 54390); Illapel, *s.col.* (BM); Illapel, hills east of town, 20 Sept. 1944, *E. Barros* 6243 (GH); Vicinity of Illapel, 6 Oct. 1914, *Mr.& Mrs. S.N. Rose* 19246 (NY, US); Road to Illapel, 250 m, 4 Dec. 1987, *A. Urzúa* s.n. (SGO 107257); Cuesta Cavilolén, road Illapel to Los Vilos, 33 km, 560 m, 21 Nov. 1938, *C.R. Worth & J.L. Morrison* 16647 (GH, K); Road to Illapel km 3-4, 24 July 2004, *S. Sepúlveda & J. Villagrán* 128 (SGO); Camino Viejo, W of Salamanca, 14 Nov. 1994, *C. Ehrhart & J. Grau* 94/301 (MSB); Caleta Nague, 60 m, 23 April 1959, *A. Consigny* s.n. (CONC 41307); Near Los Vilos, 14 Oct. 1948, *E. Kausel* 2655 (F); Los Vilos, 5 m, 25 Aug. 1954, *A. Consigni* s.n. (EIF 2955); Cerro Centinela, 27 July 1961, *H. Klempau* 375 (CONC); Pichidangui, 14 Nov. 1976, *W.A. Weber & B. Johnston* 949 (SGO); Pichidangui, 6 Oct. 1957, *G. Monsalve* s.n. (SGO 132186); Pichidangui, 70 m, 11 Nov. 2001, *C. Aedo* 6834 (CONC, MA). Región de Coquimbo, Indefinite: Prov. Coquimbo, 1839, *C. Gay* s.n. (G-DC G00147873); Litoral of Coquimbo, Sept. 1898, *K. Reiche* s.n. (GH); Coast of Coquimbo, 31 Jan. 1903, *G.T. Hastings* 583 (NY, US). Región de Valparaíso, Prov. Petorca: Los Molles, 20 m, Sept. 1905, *K. Reiche* s.n. (SGO 54392); Quebrada El Chivato, S of Punta Molles, 30 m, 13 Oct. 1948, *G. Looser* 5518 (G, GH); Road from Cabildo to Alicahue, 630 m, 10 Nov. 1988, *Bobadilla* 33 (CONC); Between La Vega and Cabildo, 300 m, 24 Oct. 2004, *F. Luebert & C. Becker* 2195A (BSB); Onthe road from San Felipe to Cabildo, ca 10 km below Cabildo, 32°26'17''S, 70°58'9''W, 314 m, 1 Oct. 2001, *M. Weigend, H.H. Hilger & J. Skrabal* 5939 (B, MSB); La Ligua, Valle Hermoso, 24 Sept. 1947, *E. Barros* 7212 (US); Palos Quemados, 400 m, 22 Jan. 1933, *G. Looser* s.n. (CONC 134788, G, M). Región de Valparaíso, Prov. San Felipe: Near Chagres, 410 m, 13 Nov. 1954, *F. Schlegel* 411 (CONC); Cuesta de Chagres, Puntilla El Romeral, 20 Aug. 1950, *Bultmann* s.n. (CONC 48649); Cuesta de Ocampo, 1862, *R.A. Philippi* s.n. (G, SGO 42245, 54395). Región de Valparaíso, Prov. Quillota: Near La Calera, Oct. 1829, *C. Bertero* 1042 (holotype of *Heliophytum stenophyllum* var. textitrosmarinifolium G-DC, isotypes BM, F, G, GH, NY, possible isotypes F 997919, G-DC G00147885, NY, US 1706268); La Calera, 13 Sept. 1953, *Kunkel* 926 (CONC); La Calera, 15 Nov. 1977, *A. Zárate* s.n. (SGO 137451); Cuesta Llaillay, 630 m, 8 May 2004, *F. Luebert & C. Becker* 1990 (BSB); Cuesta Llaillay, *J. Miers* s.n. (lectotype of Cochranea conferta BM); Cuesta Pachacama near Quillota, 1832, *T. Bridges* 235 (BM, K, lectoparatypes of *Cochranea conferta*); Pachacama, 350 m, 28 Aug. 2004, *F. Luebert* 2007 (BSB); near Valparaíso, 1831, *H. Cuming* 377 (BM, GH, K, lectoparatypes of *Cochranea conferta*); near Viña del Mar, 1863, *R.A. Philippi?* s.n. (US 1134830). Región de Valparaíso, Indefinite: Valparaíso, 1914, *A. Calvert* s.n. (BM); prov. Aconcagua, *R.A. Philippi* s.n. (B). Indefinite: N Chile, Jan. – Feb. 1975, *W. Schwabe* s.n. (B); Chili, *s.col.* (K); Cumbre, Andium Claustrum, Chili, 1825, *J. Macrae* s.n. (K); Litus chilense boreale, 1889, *F. Vidal* s.n. (SGO 42242, 54393); N Chile, *W. Lobb* 442 (K); Chile, *L. Neé* s.n. (MA 232466); Chile, *L. Neé* (MA 232441); Chile and Coquimbo, *L. Neé* s.n. (MA 218843); 'Arica', Oct. 1926, *F. Jaffuel* 12 (GH); 'Conception', *A. Caldcleugh* s.n. (K); 'Valdivia', 1862, *T. Bridges* 595 (NY); 'Perou', 1870, *s.col.* (G); s.loc., *C. Gay* s.n. (K, lectoparatype of *Cochranea conferta*); s.loc., *H. Cuming* s.n. (BM); s.loc., *T. Bridges* s.n. (K); s.loc., *T. Bridges* s.n. (M); s.loc., *Cap. King.* s.n. (G); s.loc., 1790, *T. Haenke* 2082 (NY); s.loc., *L. Neé* 40 (MA 218815).

### 13. ***Heliotropium longistylum*** **Phil.**

**CHILE**. Región de Atacama, Prov. Copiapó: Estancia Castilla, 27°43'40.5"S, 71°0'2.4"W, 92 m, 16 Sept. 2003, *F. Luebert & L. Kritzner* 1829 (BSB); Vicinity of Caleta Pajonales, 27°47'14.8"S, 71°1'35.3"W, 203 m, 15 Sept. 2003, *F. Luebert & L. Kritzner* 1826 (BSB); Vicinity of Caleta Pajonales, 27°49'4.9"S, 71°0'48.1"W, 210 m, 15 Sept. 2003, *F. Luebert & L. Kritzner* 1827 (BSB); Road to Caleta Pajonales, 27°50'10.6"S, 71°0'29.1"W, 215 m, 13 Sept. 2004, *F. Luebert, C. Becker & N. García* 2020 (BSB, SGO); Road between Totoral and Bahía Totoral, 400 m, 8 Sept. 1991, *C. von Bohlen* 1373 (SGO). Región de Atacama, Prov. Huasco: Carrizal Bajo, Quebrada Higuera, 100 m, Nov. 1985, *F. Schlegel* 8017 (CONC); Carrizal Bajo, 10 Oct. 1965, *C. Muñoz* 17 (SGO); Carrizal Bajo, Dec. 1871, *T. King* s.n. (lectotype SGO 54363, duplicates GH [fragm.], SGO 42221, possible isotype K); Carrizal Bajo, Sept. 1885, [*F. Philippi*] s.n. (lectotype of *Helioropium vernicosum* SGO 54362, duplicates GH [fragm.], SGO 42218); Carrizal Bajo, road to Huasco, 28°5'S, 71°9'W, 10 m, 25 Sept. 1993, *S. Teillier, R. Torres & J. Villarroel* 3165 (SGO); Road to Mina Oriente, 28°6'51.1"S, 71°5'49.8"W, 30 m, 19 Oct. 2005, *F. Luebert & C. Becker* 2898 (BSB); Quebrada Carrizal, 28°6'45.2"S, 71°6'57.4"W, 26 m, 15 Sept. 2003, *F. Luebert & L. Kritzner* 1822 (BSB); Quebrada Carrizal, 28°6'45.2"S, 71°6'57.4"W, 30 m, 21 Jan. 2004, *F. Luebert & R. Torres* 1971 (BSB, SGO); Cerro Negro, Carrizal Bajo–Huasco., 28°9'S, 71°9'W, 12 Oct. 1994, *S. Teillier & R.Torres* 3905 (SGO); Carrizal Bajo, road to Huasco, 28°10'S, 71°9'W, 20 m, 25 Sept. 1993, *S. Teillier, R. Torres & J. Villarroel* 3166 (SGO); Punta Lobos, 28°11'6.7"S, 71°9'25.1"W, 20 m, 14 Sept. 2003, *F. Luebert & L. Kritzner* 1812 (BSB); Cerro Negro, Carrizal Bajo–Huasco, 28°16'S, 71°13'W, 50 m, 13 Oct. 1991, *S. Teillier, J. Villarroel & R. Torres* 2570 (SGO); Punta Lobos, 28°17'31.8"S, 71°10'37.1"W, 5 m, 14 Sept. 2003, *F. Luebert & L. Kritzner* 1811 (BSB); Los Toyos on road from Carrizal Bajo to Huasco, 28°22'57"S, 71°10'44"W, 50 m, 27 Oct. 2002, *M. Ackermann* 518 (BSB).

### 14. ***Heliotropium floridum*** **(A.DC.) Clos**

**CHILE**. Región de Atacama, Prov. Chañaral: Prov. Atacama, km 1031, near Las Bombas, 10 Nov. 1969, *C. Jiles* 5497 (M); Falda Verde, 26°17'S, 70°37'W, 100 m, 5 Nov. 2005, *N. Schulz* FV58 (BSB); Chañaral, Quebradas Faldas Verdes, 27 Sept. 1952, *M. Ricardi* 2248 (CONC); 15 km N of Salado, 14 Sept. 1958, *M. Ricardi & C. Marticorena* 4618/1003 (CONC); Villa Alegre, 26°31'10.8"S, 70°41'40.1"W, 0 m, 15 Oct. 2005, *F. Luebert & C. Becker* 2838 (BSB, SGO); Atacama: km 900, 6 Oct. 1966, *C. Jiles* 4939 (CONC). Región de Atacama, Prov. Copiapó: Between Caldera and Flamenco, 20 m, 14 Oct. 1991, *S. Teillier, L.Villarroel & R. Torres* 2591 (CONC, SGO); Between Caldera and Flamenco, 40 m, 14 Oct. 1991, *S. Teillier, L.Villarroel & R. Torres* 2592 (CONC, SGO); Between Caldera and Flamenco., 30 m, 14 Oct. 1991, *S. Teillier, L.Villarroel & R. Torres* 2593 (SGO); Bahía Obospito, Panamericana km 925 , 16 Oct. 1980, *J. Grau* 2171 (BM, M); Caleta Mora, 15 m, 11 Oct. 1972, *F. Behn* s.n. (CONC 51923); Caleta Mora, 15 m, 19 Oct. 1972, *F. Behn* s.n. (CONC 51925); Between Caldera and Chañaral, 26°50'26.6"S, 70°47'29.6"W, 61 m, 17 Sept. 2003, *F. Luebert & L. Kritzner* 1840 (BSB); Unidad 5 ducto CPM, 26°51'S, 70°48'W, 13 m, 21 Sept. 2004, *G. Arancio* 15144 (ULS); Unidad 14 ducto CPM, 26°54'S, 70°47'W, 87 m, 21 Sept. 2004, *G. Arancio* 15148 (ULS); Pampa Caracoles, 17 km N of Caldera, 26°57'S, 70°47'W, 100 m, 24 Sept. 1988, *M.O. Dillon, D. Dillon & V. Poblete* 5481 (F, M); Quebrada del León, 20 km N of Caldera along the coast, 150 m, 20 Oct. 1938, *C.R. Worth & J.L. Morrison* 16150 (G, K, M); Quebrada Los Leones, 26°57'17.7"S, 70°44'7.1"W, 240 m, 16 Oct. 2005, *F. Luebert & C. Becker* 2845 (BSB); Quebrada Los Leones, 26°58'27.9"S, 70°46'13.7"W, 65 m, 17 Sept. 2003, *F. Luebert & L. Kritzner* 1838 (BSB); Quebrada Los Leones, 26°58'19.9"S, 70°46'20.1"W, 75 m, 15 Sept. 2004, *F. Luebert, C. Becker & N. García* 2049 (BSB); Caldera, dunes back of Playa Ramadas, 50 m, 12 Oct. 1999, *S. Teillier* 4736 (CONC); Caldera, Playa Ramadas, 30 m, 19 Jan. 2004, *F. Luebert & R. Torres* 1958 (BSB); 5 km N of Caldera on road to Chañaral, 6 Nov. 1987, *K.H. Rechinger & W. Rechinger* 63446 (B); Caldera, *s.col.* (K); Caldera, Sept. 1885, *F. Philippi* s.n. (SGO 42223, 54360, 54361); Caldera, Sept. 1885, *F. Philippi* 106 (BM); Caldera, 5 m, 19 Feb. 1939, *A.A. Beetle* 26122 (G, K); Caldera, Nov. 1853, *R.A. Philippi* s.n. (SGO 54358); Caldera, Sept. 1876, *R.A. Philippi* s.n. (SGO 54359); S of Caldera, in front of Copec Gas station, 27°5'26.6"S, 70°48'6.5"W, 61 m, 16 Sept. 2003, *F. Luebert & L. Kritzner* 1837 (BSB); Desert of Atacama [Caldera], Sept. – Oct. 1890, *T. Morong* 1236 (F, G, K, US); Bahía Inglesa, 27°7'S, 70°54'W, 12 Nov. 1987, *K.H. Rechinger & W. Rechinger* 63611 (B); Bahía Inglesa, 27°7'S, 70°54'W, 12 Nov. 1987, *K.H. Rechinger & W. Rechinger* 63615 (B); Bahía Inglesa, dunes, 5 m, 4 Oct. 1991, *C. von Bohlen* 1243 (SGO); Top of Morro Grande, 27°8'S, 70°56'W, 241 m, 19 Nov. 2005, *G. Arancio* 15228 (ULS); Dunes at Caleta Los Patos, 27°9'S, 70°53'W, 10 m, 21 Nov. 2005, *G. Arancio* 15345 (ULS); Caleta Los Patos, 27°10'S, 70°55'W, 49 m, 21 Nov. 2005, *G. Arancio* 15367 (ULS); Mina Los Fósiles, 27°9'S, 70°55'W, 92 m, 18 Dec. 2005, *G. Arancio* 15308 (ULS); W of Morro Chico, 27°11'S, 70°58'W, 19 m, 21 Nov. 2005, *G.*

*Arancio* 15427 (ULS); Llano Húmedo, 27°12'S, 70°56'W, 72 m, 20 Nov. 2005, *G. Arancio* 15331 (ULS); Llanos, 27°14'S, 70°55'W, 90 m, 19 Dec. 2005, *G. Arancio* 15504 (ULS); Road from Copiapó to Caldera, km 49, 24 Oct. 1971, *C. Marticorena, R. Rodríguez & E. Weldt* 1863 (CONC); Dunes N of Bahía Cisne, 27°19'S, 70°56'W, 102 m, 21 Nov. 2005, *G. Arancio* 15437 (ULS); Road between Copiapó and Caldera, km 3, 23 Oct. 1964, *M. Ricardi, C. Marticorena & O. Matthei* 1053 (CONC); El Caserón, road from Copiapó to Caldera, 175 m, 21 Sept. 1941, *C. Muñoz P. & G.T. Johnson* 1920 (SGO); Panamericana near Copiapó km 730, 11 Oct. 1971, *E. Kausel* s.n. (SGO 80552); Road from Copiapó to Bahia Salada, 27°23'52.3''S, 70°41'29.8''W, 170 m, 18 Oct. 2005, *F. Luebert & C. Becker* 2888 (BSB); Barranquilla, 27°30'43''S, 70°52'31.2''W, 60 m, 16 Sept. 2003, *F. Luebert & L. Kritzner* 1836 (BSB); Llano Travesía, 19 Sept. 1961, *F. Schlegel* 3876 (CONC); Travesía?, *C. Muñoz* s.n. (ULS 599); Road between Bahia Salada and Caldera, 27°34'31.2''S, 70°47'48.5''W, 265 m, 18 Oct. 2005, *F. Luebert & C. Becker* 2894 (BSB); Road between Bahia Salada and Caldera, 27°36'24.9''S, 70°47'4.8''W, 220 m, 16 Sept. 2003, *F. Luebert & L. Kritzner* 1835 (BSB); Totoral-Caldera, Cerca de Barranquilla, 27°37'39.7''S, 70°47'15.3''W, 130 m, 14 Sept. 2004, *F. Luebert, C. Becker & N. García* 2043 (BSB); Copiapó-Pabellon, Sept. 1885, *F. San Roman* s.n. (SGO 42224); Bandurrias, 1885, *G. Geisse* s.n. (SGO 42240, 42246); Bahíaa Salado, 13 Oct. 1965, *M. Ricardi, C. Marticorena & O. Matthei* 1274 (CONC); Road Totoral–Caldera, 27°40'45.6''S, 70°56'59.2''W, 30 m, 16 Sept. 2003, *F. Luebert & L. Kritzner* 1830 (BSB); Between Totoral and Bahia Salada, 27°49'14.1''S, 71°0'8''W, 215 m, 14 Sept. 2004, *F. Luebert, C. Becker & N. García* 2031 (BSB, SGO); Pajonales, Oct. 1888, *G. Geisse* s.n. (SGO 72727). Región de Atacama, Prov. Huasco: Chañarcito, *s.col.* (K); Carrizal Bajo, 30 m, 10 Oct. 1965, *C. Muñoz* s.n. (SGO 135276); Carrizal Bajo, Dec. 1871, *T. King* s.n. (lectotype SGO 54384, duplicates GH [fragm.] SGO 54385); Carrizal Bajo, 19 May 1875, *E.C. Reed* s.n. (BM); Carrizal Bajo, *s.col.* (K); Carrizal Bajo, Dec. 1871, *T. King* s.n. (SGO 54383); La Herradura, 28°6'45.2''S, 71°6'57.4''W, 18 m, 15 Sept. 2003, *F. Luebert & L. Kritzner* 1819 (BSB); La Herradura, 28°6'8.9''S, 71°9'0.6''W, 30 m, 21 Jan. 2004, *F. Luebert & R. Torres* 1974 (BSB, SGO); Quebrada de Carrizal, 50 m, 13 Oct. 1991, *S. Teillier, L.Villarroel & R. Torres* 2569 (SGO); Road from Carrizal Bajo to Huasco, 2 Nov. 1991, *M. Muñoz Schick, S. Teillier, I. Meza* 2956 (SGO); Carrizal Bajo, road to Huasco, 20 m, 25 Sept. 1993, *S. Teillier, R. Torres & L. Villarroel* 3167 (SGO); Punta Lobos, 28°17'31.8''S, 71°10'37.1''W, 5 m, 14 Sept. 2003, *F. Luebert & L. Kritzner* 1810 (BSB); Huasco–Carrizal Bajo, ca. 12 km N of Huasco, before Los Toyos, 24 Oct. 1997, *C. Ehrhart & J. Grau* 97/1253 (M); 11 km N of Huasco Bajo towards Carrizal Bajo (= 4 km S of Los Toyos), 28°23'38''S, 71°11'18''W, 20–70 m, 22 Oct. 1997, *U. Eggli & B.E. Leuenberger* 2997 (B, CONC, SGO); Huasco–Carrizal Bajo, 28°24'S, 71°11'W, 5 m, 3 Dec. 2002, *C. Ehrhart* 2002/144 (M); Road to Carrizal Bajo, Sept. 1997, *H. Niemeyer & C. Fernández* 9722 (SGO); Tres Playitas, 28°24'28.1''S, 71°11'22.9''W, 20 m, 14 Sept. 2003, *F. Luebert & L. Kritzner* 1801 (BSB); Dunes of Huasco, Sept. 1965, *A. Kohler* 123 (CONC); 15 km N of Vallenar, 12 Oct. 1994, *S. Teillier & R.Torres* 3902 (SGO); Isla Huacolda, 10–15 m, 26 Oct. 1938, *C.R. Worth & J.L. Morrison* 16232 (K); Chañaral de Aceituna, 23 Oct. 1971, *C. Marticorena, R. Rodríguez & E. Weldt* 1834 (CONC). Región de Atacama, Indefinite: Coquimbo [sand hill desert between Copiapó and Huasco], 1841, *T. Bridges* 1340 (BM, G, GH, K, M); Atacama, *C. Porter* s.n. (K). Región de Coquimbo, Prov. Elqui: Punta Choros, 5 km towards Carrizalillo, 29°12'58''S, 71°28'6''W, 9 Oct. 2002, *A. Moreira* 705 (SGO); Punta Choros North, 29°13'52.3''S, 71°27'33.3''W, 29 m, 13 Sept. 2003, *F. Luebert & L. Kritzner* 1761 (BSB, SGO); Punta Choros, Aug. 2004, *N. García* s.n. (BSB); Punta Choros South, 29°15'14.3''S, 71°26'39.2''W, 8 m, 13 Sept. 2003, *F. Luebert & L. Kritzner* 1775 (BSB); Quebrada Los Choros, Playa Choros, 20 Oct. 1997, *C. Ehrhart & J. Grau* 97/1163 (M). Región de Coquimbo, Indefinite: Coquimbo, 1832, *H. Cuming* 858 (BM, GH, K); Coquimbo, *T. Bridges* s.n. (BM, K); Prov. Coquimbo, 1836, *C. Gay* 1182 (holotype G-DC, isotypes F 515902 [fragm.], F 970065 [fragm.], GH, possible isotypes G, K [*C. Gay* s.n.]). Indefinite: Temperate South America, *s.col.* (BM); s.loc., *G. Arancio* 91176 (ULS); s.loc., *s.col.* (BM).

### 15. *Heliotropium linariifolium* Phil.

**CHILE**. Región de Antofagasta, Prov. Antofagasta: Paposo, road to Mina Liverpool, Quebrada Paposo, 24°56'41.2''S, 70°24'25.2''W, 950 m, 13 Dec. 2006, *M. Ackermann* 684 (BSB); Quebrada Yumbe, 25°0'S, 70°26'W, 1060 m, 14 Feb. 1998, *G. Arancio & F. Squeo* 11325 (ULS); Hills above Paposo, road to Mina Julia, 300 m, 5 Oct. 1991, *C.M. Taylor, C. von Bohlen & A. Marticorena* 10715 (CONC); Paposo road, between Paposo and Panamericana, 700 m, 9 Oct. 1983, *X. Rodríguez* 2 (K); Cuesta Paposo, 680 m, 7 Nov. 1985, *F. Schlegel* 7958 (CONC); Paposo, 17 Sept. 1958, *M. Ricardi & C. Marticorena* 4636 (CONC); Paposo, 25°1'S, 70°28'W, 50 m, 20 Oct. 2005, *N. Schulz* 63 (ULS); Paposo, near the beach, 15 Nov. 1959, *A. Torres* s.n. (SGO 135453); Paposo, road to Mina Julia ca. 5 km E of Paposo, 500 m, 16 Sept. 1991, *L. Landrum & S. Landrum* 7499 (SGO); Quebrada de Paposo, ca. 12 km E of Caleta Paposo, 25°1'S, 70°25'W, 920 m, 7 Dec. 1987, *M.O. Dillon & S. Teillier* 5121 (F, MSB); Quebrada Los Yales, Paposo, 25-26 Aug. 1992, *J.C. Torres* s.n. (SGO 128787); Quebrada Guanillo, 18 Sept. 1941, *C. Muñoz & G.T.Johnson* 2974 (SGO); Quebrada Guanillo, 950 m, 16 Sept. 1992, *S. Teillier, P. Rundel & P.García* 2757 (SGO); Quebrada Paposo, 650 m, 5 Sept. 1991, *C. von Bohlen* 1266 (SGO); Quebrada Matancilla, 25°6'44.7''S, 70°27'28.7''W, 300 m, 8 Oct. 2005, *F. Luebert & N. García* 2724/1118 (BSB); Quebrada Matancilla, 185 m, 18 Sept. 1992, *S. Teillier, P. Rundel & P.García* 2934 (SGO); Quebrada Matancilla, 185 m, 18 Sept. 1992, *S. Teillier, P. Rundel & P.García* 2938 (SGO); Quebrada Bandurrias, Taltal-Paposo, 80 m, 5 Oct. 1991, *M. Quezada & E. Ruiz* 232 (CONC); Quebrada Anchuña, 20 Sept. 1953, *M. Ricardi* 2531 (CONC); Taltal, towards La Puntilla, 1 Oct. 1940, *C. Grandjot* 4401 (CONC, SGO); Quebrada Cascabeles, 4 Oct. 1954, *M. Ricardi* 3111 (CONC); 16 km N of Taltal., 14 Sept. 1991, *C. Fernández & H. Niemeyer* (91)132 (SGO); Between Taltal and Paposo, km 6, 10 m, 13 Oct. 1983, *G. Morales* 11 (CONC); Quebrada Peralito, 16 Sept. 1953, *M. Ricardi* 2476 (CONC); Quebrada San Ramón, 10–100 m, 25 Sept. 1941, *E. Pisano & R. Bravo* 228 (SGO); 15 km S crossroad to Taltal, 25°24'S, 70°29'W, 130 m, 2 Sept. 1991, *G. Arancio* 91225 (ULS); 7-15 km N of Taltal, 25°24'S, 70°29'W, 7 Nov. 1987, *K.H. Rechinger & W. Rechinger* 63514 (B, NY); Hueso Parado, 17 Sept. 1967, *O. Zoellner* 1870 (CONC); Hueso Parado, 2 Oct. 1953, *M. Ricardi* 2705 (CONC, G); Taltal, Oct. 1887, *A. Borchers* s.n. (SGO 54351); Taltal, 26 Sept. 1940, *E. Barros* 6233 (GH); Taltal, 200 m, Oct. 1925, *E. Werdermann* 767 (B, BM, CONC, F, G, GH, K, M, NY, SGO, US); Taltal, 18 Oct. 1960, *G. Montero* 6309 (CONC); Taltal, 17 Sept. 1967, *O. Zoellner* 1735 (CONC); Taltal, 150 m, 9 Nov. 1969, *C. Jiles* 5381 (M); ca. 10 km E of Taltal, Quebrada de Taltal, 75 m, 12 Oct. 1938, *C.R. Worth & J.L. Morrison* 15796 (G, K); Cerro Perales, 25°25'S, 70°25'W, 245 m, 18 Nov. 2005, *N. Schulz* 2 (ULS); Hillsides SE of Taltal, 25 Nov. 1925, *I.M. Johnston* 5119 (US); Lomas de Taltal, 7 km S of Taltal, 25°26'45''S, 70°30'57''W, 30 m, 25 Oct. 2002, *M. Ackermann* 479 (B, CONC, F); Quebrada de Taltal, 470 m, 14 Sept. 1992, *S. Teillier, P. Rundel & P.García* 2695 (SGO); Quebrada de Taltal, 400 m, 14 Sept. 1992, *S. Teillier, P. Rundel & P.García* 2648 (SGO); Quebrada de Taltal, Road to airport, 800 m, 14 Sept. 1992, *S. Teillier, P. Rundel & P.García* 2682 (SGO); Quebrada de Taltal, Road to airport, 800 m, 14 Sept. 1992, *S. Teillier, P. Rundel & P.García* 2683 (SGO); Quebrada Las Tipias, 25°26'54.1''S, 70°26'9.1''W, 275 m, 17 Sept. 2004, *F. Luebert, C. Becker & N. García* 2079 (BSB); Quebrada Taltal, 9 km E of Taltal, 25°26'S, 70°35'W, 4 Oct. 1997, *S. Teillier* 647 (CONC, SGO); Taltal, Quebrada Changos, 21 Sept. 1953, *M. Ricardi* 2563 (CONC); Taltal, Quebrada del Ocho, 25°27'51.5''S, 70°25'44.3''W, 370 m, 10 Oct. 2005, *F. Luebert & N. García* 2754/1148 (BSB); Between Panamericana and Taltal, 25°29'S, 70°28'W, 11 Sept. 2001, *M. McMahon & L Hafford* 552 (F); Breas, 25°29'55.8''S, 70°24'2.9''W, 570 m, 10 Oct. 2005, *F. Luebert & N. García* 2731/1125 (BSB, SGO); Breas, 1888, *A. Larrañaga* s.n. (holotype of *Heliotropium longiflorum* SGO 54350, isotype SGO 54352); Aguada Breas, 12 Dec. 1949, *W. Biese* 3222 (SGO); ca. 16 km SE of Taltal, 2-5 km NE of Breas, 25°29'S, 70°22'W, 590–610 m, 29 Oct. 1988, *M.O. Dillon & D. Dillon* 5791 (F, MSB); Quebrada de Taltal, ca. 13 km E of Taltal, 580 m, 21 Oct. 1990, *E. Bayer, J. Grau, A. Marticorena & R. Rodríguez* BY5015 (NY); Road Taltal-Panamericana, 9 Nov. 1990, *O.F. Clarke* 17-08 (CONC); Ruta 5 to Taltal, crossroad to Cifuncho, 600 m, 13 April 1994, *C.M. Taylor & A. Pool* 11590 (CONC); Taltal, 800 m towards Cifuncho from Taltal crossroad, 25°30'38''S, 70°25'6.2''W, 571 m, 6 Jan. 2006, *M. Acosta, P. Guerrero & M. Rosas* 3358 (K); Quebrada Los Zanjones, 5 km SW on road (B-900) to Cifuncho, 15 km SW Taltal , 25°31'S, 70°25'W, 610–620 m, 25 Sept. 1988, *M.O. Dillon, D. Dillon & V. Poblete* 5502 (F, MSB); Taltal, Quebrada Setiembre, 6 Oct. 1954, *M. Ricardi* 3144 (CONC); Road to Cifuncho, 17 km after the crossroad, 290 m, 30 Nov. 1996, *C. Ehrhart & E. Sonderegger* 96/1010 (MSB); Road from Taltal to Cifuncho, 25°32'2.6''S, 70°26'37.1''W, 600–700 m, 24 Oct. 2009, *F. Luebert, A. Moreira & M.O. Dillon* 3005 (BSB, G, SGO); Antofagasta-Chañaral, crossroad to Taltal, 950 m, 14 April 1968, *M. Ricardi* 5524 (CONC); Las Tórtolas, Sierra de San Pedro, 25°33'30.3''S, 70°35'44.5''W, 170 m, 12 Oct. 2005, *F. Luebert & N. García* 2763/1157 (BSB); Between crossroad to Cifuncho and road to Las Tórtolas, 25°35'35.7''S, 70°31'15.8''W, 380 m, 12 Oct. 2005, *F. Luebert & N. García* 2774/1168 (BSB); Cifuncho, 24 Oct. 1964, *M. Ricardi, C. Marticorena & O. Matthei* 1083 (CONC); Sierra Cifuncho, 25°46'12.7''S, 70°34'19.4''W, 800 m, 16 Sept. 2004, *F. Luebert, C. Becker & N. García* 2067A (BSB); Cifuncho to Panamericana, S crossroad from Cifuncho, 25°48'S, 70°32'W, 690 m, 8 Dec. 2002, *C. Ehrhart* 2002/233 (M); Mineral Esmeralda, 75 km S of Taltal, 750 m, 3 Feb. 1947, *W. Biese* 2251 (SGO); Sierra Esmeralda, 25°52'2''S, 70°39'12.8''W, 500 m, 13 Oct. 2005, *F. Luebert & N. García* 2806/1200 (BSB); Aguada Cachina, , 13 Dec. 1949, *W. Biese* 3256 (SGO); Quebrada Guanillos (10 km N of Cachinal de la Costa)., 250 m, 14 Dec. 1949, *W. Biese* 3341 (SGO); Sierra Esmeralda, road to Esmeralda, 25°53'31.8''S, 70°33'33.2''W, 520 m, 12 Oct. 2005, *F. Luebert & N. García* 2778/1172 (BSB); Quebrada Agua Grande, between Pan de Azucar and Caleta Esmeralda, 660 m, 30 Oct. 1942, *E. Pisano & R. Bravo* 566 (CONC,

SGO). Región de Atacama, Prov. Chañaral: Las Lomitas, 26°0'20.2''S, 70°36'18.9''W, 820 m, 14 Oct. 2005, *F. Luebert & N. García* 2821/1215 (BSB); Pan de Azúcar National Park, Las Lomitas, 2 km E of coast, 26°1'S, 70°35'W, 720 m, 12 Nov. 1997, *M.O. Dillon & C. Trujillo* 8020 (CONC, F, MSB, SGO); Road Agua Verde-Chañaral, 1300 m, 26 Feb. 2001, *C. Latorre, C. Villagrán & A. Maldonado* 261 (CONC); Panamericana N of Chañaral, km 1000, 650 m, 12 Oct. 1980, *J. Grau* 2112 (M); Quebrada Pan de Azúcar, 450 m, 20 Oct. 1972, *F. Behn* s.n. (CONC 51924); Vicinity of Aguada Grande ("Cachinal de la Costa" of Philippi), near Antofagasta-Atacama Provincial Boundary, 16-18 Dec. 1925, *I.M. Johnston* 5808 (US); Cachinal de la Costa, Dec. 1853, *R.A. Philippi* s.n. (lectotype SGO 42217); Sierra Las Tipias, Pan de Azúcar National Park, 26°5'S, 70°37'W, 500 m, 30 Sept. 2005, *N. Schulz* 14F24-132 (ULS); Pan de Azúcar, 26°6'54.9''S, 70°34'66.7''W, 210 m, 15 Sept. 2004, *F. Luebert, C. Becker & N. García* 2055 (BSB); Pan de Azúcar, 13 Oct. 1980, *J. Grau* s.n. (M); Pan de Azúcar National Park, El Mirador, 26°7'S, 70°37'W, 340 m, 7 Dec. 2002, *C. Ehrhart* 2002/219 (M); Pan de Azucar, 26°7'55.2''S, 70°27'33.1''W, 115 m, 15 Sept. 2004, *F. Luebert, C. Becker & N. García* 2054 (BSB, SGO); Pan de Azúcar National Park, 15 Sept. 1992, *S. Teillier, P. Rundel & P.García* 2727 (SGO); 12 km from the coastal access to Pan de Azúcar National Park, 31 Oct. 1991, *M. Muñoz Schick, S. Teillier, I. Meza* 2809 (SGO); 12 km from the coastal access to Pan de Azúcar National Park, 31 Oct. 1991, *M. Muñoz Schick, S. Teillier, I. Meza* 2822 (SGO); 15 km N of Chañaral, 7 Oct. 1988, *G. Arancio* 88271 (ULS); Panamericana Las Bombas-Chañaral, km 27, 23 Oct. 1965, *M. Ricardi, C. Marticorena & O. Matthei* 1435 (CONC); Falda Verde, 26°17'S, 70°37'W, 350 m, 5 Nov. 2005, *N. Schulz* 36 (ULS); N of Chañaral, km 990, 27 Oct. 1987, *M. Muñoz S. & I. Meza* 2254 (SGO); Vicinity of Puerto de Chañaral, hills back of El Barquito, 28-29 Oct. 1925, *I.M. Johnston* 4750 (K); La Ánimas, Dec. 1853, *R.A. Philippi* s.n. (SGO 54353 [photo F, GH, MSB, NY, US]); E of El Salado, 35 km from Diego de Almagro, 26°24'S, 70°19'W, 490 m, 30 Oct. 1991, *M. Muñoz Schick, S. Teillier & I. Meza* 2784 (SGO); Caleta Flamenco, 26°34'12.9''S, 70°40'48.3''W, 0 m, 15 Oct. 2005, *F. Luebert & C. Becker* 2843 (BSB); Dunes back of Caleta Flamenco, 20 m, 14 Oct. 1991, *S. Teillier, L. Villarroel & R. Torres* 2595 (SGO). Región de Atacama, Prov. Copiapó: Panamericana km 908, N of Caldera., 11 Oct. 1980, *J. Grau* 2089 (BM, M); 16 km N of Caldera, Quebrada El León, 25 Oct. 1984, *M. Muñoz S.* 1976 (SGO); Quebrada Los Leones, 26°57'17.7''S, 70°44'7.1''W, 240 m, 16 Oct. 2005, *F. Luebert & C. Becker* 2844A (BSB, SGO); 20 km N of Caldera, 27°0'S, 70°45'W, 105 m, 2 Sept. 1991, *G. Arancio* 91163 (ULS); Caldera, 6 Nov. 1969, *C. Jiles* 5306 (CONC); Caldera, Sept. 1900, *K. Reiche* s.n. (SGO). Indefinite: S side of Chungará lake, 27 May 1968, *O. Zalensky* XV-866 (SGO); Litoral of the prov. Tarpacá and Atacama, Sept. 1909, *K. Reiche* s.n. (SGO 61446, 61447); s.loc., *s.col.* (GH).

### 16. *Heliotropium philippianum* I.M.Johnst.

**CHILE**. Región de Antofagasta, Prov. Antofagasta: Quebrada Blanco Encalada, 50–250 m, 11 Dec. 1949, *W. Biese* 3131 (SGO); 10 km S of Caleta Blanco Encalada, 200–800 m, 11 Dec. 1949, *W. Biese* 3194 (SGO); Miguel Diaz, 24°32'58.5''S, 70°32'55.2''W, 315 m, 5 Oct. 2005, *F. Luebert & N. García* 2641/1035 (BSB); Miguel Díaz, 24°32'46.9''S, 70°32'52.3''W, 400 m, 20 Sept. 2004, *F. Luebert, C. Becker & N. García* 2131 (BSB, SGO); Miguel Díaz, 23 Dec. 1853, *R.A. Philippi* s.n. (SGO 42220 [photo F, GH, MSB, NY, US]); Miguel Diaz, 24°33'16.3''S, 70°32'33.6''W, 590 m, 5 Oct. 2005, *F. Luebert & N. García* 2656/1050 (BSB); Miguel Díaz, 600 m, 17 Oct. 1994, *M. Richter* 94/4 (M); Vicinity of Aguada Miguel Díaz, 1 to 4 Dec. 1925, *I.M. Johnston* 5415 (GH); Quebrada La Plata, 24°41'S, 70°32'W, 500 m, 12 Feb. 1998, *G. Arancio & F. Squeo* 11257 (ULS); Quebrada La Plata, 20–300 m, 18 Oct. 1990, *E. Bayer, J. Grau, A. Marticorena & R. Rodríguez* BY4933 (NY); Quebrada La Plata, 300 m, 6 Oct. 1991, *M. Quezada & E. Ruiz* 274 (CONC, G); Vicinity of Aguada Cardón, 30 Nov. 1925, *I.M. Johnston* 5294 (GH, US); Aguada Panul, 24°47'42.1''S, 70°31'50.3''W, 215 m, 7 Oct. 2005, *F. Luebert & N. García* 2672/1066 (BSB); Aguada Panulcito, 24°47'55.7''S, 70°31'36.6''W, 345 m, 19 Sept. 2004, *F. Luebert, C. Becker & N. García* 2124 (BSB, SGO); Aguada Panulcito, 24°48'2.2''S, 70°31'32.6''W, 375 m, 19 Sept. 2004, *F. Luebert, C. Becker & N. García* 2108 (BSB); Aguada Panulcito: along trail of the old Andacolla mine on slope above the waterhole, 5 Dec. 1925, *I.M. Johnston* 5478 (GH); Quebrada Los Médanos, 22 km N of Paposo, 400 m, Nov. 1987, *A. Hoffmann & X. Rodriguez* 150b (CONC); Quebrada El Médano, 7 Oct. 1991, *M. Quezada & E. Ruiz* 318 (CONC, M); Quebrada El Médano, near the waterhole, 24°49'43.9''S, 70°31'11.7''W, 300–400 m, 23 Oct. 2009, *F. Luebert & A. Moreira* 3003 (BSB, G, SGO); Quebrada La Rinconada, ca. 5 km N of Paposo, 24°56'S, 70°29'W, 500 m, 18 Nov. 1997, *M.O. Dillon, C. Trujillo & M. Villarroel* 8065 (CONC, F, MSB, SGO); Paposo, 19 Dec. 1853, *R.A. Philippi* s.n. (SGO 42216 [photo F, GH, MSB, NY, US]); Paposo, hillsides, 10 Oct. 1983, *M. Elgueta* 48 (SGO); Vicinity of Paposo; hill directly back of Punta Grande, 29 Nov. 1925, *I.M. Johnston* 5233 (holotype GH, isotypes K, US). Indefinite: Desert Atacam, 1861, *R.A. Philippi* s.n. (G).

**17. *Heliotropium eremogenum* I.M.Johnst.**
**CHILE**. Región de Tarapacá, Prov. Iquique: Iquique, Dec. 1913, *E. Salinas* s.n. (GH); Punta Gruesa, May 2003, *R. Pinto* 761 (SGO); Punta Gruesa, 20°22'41''S, 70°7'53''W, 1015 m, 23 Sept. 2004, *F. Luebert, C. Becker, N. García & R. Pinto* 2159 (SGO). Región de Antofagasta, Prov. Tocopilla: Quebrada La Higuera, N of Tocopilla, 22°3'6''S, 70°10'34''W, 150 m, 29 Sept. 2005, *F. Luebert & N. García* 2566/960 (BSB). Región de Antofagasta, Prov. Antofagasta: Morro Moreno, 830 m, 31 Oct. 1985, *F. Schlegel* 7819 (CONC); Morro Moreno, 10 Nov. 2002, *R. Pinto* 566 (SGO); Morro Moreno, 10 Nov. 2002, *R. Pinto* 568 (SGO); Cerro Moreno, 930 m, 19 Oct. 1994, *M. Richter* 94/10 (M); Cerro Moreno, 23°29'19.1''S, 70°35'31''W, 670 m, 2 Oct. 2005, *F. Luebert & N. García* 2575/969 (BSB, SGO); Cerro Moreno, 1000 m, 17 July 1969, *O. Zoellner* 3358 (CONC); Peninsula Moreno, hills W of J. López, 23°30'S, 70°33'W, 830 m, 18 Oct. 1992, *G. Baumann* 39 (CONC, ULS); Peninsula Moreno, hills in front of J. López, 300 m, 29 Sept. 1991, *M. Quezada & E. Ruiz* 55 (CONC); Quebrada de La Chimba, 300 m, 16 Nov. 1987, *A. Hoffmann & X. Rodríguez* 7 (CONC); Quebrada La Chimba, 300 m, 30 Sept. 1991, *M. Quezada & E. Ruiz* 85 (CONC, M); Quebrada La Chimba, 1 Oct. 1954, *M. Ricardi* 3039 (CONC); La Chimba, Oct. 1959, *O. Astudillo* s.n. (CONC 121853); La Chimba, 7 Dec. 2002, *R. Pinto* 595 (SGO); Antofagasta, open rocky canyon, 100–300 m, 3 April 1925, *F.W. Pennel* 13022 (NY); Antofagasta, 29 Oct. 1930, *F. Jaffuel* 1120 (holotype GH); Antofagasta, 6 Nov. 1931, *F. Jaffuel* 2639 (G, GH). Indefinite: Putre, 5 Dec. 1946, *R.P.B. Kuschel* s.n. (SGO 66193).

# Appendix F: Supplementary data to Chapter 7

## Specimens from cultivation of *H. arborescens*, *H. corymbosum* and putative interspecific hybrids

Note: ‘o.d.’ indicates original determination.

***Heliotropium arborescens* L.** (style shorter than or equal to the stigmatic heads; agreeing with Miller’s specimens): cultivated in Madrid, Spain, 1800 (MA [o.d. *H. peruvianum*]); cultivated in Madrid, Spain, 1805 (MA [o.d. *H. peruvianum*]); cultivated in Madrid, Spain, 1808 (MA [o.d. *H. peruvianum*]); cultivated in Lausanne, Switzerland, 1811 (K [o.d. *H. peruvianum*]); cultivated in Toulon, France, 1819 (K [o.d. *H. grandiflorum*]); cultivated in England, 1819 (K [o.d. *H. peruvianum*]); cultivated in Bonn, Germany, 1821 (B [o.d. *H. corymbosum*]); cultivated in Bonn, Germany, 1830 (B [o.d. *H. voltairianum* Hort.]); cultivated in Bonn, Germany, 1841 (B [o.d. *Heliotropium*]); cultivated in Nantes, France, 1842 (BM [o.d. *H. peruvianum var. voltairianum*]); cultivated in Berlin, Germany, 1898 (B [o.d. *H. peruvianum*]); cultivated in Kenya, 1953 (K [o.d. *H. corymbosum*]); cultivated in Berlin, Germany, 1975 (B [o.d. *H. arborescens*]); cultivated in Berlin, Germany, 1988 (B [o.d. *H. arborescens*]); cultivated in Buenos Aires, Argentina, 1993 (BSB [o.d. *H. peruvianum*]); cultivated in Asturias, Spain, 2001 (MA [o.d. *H. arborescens*]); cultivated in Kew, England, 2003 (K [o.d. *H. arborescens*]); cultivated in Malaga, Spain, 2004 (MA [o.d. *H. arborescens*]); cultivated in South Carolina, U.S.A., 2006 (BSB [o.d. *Heliotropium*]).

***Heliotropium corymbosum* Ruiz & Pav.** (style longer than the stigmatic heads): cultivated in Nantes, France, 1816 (K [o.d. *H. corymbosum*]); cultivated in Lisbon, Portugal, 1840 (BM [o.d. *H. peruvianum*]); cultivated in Paris, France, 1841 (MA [o.d. *H. grandiflorum*]); cultivated in Munich, Germany, 1841 (M [o.d. *H. grandiflorum*]).

**Putative interspecific hybrids**: cultivated (Herb. Déséglise), 1817 (BM [o.d. *H. peruvianum*]); cultivated in Saxony, Germany, 1896 (B [o.d. *H. peruvianum*]).