Studies on the systematics, evolution, and biogeography of *Oxalis* sections *Caesiae*, *Carnosae*, and *Giganteae*, endemic to the Atacama Desert of northern Chile

Diplomarbeit

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INTRODUCTION

With more than 450 species the genus *Oxalis* L. is not only species rich (Lourteig, 2000), but it is also widely distributed and ecologically diverse. Species of *Oxalis* occur in all kinds of habitats from Andean cloud forests over Eurasian temperate woodlands to coastal deserts of South America and South Africa and from sea level in the Patagonian steppe to the Puna in the Andes at more than 3700 meters altitude. Life forms found in *Oxalis* are correspondingly diverse. There are annuals (often invasive), perennial herbs that form rhizomes, tubers or bulbs for dormancy, cushion-like dwarf shrubs, shrubs and lianas that reach up to 6 meters. Many species in the genus tend to form of fleshy stems and leaves.

Succulence of *Oxalis* in the Atacama Desert. A marked case of succulence is the development of water-storing stems found in various but not all species of *Oxalis* that inhabit the coastal desert of Atacama in northern Chile. Most of these species occur more or less exclusively in fog oases along the Pacific coast of the Atacama desert. Few species also inhabit the semi desert and mediterranean region subjected to various degrees of winter rainfall. Although the ecological conditions under which most of these species grow are quite similar, they show marked differences in life form. Many *Oxalis* species in the Atacama developed water-storing tissues in root tubers, stems and leaves. Different species show different degrees of succulence apparently allocating between above ground and below ground storage of water. In contrast, a few species do not show notable succulence grow as compact dwarf shrubs.

Different life forms of *Oxalis* found in the Atacama desert raise the question of how they originated. Previous floristic investigations suggested that formation of the Atacama desert had a substantial influence on survival, diversification and extinction of species depending on their life form (Armesto & Vidiella, 1993). Reconstructions of the paleoclimates for the Atacama region show that the arid environment developed recently. Tertiary climates were generally warmer and wetter than at present (Solbrig, 1976), and tropical forests covered most of the mountain less South American landscape. Gradual desiccation of the Atacama region began in the middle Eocene and was intensified in the late Miocene due to formation of the Humboldt Current and Andean uplift. Hyper arid conditions, however, did not develop until the Pleistocene (Solbrig, 1976; Arroyo et el. 1988). Increasing aridity constitutes a selection pressure that acted upon desert plants and should also have been responsible for shaping

different life forms in *Oxalis*. More than 75% of species of *Oxalis* in the Atacama desert are succulent, but a small minority appears to be constraint to cushion-like growth patterns for reducing water loss. Development of water-storing tissues, however, seems to represent a favorable adaptation in the present context. There are two evolutionary scenarios that could have potentially led to the formation of succulence:

(1) A multiple origin of succulence due to convergent evolution would be a likely explanation since populations are found isolated in fog oases that are geographically separated. Gene flow and seed dispersal should be limited under present climatic conditions.
(2) On the other hand, Arroyo et al. (1988) argue that the Pleistocene climate showed marked changes due to glacial and interglacial events. Wet glacial periods led to a snowline depression and subsequent descend of Andean floristic elements (Solbrig, 1976). Armesto and Vidiella (1993) suggest that these species could have reached the Pacific coast and integrated into the coastal desert flora. If this is true, dispersal between adjacent fog oases could have been possible during glacials and a preadapted genotype could indeed have dispersed prior to specification due to genetic isolation.

The study group of Atacama-inhabiting *Oxalis* consists of three sections: *Caesiae*, *Giganteae* and *Carnosae*. Taxonomic delimitations of many of its species are still poorly defined in comparison to other sections of *Oxalis.* Previous classifications (Philippi 1860, Philippi, 1893; Reiche, 1894; Knuth, 1930; Lourteig 2000) were exclusively based on examination of herbarium material, which is difficult to preserve due to the fragileness of succulent specimens. Therefore, as a first part of the study, the classification of the study group was reviewed using field observations and greenhouse cultivations in addition to herbarium specimens. The investigation of life material was hoped to grant a better approach to the classification of succulent species.

Character evolution in the west-Andean *Oxalis*. As a second part of the study, a molecular phylogeny was established in order to gain understanding of the origin of succulence in desert inhabiting *Oxalis*. In doing so, it is necessary to construct a phylogeny that also includes other sections of *Oxalis* of putative affinity. Table 1 gives an overview of life form, habitat and distribution over all sections of *Oxalis* represented in the phylogenetic analysis. Throughout this study, they will be referred to as ‘west-Andean alliance’.

Table 1: Life form, habit and distribution for eight sections of Oxalis in the 'west-Andean alliance'. The study group consists of *Caesiae*, *Giganteae* and *Carnosae* with a center of diversity in the Atacama desert. The remaining sections are distributed around the Atacama desert and are included in the phylogenetic analysis.

	Section	Life form	Habitat	Distribution
Atacama	*Caesiae*	dwarf shrubs	dry	Atacama desert
	Giganteae	succulent shrub	dry	Atacama desert and semi desert of Chile
	Carnosae	succulent subshrub	dry	Atacama desert, semi desert and mediterranean region of Chile
Non-Atacama	*Alpinae*	suffrutescent perennials	dry	Andes of Argentina and Chile
	Herrerae	succulent perennials	dry to humid	Andes of Colombia, Ecuador, Peru and Bolivia
	Roseae	herbaceous annuals	humid	mediterranean and temperate Chile
	Corniculatae	herbaceous	dry to humid	cosmopolitan
	Palmatifoliae	herbaceous perennials	dry	Patagonia of Chile and Argentina

The non-Atacama sections were selected according to their biogeography under the assumption that Andean orogenesis and formation of the Atacama Desert have played a key role in the evolution of the study group. They show Andean or Pacific coastal distribution (Figure 1). A brief description of the non-Atacama sections is given. Section *Alpinae* is restricted to the Andes of Argentina and Chile. It contains 25 species of suffrutescent perennial herbs and cushion-like dwarf shrubs. They are found from the piedmont to the snowline in dry habitats with stony or sandy substrate. The four species of section *Herrerae* are found in open habitats the Andes of Columbia, Ecuador, Peru and Bolivia, where they prefer stony substrate and dry to humid conditions. Like many Atacama-inhabiting species, those of *Herrerae* show pachycaulous habits. Section *Roseae* consist of only one species *sensu* Lourteig (2000), which is endemic to the mediterranean and temperate climate zone of central Chile, ranging from La Serena to the Taitao peninsula. It is a mesophytic herb that grows in humid habitats. Section *Corniculatae* is not depicted in the map (Figure 1) because of its cosmopolitan distribution. Its members are mainly distributed in South America, where the section presumably originated. Four species are found in Chile. One of them, *O. corniculata*, is introduced while the other three species are endemic to Chile, occurring more or less sympatrically with *O. rosea*. The species are all creeping herbs that occur in a wide variety of habitats. Section *Palmatifoliae*, finally, consists of five species endemic to the cold

steppes of Patagonia. They grow as cushion-like, acaulescent, perennial herbs and are distinguished in having pinnate leaves with 5-14 leaflets instead of trifoliolate leaves as is typical for *Oxalis*.

Aims. The present study aimed at a better understanding of the systemtics and biogeography of three sections of genus *Oxalis* that inhabit the Atacama Desert in northern Chile. It addressed three major questions:

(1) The current classification of the study group was revised based on morphological investigation of living material and herbarium specimens.

(2) Evolution relationships among sections of the west-Andean Oxalis and among species of the study group were inferred by construction a molecular phylogeny (*trnL-L-F* and *psbA-trnH*).

(3) Morphological and molecular evidence was used in order to reconstruct the origin of stem succulence and to discuss xerophytic adaptations in Atacama endemic *Oxalis* in a biogeographical context.

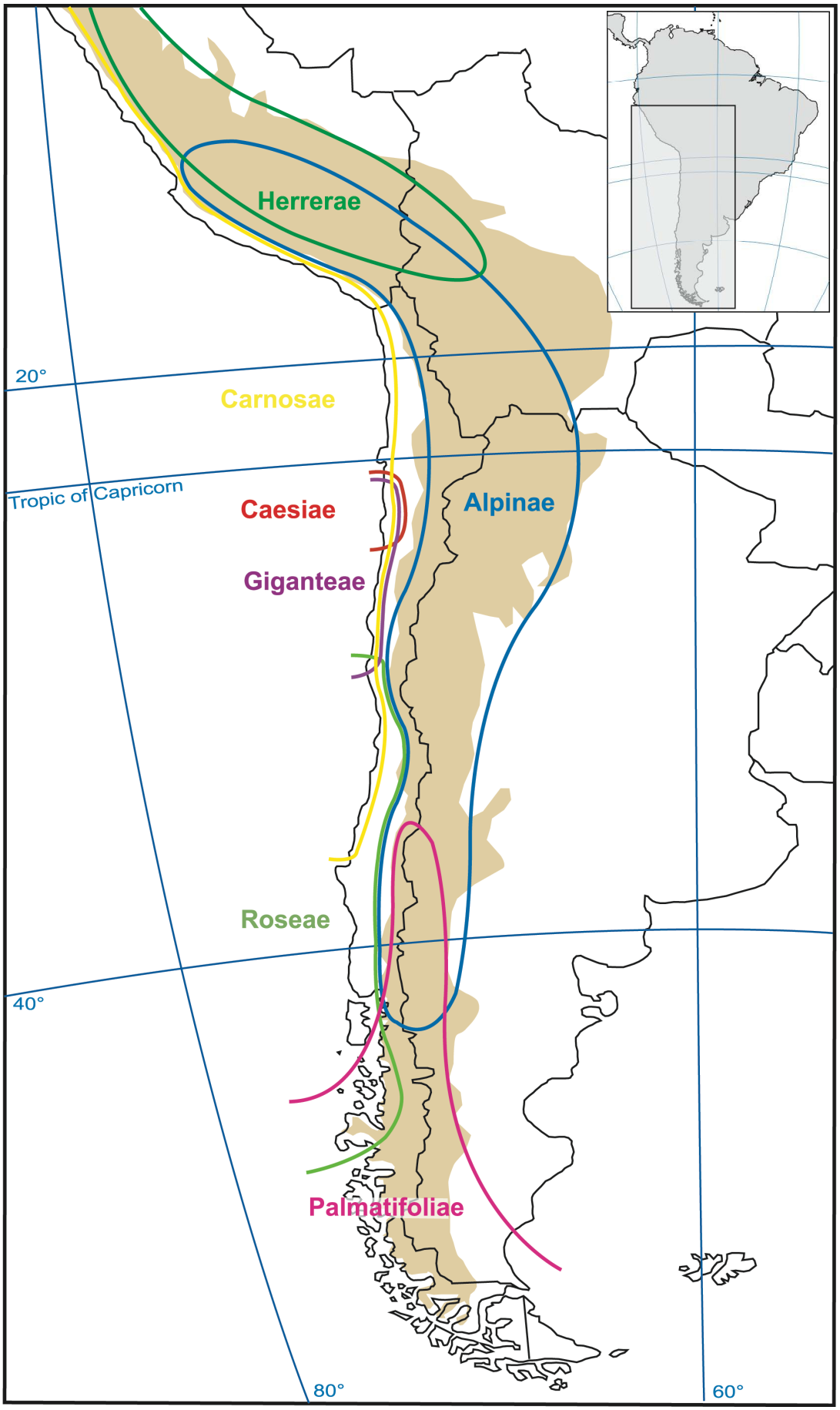


Figure 1: Approximate distributional ranges of sections of *Oxalis* of the 'west-Andean alliance'.

MATERIAL & METHODS

Study area

The desert of Atacama means different things to different investigators depending on the characteristics that are used for its delimitation. Coastal fogs as a main source of plant life in the Atacama Desert are not easily measured (Larrain et al., 2002) and are usually not registered in the climate records. As a result, more water is available for plant development than predicted by meteorological data and circumscription of the Atacama Desert using patterns of vegetation will differ from those using patterns of precipitation. Therefore, considering both meteorological and vegetation data, a classification of biomes of northern and central Chile will be given with a special emphasis on the coastal fog ecosystems.

Climate. The Atacama Desert is part of a coastal desert belt that extends from the Sechura desert in Peru (5 °S) to the southern limit of the Chilenean Atacama desert at Copiapó (27°). In contrast to many other hot deserts of the world it hardly ever experiences rainfall with he exception of El Niño Southern Oscillation (ENSO) events. The extreme aridity is due to the concerted action of the cold Humboldt Current (Börgel, 1973; Caviedes, 1973; Lydolph, 1973), the eastern Pacific anticyclone (Lauer & Frankenberg, 1983; Arroyo et al., 1988) and the rain shadow of the Andean mountain range (Arroyo et al., 1988). The Humboldt Current is derived from the West Wind Drift, an east-flowing circum Antarctic current that is in part deflected northward after hitting the South American coast. Its upwelling of cold waters produced by the Coriolis effect and the northward deflection of westerly winds in central and southern Chile cools the air above. The result is a stable inversion layer that prevents mixing of the warm, dry air above with the cool, dry air below. As a consequence, no sufficient increase in air moisture is possible to cause any precipitation inland of the coast.

The high-pressure cell of the eastern Pacific anticyclone is responsible for deflecting the influences of the Polar Fronts southward. With the seasonal migration of the eastern Pacific anticyclone central Chile is subjected to rainfall mainly in winter giving rise to Mediterranean type climate. Further north, the polar fronts are permanently blocked by the high-pressure cell and precipitations reach the continent only during ENSO events when change in winds and ocean currents cause the eastern Pacific anticyclone to break down.

Finally the Andean mountain range intercepts moist trade winds causing increased precipitation on the eastern slopes. This precipitation is received predominantly from

November to March (Fig. 4b), a phenomenon known as “invierno boliviano” in the central Andes. The dried air descends on the western side of the Andes causing a rain-shadow effect from 30° S north almost to the equator thereby adding to the effects of the Humboldt Current and the eastern Pacific anticyclone.

Classification of northern and central Chilean biomes. Classification of northern and central Chile follows a general view recognizing four major regions: Andean, desert, semi-desert and Mediterranean climate. The southernmost part of the study area lies in the transition zone to temperate climate, recognized as a fifth region. These major regions are further subdivided according to water supply and the vegetation types it gives rise to. Table 2 gives an overview over the classification used in the present study. The map in figure 3 shows the approximate distribution of each region. This map is based on the work of Schmidhüsen (1956) and modified according to considerations explained below.

Table 2: Major biomes of northern and central Chile and their subdivisions based on main water source and vegetation type.

	Water source	Vegetation
1 Andean climate		
1a	summer rainfall	dwarf shrubs, tussock grasses
1b	winter rainfall	dwarf shrubs, herbaceaous geophytes
2 Desert climate		
2a	hyper arid	mainly absent, desert ephemerals
2b	coastal fog	xeromorphic shrubs, succulents
3 Semi desert climate		
3a	variable winter rainfall	xeromorphic shrubs, sporadically desert ephemerals
3b	variable winter rainfall and coastal fog	succulents, xeromorphic shrubs
4 Mediterrenean climate		
4a	notable winter rainfall	xeromorphic shrubs, succulents
4b	notable winter rainfall	xeromorphic shrubs, succulents, regular spring time flowering of herbaceous annuals and geophytes,
4c	regular winter rainfall	sclerophyll forests
5 Temperate climate		
5	rainfall year round	summer green deciduous forest

The Andean climate (1) is characterized by small atmospheric humidity and great intensity of solar radiation. According to Arroyo et al. (1988), there is a transition zone between 24°-25° S where influences of Amazonic trade winds give way to influences of westerlies from the Pacific. Consequently, the Andean region is subdivided based on the timing of rainfall: The northern part (1a) receives rainfall in summer (November to March), while the southern part (1b) receives rainfall during the winter months from May to August. Summer rainfall in the northern Chilean Andes can also be regarded as a modification of the otherwise hyper arid desert conditions that prevail in the tectonic basins found at the west-Andean foothills (Pampas del Tamarugal, Desierto de Atacama) at that latitude (Fig. 2).

The desert climate (2) is characterized by the absence of any regular precipitation in the form of rain. Its center (2a) is hyper arid and precipitation has never been recorded in historical times (e.g., in Calama, Fig. 4a). Fog oases (2b) constitute an important modification of the hyper arid desert climate along the Pacific coast (Fig. 2) that is particularly important in the present context. Where the coastal mountain range intercepts the thermal inversion layer that forms above the sea, frequent fog events allows notable plant life to develop on the windward slopes (Fig. 2). These fogs occur year round, but are more intense in winter and spring and least intense from January to March (Cereceda et al., 2002, Richter, 1995). Fog formation along the northern Chilean coast takes two forms (Cereceda et al., 2002). Advective fog results from stratocumulus clouds generated over the ocean far from the continent and trapped below the thermal inversion layer, which are transported by the wind to the coast where they intercept with the relief. Orographic fog is formed on the first windward slope facing the sea, when sea winds are forced upward by the relief. Except for ENSO events, these two types of fog constitute the only source of water for local plant communities. Therefore, this type of habitat has been often characterized as fog oasis. Apart from abundant lichens and some members of Bromeliaceae, that can absorb humidity directly from the air most inhabitant of these fog oases are not true fog plants. They rely on water that condenses on rock surfaces, leaves or cactus spines and drops to the ground where it can be taken up by their roots.

The semi desert climate (3) is best understood as a transition zone between the desert and the Mediterranean climate. This region receives winter rainfall (April to July) of varying intensities between 0-200 mm (Armesto & Vidiella, 1993; Muñoz, 1985). This high variation in precipitation is the result of irregularities in the position of the south Pacific anticyclone as explained above. Again, the semiarid inland (3a) is modified along the Pacific coast by frequent fog events (3b). Occasionally, when ENSO events cause abundant rainfalls, the phenomenon of the ‘flowering desert‘ can be observed extending up north reaching the

surroundings of Copiapió. Herbaceous annuals and geophytes then cover the landscape for some weeks.

The Mediterranean climate (4) is characterized by winter rainfalls that increase in intensity from north to south (Figures 4c, 4d, and 4e). Xerophytic shrubs and trees along with succulents dominate the vegetation of the northern part (4a). Schmidhüsen (1956) designated the surroundings of La Serena as a proper region (4b) because of regular springtime flowering of annuals and geophytes after winter rainfall. The occurrence of relict forests in fog oases in Fray Jorge, Talinay and Pichidangui are another remarkable feature of this region (Muñoz & Pisano, 1947; Skottsberg, 1948). Further south, the xerophytic vegetation passes gradually into sclerophyllous woodland (4c).

The transition zone to the temperate climate (5) still shows marked seasonal differences in rainfall but there is no pronounced summer dry season as in the Mediterranean region and precipitation occurs year round. The natural vegetation of this zone consists of summer green deciduous woodland.

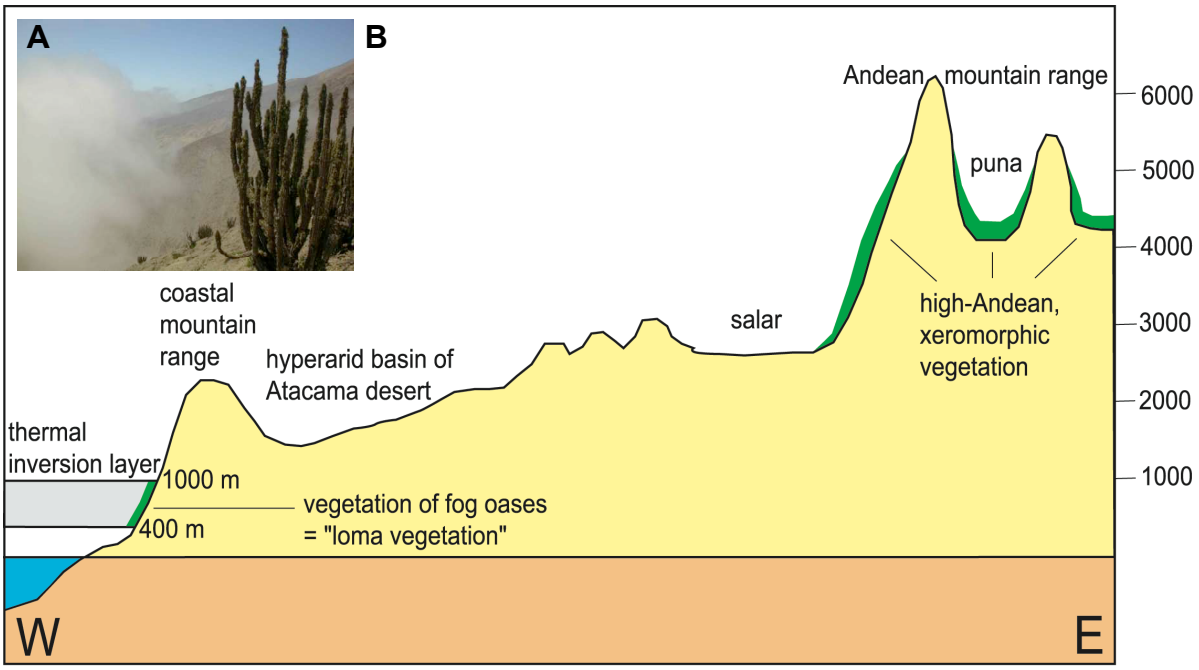
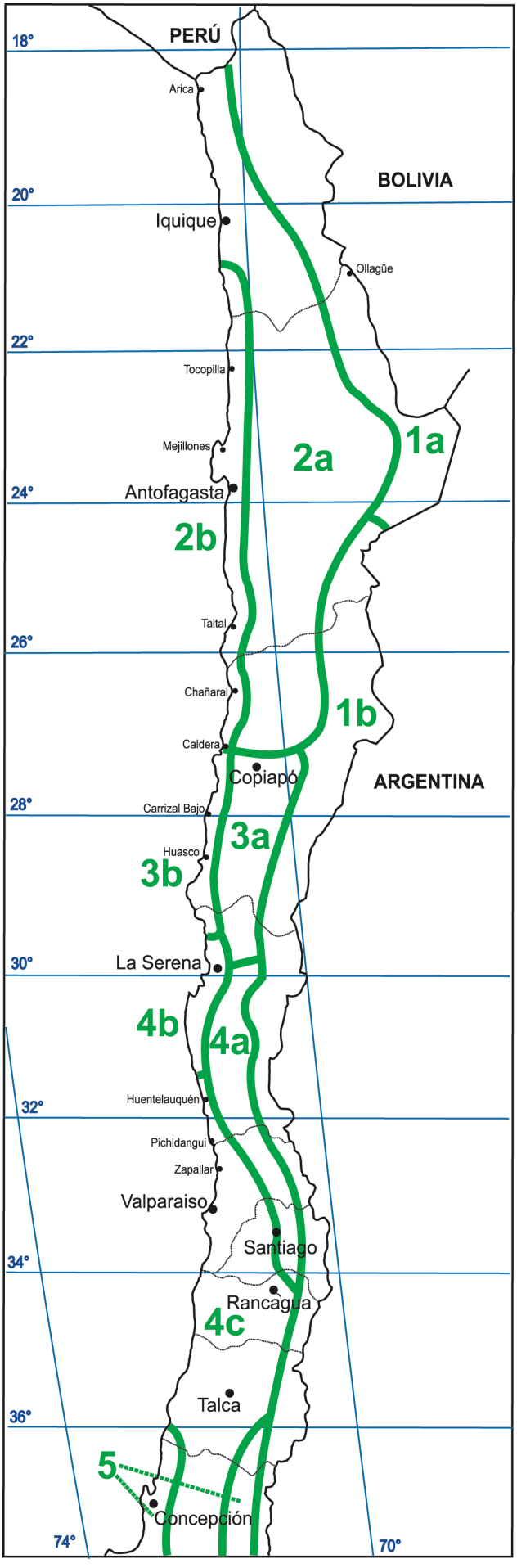


Figure 2: **A** Fog oasis near Caleta Colorada, Chile (24,5°S). **B** Schematic E-W profile of the Atacama Desert at 26° S, showing the modification of the hyper arid conditions towards the borders of the desert.

The Atacama Desert. Pisano (1966) defined northern Chile from the limit with Peru in the North to La Serena, which is characterized by the absence of regular winter rainfall, as ‚xeromorphic vegetation'. Grau (1995) refers to the same region as ‚Atacama Desert' in a phytogeographical meaning. According to these authors, I will be use the name Atacama Desert to denote desert (2a, 2b) and semi desert (3a, 3b) ecosystems, which receive their water either from coastal fogs or occasional, irregular winter rainfall (see table 2, fig. 3).



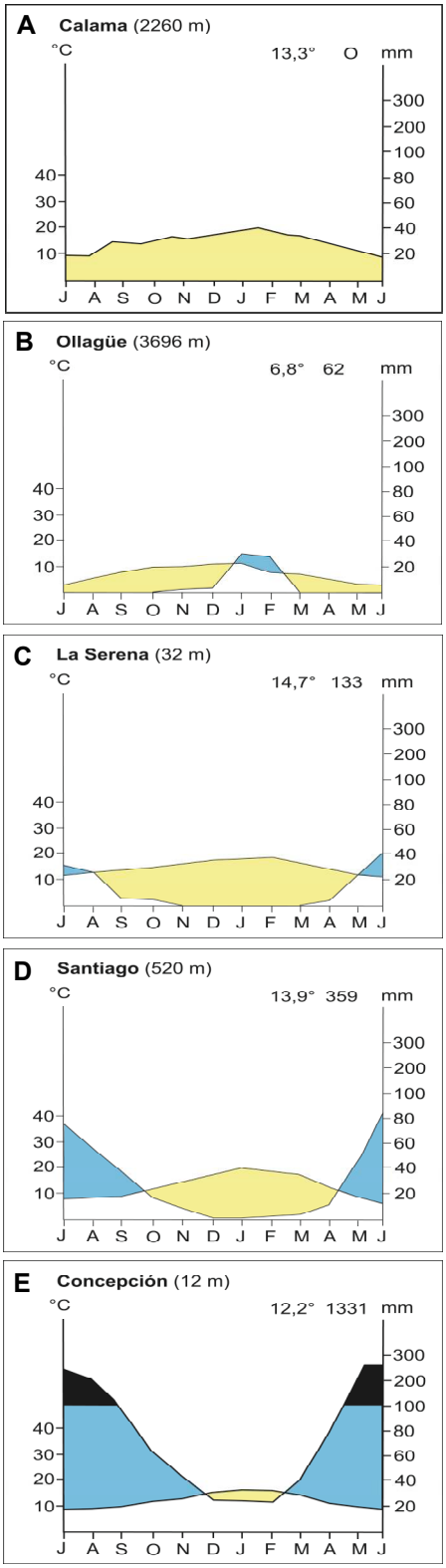


Figure 4: Climate diagrams of five representative stations of northern and central Chile.

Figure 3: Biomes of northern and central Chile: **1a** Andean/summer rainfall, **1b** Andean/winter rainfall, **2a** hyper arid desert, **2b** coastal fog desert, **3a** semi desert/sporadic winter rain, **3b** semi desert/sporadic winter rain and fog, **4a, 4b** Mediterranean thornscrub, **4c** Mediterranean sclerophyll forests, **5** temperate summer green deciduous forest.

Material studied

The delimitation of taxa relied on both herbarium specimens and greenhouse cultivation. Special emphasis was given to the investigation of living material due to the fact that herbarium material of succulent plants is often difficult to interpret. DNA probes were collected during a fieldtrip in December 2004 and dried and stored in silica gel. Additionally, DNA was isolated from living material cultivated in the greenhouses in Munich and, in a few cases, from herbarium specimens. Table 3 lists locality, date of collection, collector, and accession number for all accessions investigated in the present study. The last column gives information about the sort of observation made on the specimens: field observations, green house cultivation and/or dead herbarium material including type specimens.

Greenhouse cultivation. Plants were grown from root tubers that have been collected by workers of the Institute of Systematic Botany, LMU München during various fieldtrips to northern Chile from 1980 onwards. Root tubers were planted in pots containing a mixture of humus, sand and pumice-stone and irrigated every two days. Generally, dormancy was broken within a few days, but some individuals kept dormant for many weeks. Dormant root tubers are at risk of putrefaction and irrigation intensity had to be adapted to the state of dormancy. Eventually, all accessions showed vegetative growth and nearly all of them also flowered. Despite some artifacts of greenhouse cultivation like slight etiolation or changes in the indumentum in some plants, many characteristics could be judged more reliably in greenhouse cultivation than in herbarium specimens.

Herbarium specimens. It is difficult to make herbarium specimens of succulent *Oxalis*. Their bulky stems together with delicate leaves and inflorescences, that easily break apart at their pulvini, make many herbarium specimens resemble a game of pick-up sticks. Nevertheless, the indumentum and small characters like seeds and calyces can be reasonably investigated in most herbarium specimens. Careful comparisons of plants observed during a fieldtrip in December 2004 with their corresponding herbarium specimens were made in order to try to "translate" between a certain character state and its appearance in a dried specimen. These characters involved mainly surface structure of succulent plant parts with together with patterns of coloration and light reflection on surfaces (waxy, shiny, dull, etc.)
Due to the brevity of the study only a rather small number of herbarium specimens could be obtained and investigated. Among these are those kept at the herbarium of the Botanische

Staatssammlung München (M) and material that was collected by members of the Botanical Institute of the University of Munich, on five field trips to the Atacama Desert between 1980 and 2004 and which has not yet been deposited in the herbarium. Additionally, the herbaria F, G, GH, L, P, and SGO kindly provided type specimens that were critical for some taxonomic delimitation.

Table 3: List of specimens investigated in the present study

Locality	**Collector, accession number**	Date	**F**: field observation **C**: greenhouse cultivation **H**: herbarium specimen **T**: type specimen
***Oxalis arbuscula* Barnéoud**			
Tierra Amarilla, Copiapó, Chile	Werdermann, 400	IX-1924	H (M)
Copiapó, Chile	Gay, s.n.	18..	T (P)
***Oxalis atacamensis* Reiche**			
Paposo, II, Chile	Philippi, s.n.	XII-1853	T (GH)
Quebrada Guanillos, II, Chile	Biese, 3310	12-XII-1949	H (SGO)
Quebrada Bandurrias, II, Chile	Pisano & Bravo, 470	16-X-1941	H (SGO)
Quebrada El Médano, II, Chile	Bayer & Grau, 4966	19-X-1990	C, H (M)
Quebrada Rincón, II, Chile	Bayer & Grau, 4976	20-X-1990	H (M)
Vic. of Q. Matancilla, II, Chile	Heibl, 01-052	8-XII-2004	F, C, H (M)
Vic. of Q. Matancilla, II, Chile	Heibl, 01-054	8-XII-2004	F, H (M)
Vic. of Q. Matancilla, II, Chile	Heibl, 01-055	8-XII-2004	F, H (M)
Quebrada Bandurillas, II Chile	Heibl, 01-060	9-XII-2004	F, C, H (M)
Cerro Carnero, II, Chile	Heibl, 01-073	10-XII-2004	F, C, H (M
Falda Verde, II, Chile	Heibl, 01-077	12-XII-2004	F, C, H (M
***Oxalis bulbocastanum* Philippi**			
II, Chile	Herzog, s.n.	IX-1911	T (L)
3 km north of Taltal, II, Chile	Muñoz & Meza, 2277	27-X-1987	H (SGO)
Quebrada La Chimba, II, Chile	Teillier, 443	30-IX-1987	H (SGO)
Punta Gualaguala, II, Chile	Biese, 2269	16-X-1949	H (SGO)
Punta Cobija, II, Chile	Biese, 2285	16-X-1949	H (SGO)
Quebrada Anchuña, II, Chile	Heibl, 01-066	9-XII-2004	F, C, H (M, CONC)
Cerro Carnero, II, Chile	Heibl, 01-071	10-XII-2004	F, H (M)
***Oxalis caesia* Philippi**			
Quebrada Paposo, II, Chile	Grau, 2149	14-X-1980	H (M)
Quebrada Paposo, II, Chile	Quezada & Ruiz, 210	4-X-1991	H (M)
***Oxalis ericoides* Knuth**			
no material available			
***Oxalis gigantea* Barnéoud**			
5 km E of Carrizal Bajo, III, Chile	Ehrhart, 2002-153	3-XII-2004	H (M)
Caleta Esmeralda, II, Chile	Ehrhart, 2002-244	8-XII-2004	C, H (M)
Quebrada El Médano, II, Chile	Heibl, 01-035	6-XII-2004	F, H (M)

***Oxalis johnstonii* Knuth**

Aguada Miguel Díaz, II, Chile	Johnston, 5400	4-XII-1925	T (GH)
Quebrada Los Peralitos, II, Chile	Brinck, s.n.	18-X-1991	H (SGO)
Quebrada Rincón, II, Chile	Ehrhart & Sonderegger, 96/971	22-XI-1996	H (M)
Cerro del Obispo, III, Chile	Heibl, 01-080	12-XII-2004	F, C, H (M)

***Oxalis leucophylla* Philippi**

Quebrada León, III, Chile	Werdermann, 438	X-1924	H (M)

***Oxalis matancillae* Lourteig**

Quebrada de Matancilla, II, Chile	Dillon, 5749	27 X 1988	T (P, GH)
Aguada Miguel Díaz, II, Chile	Dillon & Teillier, 5288	15-XII-1987	H (GH)
Quebrada Bandurillas, II, Chile	Ehrhart, 2002/256	9-XII-2002	H (M)
Vic. of Q. Matancilla, II, Chile	Heibl, 01-056	8-XII-2004	F, H (M)
Vic. of Q. Bandurillas, II, Chile	Heibl, 01-059	9-XII-2004	F, H (M)
Quebrada Anchuña, II, Chile	Heibl, 01-064	9-XII-2004	F, C, H (M)
Quebrada Anchuña, II, Chile	Heibl, 01-065	9-XII-2004	F, H (M, CONC)

***Oxalis megalorrhiza* [Feuillée] Jacquin**

La Campana, V, Chile	Grau, s.n.	1980	C
Putú, VII, Chile	Grau, s.n.	1980	C
Caleta Obispo, III, Chile	Bayer & Grau, 5027	21-X-1991	C
Putú, VII, Chile	Bayer & López, 5154	4-XI-1991	C
Angostura Paine, M, Chile	Bayer & López, 5251	9-XI-1991	C
Zapallar, V, Chile	Kraus, 96	30-XI-1991	C
Villa Prat, VII, Chile	Kraus, 135	07-IV-1992	C
Hualpén, VIII, Chile	Kraus, 139	12-IV-1992	C

***Oxalis morenoensis* Lourteig**

Cerro Moreno, II, Chile	Ricardi et al., 1408	22-X-1965	T (CONC)
Cerro Moreno, II, Chile	Heibl, 01-009	3-XII-2004	F, H (M)
Quebrada La Plata, II, Chile	Heibl, 01-026	5-XII-2004	F, C, H (M)

***Oxalis ornata* Philippi**

Paposo, II, Chile	Philippi, s.n.	XII-1853	T (SGO)
Cerro Carnero, II, Chile	Heibl, 01-072	10-XII-2004	F, C, H (M)

***Oxalis ornithopus* Philippi**

Paposo, II, Chile	Muñoz & Meza, 2295	27-X-1987	H (SGO)
Quebrada Cachina, II, Chile	Grau, 2126	13-X-1980	H (M)
Quebrada Iscuña, III, Chile	Kraus, 78	19-10-91	C
Caleta Colorada, II, Chile	Heibl, 01-018	4-XII-2004	F, C
Quebrada La Plata, II, Chile	Heibl, 01-024	5-XII-2004	F, H (M, CONC)

***Oxalis ovalleana* Philippi**

Quebrada Taltal, II, Chile	Teillier et al., 2700	14-IX-1992	H (SGO)
Quebrada Yales, II, Chile	Torres, s.n.	25-VIII-1992	H (SGO)
Quebrada Guanillos, II, Chile	Teillier et al., 2790	16-IX-1992	H (SGO)

***Oxalis pachyrhiza* Weddell**

Arequipa, Peru	Pennell, 13192	7-IV-1925	T (GH)
La Compuerta, Arequipa, Peru	Weddell, 4508	II-IV1847	T (P)
La Paz, Bolivia	Buchtien, 614	29-IV-1939	H (M)

***Oxalis paposana* Philippi**

Paposo, II, Chile	Philippi, s.n.	XII-1853	T (SGO)
10 km south of Cta. Blanco Encalada, II, Chile	Biese, 3216	11-XII-1949	H (SGO)
Quebrada Cachina, II, Chile	Biese, 3283	13-XII-1949	H (SGO)
Quebrada Guanillo, II, Chile	C.Muñoz & Johnston, 2960	18-IX-1941	H (SGO)
Escayache, Tarija, Bolivia	Fiebrig, 30/6	30-I-1904	H (M)
Quebrada La Plata, II, Chile	Bayer & Grau, 4920	18-X-1990	C, H (M)
Quebrada La Plata, II, Chile	Heibl, 01-023	5-XII-2004	F, H (M)
Punta Rincón, II, Chile	Heibl, 01-068	10-XII-2004	F, C, H (M)
Cerro Carnero, II, Chile	Heibl, 01-069	10-XII-2004	F, C, H (M)

***Oxalis ricardii* Lourteig**

Quebrada Cascabeles, II, Chile	von Bohlen, 1318	6 IX 1991	H (SGO)
Quebrada Bandurillas, II Chile	Heibl, 01-061	9-XII-2004	F, G, H (M)

***Oxalis squarrosa* Barnéoud**

Guanta, Coquimbo, IV, Chile	Gay, 352	XI 1835	T (P)
La Serena, Coquimbo, IV, Chile	Gay, 1778	1838	T (P)
Guanta, VI, Chile	Gay, s.n.	18..	T (G)
Cerro Tololo, IV, Chile	Jiles, 5814	26-X-1971	H (M)

***Oxalis tortuosa* Lindley**

Coquimbo, IV, Chile	Gay, 346	1839	T (P)
La Serena, Coquimbo, IV, Chile	Gaudichaud, 197	IX 1836	T (P)
Valparaiso, V, Chile	MacRae, s.n.	X 1825	T (GH, L)
Playa Ancha, Valparaiso, V, Chile	Bertero, 1767	VII-1830	T (M)
Baños de Cauquenes, VII, Chile	Dessauer, s.n.	1875	H (M)
Fischermannsbai	Dessauer, s.n.	1887	H (M)
	Zuccarini, s.n.		H (M)
Cultivation Botanical Garden Munich	Kummer, s.n.	1855	H (M)
Zapallar, V, Chile	Kraus, 94	30-11-91	C

***Oxalis virgosa* Molina**

Chungungo-El Tofo, IV, Chile	Ehrhart, 6-109	29-XI-2002	H (M)
Bahía Sarco, III, Chile	Ehrhart, 6-119	1-XII-2002	H (M)
Bahía Sarco, III, Chile	Ehrhart, 6-134	1-XII-2002	C, H (M)

DNA isolation, amplification, sequencing and alignment

DNA Isolation. DNA was extracted mainly from leaflet tissue of three different sources: lyophilized tissue from accessions cultivated in the greenhouse, tissue probes dried and stored in silica gel and herbarium specimens. If possible, lyophilized tissue was used as it was expected to yield high quantities of undegraded DNA. When accessions died prior to their establishment in the greenhouse, DNA was extracted from leaflet probes that were collected during the fieldwork. Drying succulent leaf material in silica gel can sometimes pose a problem because closure of stomata leads to delayed desiccation and subsequent degradation of DNA. Nevertheless in the present case tissue the samples dried rapidly in the arid desert climate and extraction was expected to lead to results comparable to those from lyophilized fresh material. Only when no material from the other two sources was available, I resorted to DNA extraction from herbarium specimens. Theoretically, DNA can be successfully extracted from herbarium specimens even fifty years or more after their collection, but heat treatments during preparation and conservation could potentially lead to the degradation of their DNA.

Fresh leaflet tissue was lyophilized in a Christ BETA 1-8 freeze dryer (Martin Christ Gefriertrocknungsanlagen GmbH, Osterode am Harz) between 12 – 60 hours and then stored at 4 °C. In each case 10 mg of lyophilized material, 10 mg of silica probes or 20 mg of herbarium material were homogenized in a Retsch® MM200 mixer mill (Retsch GmbH & Co. KG, Haan, Germany) adding a glass bead to the tube. Well-homogenized material is crucial for subsequent cell lysis because plant cells are very robust. Milling was therefore extended to up to six minutes and every two minutes the tubes were shaken by hand in order to secure complete homogenization.

DNA was extracted from the homogenate using the NucleoSpin® Plant kit (Machinerey-Nagel, Düren, Germany): Cells are suspended in a lysis buffer (C1) based on the CTAB Method (Doyle & Doyle 1990, Reichardt & Rogers 1994) and incubated 30 minutes in a 60° C water bath. During this incubation any RNA is degraded by the RNAse that is also added. The lysate is cleared by centrifugation in order to remove polysaccharides, contamination and residual cellular debris. The clear supernatant is mixed with binding buffer (C4) and ethanol to create conditions for optimal binding of DNA to a silica membrane where it is further purified by application of two washing buffers (CW, C5) and finally eluted with 50 □l elution buffer (CE). All obtained DNA samples were stored at 4° C.

Molecular markers and primers. Two regions from the large single copy region (LSC) of the chloroplast genome were chosen as phylogenetic markers for the analysis: *trnL-trnL-trnF* and *psbA-trnH*. Both of them constitute non-coding regions. They should evolve more rapidly than coding regions but still more slowly than comparable nuclear non-coding regions (Page & Holmes, 1998). This could be problematic when to little variation is observed in comparisons between taxa on a lower taxonomic level. An important advantage of chloroplast markers, though, is that they are single-copied and one has not to deal with the problem of identifying potential paralogs. This is important because confusion between orthologous and paralogous gene regions leads to erroneous hypotheses of sequence homology. In the worst case, when intraspecific variation is greater than interspecific variation, reconstruction of the phylogeny is made impossible.

TrnL-trnL-trnF was selected for the present study because since the introduction of six universal primers (Taberlet et al 1991) a lot of studies on plant phylogenetics have used this region. Oberlander et al (2004) used *trnL-trnL-trnF* for reconstruction of systematic relationships in southern African *Oxalis.* Their alignment included 1062 characters of which 141 (13%) were potentially parsimony-informative (e.g., synapomorphic). It seemed therefore promising to use their sequences from Genbank (No. AJ852290-AJ852367) as a starting point for alignment and also as source of potential outgroups. Primers C and F were used for PCR and primers D and E were used as additional sequencing primers in the cycle sequencing reaction (Taberlet et al., 1991). Primer sequences are given in table 4.

Because *ex ante*-sequencing of two members from the study group showed little variation in *trnL-trnL-trnF*, the use of a second marker was hoped to reveal relationships between these closely related taxa. *PsbA-trnH* should be suited for this purpose as is discussed by Shaw et al (2005). They report in their review several studies that have successfully used *psbA-trnH* even on an intraspecific level (Holdegger & Abbott 2003), while studies on an above-generic level showed *psbA-trnH* to be largely unalignable (Renner, 1999, Soltis et al., 2001; Hamilton et al, 2003). Therefore the combination of both markers should be favorable for the present study: *trnL-trnL-trnF* resolving relationships between the sections of the west-Andean alliance and *psbA-trnH* tracing the phylogeny of species in the Atacama endemics. For amplification and cycle sequencing of *psbA-trnH* the forward primer psbAF (Sang et al., 1997) and the reverse primer trnH2 (Tate & Simpson, 2003) were used. Their sequences are given in table 4.

Table 4: Sequences of primers used for amplification of the *trnL-L-F* gene region (C, D, E, F) and for the psbA-trnH gene region (psbAF and trnH2) together with their first citation.

Name	Sequence 5' – 3'	Citation
C	CGA AAT CGG TAG ACG CTA CG	Taberlet et al., 1991
D	GGG GAT AGA GGG ACT TGA AC	Taberlet et al., 1991
E	GGT TCA AGT CCC TCT ATC CC	Taberlet et al., 1991
F	ATT TGA ACT GGT GAG ACG AG	Taberlet et al., 1991
psbAF	GTT ATG CAT GAA CGT AAT GCT C	Sang et al., 1997
trnH2	CGC GCA TGG TGG ATT CAC AAT CC	Tate & Simpson, 2003

Polymerase chain reaction. Since its invention in the mid-80ies (Mullis et al., 1986), the polymerase chain reaction (PCR) has become a standard tool in molecular genetics. The principle is simple and elegant: Denaturing of DNA double strands at about 96°C is followed by cooling to temperatures ranges between 40-60°C in order to allow for annealing of primers and subsequent elongation of primers by heat-stable DNA-polymerase at 72°C. Iteration of this cycle up to 35 times is used to amplify the region of interest to a large number. Alteration of annealing temperature can be used to create different primer binding conditions: PCR yields more specific products when annealing temperatures are increased. Consequently, slightly degraded DNA (e.g., herbarium specimens) or sequences that possess a point mutation in the primer binding site can potentially be amplified by lowering the annealing temperature.

As a standard procedure *Taq*-DNA-polymerase (BioTherm, eEnzymes LLC, Gaithersburg, USA) was used. In some cases, when conventional *Taq*-DNA-polymerase failed to amplify the markers, a proofreading DNA-polymerase (Phusion™, Finnzymes, Espoo, Finland) was also tried. PCR protocols for both enzymes are given in table 5, including the set of annealing temperatures that gave best results for each marker and source of DNA. All PCR reactions were conducted on a Biotherm T1 thermocycler (Göttingen, Germany) and stored at 4°C.

Table 5: PCR conditions for *Taq* Polymerase and proof reading polymerase and cycle sequencing conditions.

	Taq Polymerase		Proof reading Polymerase		Cycle sequencing	
Initial denaturing	300 s	95°C	30 s	98°C	60 s	96°C
Denaturing	30 s	95°C	5 s	98°C	10 s	96°C
Primer annealing (*trnL-L-F*)	60 s	55°C	15 s	55°C	5 s	50°C
Primer annealing (*psbA-trnH*, all herbarium specimens)	60 s	48°C	15 s	48°C	-	-
Elongation	100 s	72°C	45 s	72°C	240 s	60°C
Final elongation	420 s	72°C	420 s	72°C	-	-
Number of cycles	34		34		24	

Purification of PCR-Products. Before continuing with the cycle sequencing reaction, excess of nucleotides and primers has to be removed from the PCR product. This was done with help of the Wizard® SV Gel and PCR Clean-Up System (Promega, Madison, USA). DNA is bound to silica membrane in the presence of chaotropic salts. After washing the PCR product, the DNA is eluted in water and stored at 4°C.

Sequencing. Purified PCR products were used in a BigDye^{TM} terminator cycle sequencing reaction to generate fluorescently labeled DNA templates for subsequent capillary electrophoresis on an ABI Prism® 3100 Genetic Analyzer (Applied Biosystems-Hitachi). The underlying principle is shortly outlined: In addition to normal nucleotides the BigDye^{TM} terminator contains a certain fraction of dideoxynuclotides, which are labeled with a different dye for each base. Because of lack of a hydroxyl group on the 3' carbon, elongation is terminated every time a dideoxynucleotide is built in. As a result cycle sequencing yields for each nucleotide position in the sequence a fragment of different length that can be separated by capillary electrophoresis and assorted to the corresponding base by its fluorescent labeling. Cycle sequencing was perfumed with 5 ml reaction batches each containing 1 ml DigDye, 0,5 reaction buffer, 0,15 ml 10□M primer. The DNA content of each was adjusted by adding 0,5 – 2 ml of purified PCR product according to the intensity of the respective band in the gel electrophoresis and the rest was filled with ddH_2O. Cycle sequencing conditions are given in table 5 in the right column.

Before proceeding to the electrophoresis of the cycle sequencing products, they have be purified once more because unincorporated dye-terminators as well as residual salts and proteins can interfere with capillary electrophoresis. Their removal was achieved by gel filtration using Sephadex® G-50 superfine (Sigma-Aldrich Chemie GmbH, Munich, Germany).

Processing of raw sequence data. The software package Sequencher ^{TM} 4.2.2 was used to prepare DNA sequences for alignment. Quality of sequences was assessed by examination of the electropherogram before sequences were assembled from the four (*trnL-L-F*) or two (*psbA-trnH*) different sequencing reactions. Ambiguous sites in the resulting consensus sequences are corrected using information from comparisons of the corresponding electropherograms.

Alignment of sequences. Phylogenetic analysis is based on the comparison of homologous characters. By definition, homologous characters are those that are derived from a common ancestral character. Only they can be used to infer evolutionary relationships and their correct identification is crucial. In phylogenetic analyses of DNA, the process of establishing homology among nucleotide sites is known as alignment. It can be done be computer algorithms but always has to be controlled and corrected by eye. In the present case sequence alignment was done manually in MacClade 4.06 (Maddison & Maddison, 2005).

Phylogenetic Analyses

The task of phylogenetics is to convert information in morphological or molecular data matrices into an evolutionary tree. A great number of methods have been developed for doing this, and three of them were chosen for the present analysis, because they are widely accepted and used in molecular phylogenetics: Maximum parsimony, maximum likelihood and Bayesian inference. Maximum parsimony and maximum likelihood trees are calculated in PAUP 4.0 b10 (Swafford, 1998). MrBayes 3.1 (Huelsenbeck & Ronquist, 2001) is used for Bayesian inference of the evolutionary tree.
Nexus files were written for both applications separately. The whole alignment was placed into the nexus files, but unalignable AT-rich microsatellite regions were excluded from the analysis. The alignment contained numerous insertions/deletion (indels). Several possibilities are described in the literature for coding indels (Simmons & Ochoterena, 2000). Nevertheless for the present study a rather conservative approach was taken by treating gaps as missing characters.

Maximum parsimony. Mutations, which are the underlying cause of all evolutionary change, are generally thought to be rare and independent events (Poisson distribution; see Sokal & Rohlf, 1995). Hence, if a group of organisms shows a certain evolutionary novelty it is more easily explained to have arisen only once in the common ancestor of the group than several times independently. Considering this, Edwards & Cavalli-Sforza (1963) suggested the principle of maximum parsimony (MP) to reconstruct the phylogeny that involves a minimum amount of evolution. This corresponds to the phylogeny that contains the fewest possible evolutionary changes.

Parsimony affords an assumption of how evolutionary changes take place. When working with morphological data, we can think of multiple character states as being ordered by a series of character state changes corresponding to the evolutionary development of certain features from the primitive to the derived state. Besides, character state changes can be thought to be rather irreversible, especially in constant and homogeneous environments (e.g., evolution of cetaceans from ungulate ancestors). For non-coding DNA sequences, however, it is most reasonably assumed that evolutionary changes are reversible and unordered. These assumptions are implemented in the Fitch-Algorithm (Fitch, 1971), which is the default in PAUP and used in the present study.

MP has also to deal with homoplasy, which is the ambiguity in a data set caused by convergence, parallelism and reversal. When such homoplasious characters contradict those characters that track the real genealogy, MP gives rise to several or many equally most parsimonious trees of contradicting topologies. We cannot tell synopomorphies from homoplasy but we can decide which kind of homoplasy we believe to be most likely in order to implement this information for inference of ancestral character states. Accelerated transformation (ACCTRAN) assumes that homoplasy is produced by reversals, while delayed transformation (DELTRAN) prefers topologies that assume all homoplasy to be due to analogies (Swafford & Maddison, 1987; Swafford & Maddison, 1992). ACCTRAN character-state optimization was used for the present analysis.

In order to search for the best tree, the 'tree space' (e.g., the set of all possible trees for a given number of terminal nodes) has to be explored using certain algorithms or search strategies. PAUP offers three of them: exhaustive search, branch and bound search and heuristic search.

Finding the best tree by exhaustive search in a MP (as well as in ML) analysis is NP-complete for larger data sets (Foulds and Graham, 1982). Yet, it is not known if NP-complete problems can be solved in polynomial time (Garey & Johnson, 1976); that means no algorithm for doing this has been developed so far. Consequently, PAUP does not allow exhaustive search for data sets containing 12 or more taxa. Fortunately, also the branch and bound algorithm is (Hendy & Penny, 1982) guaranteed to find the best tree. It reduces computational effort considerably, because it analyzes only a subset of the tree space. This is possible because trees in tree space themselves are related in a tree-like pattern according to their similarity in topology. This allows the algorithm to look at trees systematically. If a branching pattern in a certain tree is found, that makes it less parsimonious (or less likely) than the best tree found so far, the branch containing all related trees is discarded from the analysis, because none of them will be the best tree.

Branch and bound search was used in the present study to infer the most parsimonious tree(s).

All evolutionary trees are of hypothetical character. When assessing the credibility of trees, two types of questions have to be distinguished: (1) Does the tree depict the real phylogeny?

(2) How well do tree and data fit and did we recover really all of the best trees? These questions are referred to as those about the accuracy and the precision of the tree, respectively. The question of accuracy lies completely in the hand of the investigator and depends basically on well-founded selection of taxa and characters for the analysis. Precision

could be rigorously tested by statistical methods. These, however, afford independent sampling of replicates. We would have to repeat the whole process from DNA-isolation to tree search, but this is of course impossible. As a resort, methods have been developed that use pseudoreplicates of the data set in order to simulate independent sampling from the population. Bootstrapping (Felsenstein; 1985) is the most widely used. It creates a number of pseudoreplicates of the same size as the original data set by resampling with replacement. Because resampling is done with replacement, the pseudoreplicates will contain some characters several times, while some will be missing just by chance. A majority-rule consensus tree of all pseudoreplicates, then, gives an impression of the fit between the data set and the different parts of the tree topology.
Precision estimates for the present data set were obtained by bootstrap analysis, performed in PAUP with 1000 replicates under a heuristic search strategy and equal settings as in the MP tree search (see above).

Maximum Likelihood (ML). Like MP, ML is a method that aims to find the best tree based on an optimality criterion. In this case the optimality criterion is the likelihood of the tree. The likelihood L of a tree is defined as the probability of the aligned data D conditioned on the tree hypothesis H:

$$L = P(D \mid H)$$

The tree hypothesis H consists of a model of sequence evolution and the tree itself. The model of sequence evolution specifies the substitution probabilities of one base by another and variation in the substitution rates among different sites. It has to be derived from the data (see below). The requirement of an explicit model of sequence evolution can be regarded as a strength and as well as a weakness of the method. It makes us aware of the assumptions concerning the processes of evolutionary change, but at the same time the question remains of how to correctly infer the parameters used in the model.
In order to find the tree(s) with the maximum likelihood, analysis is started by calculating the likelihood score for a starting tree according to the chosen model of sequence evolution. The tree topology is then modified and the likelihood score of the new tree is compared to that of the previous tree. The higher scoring tree is used for further modifications and, by doing this, the search algorithm moves through tree space until it reaches an optimum likelihood score. It is impossible to distinguish between a local and a global optimum, but modification of the

tree topology during the search should be profound enough to prevent the search algorithm to be stuck on a local optimum.

The model of sequence evolution was chosen with DTModSel (Minin et al., 2003). DTModSel is based on Bayesian inference, but it incorporates relative branch-length errors in as a performance measure in a decision theory framework. It selects models that are simpler than those chosen by conventional techniques, which are based on likelihood-ratio tests. The model of sequence evolution as inferred by DTModSel was implemented in the likelihood settings in PAUP.

Due to the size of the data set, heuristic search had to be adopted as a search strategy instead of branch-and-bound search. The starting tree was created by stepwise addition "as-is". Branch swapping of the tree topology was achieved by tree bisection and reconnection (TBR), which is discussed by Felsenstein (2004) to be more effective than nearest-neighbor interchange (NNI) or subtree pruning and regrafting (SPR). In order to save computational time, branch swapping was conducted on best trees only.

Bayesian Approach. Bayesian inference is gaining in popularity because it allows for the use of an explicit model of sequence evolution and, at the same time, offers statistically meaningful confidence intervals obtained with reasonable computational effort. The basic idea is to sample trees from a posterior probability distribution using Bayes theorem:

$$P(H \mid D) = \frac{P(H)P(D \mid H)}{\prod_{i=1}^{n} P(H)P(D \mid H)}$$

D stands for the data matrix and H for the tree hypothesis. The product of the prior probability P (H) and by the likelihood P (D|H) is termed the 'joint probability'. The posterior probability of a tree P (H|D) is equal to the joint probability of this tree divided by the joint probability summed over all trees. The denominator is usually too complex to be calculated directly, but it can be approximated using Markov chain Monte Carlo (MCMC) algorithms.

One of them, which is widely used in phylogenetics, is the Metropolis-Hastings-Green algorithm (Green, 1995; Hastings, 1970; Metropolis, 1953). It compares a given tree T_i with a new tree T_j, which is adjacent in tree space, calculating the ratio R between both posterior probabilities: R = posterior probability T_j /posterior probability of T_i. The new tree is accepted, if one of the following two conditions is met: (1) R ≥ 1 or (2) R > than a randomly chosen number between 0 and 1. Otherwise, it is rejected and analysis continued with the old tree. Repeating this procedure for a number of n generations and sampling every mth tree, a

markov chain of n/m samples drawn from the posterior probability is created. Eventually, after some x generations, the posterior probability will level off reaching a stable value. Summing these (n-x)/m trees in a majority-rule consensus tree, the fraction of trees that contains a certain clade corresponds to the posterior probability of the clade.

The program MrBayes implements Metropolis-coupled MCMC (Geyer, 1991), a variant that runs one or more so called 'heated chain(s)' parallel to the 'cold chain' described above. The posterior probabilities of the heated chains are raised to the power of some value of $\lambda > 1$. Thus, it is more feasible for the heated chains to leave suboptimal, local tree islands. When they do so, a swap is made between the cold chain and the heated chain, which transfers the cold chain onto the new tree island to continue search there.

MrBayes was run for 1000000 generations using four chains and sampling every ten generations. The parameters of the model of sequence evolution were used as inferred from DTModSel (see above). In MrBayes, it is only possible to specify certain evolutionary models. In case that the model-selection algorithm suggests a model, that is not available in MrBayes, the authors recommend to select the next more complex model (Ronquist et al., 2005). They state that Bayesian techniques are especially robust to over parameterization.

RESULTS

Morphological characters

The following section presents a brief summary of the results of analysis of morphological characters that have been of taxonomic value.

Stem axis. Branching pattern, occurrence of short shoots and the presence or absence of sclerified leaf bases could used to classify three types of stem axis in the study group (Fig. 5). The ‘arbuscula type’ (Fig. 5, left) shows long shoots that develop in the leaf axils on the main axis. These shoots might themselves bear lateral branches. The whole plant is densely ramified and appears more or less cushion-like (Fig. 12A, 13A).

The remaining two types are characterized by the presence of short shoots and sclerified leaf bases. The latter develop when leafs are shed entering dormancy and stipules and leaf bases remain as scale-like or spike-like, sclerified appendages.

The ‘gigantea type’ (Fig. 5, middle) develops normal leaves on first year shoots. After senescence, they leave characteristic spine-like leaf bases. From their axils, the plant develops short shoots in the next growing season which bear leafs and flowers (Fig. 14E). Eventually those short shoots die and only the sclerified leave bases remain on the stem.

Finally, the ‘megalorrhiza type’ (Fig. 5, right) is characterized by its comose appearance, as leaves are concentrated in a short shoot at the apical end of the stem axis. Leaves are relatively short-lived. After their senescence the stem is entirely covered by the scale-like, sclerified leaf bases (Fig. 16H). Stems measure 4-8 mm in diameter and usually do not exceed 10 cm. When they do, as in some specimens, stems increase in girth up to 20 mm due secondary growth. The leaf bases are shed and replaced by a greyish periderm (Fig. 21A).

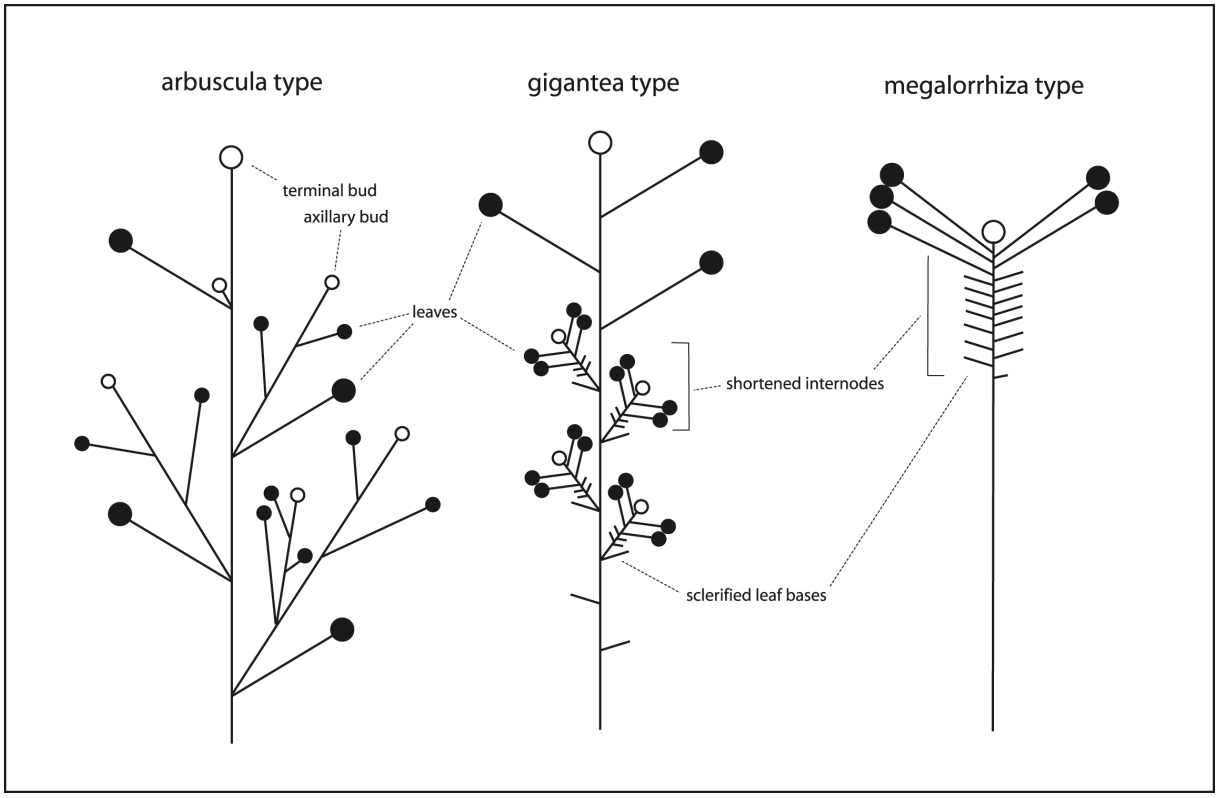


Figure 5: Three types of branching pattern, occurrence of short shoots and the presence or absence of sclerified leaf bases in Atacama endemic *Oxalis*.

Indumentum. Judd et al. (2002) point out that most indumentum terms are ambiguous and recommend careful investigation of morphology, density and distribution of hairs instead. Following this approach, pubescence was investigated with aid of a dissecting microscope (6,4-40 x) giving approximate length, shape and density for each organ separately. Developing leaves and flowers are often densely pubescent in the beginning but will loose their pubescence rapidly. Therefore only fully developed organs were used for investigation and no distinction was made between glabrous and glabrescent.

The Atacama endemics showed considerable variation in presence, density and type of pubescence. Investigation of the indumentum proved especially useful at the species level (see species descriptions for details).

Root system. The study group possesses a well-developed root system. Almost all species form root tubers. Two groups of root tubers can be discerned according to their shape. Prolonged napiform root tubers (Fig. 15F, 21A, 26A, 27B) that pass gradually into the fibrous roots are present in a few species. The majority of species develop ovoid to conical root tubers, which are sharply stepped from the fibrous roots (Fig. 16G, 17H, 18A, 19A).

There seem to be no root tubers in *O. arbuscula*, *O. caesia* and *O. ericoides*.

Leaves. Most species of the study group showed trifoliolate leaves typical for the genus (Fig. 15B, 17F, 23 B, 28B, 30D). A few species, however, have ternate-pinnate leaves (Fig. 12B, 13D). Petioles and leaflets are all more or less succulent and vary greatly in size, shape and indumentum. They showed to be useful for classification at the species level (see species descriptions).

Inflorescences. All Atacama endemics possess many-flowered to few-flowered inflorescences of cymose branching. A schematic representation of a dichasial cyme of *Oxalis* is presented in figure 6. Their paraclades consist of scorpiod cymes or concinni, which are defined as monochasial cymose inflorescence branching alternately from a prophyll on one side of a pedicel and then from one on the other side. Some authors have restricted the term scorpiod cymes to inflorescences having circinate distal ends, while using the term concinnus for uncoiled inflorescences. I will use both terms synonymously and mention the occurrence of coiled inflorescences explicitly in the species descriptions. Scorpiod cymes can be recognized by bearing flowers in two rows as observed in *Oxalis* and indicated in figure 6 (Buys & Hilger, 2003). Detailed description of the inflorescence useful for classification at the species level since the ratio between concinni length and pedicel length varies substantially and gives rise to a "spike-like" or "umbel-like" aspect of the inflorescences in some species.

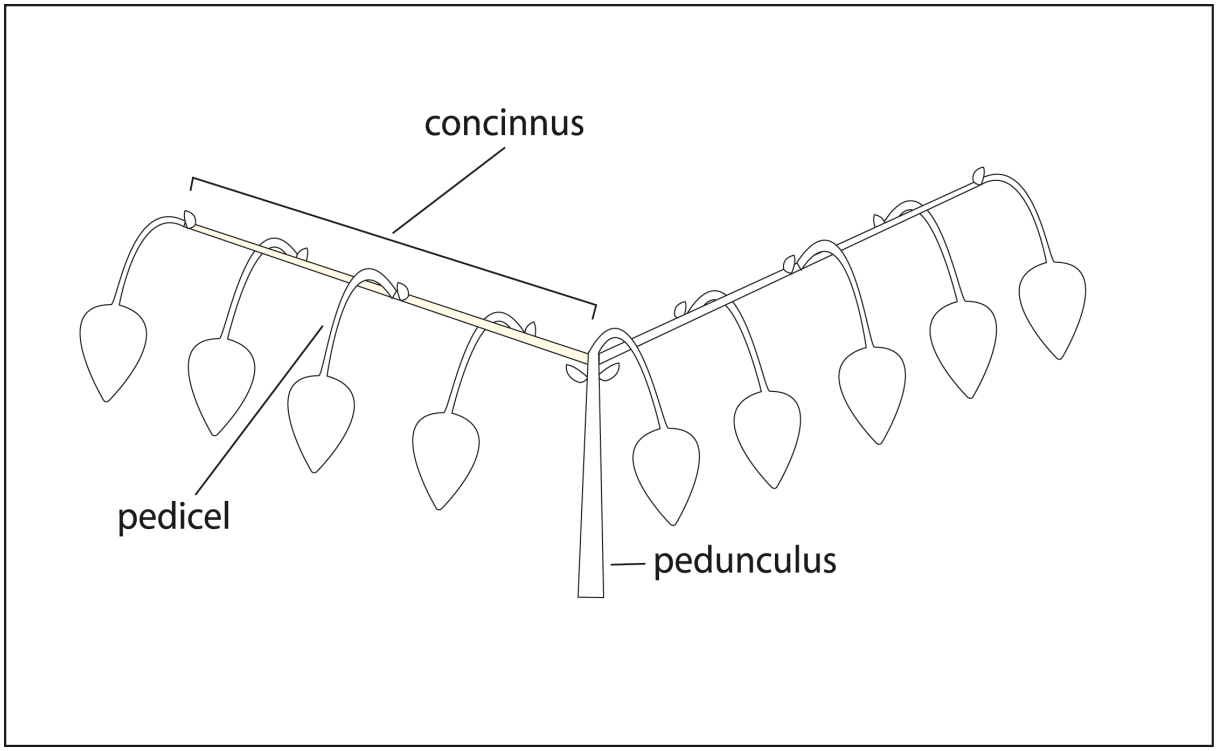


Figure 6: Dichasial cymes of *Oxalis*. The axillary buds of both bracts subtending the terminal flower develop into concinni.

Flowers. The 5-merous flowers of *Oxalis* are quite uniform. The corolla is synpetalous with the petals being connate at the base. The calyx generally shows radial symmetry, but can also be strongly asymmetric in some species. These asymmetric calyces consist of two outer and two inner sepals strongly distinguished by their shape. The fifth sepal is intermediate and can be described as being longitudinally split in two halves, one resembling the outer sepals and the other the inner sepals (e.g. fig 17D, 19C, 30E). This quite distinctive character was expected to be of particular taxonomic value as it was already used by Lourteig (2000) to delimit *Oxalis* section *Carnosae*. Sepals are distinct and vary considerably in shape and indumentum between species, which also proved to be of high taxonomic usefulness.
Androecia and gynoecia were difficult to investigate for two reasons. All members of the genus are heterostylous (Fig. 17C, 18D, 22I, 23I). Hence to obtain a complete description of a species' floral morphology, samples of longs, mids and shorts and samples of longs and shorts have to be examined for tristylous and distylous species, respectively. However, shorts were strongly overrepresented in all accessions examined and description had to rely partly on previous studies found in the literature. These studies, though, might themselves have suffered the same shortcoming. The second reason is that the investigation of gynoecia and androecia affords destructive sampling of vouchers. For that reason, types specimens could not be investigated and I also tried to reduce destructive sampling of old and rare vouchers to a minimum, particularly when they were loans from other herbaria.

Fruits and seeds. Fruits and seeds could be investigated only when present in herbarium specimens. Greenhouse cultivations normally did not produce seeds because they were deprived of potential mating partners due tristyly and the self-incompatibility reactions in most cases. Nevertheless, data on seed surface structure from herbarium specimens, supplemented by data from the literature, was expected to be potentially useful for classification. Most accessions showed seed surfaces that were more or less regularly transversally striated or grooved. There was not enough material to look for consistent variation in striation patterns between species. Rather, all of these seeds were classified as 'transversally striated' as opposed to seed with smooth seed coat found in some species.

Revised classification of *Oxalis* section *Carnosae*, *Giganteae* and *Caesiae*

In this section a revised classification of species of *Oxalis* endemic to the Atacama Desert is presented together with keys for their identification. Keys were based on vegetative characters as far as possible in order to allow for the identification of non-flowering individuals. Note that *O. lomana* from section *Carnosae* is not included in the present classification because it has never been collected in the Atacama Desert and seems to be restricted to the Peruvian coastal desert. A description of *O. lomana* is given by Lourteig (2000).

Key to sections of *Oxalis* endemic to the Atacama Desert

1 Densely ramified dwarf shrubs with woody stem base, not succulent. Leaves ternate-pinnate …… **Sect. *Caesiae***

- Subshrubs to shrubs with succulent stems covered with lignified leaf bases. Leaves trifoliate..…… **2**

2 Pachycaulous shrubs, up to 2 m; densely branched with succulent, erect branches. Leaves and flowers in brachyblasts along the main axis. Calyx regular, all sepals ovate. Seeds smooth …… **Sect. *Giganteae***

- Pachycaulous subshrubs up to 30 cm. Leaves apically crowded together. Calyx asymmetrical: outer sepals deltoid, rhomboid, lanceolate or hastate, rarely ovate, inner sepals narrowly oblong. Seeds transversally striated …… **Sect. *Carnosae***

Sect. ***Caesiae*** Knuth

R. Knuth, Ein Beitrag zur Systematik und der Verbreitung der Oxalidaceen. Bot. Jahrb. 50 Suppl. 215-23, fig. 1-5. 1914

Perennial dwarf shrubs, densely ramified, densely foliated. Fibrous root system. Leaves glaucous, ternate-pinnate. Inflorescence a dichasial cyme, flowers rather small (8-15 mm), yellow. Calyx regular, sepals elliptic. Tristylous. Stamens connate near base, long filaments pubescent, mid and short filaments glabrous. Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed. Capsule cylindrical (1-4 x 2 mm), loculicidal dehiscence. Seeds ovoid (± 1 mm) reddish brown, smooth.

Key to species of section *Caesiae*

1 Leaflets cuneate, apex emarginate (± "heart-shaped") ……...… ***O. arbuscula***

- Leaflets linear or linear to lanceolate.…… **2**

2 Leaflets linear, cylindrical..…..…….…….…... ***O. caesia***

- Leaflets linear to lanceolate, flat, revolute……..……..… ***O. ericoides***

Oxalis arbuscula Barnéoud

F. M. Barnéoud, in C. Gay, Historia Física y Política de Chile 1: 443-444. 1845

Type: Chile, Copiapó. Gay. 18… P

Includes: *O. fruticula* Philippi, *Acetosella arbuscula* (Barn.) Kuntze, *A. fruticula* (Phil.) Kuntze.

Color plate: Fig. 12 (page 90).

Habit: Perennial. Dwarf shrub, suffrutescent, densely ramified, densely foliated, up to 20 cm.

Roots: Fibrous root system.

Leaves: Ternate-pinnate, glaucous; petioles up 30 mm, glabrous; raquis ±1 mm; leaflets 2-8 x 1-6 mm, cuneate, apex emarginate, base cuneate; surface colliculate, glabrous.

Inflorescence: Dichasial cyme, internodes of concinni well developed; peduncle (up to 3 cm), and pedicel (2-3 mm) glabrous.

Calyx: Regular; sepals (2-4 x 1,5 mm) light green with red dots, elliptic, apex rounded; glabrous.

Corolla: 8-15 mm diameter; petals yellow, broadly spathulate to cuneate, apex subtruncate.

Androecium: Stamens connate near base, long filaments pubescent, mid and short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (1-4 x 2 mm), loculicidal dehiscence.

Seeds: Ovoid (± 1 mm) reddish brown, smooth.

Chromosome number: Unknown.

Distribution: Stony soils, collected at Paposo in the coastal fog desert and south of Copiapó in the inland semi desert (Map 1, appendix A).

Oxalis caesia Philippi

R. A. Philippi, Reise durch die Wüste Atacama auf Befehl der chilenischen Regierung im Sommer 1853-54: 13. 1860

Type: Chile, Antofagasta, Valle Guanillo, Paposo. Philippi. 299. XII 1853. SGO

Includes: *Acetosella caesia* (Phil.) Kuntze

Color plate: Fig. 13 (page 91).

Habit: Perennial. Cushion-like dwarf shrub, suffrutescent, densely ramified, densely foliated, up to 10 cm.

Roots: Fibrous root system.

Leaves: Ternate-pinnate, glaucous; petioles up 5 mm, sparsely pubescent with short (± 0,5 mm), single, glandular hairs containing a reddish fluid; raquis 0,1-0,25 mm; leaflets 2-4 x 0,2-0,4 mm, linear, ± cylindrical; surface colliculate, glabrous.

Inflorescence: Dichasial cyme, internodes of concinni well developed; peduncle (up to 5 mm), and pedicel (± 0,1 mm) sparsely pubescent with short (± 0,5 mm), single, glandular hairs containing a reddish fluid.

Calyx: Regular; sepals (2-3 x 0,5-0,7 mm) wine-red, elliptic, apex rounded; apex and margins of sepals pubescent with short (± 0,5 mm), single, glandular hairs containing a reddish fluid.

Corolla: ± 8 mm diameter; petals yellow, broadly spathulate to cuneate, apex subtruncate.

Androecium: Stamens connate near base, long filaments pubescent, mid and short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (1-4 x 2 mm), loculicidal dehiscence.

Seeds: Ovoid (± 1 mm) reddish brown, smooth.

Chromosome number: Unknown.

Distribution: Stony slopes in the coastal fog desert from Aguada Miguel Díaz to Quebrada Guanillos (Map 2, appendix A).

Oxalis ericoides Knuth

R. Knuth, Oxalidaceae, in A. Engler, Das Pflanzenreich, IV 130: 182-183. 1930

Type: Chile, Antofagasta, Taltal, Aguada Panulcito, along trail to the old Andacolla Mine on slopes above the waterhole. Johnston *5466*. 5 XII 1925. Holotype GH, Isotype S, US.

Habit: Perennial. Cushion-like dwarf shrub suffrutescent, densely ramified, densely foliated, up to 15 cm.

Roots: Fibrous root system.

Leaves: Ternate-pinnate, glaucous; petioles up 10-15 mm, indumentum unknown; raquis 0,5-1 mm; leaflets 10-15 x 1,5-2 mm, linear to sublanceolate, apex rounded to acute, flat, revolute; surface colliculate, indumentum unknown.

Inflorescence: Dichasial cyme, internodes of concinni well developed; peduncle (up to 4 cm), and pedicel (1-1,5 mm) sparsely pubescent with short (± 0,5 mm), single, glandular hairs containing a reddish fluid.

Calyx: Regular; sepals (2-3 x 1-1,5 mm) reddish, ovate, apex mucronate; glabrous or margins of sepals sparsely pubescent with single, nonglandular hairs.

Corolla: ± 8 mm diameter; petals yellow, broadly spathulate to cuneate, apex subtruncate.

Androecium: Stamens connate near base, long filaments pubescent, mid and short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (1-4 x 2 mm), loculicidal dehiscence.

Seeds: Ovoid (± 2 mm) reddish brown, smooth.

Chromosome number: Unknown

Distribution: Has only been collected once in the coastal fog desert at Aguada Panulcito (Map 3, appendix A).

Sect. ***Giganteae*** Lourteig

Lourteig, *Oxalis* L. Subgéneros Monoxalis (Small) Lourt., Oxalis y Trifidus Lourt., Bradea 7(2): 311. 2000.

Perennial, pachycaulous shrubs up to 2 m, densely branched with succulent, erect branches giving superficial resemblance to *Euphorbia lactiflua* which occurs sympatrically. Napifrom tubers. Leaves green, trifoliate, alternate on first year's shoots. When entering dormancy, first the leaflets, then the petioles are shed and the sclerified leaf bases remain as spine-like structures. Smaller leaves and flowers are born in brachiblasts in the axils of these leaf bases in the next growing season. Flowers yellow, mid-sized (± 20 mm), single or in a pauciflorous dichasial cyme bearing concinni. Calyx regular, sepals elliptic. Tristylous. Stamens connate near base, long filaments pubescent, mid and short filaments glabrous. Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed. Capsule cylindrical (6 x 2 mm), loculicidal dehiscence. Seeds ovoid (± 1 mm) reddish brown, smooth.

Key to species of section Gigantea

1 Cymes reduced, uniflorous. Petiole glabrous, pubescent only at the apical end. Leaflets glabrous. Sepals pubescent with short hairs not exceeding 0,1 mm ……. ***O. gigantea***

- Cymes umbel-like contracted, pluriflorous. Petiole pubescent. Leaflets pubescent. Sepals pubescent with short hairs up to 0,4 mm …… ***O. virgosa***

Oxalis gigantea Barnéoud

F. M. Barnéoud, in C. Gay, Historia Física y Política de Chile 1: 433-434. 1845.
Type: Chile, Coquimbo. Gay *78*. 18.. . Holotype P

Color plate: Fig. 14 (page 92).

Habit: Perennial, pachycaulous shrub up to 2 m, densely branched with succulent, erect branches, leaves and flowers are in brachiblasts, brachiblasts are born in axils of the sclerified remains of stipules and leaf bases.

Roots: Root tubers at the stem base, napiform, prolonged, passing gradually into fibrous roots.

Leaves: 3-foliolate, succulent; petioles (up to 3cm) succulent, glabrous, at the apical end pubescent; leaflets 1-7,5 x 1-7,5 mm, narrowly to broadly cuneate, apex truncate to retuse, base cuneate; upper leaflet surface smooth, glabrous; lower leaflet surface alveolate, glabrous, midvein pubescent with short (± 0,3 mm) single, nonglandular hairs.

Inflorescence: Reduced, uniflorous; pedicel (3-6 mm) sparsely pubescent with very short (± 0,1 mm), single, nonglandular hairs.

Calyx: Symmetric; sepals (3,5-6 x 1,5-3 mm) broadly elliptic, apex obtuse to acute, in some individuals retuse; sparsely pubescent with very short (± 0,1 mm), single, nonglandular hairs.

Corolla: ± 20 mm diameter; petals yellow, broadly spathulate to cuneate, apex truncate.

Androecium: Stamens connate near base, long filaments pubescent, mid and short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (6-9 x 2-3 mm), loculicidal dehiscence.

Seeds: Round (± 1 mm) reddish brown, smooth.

Chromosome number: 2n = 18.

Distribution: Alluvial fans and stony slopes in the coastal fog desert and semi desert from Quebrada El Médano to Cordón Panulcillo near Huasco. One accession inland in the semi desert at Cuesta de las Cardas near La Serena (Map 4, appendix A).

Oxalis virgosa Molina

I.J. Molina, Saggio sulla storia naturale de Chili, 1: 132-133, 352. 1782

Neotype: Chile, Atacama, 3 km W of Huasco, 35 m, Worth & Morrison *16242*.27 X 1938. Holotype K. Isotype GH, NA, UC.

Includes: *O. subcarnosa* Klotzsch ex Walpers, *Acetosella virgosa* (Mol.) Kuntze, *A. savignyana Kuntze*, *A. subcarnosa* (Kl. ex Waplers) Kuntze.

Color plate: Fig. 15 (page 93).

Habit: Perennial. Pachycaulous shrub up to 2 m, densely branched with succulent, erect branches; leaves and flowers in brachiblasts, brachiblasts are born in axils of the sclerified remains of stipules and leaf bases.

Roots: Root tubers at the stem base, napiform, prolonged, passing gradually into fibrous roots.

Leaves: 3-foliolate, succulent; petioles (up to 3,5 cm) succulent, pubescent with short (± 0,4 mm) single, nonglandular hairs; leaflets 2,5-10 x 3-6 mm, broadly obovate to cuneate, apex emarginate, base cuneate; upper leaflet surface smooth, pubescent with short (± 0,4 mm) single, nonglandular hairs; lower leaflet surface alveolate, pubescent with short (± 0,4 mm) single, nonglandular hairs.

Inflorescence: Dichasial cyme, internodes of concinni contracted giving rise to an umbel-like inflorescence; peduncle (1-3 cm), succulent; pubescent with short (± 0,4 mm) single, nonglandular hairs; pedicel (2-3 mm) pubescent with short (± 0,4 mm) single, nonglandular hairs.

Calyx: Symmetric; sepals (3,5-6 x 1,5-3 mm) broadly elliptic, apex obtuse to acute, in some individuals retuse; sparsely pubescent with very short (± 0,1 mm), single, nonglandular hairs.

Corolla: ± 20 mm diameter; petals yellow, broadly spathulate to cuneate, apex truncate.

Androecium: Stamens connate near base, long filaments pubescent, mid and short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (6-9 x 2-3 mm), loculicidal dehiscence.

Seeds: Round (± 1 mm) reddish brown, smooth.

Chromosome number: Unknown.

Distribution: Stony slopes and plateaus in the coastal fog oasis of the semi desert from Carrizal Alto to Punta Herradura. Also found inland (Map 5, appendix A).

Sect. ***Carnosae*** Reiche

K. Reiche, Zur Kenntnis der chilenischen Arten der Gattung *Oxalis*, in A. Engler, Botanische Jahrbücher für Systemtik, Pflanzengeschichte und Pflanzengeographie 18: 286. 1894

Perennial subshrubs up to 40 cm, stems are slightly succulent and covered by imbricate scales consisting of the sclerified remains of stipules and leaf bases or pachycaulous with a greyish, cracked periderm as in section *Giganteae*. Ovoid to conical root tubers, well separated from the fibrous roots. Leaves green, trifoliate, apically grouped together. Flowers yellow, mid to large-sized (20-45 mm), pauciflorous to pluriflorous dichasial cymes bearing concinni. Calyx asymmetrical, outer sepals deltoid, rhomboid, lanceolate or hastate, rarely ovate inner sepals narrowly oblong. Tristylous (as far as known). Stamens connate near base, long filaments pubescent, mid and short filaments glabrous. Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed. Capsule cylindrical (6 x 2 mm), loculicidal dehiscence. Seeds ovoid (± 1 mm) reddish brown, transversally striated.

Key to species of section *Carnosae*

1 Leaflets more than 2 times as long as wide, linear to narrowly elliptic. ……..…… **2**

- Leaflets less than 2 times as long as wide, cuneate, obovate or suborbicular. …… **3**

2 Outer sepals more than 1,5 times as long as wide, lanceolate. Sympodial main axes of concinni not shortened, cymes not umbel-like..…..……... ***O. ornithopus***

- Outer sepals less than 1,5 times as long as wide, broadly hastate with rounded lobes. Sympodial main axes of concinni strongly shortened, resulting in a contracted, umbel-like appearance of cymes…..……..……..…… ***O. tortuosa***

3 Leaflet apex emarginate to bilobed, lobes ± divergent ……..…….…... **4**

- Leaflet apex rounded to retuse ……..……..…….. **5**

4 Glabrous or nearly so ……...…… ***O. ovalleana***

- Densely pubescent …….……..…….. ***O. leucophylla***

5 Upper leaflet surface pubescent …… **6**

- Upper leaflet surface glabrous ……..…… **8**

6 Glandular hairs absent …… ***O. morenoensis***

- Glandular hairs on leaves and inflorescences ……..…… **7**

7 Glandular hairs ± 0,3 mm, clinging. Distal end of concinni circinate. Pedicels ± 1 mm, concinni appearing spike-like ……..……. ***O. squarrosa***

- Glandular hairs 0,8-1,5 mm, distant. Distal end of concinni not circinate. Pedicels 10-25 mm, concinni laxiflorous. ……..…… ***O. johnstonii***

8 Leaflets cuneate …….…….. ***O. matancillae***

- Leaflets broadly obovate to circular ……..…… **9**

9 Leaflet apex emarginate to bilobed ……..…… ***O. paposana***

- Leaflet apex rounded to retuse ……..…… **10**

10 Lower leaflet surface glabrous ……..…… **11**

- Lower leaflet surface pubescent ……..……. **13**

11 Sepals rhomboid …… ***O. bulbocastanum***

12 Sepals deltoid to slightly hastate ……..…… **12**

13 Leaflets up to 11 mm long ……..…… ***O. pachyrhiza***

- Leaflets more than 15 mm long ……..…… ***O. megalorrhiza***

14 Calyx pubescent with glandular hairs ……..…… ***O. atacamensis***

- Calyx pubescent with nonglandular hairs ……..…… **14**

15 Sepals hastate, lobes obtuse. Pubescence on sepals more intense at the apex and the margins. Hairs on lower leaflet surface 0,6-1,2 mm long …… ***O. ornata***

- Sepal obovate to deltoid. Pubescence on sepals evenly distributed. Hairs on lower leaflet surface ± 0,3 mm long ……..…… ***O. ricardii***

Oxalis atacamensis Reiche

K. Reiche, Zur Kenntnis der chilenischen Arten der Gattung *Oxalis*, in A. Engler, Botanische Jahrbücher für Systemtik, Pflanzengeschichte und Pflanzengeographie 18: 286. 1894.
Nom. nov. pro. *O. trichocalyx* R. A. Philippi, Reise durch die Wüste Atacama auf Befehl der chilenischen Regierung im Sommer 1853-54: 13. 1860.
Type: Chile, Atacama, Paposo. Philippi. XII 1853 . Holotype SGO. Isotype GH
Includes: *Acetosella trichocalyx* (Phil.) Kuntzsch.

Color plate: Fig. 16 (page 94).

Habit: Perennial. Subshrub with slightly succulent stems, up to 20 cm; leaves apically crowded together; stem ± 8 mm diameter, covered by sclerified, pubescent remains of stipules and leaf bases.
Roots: One to few root tubers sit at the stem base, ovoid to conical, sharply separated from the fibrous roots.
Leaves: 3-foliolate, succulent; petioles (1,5-15 cm) succulent, pubescent with single, nonglandular hairs; leaflets 12-30 x 15-25 mm, suborbicular, but sometimes quite irregular, apex rounded to retuse, base obtuse to cuneate; upper leaflet surface waxy-shining, glabrous; lower leaflet surface colliculate, pubescent with short (0,3-0,5 mm), single, nonglandular hairs.
Inflorescence: Dichasial cyme, internodes of concinni well developed, laxiflorous; peduncle (up to 25 cm) and pedicel (7-22 mm) pubescent with short (0,3-0,5 mm), single, nonglandular hairs.
Calyx: Asymmetric; outer sepals (6-9 x 3-4 mm) lanceolate, apex obtuse; inner sepals (6-9 x 1,5-2 mm) narrowly oblong, apex truncate to retuse; pubescent with multicelular, glandular hairs (e.g. glandulous), filled with a violet, rarely colorless fluid.
Corolla: 26-44 mm diameter; petals yellow, broadly spathulate, apex obtuse to subtruncate.
Androecium: Stamens connate near base, long filaments pubescent, mid and short filaments glabrous.
Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.
Capsule: Cylindrical (6 x 2 mm), loculicidal dehiscence.
Seeds: Ovoid (± 1 mm) reddish brown, transversally striated.
Chromosome number: Unknown.

Distribution: Stony slopes in the coastal fog desert from Quebrada El Médano to Falda Verde (Map 6, appendix A).

Oxalis bulbocastanum Philippi

R. A. Philippi, Plantas nuevas chilenas, Anal. Univ. Chile 82: 74. 1893

Type: Chile, Vallenar, Caldera. Geisse. 18.. . Holotype SGO.

Includes: *O. breana* Philippi, *O. thyrsoidea* Reiche, *O. occidentalis* Knuth.

Color plate: Fig. 17 (page 95).

Habit: Perennial. Apparently subacaulescent.

Roots: One to few root tubers sit at the stem base, ovoid to conical, sharply separated from the fibrous roots.

Leaves: 3-foliolate, succulent; petioles (up to 13 cm) succulent, glabrous; leaflets 8-33 x 10-35 mm, broadly obovate, apex emarginate, base obtuse; upper leaflet surface smooth, waxy-shining, glabrous; lower leaflet surface colliculate, glabrous.

Inflorescence: Dichasial cyme, internodes of concinni well developed, laxiflorous; peduncle (up to 18 cm), succulent, glabrous; pedicel (up to 20 mm) glabrous.

Calyx: Asymmetric; outer sepals (8-10 x 5-8 mm) broadly ovate to rhomboid, apex obtuse; inner sepals (8-10 x 1,5-2 mm) narrowly oblong, apex obtuse, rarely retuse; glabrous, few hairs at the apex.

Corolla: ± 38 mm diameter; petals yellow, broadly spathulate, apex obtuse to subtruncate.

Androecium: Stamens connate near base, long filaments pubescent, mid and short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (6 x 2 mm), loculicidal dehiscence.

Seeds: Ovoid (± 1 mm) reddish brown, transversally striated.

Chromosome number: Unknown.

Distribution: Stony slopes in the coastal fog desert from Perú to Taltal (Map 7, appendix A).

Oxalis johnstonii Knuth

R. Knuth, Oxalidaceae, in A. Engler, Das Pflanzenreich, IV 130: 189-190. 1930.

Type: Chile, Antofagasta, Taltal, vicinity Aguada de Miguel Díaz. Johnston *5400*. 4 XII 1925. Holotype GH.

Color plate: Fig. 18 (page 96).

Habit: Perennial. Subshrub with slightly succulent stems, up to 20 cm; leaves apically crowded together; stem 5-7 mm diameter, covered by sclerified, pubescent remains of stipules and leaf bases.

Roots: One to few root tubers sit at the stem base, ovoid to conical, sharply separated from the fibrous roots.

Leaves: 3-foliolate, succulent; petioles (3-15 cm) succulent, pubescent with multicelular, glandular hairs; leaflets 15-25 x 10-30 mm, broadly obovate, apex obtuse to subtruncate, base ± obtuse; upper leaflet surface smooth, pubescent with multicelular, glandular hairs (0,8-1,0 mm); lower leaflet surface colliculate, pubescent with multicelular, glandular hairs (0,8-1,0 mm).

Inflorescence: Dichasial cyme, internodes of concinni well developed, laxiflorous; peduncle (up to 22 cm, succulent) and pedicel (10-25 mm) pubescent with multicelular, glandular hairs (0,8-1,2 mm)

Calyx: Asymmetric; outer sepals (5,5-9 x 2,5-3 mm) lanceolate to hastate, apex rounded; inner sepals (6-9 x 1-1,5 mm) narrowly oblong, apex truncate to retuse; pubescent with multicelular, glandular hairs (± 1,5 mm), filled with a reddish, sometimes colorless fluid.

Corolla: 20-24 mm diameter; petals yellow, narrowly obovate to cuneate, apex truncate, slightly erose.

Androecium: Stamens connate near base, long filaments pubescent, mid and short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (6 x 2 mm), loculicidal dehiscence.

Seeds: Ovoid (± 1 mm) reddish brown, transversally striated.

Chromosome number: Unknown.

Distribution: Stony slopes in the coastal fog desert from Quebrada La Chimba to Quebrada del Higuero (Map 8, appendix A).

Oxalis leucophylla Philippi

R. A. Philippi, Plantas nuevas chilenas, Anal. Univ. Chile 81: 911. 1893.

Type: Chile, Atacama, Caldera. Geisse. 1870. Holotype SGO.

Color plate: Fig. 19 (page 97).

Habit: Perennial. Subshrub with slightly succulent stems, densely pubescent, densely foliated, up to 10 cm; leaves apically crowded together; stem ± 5 mm diameter, covered by sclerified, pubescent remains of stipules and leaf bases.

Roots: One to few root tubers sit at the stem base, ovoid to cylindrical, sharply separated from the fibrous roots.

Leaves: 3-foliolate, succulent; petioles (up to 7 cm) succulent, pubescent with single, nonglandular hairs (± 0,5 mm); leafleats 9-15 x 8-12 mm, cuneate, apex bilobed, lobes narrowly oblong, divergent; upper leafleat surface smooth, glabrous; lower leaflet surface colliculate, densely pubescent with single, nonglandular hairs (± 0,5 mm).

Inflorescence: Dichasial cyme, internodes of concinni well developed, laxiflorous; peduncle (up to 7,5 cm) and pedicel (5-6 mm) pubescent with short (0,3-0,5 mm), single, nonglandular hairs.

Calyx: Asymmetric; outer sepals (5-6,5 x 5 mm) hastate with rounded lobes, apex rounded; inner sepals (5-6,5 x 1-1,5 mm) narrowly oblong, apex rounded; densely pubescent, especially at the apex and the lobes with pubescent with single, nonglandular hairs (± 0,5 mm);

Corolla: 12-18 mm diameter; petals yellow, shape unknown.

Androecium: Stamens connate near base, long filaments pubescent, mid and short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (6 x 2 mm), loculicidal dehiscence.

Seeds: Ovoid (± 0,5 mm) brown, transversally striated.

Chromosome number: Unknown.

Distribution: Sandy soils at Quebrada Leones (Map 9, appendix A).

Oxalis matancillae Lourteig

A. Lourteig, *Oxalis* L. Subgéneros Monoxalis (Small) Lourt., Oxalis y Trifidus Lourt., Bradea 7(2): 351-352. 2000.

Color plate: Fig. 20 (page 98).

Type: Chile, Antofagasta, Quebrada de Matancilla, ca. 5 km S of Punta Grande, 35 km No of Taltal, 170-350m (25°07´S, 70°27´W). Dillon, Ascensio & Villaroel *5749*. 27 X 1988. Holotype P. Isotype F.

Habit: Perennial. Subshrub with slightly succulent stems, up to 20 cm; leaves apically crowded together; stem ± 4 mm diameter, covered by sclerified remains of stipules and leaf bases.

Roots: Many, branching root tubers sit at the stem base, napiform, gradually passing into the fibrous roots.

Leaves: 3-foliolate, succulent; petioles (up to 7 cm) succulent, glabrous; leafleats 5-13 x 2-8 mm, narrowly to broadly deltoid, apex retuse to emarginate, base cuneate; upper leafleat surface smooth, glabrous; lower leaflet surface colliculate, pubescent with short (± 1,5 mm) single, nonglandular hairs.

Inflorescence: Dichasial cyme, internodes of concinni well developed, laxiflorous; peduncle (up to 13 cm) succulent, glabrous and pedicel (up to 20 mm) glabrous with very few scattered, short (± 0,3 mm), single, nonglandular hairs.

Calyx: Asymmetric; outer sepals (7-8 x 4 mm) hastate, lobes rounded, curved outwards, apex rounded; inner sepals (7-8 x 1-1,5 mm) narrowly oblong, apex retuse; pubescent, especially at the apex, with short (± 0,3 mm), single, nonglandular hairs; apex and margins of sepals often reddish, sometimes sepals entirely reddish.

Corolla: 25-30 mm diameter; petals yellow, broadly spathulate to cuneate, apex subtruncate.

Androecium: Stamens connate near base, long filaments pubescent, mid and short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (6 x 2 mm), loculicidal dehiscence.

Seeds: Ovoid (± 1 mm) reddish brown, transversal wrinkles.

Chromosome number: Unknown.

Distribution: Stony slopes in the coastal fog desert from Aguada Miguel Díaz to Quebrada Anchuña (Map 10, appendix A).

Oxalis megalorrhiza [Feuillée] Jacquin

J. N. v. Jacquin, *Oxalis* Monographia, iconibus illustrata 33. 1794.
Type: There is no voucher. Joaquin's description refers to a short description and a color plate of a plant found in Valle del Ylo, Moqueguá, Peru by Feuillée: L. E. Feuillée. Journ. Observ. 2. 734-35, plate 25. 1725.
Includes: *O. carnosa* auctore multitoties non Molina, *O. bicolor* Savigny, *O. mirbelii* Dernhardt, *O. rubrocincta* Lindley, *O. succulenta* Barnéoud, *O. reticulata* Steudel, *O. arborescens* Hort., *O. tarapacana* Philippi, *O. illapelina* Philippi, *O. brevis* Philippi, *O. paniculata* Reiche, *O. borchersii* Philippi. *O. darapskyi* Philippi ex Reiche, *O. solarensis* Knuth, *Otoxalis rubrocincta* Lindley (Small), *Acetosella megalorrhiza* (Jacq.) Kuntze, *A. reticulata* (Steud.) Kuntze, *A. rubrocincta* (Lindley) Kuntze, *A. succulenta* (Barn.) Kuntze.

Color plate: Fig. 21 (page 99).

Habit: Perennial. Pachycaulous subshrub, up to 30 cm; leaves apically crowded together; stem ± 10 mm diameter, covered by sclerified remains of stipules and leaf bases, which are later replaced by a greyish, cracked periderm.
Roots: Many, branching root tubers sit at the stem base, napiform, gradually passing into the fibrous roots.
Leaves: 3-foliolate, succulent; petioles (up to 20 cm) succulent, glabrous; leafleats 15-25 x 10-30 mm, circular to broadly obovate, apex rounded to retuse, sometimes obtuse, base ± obtuse; upper leafleat surface smooth, glabrous; lower leaflet surface colliculate, glabrous.
Inflorescence: Dichasial cyme, internodes of concinni well developed, laxiflorous; peduncle (up to 30 cm) succulent, glabrous; pedicel (7-25 mm) glabrous.
Calyx: Asymmetric; outer sepals (8-9 x 5-6 mm) deltoid to slightly hastate, apex broadly obtuse; inner sepals (8-9 x 1,5-2 mm) narrowly oblong, apex truncate to retuse; glabrous.
Corolla: 20-25 mm diameter; petals yellow, spathulate, apex truncate.
Androecium: Stamens connate near base, long filaments pubescent, mid and short filaments glabrous.
Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.
Capsule: Cylindrical (6 x 2 mm), loculicidal dehiscence.
Seeds: Ovoid (± 1 mm) reddish brown, transversally striated.
Chromosome number: 2n = 18.

Distribution: Between rocks along the coast from Pichidangui to Hualpén near Concepción in a mediterrenean type climate. One accession in the coastal desert at Caleta Obispo is probably not correctly identified (Map 11, appendix A).

Oxalis morenoensis Lourteig

A. Lourteig, *Oxalis* L. Subgéneros Monoxalis (Small) Lourt., Oxalis y Trifidus Lourt., Bradea 7(2): 359-360. 2000.

Type: Chile, Antofagasta, cumbres del lado sur del Cerro Moreno. Ricardi, Marticorena & Matthei *1408*. 22 X 1965 . Holotype CONC.

Color plate: Fig. 22 (page 100).

Habit: Perennial. Subshrub with sligthly succulent stems, up to 10 cm; leaves apically crowded together; stem ± 6 mm diameter, covered by sclerified, pubescent remains of stipules and leaf bases.

Roots: One to few root tubers sit at the stem base, ovoid to cylindrical, sharply separated from the fibrous roots.

Leaves: 3-foliolate, succulent; petioles (up to 2 cm) succulent, densely pubescent with single, nonglandular hairs; leafleats 14-17 x 17-20 mm, broadly obovate, apex emarginate, base cuneate; upper leafleat surface smooth, pubescent with short (± 0,3 mm) single, nonglandular hairs; lower leaflet surface colliculate, pubescent with short (± 1 mm) single, nonglandular hairs.

Inflorescence: Dichasial cyme, internodes of concinni well developed, laxiflorous, pauciflorous; peduncle (up to 2 cm) and pedicel (up to 10 mm) pubescent with short (± 0,3 mm), single, nonglandular hairs.

Calyx: Asymmetric; outer sepals (5-6 x 4-4,5 mm) deltoid to subrhomboid, apex rounded; inner sepals (5-6 x 2 mm) narrowly oblong, apex retuse, margin membranous; densely pubescent with short (± 0,4 mm) single, nonglandular hairs.

Corolla: 20-24 mm diameter; petals yellow, broadly spathulate, apex subtruncate, irregular.

Androecium: Stamens connate near base, long filaments pubescent, mid and short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (4 x 2 mm), loculicidal dehiscence.

Seeds: Ovoid (± 1 mm) reddish brown, transversally striated.

Chromosome number: Unknown.

Distribution: Stony slopes in the coastal fog desert from Morro Moreno at Peninsula Mejillones to Quebrada La Plata (Map 12, appendix A).

Oxalis ornata Philippi

R. A. Philippi, Reise durch die Wüste Atacama auf Befehl der chilenischen Regierung im Sommer 1853-54: 13. Santiago. 1860.

Non *O. ornata* Poeppig ex Progel, 1877

Type: Chile, Antofagasta, Paposo. Philippi. XII 1853. Holotype SGO. Isotype W.

Color plate: Fig. 23 (page 101).

Habit: Perennial. Subshrub with sligthly succulent stems, up to 20 cm; leaves apically crowded together; stem ± 6 mm diameter, covered by sclerified, pubescent remains of stipules and leaf bases.

Roots: One to few root tubers sit at the stem base, ovoid to cylindrical, sharply separated from the fibrous roots.

Leaves: 3-foliolate, succulent; petioles (± 10 cm) succulent, sparsely pubescent with short (± 1 mm) single, nonglandular hairs; leafleats 20-30 x 18-24 mm, broadly obovate, apex rounded to emarginate, base cuneate to slightly decurrent; upper leafleat surface smooth, glabrous; lower leaflet surface colliculate, densely pubescent with short (± 1,5 mm) single, nonglandular hairs, pubescence extending to upper leaflet surface, covering a zone of 2 mm measured from leaf margin and giving a ciliate appearance when viewed from above.

Inflorescence: Dichasial cyme, internodes of concinni well developed, laxiflorous; peduncle (up to 12 cm) sparsely and pedicel (± 14 mm) densely pubescent with short (0,6-1,2 mm), single, nonglandular hairs.

Calyx: Asymmetric; outer sepals (8-9 x 4-5 mm) hastate, lobes obtuse, apex rounded; inner sepals (8-9 x 2 mm) narrowly oblong, apex rounded; pubescent with single, nonglandular hairs, pubescence getting denser at margins and apex.

Corolla: 40-45 mm diameter; petals yellow, broadly spathulate to deltoid, apex subtruncate.

Androecium: Stamens connate near base, long filaments pubescent, mid and short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (6 x 2 mm), loculicidal dehiscence.

Seeds: None available for investigation.

Chromosome number: Unknown.

Distribution: Stony slopes in the coastal fog desert, up to date only collected in the surroundings of Paposo (Map 13, appendix A).

Oxalis ornithopus Philippi

R. A. Philippi, Reise durch die Wüste Atacama auf Befehl der chilenischen Regierung im Sommer 1853-54: 13. 1860.

Type: Chile, Atacama, Cachinal de la Costa. Philippi. X 1853. Holotype SGO.

Includes: *Acetosella ornithopus* (Phil.) Kuntze

Color plate: Fig. 24 (page 102).

Habit: Perennial. Subshrub with sligthly succulent stems, up to 30 cm; leaves apically crowded together; stem ± 6 mm diameter, covered by sclerified, pubescent remains of stipules and leaf bases.

Roots: One to few root tubers sit at the stem base, ovoid to cylindrical, sharply separated from the fibrous roots.

Leaves: 3-foliolate, succulent; petioles (up to 13 cm) succulent, glabrous; leafleats 10-30 x 2-10 mm, narrowly elliptic or lanceolate to linear, apex rounded, sometimes retuse, base acute; upper leafleat surface smooth, glabrous; lower leaflet surface colliculate, pubescent with short (± 1,5 mm) single, nonglandular hairs.

Inflorescence: Dichasial cyme, internodes of concinni well developed, laxiflorous; peduncle (up to 15 cm) succulent, glabrous; pedicel (5-10 mm) glabrous.

Calyx: Asymmetric; outer sepals (6-8 x 4 mm) lanceolate, apex obtuse or retuse; inner sepals (5-8 x 2 mm) narrowly oblong, apex truncate to retuse; blade sparsely, apex and lobes densely pubescent with short (± 0,6 mm) single, nonglandular hairs, sometimes pubescence limited to apex

Corolla: ± 30 mm diameter; petals yellow, cuneate, apex truncate.

Androecium: Stamens connate near base, long and mid filaments pubescent, short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (6 x 2 mm), loculicidal dehiscence.

Seeds: Ovoid (± 1 mm) reddish brown, transversally striated.

Chromosome number: Unknown.

Distribution: Stony slopes in the coastal fog desert from Caleta Duendes to Quebrada Leones (Map 14, appendix A).

Oxalis ovalleana Philippi

R. A. Philippi, Plantas nuevas chilenas, Anal. Univ. Chile 81: 910. 1893.

Type: Chile, Coquimbo, Ovalle. Philippi. … . Holotype SGO.

Color plate: Fig. 25 (page 103).

Habit: Perennial. Subshrub with sligthly succulent stems, up to 30 cm; leaves apically crowded together; stem ± 4 mm diameter, covered by sclerified, pubescent remains of stipules and leaf bases.

Roots: One to few root tubers sit at the stem base, ovoid to cylindrical, sharply separated from the fibrous roots.

Leaves: 3-foliolate, succulent; petioles (up to 11 cm) succulent, glabrous; leafleats 3,5-16 x 3,5-18 mm, broadly deltoid, apex emarginate to bilobed (up to 40 % incised), lobes divergent, rounded, base cuneate to decurrent; upper leafleat surface smooth, glabrous; lower leaflet surface colliculate, pubescent with short (± 0,6 mm) single, nonglandular hairs.

Inflorescence: Dichasial cyme, internodes of concinni well developed, laxiflorous; peduncle (up to 25 cm) succulent, glabrous and pedicel (± 20 mm) glabrous.

Calyx: Asymmetric; outer sepals (5-7 x 2,5-6 mm) lanceolate to subrhomboid, apex rounded; inner sepals (5-7 x 0,5-2 mm) narrowly oblong, apex truncate to retuse; glabrous, apex ± pubescent with short (± 0,5 mm), single, nonglandular hairs.

Corolla: ± 30 mm diameter; petals yellow, broadly spathulate, apex obtuse to subtruncate.

Androecium: Stamens connate near base, long filaments pubescent, mid and short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (6 x 2 mm), loculicidal dehiscence.

Seeds: Ovoid (0,5-0,7 mm) reddish brown, transversally striated.

Chromosome number: Unknown.

Distribution: Stony slopes in the coastal fog desert from Aguada Miguel Díaz to Pan de Azúcar (Map 15, appendix A).

Oxalis pachyrhiza Weddell

H.A. Weddell, Chloris andina: 290, 1861.

Type: Peru, in cavitatis scopulorum loco dicto La Compuerta, sur la route de Puno à Arequipa, 4000 m. Weddell *4508*. II-IV 1847. Holotype P.

Includes: *O. sepalosa* Diels, *O. juninensis* Knuth, *O. buchtienii* Bruns, *O. arequipensis* Knuth, *O. xerophyton* Knuth.

Color plate: Fig. 26 (page 104).

Habit: Perennial. Subshrub with sligthly succulent stems, up to 10 cm; leaves apically crowded together; stem ± 6 mm diameter, covered by sclerified, pubescent remains of stipules and leaf bases.

Roots: One to few root tubers sit at the stem base, ovoid to cylindrical, sharply separated from the fibrous roots.

Leaves: 3-foliolate, succulent; petioles (2-6 cm) succulent, glabrous; leafleats 5-11 x 5-11 mm, broadly obovate, apex subtruncate to retuse, base obtuse to slightly decurrent; upper leafleat surface smooth, glabrous; lower leaflet surface colliculate, glabrous.

Inflorescence: Dichasial cyme, internodes of concinni well developed, laxiflorous; peduncle (up to 9 cm) succulent, glabrous; pedicel (up to 8 mm) glabrous.

Calyx: Asymmetric; outer sepals (5-6 x 4 mm) deltoid to sligthly hastate, apex broadly obtuse; inner sepals (5-6 x 1 mm) narrowly oblong, apex truncate to retuse; glabrous.

Corolla: ± 20 mm diameter; petals yellow, shape unknown.

Androecium: Stamens connate near base, long and mid filaments pubescent, short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (6 x 2 mm), loculicidal dehiscence.

Seeds: Ovoid (± 0,5 mm) reddish brown, transversally striated.

Chromosome number: 2n = 18.

Distribution: Stony habitats in the Central Andes slopes, collected from Arequipa, Peru, to La Paz, Bolivia. Occurrence in the Atacama Desert uncertain. Needs further investigation.

Oxalis paposana Philippi

R. A. Philippi, Reise durch die Wüste Atacama auf Befehl der chilenischen Regierung im Sommer 1853-54: 13. 1860.

Type: Chile, Antofagasta, Paposo. Philippi. XII 1853. Holotype SGO. Isotype W.

Color plate: Fig. 27 (page 105).

Habit: Perennial. Pachycaulous subshrub, up to 40 cm; leaves apically crowded together; stem ± 12 mm diameter, covered by sclerified remains of stipules and leaf bases, which are later replaced by a greyish, cracked periderm.

Roots: Branching root tubers sit at the stem base, napiform, gradually passing into the fibrous roots.

Leaves: 3-foliolate, succulent; petioles (up to 5 cm) succulent, glabrous; leafleats 7-15 x 8-16 mm, broadly obovate, apex emarginate to bilobed, lobes oblong, base obtuse to cuneate; upper leafleat surface smooth, glabrous; lower leaflet surface colliculate, glabrous to pubescent with short (± 0,5 mm) single, nonglandular hairs.

Inflorescence: Dichasial cyme, internodes of concinni well developed, laxiflorous; peduncle (up to 10 cm) succulent, glabrous; pedicel (10-20 mm) glabrous.

Calyx: Asymmetric; outer sepals (5-7 x 3-4 mm) lanceolate, apex retuse; inner sepals (5-7 x 1,5-2 mm) narrowly oblong, apex retuse; glabrous, apex pubescent with few short (± 0,3 mm) single, nonglandular hairs.

Corolla: ± 30 mm diameter; petals yellow, broadly spathulate, apex obtuse to subtruncate.

Androecium: Stamens connate near base, long and mid filaments pubescent, short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (6 x 2 mm), loculicidal dehiscence.

Seeds: Ovoid (± 1 mm) reddish brown, transversally striated.

Chromosome number: Unknown.

Distribution: Stony slopes in the coastal fog desert from Punta Tragagente to Quebrada Guanillos (Map 16, appendix A).

Oxalis ricardii Lourteig

A. Lourteig, *Oxalis* L. Subgéneros Monoxalis (Small) Lourt., Oxalis y Trifidus Lourt., Bradea 7(2): 352-353. 2000.

Type: Chile, Antofagasta, Taltal, El Rincón. Ricardii *3553*. 5 X 1955. Holotype CONC.

Color plate: Fig. 28 (page 106).

Habit: Perennial. Subshrub with sligthly succulent stems, up to 10 cm; leaves apically crowded together; stem ± 7 mm diameter, covered by sclerified, pubescent remains of stipules and leaf bases.

Roots: One to few root tubers sit at the stem base, ovoid to cylindrical, sharply separated from the fibrous roots.

Leaves: 3-foliolate, succulent; petioles (up to 10 cm) succulent, pubescent with short (± 0,3 mm) single, nonglandular hairs; leafleats 16-18 x 16-18 mm, suborbicular to broadly obovate, apex rounded to truncate or retuse, base cuneate to slightly decurrent, sometimes shape quite irregular; upper leafleat surface, smooth, waxy-shining, glabrous; lower leaflet surface colliculate, densely pubescent with short (± 0,3 mm) single, nonglandular hairs, pubescence extending to leaf margin giving a ciliate appearance when viewed from above.

Inflorescence: Dichasial cyme, internodes of concinni well developed, laxiflorous; peduncle (2-13 cm) succulent, pubescent with short (± 0,3 mm) single, nonglandular hairs; pedicel (5-25 mm) pubescent with short (± 0,3 mm) single, nonglandular hairs.

Calyx: Asymmetric; outer sepals (5,5-7 x 3,2-5 mm) obovate to deltoid, sometimes sligthly lobed, apex rounded; inner sepals (5-8 x 1,8-2,5 mm) narrowly oblong, apex truncate to retuse; sparsely to densely pubescent with short (± 0,3 mm) single, nonglandular hairs.

Corolla: 30-40 mm diameter; petals yellow, broadly spathulate, apex subtruncate.

Androecium: Stamens connate near base, long and mid filaments pubescent, short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (6 x 2 mm), loculicidal dehiscence.

Seeds: Ovoid (± 0,6 mm) reddish brown, transversally striated.

Chromosome number: Unknown.

Distribution: Stony slopes in the coastal fog desert from Punta Rincón to Quebrada Aguas de Cascabeles (Map 17, appendix A).

Oxalis squarrosa Barnéoud

F. M. Barnéoud, in C. Gay, Historia Física y Política de Chile 1: 445-446. 1845.

Type: Chile, Coquimbo, Cordillère de Guanta, depuis 1335 m a jusqu´ à 2669 m, terrain granitique. Gay *352*. XI 1839. Holotype P. Isotype K, P.

Includes: *O. glutinosa* Philippi, *O. coquimbana* Philippi, *O. briquetti* Knuth, *Acetosella squarrosa* (Barn.) Kuntze, *A. glutinosa* (Phil.) Kuntze, *A. coquimbana* (Phil.) Kuntze.

Color plate: Fig. 29 (page 107).

Habit: Perennial. Subshrub with sligthly succulent stems, densely foliated, up to 30 cm; leaves apically crowded together; stem ± 8 mm diameter, covered by sclerified, pubescent remains of stipules and leaf bases.

Roots: One to few root tubers sit at the stem base, ovoid to cylindrical, sharply separated from the fibrous roots.

Leaves: 3-foliolate, succulent; petioles (3-15 cm) succulent, sparsely pubescent with short (0,2-0,3 mm) glandular hairs; leafleats 12-13 x 12-13 mm, broadly obovate, apex retuse, base cuneate; upper leafleat surface smooth, sparsely pubescent with short (± 0,3 mm), glandular hairs; lower leaflet surface ± colliculate, pubescent with short (± 0,3 mm), glandular hairs.

Inflorescence: Dichasial cyme, internodes of concinni well developed, distal ends circinate; peduncle (up to 15 cm) succulent, sparsely pubescent with short (± 0,3 mm) glandular hairs; pedicel very short (± 1 mm), sparsely pubescent with short (± 0,3 mm) glandular hairs.

Calyx: ± asymmetric; outer sepals (3-5 x 2-2,5 mm) ovate, apex truncate; inner sepals (3-5 x 1-1,5 mm) narrowly oblong, apex truncate to retuse; densely pubescent with short (± 0,3 mm) simple, glandular hairs.

Corolla: 16-18 mm diameter; petals yellow, shape not known (perhaps spathulate).

Androecium: Stamens connate near base, long and mid filaments pubescent, short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (4 x 2-3 mm), loculicidal dehiscence.

Seeds: Ovoid (± 1,4 mm) reddish brown, irregularly transversally striated.

Chromosome number: Unknown.

Distribution: Stony terrain in the semi desert at the Andean foot hills from 29°-31°S. Never collected along the coast. (Map 18, appendix A).

Oxalis tortuosa Lindley

J. Lindley, Edward´s Botanical Register 15: 1249. (1829)

Type: Chile, near Valparaíso. MacRae. X 1825. Holotype K. Isotye G, L.

Includes: *O. glomerata* Hooker et Arnott, *O. bridgesii* Bert. ex Colla, *O. maritima* Barnéoud, *O. gaudichaudii* Barnéoud, *O. zonata* Liebmann, *Acetosella tortuosa* (Lindl.) Kuntze, *A. bridgesii* (Bert. ex Colla) Kuntze, *A. maritima* (Barn.) Kuntze, *A. gaudichaudii* (Barn.) Kuntze, *A. zonata* (Liebm.) Kuntze.

Color plate: Fig. 30 (page 108).

Habit: Perennial. Subshrub with sligthly succulent stems, up to 30 cm; leaves apically crowded together; stem ± 6 mm diameter, covered by sclerified, pubescent remains of stipules and leaf bases.

Roots: One to few root tubers sit at the stem base, ovoid to cylindrical, sharply separated from the fibrous roots.

Leaves: 3-foliolate, succulent; petioles (up to 30 cm) succulent, glabrous; leafleats 10-30 x 1,5-5 mm, linear to narrowly elliptic, often quite irregularly shaped and tortuous, apex acute, base acute; upper leafleat surface smooth, glabrous; lower leaflet surface colliculate, glabrous to very sparsely pubescent with short (0,6-0,8 mm) single, nonglandular hairs.

Inflorescence: Dichasial cyme, internodes of concinni contracted giving rise to an umbel-like inflorescence; peduncle (up to 30 cm) succulent, glabrous; pedicel (2-10 mm) glabrous.

Calyx: Asymmetric; outer sepals (4-6 x 4 mm) hastate, lobes rounded, strongly curved outwards, apex rounded; inner sepals (4-6 x 1,5 mm) lanceolate, apex rounded; glabrous, only apex pubescent with few, short (± 0,3 mm), single, nonglandular hairs.

Corolla: ± 15 mm diameter; petals yellow, narrowly spathulate to deltoid, deflexed, apex rounded to subtruncate.

Androecium: Stamens connate near base, long and mid filaments pubescent, short filaments glabrous.

Gynoecium: Pistil glabrous, styles distinct, pubescent in long or mid position, stigmas distinct, bilobed.

Capsule: Cylindrical (6 x 2 mm), loculicidal dehiscence.

Seeds: Ovoid (± 1 mm) reddish brown, transversally striated.

Chromosome number: Unknown.

Distribution: Between rocks along the coast of the semi desert from Cerro El Tofo to Valparaiso. Also collected at Baños de Cauquenes. (Map 17, appendix A).

Phylogeny of the west-Andean alliance as inferred from *trnL-L-F* and *trnH-psbA*

Isolation, amplification, and alignment of *trnL-L-F* and *psbA-trnH*. DNA isolation and amplification from silica-dried and freeze-dried vouchers was carried out without considerable problems except for one case: Neither the *trnL-L-F* nor the *psbA-trnH* fragments could be amplified for *O. ptychoclada* (Section *Herrerae*). The reasons for the failure remain unclear. There was no other material available for *Herrerae* and the section is therefore represented only by *O. teneriensis* in the phylogenetic analysis. DNA isolation and amplification from herbarium vouchers proved to be difficult, but was successful in seven specimens: *O. arbuscula*, *O. aureo-flava*, *O. caesia*, *O. cinera*, *O. rosea* and *O. teneriensis*. *Averrhoa* and *Sarcotheca* were used as outgroups in the analysis. Their *trn-L-L-F* sequences (Oberlander et al., 2004) were downloaded from Genbank.
The final aligned matrix consisted of 25 taxa and 1524 characters. It contained an interleaved data set of *trnL-L-L* and *psbA* chloroplast markers. Several polyT regions in *psbA-trnH* were largely unalignable and all together 210 characters had to be excluded from further analysis.

Phylogenic analysis. Of 1524 characters in the maximum parsimony analysis 1249 were constant. 138 characters were autapomorphies and therefore parsimony-uninformative. 137 were scored as potentially parsimony-informative. That means they are either homoplasies or synapomorphies. Branch-and-bound search yielded 30 trees of equal length. The consensus of these 30 trees is summarized in the majority-rule tree shown in figure 7. Bootstrap credibility is depicted on all branches receiving values over 50. The following clades received bootstrap support of 90 and more: *Oxalis* (100), *Corniculatae* (100), *Caesiae* (99), *Palmatifoliae* (100), *Alpinae* (93) and *Carnosae* (97). *Giganteae* show only moderate bootstrap support of 81. Relationships between sections are almost fully resolved (bootstrap values between 90 and 100) with exception of *Corniculatae* and *Caesiae* whose relationship to a clade of the remaining species remains unclear (low bootstrap value of 59). Relationships among species of *Carnosae* are essentially unresolved, but two clades are indicated: A clade of species from central Chile and another clade of species from northern Chile (but see low bootstrap values 74 and 83, respectively).

The model of sequence evolution for the maximum likelihood analysis inferred by DTModSel was the Kimura-3-parameter model (Kimura, 1981) with unequal base frequencies. Table 6 shows the substitution probability matrix as implemented in the model. This model is extended by two parameters modeling variation of rates of substitution among sites: I means a proportion of invariable sites in the data set and G stands for a gamma-shaped distribution of variable sites.

ML analysis was conducted under this model in PAUP. Heuristic search was terminated after 15h 47min and yielded one tree with -Ln likelihood = 4100.2894. Base frequencies were A=0.35275, C=0.15829, G=0.16250 and T=0.32645. The estimated value of proportion of invariable sites was 0.541280 and the value of the gamma shape parameter was estimated to be 19.191374. The resulting phylogram is shown in figure 8. The topology agrees exactly with the MP consensus tree. Atacama succulents show markedly fewer substitutions in comparison to the rest of the taxa.

Table 6: Substitution probability matrices of the Kimura-3-parameter model (K3P) and the general time-reversible model (GTR) used in maximum likelihood analysis and Bayesian approach, respectively.

	K3P (3 parameters)				**GTR** (6 parameters)			
	A	G	C	T	A	G	C	T
A	-	$\square_G$	$\square_C$	$\square_T$	-	$\square_G$	$\square_C$	$\square_T$
G	$\square_A$	-	$\square_C$	$\square_T$	$\square_A$	-	$\square_C$	$\square_T$
C	$\square_A$	$\square_G$	-	$\square_T$	$\square_A$	$\square_G$	-	$\square_T$
T	$\square_A$	$\square_G$	$\square_C$	-	$\square_A$	$\square_G$	$\square_C$	-

Bayesian tree search had been conducted under a GTR + I + G model of sequence evolution, because the model suggested by DTModSel (K3P + I + G) is not available in MrBayes. The GTR (general time-reversible) model assumes a specific substitution probability for each pair of bases, which is the same in either direction (e.g. time reversible). A gamma shaped substitution rate variation with four discrete rate categories together with a proportion of in variant sites (I + G) was implemented as suggested by DTModSel. Two runs were run simultaneously. The likelihoods of the best state for the cold chain of run 1 and 2 were -4104.41 and -4106.95, respectively. That means that two independent searches starting from different seeds arrived at the same topology. This is a hint (not a proof) that analysis had not been stuck on a local maximum of likelihood. A majority-rule consensus tree was constructed from both runs discarding the first 5000 trees from each run as „burn in“. Figure 9 gives the tree together with the posterior clade probabilities. The topology of the Bayesian estimate concords exactly with the MP and the ML trees. The genus *Oxalis* and all sections are well supported by posterior clade probabilities between 97 and 100. Here also *Giganteae* obtain

100 % support. The Bayesian estimate also fails to establish the potential sister relationship of *Corniculatae* and *Caesiae* (posterior clade probability of 65) to the remaining clade. Relationships among sections of the remaining clade again are well resolved with posterior clade probabilities between 97 and 100. The two clades of *Carnosae* indicated in the MP analysis receive strong support here with posterior clade probabilities of 97 and 100 for the central and northern Chilean clade, respectively.

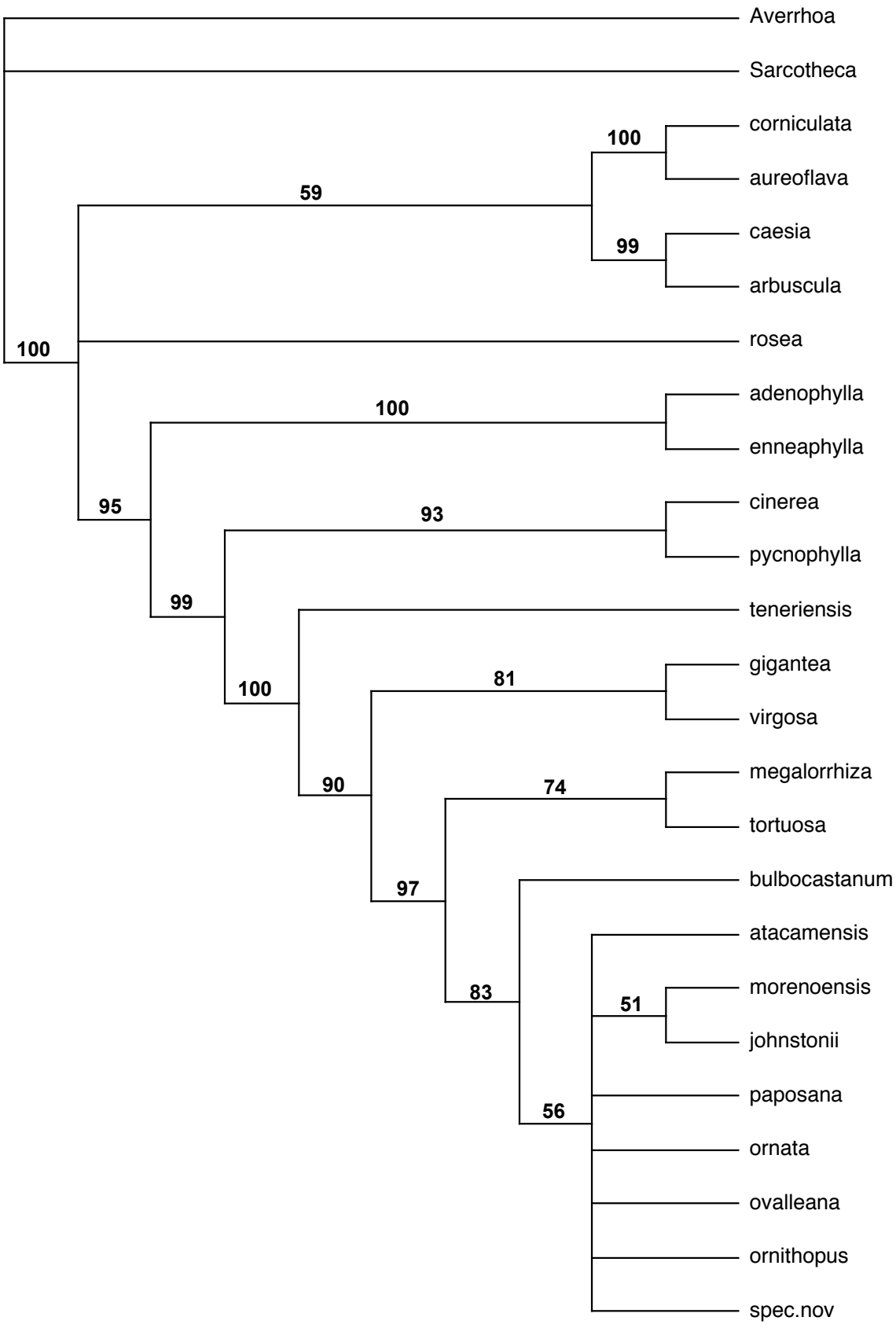


Fig. 7: Majority-rule consensus tree of 1000 bootstrap replicates under heuristic search in a maximum parsimony (MP) analysis of the *trnL-L-F/psbA-trnH* data set.

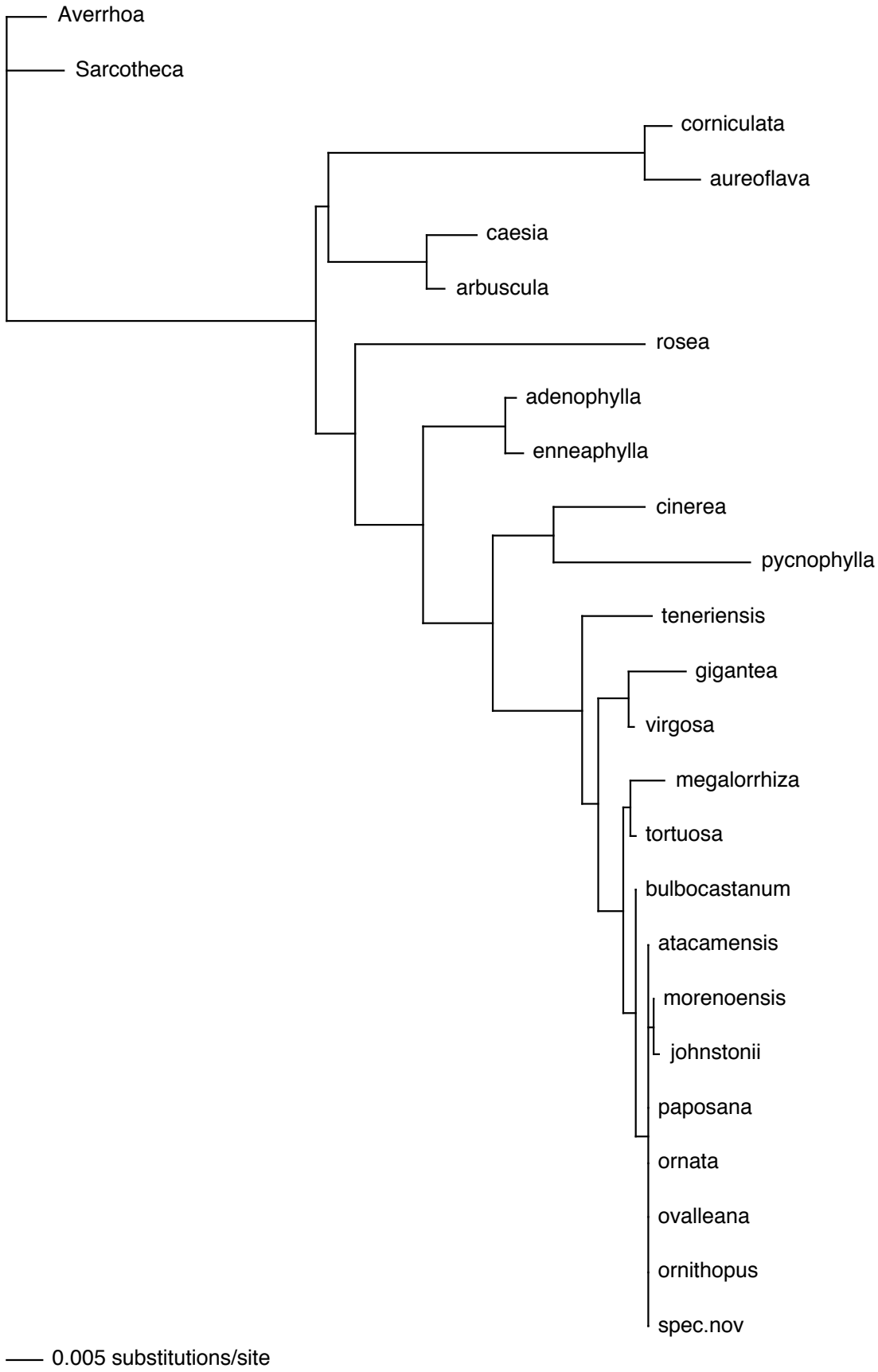


Fig. 8: Phylogram obtained under heuristic search in a maximum likelihood (ML) analysis of the *trnL-L-F/psbA-trnH* data set using K3P + I + G as model of sequence evolution.

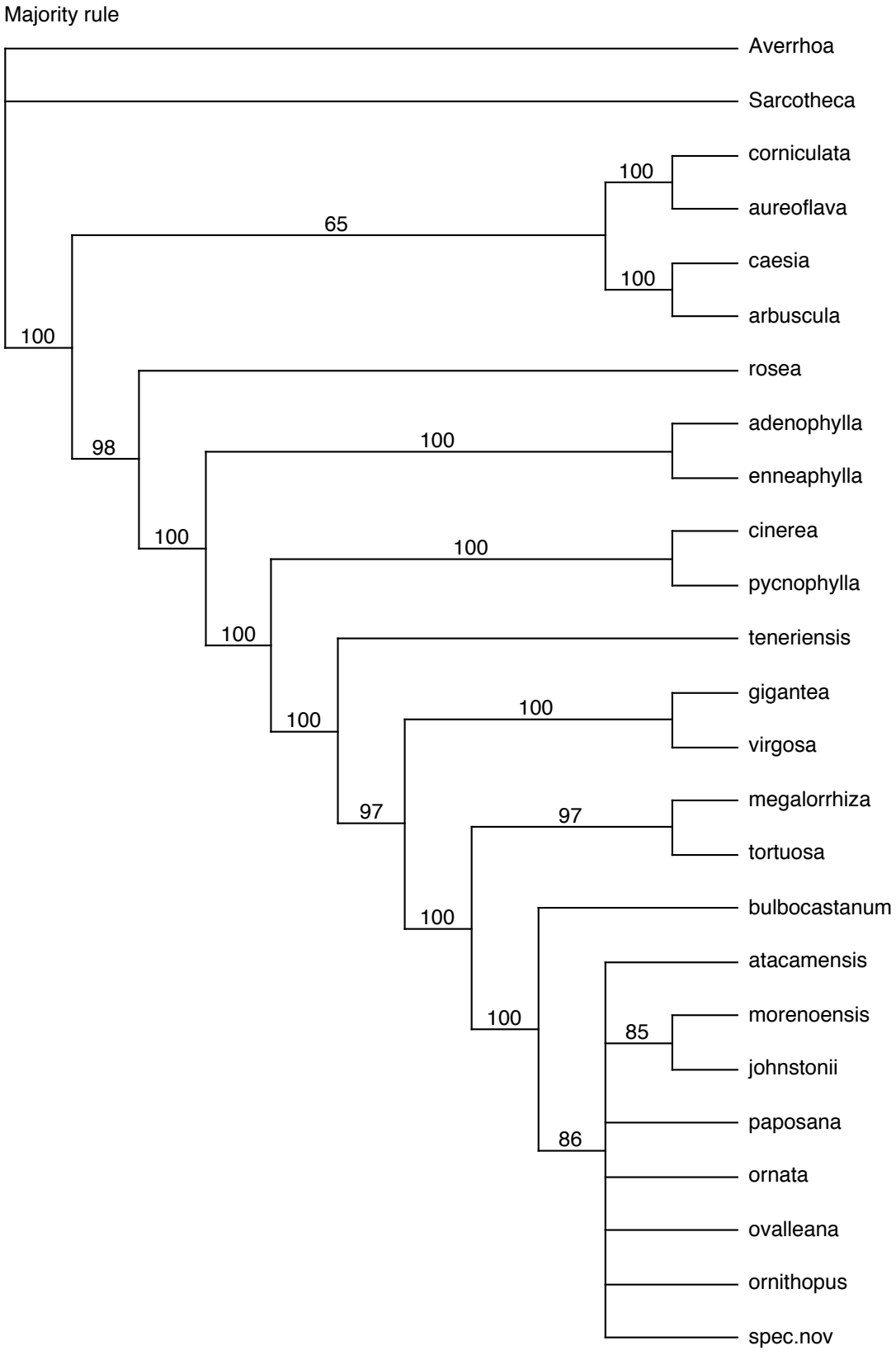


Fig. 9: Majority-rule consensus tree summarizing tree samples from the posterior probability distribution drawn by Bayesian analysis (Metropolis coupled Marcov chain Monte Carlo) using GTR + I + G model of sequence evolution. Posterior clade probabilities are depicted for branches receiving more than 50 % support.

Evolutionary relationships and character evolution in the west-Andean alliance

Figures 10 and 11 show a strict consensus tree that sums the topologies of MP, ML and Bayesian analysis. It contains only branches that receive bootstrap support of 74 and higher and Bayesian posterior clade probabilities of 97 and higher.

Two evolutionary lineages in the Atacama Desert. Tree topology in figure 10 indicates two evolutionary lineages of Oxalis in the Atacama Desert. The first lineage is represented by section *Caesiae*. Sister group relationships remain unclear here. In phylogenetic analyses, *Caesiae* cluster either with *Corniculatae* or with *Roseae*. These lineages are presumably quite old and analysis of *trnL-L-F* data might have suffered from long-branch attraction.
The second lineage consists of sections *Carnosae* and *Giganteae*. They show clear a sister ship to the Andean sections *Herrerae* (*O. teneriensis*) and *Alpinae*. Within this lineage, we can discern three groups: section *Giganteae* and a central Chilean clade (*O. tortuosa* and *O. megalorrhiza*) as well as a northern Chilean clade in section *Carnosae*. Support for a separation of the latter two, however, is not very high (Fig. 7 and 8, but see fig. 9).

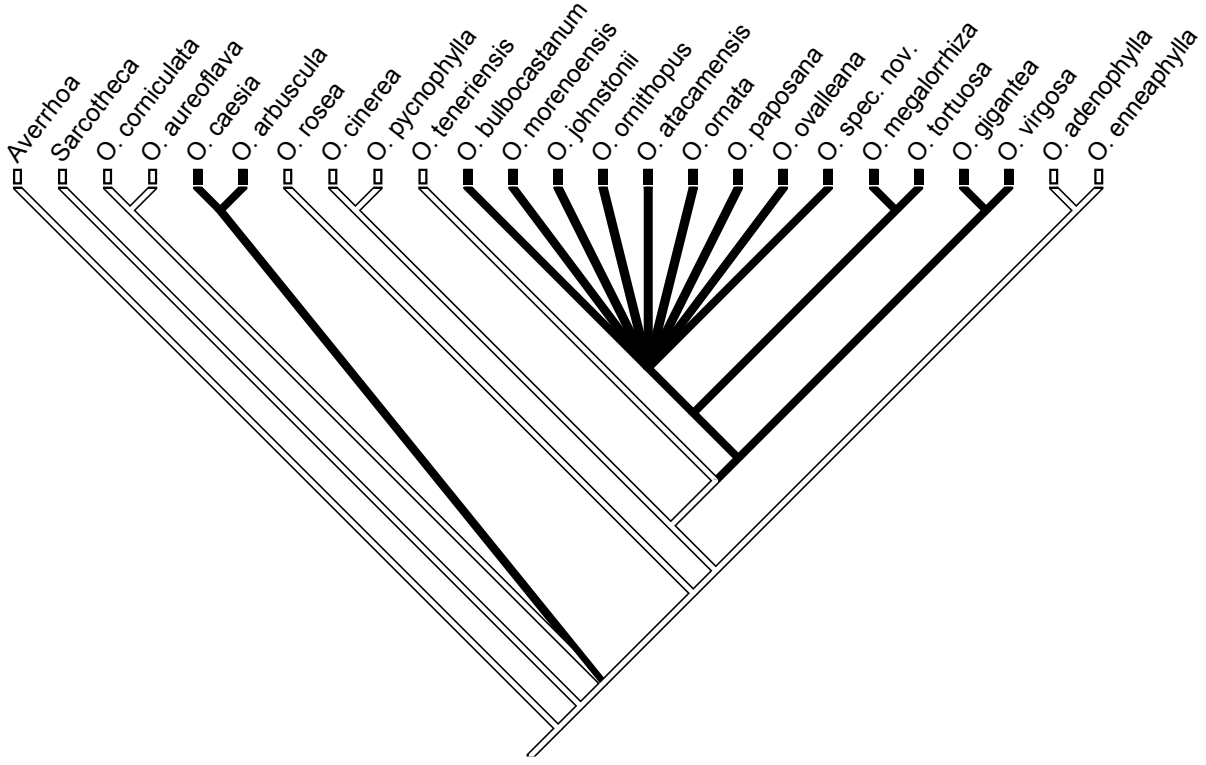


Figure 10: Evolutionary lineages of *Oxalis* in the Atacama Desert (shown in black) mapped on a strict consensus tree summing results of MP, ML and Bayesian analysis of the cp-DNA data set (*trnL-L-F* and *psbA-trnH*).

Monophyly of stem succulence. Evolutionary relationships depicted in figure 11 suggest a monophyletic origin of stem succulence in the west-Andean alliance. The evolution of water-storing stems is found in the common ancestor of sections *Herrerae*, *Giganteae*, and *Carnosae*. Lineages in *Carnosae* that show reduced stem succulence are scattered among pachycaulous lineages.

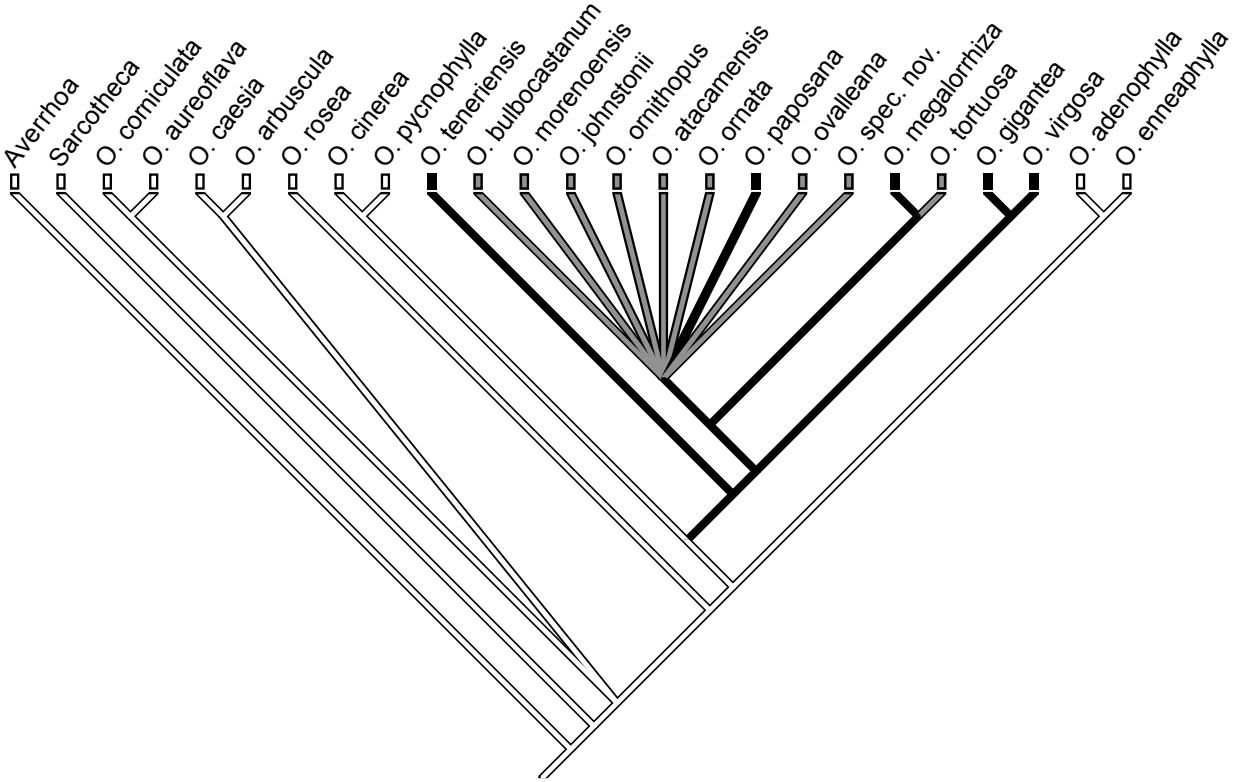


Figure 11: Occurrence of stem succulence (shown in black) and reduced stem succulence (shown in grey) in the west-Andean alliance mapped on a strict consensus tree summing results of MP, ML and Bayesian analysis of the cp-DNA data set (*trnL-L-F* and *psbA-trnH*).

DISCUSSION

Towards a complete revision of Atacama-inhabiting *Oxalis*

History of exploration. Botanical exploration of arid northern Chile is divided into two different stages. This division is also apparent in the investigation of the genus *Oxalis*. At first, species have been described only from the semi desert and the xerophytic shrub land in the southern Atacama Desert. Six of them, *O. virgosa* (Molina, 1782), *O. megalorrhiza* (Jacquin, 1794), *O. tortuosa* (Lindley, 1829), *O. gigantea*, *O. arbuscula* and *O. squarrosa* (Barnéoud, 1845), are still recognized today.

Later, systematic exploration of the coastal fog desert began with the expedition of Philippi in 1860, which was commissioned by the Chilean government in order to explore the largely unknown Atacama Desert. Philippi described a great number of species of *Oxalis* from the coastal fog desert (Philippi, 1860; Philippi, 1893), but his descriptions have to be interpreted with caution. Apparently he described species from his memory and many species have been described several times by Philippi (Grau, pers. comm.) Only seven of his species are recognized in the present study: *O. atacamensis, O. caesia, O. leucophylla, O. ornata, O. ornithopus, O. ovalleana and O. paposana*. At the same time Weddell (1861) described *O. pachyrhiza* from the coastal desert in Peru and a bit later Knuth (1930) reported two more species, *O. johnstonii* and *O. ericoides*, for the Chilean fog desert.

During her enormous attempt of a revision of the complete genus of *Oxalis*, Lourteig (2000) synonymized a great number of Philippi's species. At the same times she described three new species for the coastal fog desert from previously undetermined herbarium specimens: *O. matancillae*, *O. morenoensis* and *O. ricardii* (Lourteig, 2000).

Finally, the present study tried to add to better understanding of the group's systematics. Lourteig's revision proved to be a valuable guideline and her classification has been largely, but not entirely confirmed. Two results, which differ from her treatment, are discussed in the following sections: Taxonomic delimitation of *O. megalorrhiza* [Feuillée] Jacquin and the transfer of *O. arbuscula* from section *Carnosae* to section *Caesia*.

***Oxalis megalorrhiza* group.** Lourteig (2000) synonymized sixteen different names that have been described by various authors between 1797 and 1919; under the name of *O. megalorrhiza* (see results, p. 44). Some of these names are clearly synonymous. For example,

Savigny described O. bicolor from Feuillée's illustration. The very same illustration that Jacquin had used for his description three years earlier. Also, there is evidence that species described from material cultivated in botanical gardens in Europe and Russia from around 1825 onward (e.g. *O. mirbelii*, *O. rubrocincta* and *O. arborescens*) are synonyms to the plant that was mentioned and illustrated by Feuillée. For example, *O rubrocincta* was described from plants that were grown from seeds that "came among the earth of Mr. Hartwegs Guatemala plants". Lourteig (2000), however, refuted the putative provenance of this specimen from Guatemala and it seems likely that the plants stemmed from seeds of *O. megalorrhiza*. So far, *O. megalorrhiza* it the only species of section *Carnosae* that is known to lack self-incompatibility and produces fertile offspring by selfing in greenhouses around the world. Therefore, a great deal of uncertainty around this species has to be attributed to its early discovering and rapid distribution due to its unique reproductive biology, but also to the fact that there is no type specimen.

Nonetheless, observations made in the field and on greenhouse cultivations show that *O. megalorrhiza sensu* Lourteig comprises more than one species. Two of them could be identified in the present study. *O. paposana* Philippi is clearly separated from *O. megalorrhiza* according to considerably smaller leaflets, emarginate to bilobed leaflet apices, pubescent lower leaflet surfaces (Fig. 27F) and lanceolate outer sepals (Fig. 27D). These characters remain stable under 'common garden' conditions in the greenhouse and are not blending into each other. The two species are united by possessing distinctive pachycaulous stems with considerably secondary growth, reaching diameters of up to 20 mm, and development of a periderm. This resemblance in habit could have been a potential source of confusion, especially when working with herbarium material. O. *ornata* Philippi has also to be separated from *O. megalorrhiza*. It differs mainly in habit (Fig. 23A), dense pubescence of lower leaflet surfaces (Fig. 23F) and dense pubescence of margins and apex of sepals (Fig. 23D). Especially the pubescence of lower leaflet surfaces are a distinctive characters, because the give a ciliated appearance of the leaves when they are viewed from above (Fig.23C). Again these characteristics are stable under greenhouse conditions. For both *O. paposana* and *O. ornata*, careful investigation of type specimens and first descriptions confirmed these results.

Furthermore, the separation of both species from *O. megalorrhiza* is also suggested by molecular evidence. MP, ML and Bayesian inference of non-coding cp-DNA (*trnL-L-F* and *psbA-trnH*) places *O. paposana* and *O. ornata* in northern Chilean subclade of *Carnosae*, while *O. megalorrhiza* is part of the central Chilean subclade (Fig. 7, 8, 9, 10).

Changes in the intrageneric classification. Reiche (1894) was the first to attempt an intrageneric classification of Chilean *Oxalis* based on sections. He described the sections *Fruticulosae* and *Carnosae* in order to unite species with woody and with succulent stems, respectively. Fruticulosae contained *O. arbuscula*, *O. atacamensis* and *O. squarrosa*, plus some species today regarded as synonymous. *O. ornata*, *O. paposana*, *O. ovalleana*, *O. gigantea* and synonymous species of *O. megalorrhiza* were among the species put into *Carnoase*. The remaining Atacama endemic species were distributed over three more sections: *O. ornithopus* and *O. tortuosa* were put in *Angustifoliae* due to their linear leaflets. *O. leucophylla* and *O. caesia* were classified as members of the mostly Andean *Berteroanae*, because of their cushion-like growth pattern. Finally, *O. bulbocastanum* was considered a member of *Euoxys* due to its acaulescent habit.

Knuth (1930) accepted the classification of Reiche with some modifications. He recognized the relationships between *O. caesia* and the newly described *O. ericoides* and put them together in a new section *Caesiae*. Consequently, *O. leucophylla* was transferred to section Carnoase, together with the newly described *O. johnstonii*. Yet, he did not recognize the affiliation of *O. bulbocastanum* to section Carnoase, putting it into section *Articulatae*. *O. pachyrhiza*, which was unknown to Reiche, was considered to lie in section *Acetosellae* by Knuth.

It was up to Lourteig (2000) to propose the asymmetrical calyx as synapomorphy of section *Carnosae*. As a consequence, she included *O. pachyrhiza*, *O. bulbocastanum*, *O. ornithopus*, *O. tortuosa, O. atacamensis* and *O. squarrosa* as well as the newly described *O. matancillae*, *O. morenoensis* and *O. ricardii* in section Carnoase. *O. arbuscula* was also transferred to this section for reasons not known. Another consequence was the placement of *O. gigantea* and *O. virgosa* into their own section *Giganteae*, because these species possess regular calyces.

Her results have been confirmed in the present study by both morphological and molecular data with only one exception: *O. arbuscula* is clearly placed in section *Caesia*.

Monophyly of all three sections is strongly suggested by the evolutionary trees obtained from MP, ML and Bayesian analysis of the non-coding cpDNA data set (Fig. 7, 8, 9). Consistently, all trees group *O. arbuscula* together with of *O. caesia* with high support (bootstrap value and posterior clade probability of 99 and 100, respectively). Each of these clades is supported by morphological synapomorphies: (1) Section *Caesiae* has ternate pinnate leaves, (2) section *Giganteae* bears leaves and flowers in brachyblasts along the pachycaulous main axis and (3) section *Carnosae* is characterized asymmetrical calyces with the outer sepals being deltoid,

rhomboid, lanceolate or hastate, rarely ovate and inner sepals being narrowly oblong (e.g. fig 17D, 19C, 30E). Furthermore, the molecular phylogeny is consistent with branching pattern, occurrence of short shoots and the presence or absence of sclerified leaf bases (Fig. 5). The arbuscaula type, gigantea type and megalorrhiza type correspond exactly to the sections *Caesiae*, *Giganteae* and *Carnosae*, respectively.

Future perspective. Due to the combined investigation of morphological and molecular characters complemented by field observation and greenhouse cultivation, the present study can be regarded as the most comprehensive approach to understanding systematics of *Oxalis* in the Atacama Desert up to date. Nevertheless, for its brevity and limited amount of material that could be studied, it remains modest and leaves many questions open. Many species, especially *O. ericoides* and *O. leucophylla*, have been collected only few times. Their morphological variation and their distributions are still poorly known. It is not even known if they still exist, as many species are local endemics and potentially endangered by climatic shifts and human activities such as mining and street construction. Sampling those rare species is essential for a better understanding of their systemtics.
Furthermore, a huge number of unidentified herbarium specimens show that many taxonomic challenges remain. During a fieldtrip of only three weeks in December 2004 at least one undescribed species was collected and probably there are more among unidentified accessions cultivated in the greenhouse. This shows that the diversity of *Oxalis* in the Atacama Desert could be considerably higher than the present study suggests and more work is needed for a more satisfying picture of the systematics of Atacama endemic *Oxalis*.

Credibility and limitations of the cpDNA-based phylogeny

General considerations. Genes trees not necessarily track the history of the species in concern (Page & Holmes, 1998; Judd et al. 2002). There are three main reasons for this: (1) Since nuclear genomes recombine frequently, most nuclear genes have undergone duplications and are arranged in multigene families. All descendents of a certain gene in a gene family are said to be orthologous to each other, but they are termed paralogous when compared to all descendents of other members of the same gene family. Comparing paralogous genes in a phylogenetic analysis will yield a tree topology, which does not reliably reflect speciation events because it is blurred by gene duplication events. There is only one

exception: A phenomenon called ‘concerted evolution’ tends to homogenize functional members of a gene family. Phylogenetic relationships can be confidently inferred from homogenized paralogous genes, but they have to be checked for polymorphism by cloning techniques. (2) Even if only orthologous genes are compared, lineage sorting can be problematic in phylogenetic analyses, when coalescence times are longer than the time interval between two successive speciation events. In this case, polymorphisms persist in the population during speciation events and are randomly sorted. Just by chance, one of the daughter populations can receive a paraphyletic set of copies. Some of these copies, then, are in fact more closely related to the gene copies in the other daughter population. In this case, again the gene tree might not reflect the species tree. (3) Introgression of genetic material of one lineage into another during hybridization is another cause of error in phylogenic analysis.

The *trnL-L-F* and *psbA-trnH* data set. *TrnL-L-F* and *psbA-trnH* are both single copied chloroplast markers. Their sequencing is straightforward because it does not afford troublesome cloning techniques. Still, the problems of lineage sorting and hybridization remain. A single gene tree must therefore be interpreted with care for the reasons explained above. Nevertheless, we can gain confidence by combining two or more gene trees, although it is still possible that none of them reflect the true evolutionary tree (Judd et al., 2002). In the present case, where work had to be completed in a given time of nine month, the analysis of a two-chloroplast data set seemed to be good compromise. The congruence of the tree topology (see above) adds further confidence into the evolutionary tree predicted from the cpDNA data set.

Yet, another point is the usefulness of the markers utilized. Initial analysis of a *trnL-L-F* data set showed that variation in this marker is perfectly suitable for resolving evolutionary relationships on a section level, while failed to resolve relationships of the sections *Carnosae* and *Gigantea* on a species level. The second marker (*psbA-trnH*) should have done better for the on the species level as it is known to evolve more rapidly than trnL-L-F (Shaw et al., 2005; Holdegger & Abbott, 2003). Nevertheless, the use of psbA-trnH could not fully resolve relationships among the northern Chilean clade in section *Carnosae* either (Fig. 7, 8, 9). In fact, five out of nine species sequences in this clade (*O. atacamensis, O. ornata, O. ornithopus, O. ovalleana, and O. paposana*) were genetically identical in both markers (Fig. 8). These species are all well distinguished by morphological characters (Fig. 16, 23, 24, 25, 27). This finding is interesting as it points towards a possible adaptive radiation in this clade that left a hard polytomy as a trace.

Recently, *psbA-trnH* has been proposed for 'DNA bar-coding' (Kress et al., 2005) that it should allow the identification of species on a DNA level. The present case, however, shows that *psbA-trnH* is not suited for the identification of species of *Oxalis* section *Carnosae*. It is important to stress, however, that a hard polytomy, like in this case, cannot be resolved by any molecular marker by definition and these results therefore do not speak against the general use of *psbA-trnH* in DNA bar-coding.

Evolution and biogeography of Atacama endemic *Oxalis*

Apart from a revision of Atacama endemic *Oxalis*, the present study aimed at giving insights into the evolution and biogeography of the species studied. Under the assumption that increasingly arid conditions during desert formation, together with orogenic processes, were among the ecological key factors influencing desert life, evolution of xerophytic morphology was hypothized to be of major importance in Atacama-inhabiting *Oxalis*.

Desert formation as a background for biotic evolution. The climate of the Atacama region during Cretaceous is thought to have been warmer and wetter than today (Solbrig 1976). No significant mountain chains were present in the South American and uniform, tropical vegetation covered the continent. A slight rise of the Chilean Andes began in the middle Cretaceous (Solbrig, 1976), but they reached their final dimensions only in the Pliocene (see below). The warm-wet climate continued during the Paleocene and Eocene, when tropical

elements reached furthest south, until a gradual deterioration of the climate can be registered from the middle Eocene onwards (Hüniken, 1966; Menéndez, 1972). This climatic deterioration continued during the Oligocene and the Miocene (Solbrig, 1976). The desiccation process along the Pacific coast of subtropical South America was strongly intensified at the Miocene-Pliocene boundary when cooling of the Humboldt Current began (Zinsmeister, 1978). This change is evidenced by biogeographical and geological events: Marine fauna declined in species richness and shifted towards coldwater elements in southern Peru (Herm, 1969) and northern Chile (Muizon & De Vries 1985). At the same time canyon cutting ceased in the area of the present Atacama Desert as a result of strongly reduced precipitation (Mortimer, 1973). Arroyo et al. (1988) suggest a gradual transition from closed Miocene forest into more open, savanna like vegetation for low elevation of the Atacama region. During the same time, the dry highlands of the Altiplano of Peru and Bolivia were created and the Chilean Andes continued to rise (Solbrig, 1976). Continued desiccation of the Atacama region due to increased rain shadow effects and continued influence of the Humboldt Current, finally led to the establishment of hyper arid conditions in the Atacama Desert during the Pleistocene (Solbrig, 1976, Arroyo et al. 1988). A meteorological model developed by Damuth & Fairbridge (1970) proposed warm-dry and wet-cold climatic cycle due to changes in the wind system. These changes are witnesses by formation of salt lakes in the high Andes (Stoertz & Ericksen, 1974; Naranjo & Paskoff, 1980), a snowline depression in the Andes of as much as 4000 m (Hastenrath, 1967; Simpson Vuilleumier, 1971) and a northward migration of temperate element as suggested by pollen deposits (Heusser, 1983; Villagran & Armesto, 1993). Andean uplift continued throughout the Pleistocene and Arroyo et al. (1988) suggested therefore that aridity should have intensified at each new interglacial. Solbrig (1976) proposed that the continued cycles of warm-dry and wet-cold climate were responsible for the extinction of many tropical and subtropical elements that had occupied the area since the Tertiary. At the same time, these conditions could have allowed the invasion and adaptive radiation of cold and dry-adapted Andean elements.

Summing these results, we can state that gradual desiccation began in the mid Eocene and culminated only recently in the Pleistocene when the Atacama Desert reached its present hyper arid conditions. Ever increasing selection pressures towards xeromorphic adaptation should have acted upon plant life in the Atacama region since the Eocene. Evolution of Atacama-inhabiting *Oxalis* will be discussed in the next section against this background.

Different evolutionary lineages. Both lineages of *Oxalis* in the Atacama evolved towards increased drought resistance section, but they did so in different ways.

The first lineage, section *Caesiae*, seems to never have evolved notable succulence. Instead they rely on low cushion growth, thick layers of epiculticular waxes and small, often needle-like leaves. The basal position of *Caesiae* in the west-Andean alliance, together with the low number of three species, suggests that its members represent survivors of an old lineage.

Phylogenetic analysis indicates that their next close relatives are to be found among mesophytic herbs from central Chile (sections *Roseae* and *Corniculate*, Fig. XX). During the formation of the desert, the ancestors of today's *Caesiae* might have been 'trapped' in fog oases along the Pacific coast and taken an evolution different from the central Chilean elements.

The second lineages consist of the two sections *Carnosae* and *Gigantea*. They share their pachycaulous habit with section *Herrerae* from the Andes of Colombia, Ecuador, Peru and Bolivia. Monophyly of these three sections indicates that stem succulence originated only once in a common ancestor somewhere in the Andes in the Altiplano region. As suggested by Solbrig (1976) and Armesto & Vidiella (1993) cold-wet climates during Pleistocene glacials could be invoked to explain the migration of preadapted *Oxalis* genotypes from the Andes to the Atacama lowlands. This scenario is consistent with the finding of strong floristic affinities between Atacama and Andean elements (Solbrig, 1976; Armesto & Vidiella, 1993).

Stem succulence, as an apparent key innovation in their new habitat, allowed for a subsequent diversification of *Giganteae* and *Carnosae* in the Atacama Desert. Limited genetic divergence, especially between species of *Carnosae*, suggests a recent origin of most species. The hard polytomy in the northern Chilean clade of section *Carnosae* indicates a possible adaptive radiation.

Interestingly, many species in section *Carnosae* show reduced stem succulence and seem to allocate biomass towards belowground storage of water in root tubers. This tendency is most pronounced in the acaulescent *O. bulbocastanum*, which relies entirely on water storing root tubers. The tree topology in figure XX offers two possible evolutionary explanations for this pattern: (1) Reduced stem succulence constitutes a synapomorphy for section *Carnosae* and two species (O. *megalorrhiza* and O. *paposana*) regained the pachycaulous habit later on. (2) The common ancestor of section *Carnosae* was stem succulent and stem succulence was repeatedly reduced due to convergent evolution. At present, there is no data to prefer one explanation. Nevertheless, convergent evolution of reduced stem succulence might be a reasonable explanation in a homogenous but extreme environment as the Atacama Desert.

Abstract

The present study aimed at a better understanding of the systemtics and biogeography of three sections of *Oxalis* that inhabit the Atacama Desert in northern Chile. The hyper arid Atacama Desert formed recently in the Pleistocene and offers an interesting scenario for the investigation of plant adaptation to increasing aridity. The study involved a revision of the Atacama-inhabiting *Oxalis* based on morphology and the construction of a molecular phylogeny (*trnL-L-F* and *psbA-trnH*) of representatives of all west-Andean sections of *Oxalis*. Morphological systematics mainly confirmed the revision of Lourteig (2000) with two exceptions. First, morphological and molecular data strongly suggest the transfer of *O. arbuscula* from section *Carnosae* to section *Caesiae*. Second, *O. ornata* and *O. paposana*, both considered synonyms of *O. megalorrhiza* by Lourteig, are recognized again.

Molecular data suggest two evolutionary lineages of Oxalis in the Atacama Desert. (1) A clade of three species (section *Caesiea*) represents the survivors of an old lineage of cushion shrubs. This lineage failed to evolve water-storing tissues, instead relying on low cushion growth, thick layers of epiculticular waxes and small, often needle-like leaves.

(2) A second clade (sections *Giganteae* and *Carnosae*) diversified after evolving water-storing tissues, apparently a key innovation. Limited genetic divergence among species suggests a recent origin and possibly an adaptive radiation. Within this group, species that live in more arid fog desert allocate more biomass towards belowground water storing tubers than species that receive winter rainfall.

Zusammenfassung

Die vorliegende Arbeit hatte ein besseres Verständnis der Systematik und der Biogeographie dreier Sektionen der Gattung *Oxalis* aus der Atacamawüste im Norden Chiles zum Ziel. Die hyperaride Atacamawüste entwickelte sich erst während des Pleistozäns und bietet ein interessantes Szenario für die Untersuchung von Anpassungen an eine immer steigende Aridität. Die Arbeit umfasste eine auf morphologischen Merkmalen basierende Revision der Atacama bewohnenden *Oxalis*-Arten und die Erstellung einer molekularen Phylogenie (*trnL-L-F* and *psbA-trnH*) von Repräsentanten aller westandinen Sektionen von *Oxalis*.

Die Ergebnisse der morphologischen Arbeit bestätigen im wesentlichen die Revision von Lourteig (2000) mit zwei Ausnahmen: Erstens, morphologische und molekulare Daten legen eine Klassifikation von *O. arbuscula* in Sektion *Caesiae* und nicht wie bisher in Sektion

Carnosae nahe. Zweitens, *O. ornata* und *O. paposana*, beide von Lourteig als Synonyme von *O. megalorrhiza* angesehen werden wieder anerkannt.
Die molekulare Phylogenie lässt zwei evolutionäre Linien von Oxalis in der Atacamawüste erkenne. (1) Eine monophyletische Gruppe aus drei Arten (Sektion *Caesiae*) repräsentiert Überlebende einer alten Linie von Zwergsträuchern. Diese Linie hat keine wasserspeichernden Gewebe entwickelt und ist daher auf niedrigen Polsterwuchs, dicke Schichten epikultikulärer Wachse und kleine, oftmals nadelförmige Blätter angewiesen.
(2) Eine zweite monophyletische Gruppe (Sektionen *Giganteae* und *Carnosae*) begann sich nach der Evolution von wasserspeichernden Geweben, einer offensichtlichen Schlüsseladaptation, aufzuspalten. Geringe genetische Divergenz zwischen den einzelnen Arten deutet auf deren kürzliche Entstehung und eventuell eine adaptive Radiation. Einige Arten aus der Nebelwüste investieren vermehrt Biomasse in wasserspeichernde Wurzelknollen, verglichen mit Arten aud Winterregengebieten.

Resumen

La finalidad del presente estudio fue alcanzar una mejor comprensión de la sistemática y biogeografía de tres secciones del género *Oxalis* que habitan en el desierto de Atacama, en el norte de Chile. Este desierto de extrema aridez se ha formado recientemente durante el Pleistoceno y ofrece un escenario interesante para el estudio de adaptaciones de plantas a la creciente sequía. El estudio consistió de una revisión de las especies del género *Oxalis* que habitan el desierto de Atacama, basado en rasgos morfológicos y la construcción de una filogenia molecular (*trnL-L-F* y *psbA-trnH*) de representantes de todas las secciones de *Oxalis* presentes al oeste de los Andes.
La sistemática morfológica básicamente se ajustó a la revisión de Lourteig (2000), con sólo dos excepciones. Primero, los datos morfológicos y moleculares indican el traspaso de *O. arbuscula* de la sección *Carnosae* a la sección *Caesiae*. Segundo, *O. ornata* y *O. paposana*, ambos considerados sinónimos a *O. megalorrhiza* según Lourteig, son nuevamente reconocidos.
Según los resultados de la filogenia molecular existen dos líneas evolutivas de *Oxalis* en el desierto de Atacama. (1) Un grupo monofilético de tres especies (sección *Caesiae*) que representa los sobrevivientes de un antiguo linaje de arbustos enanos. Este linaje no desarolló tejidos de almacenamiento de agua y las plantas dependen de un crecimiento en cojines bajos, capas gruesa de cera epicular y hojas pequeñas, a menudo lineares. (2) Un segundo grupo monofilético (secciones *Giganteae* y *Carnosae*) se diversificó después de haber evolucionado

tejidos de almacenamiento de agua, aparentemente una innovación clave. La limitada divergencia genética entre las especies de este grupo, sugiere un órigen reciente y posiblemente una radiación adaptiva. En este grupo, ciertas especies que crecen en la zona de camanchacas muestran mayor asignación de biomasa al desarollo de tubérculos que las especies que reciben lluvias invernales.

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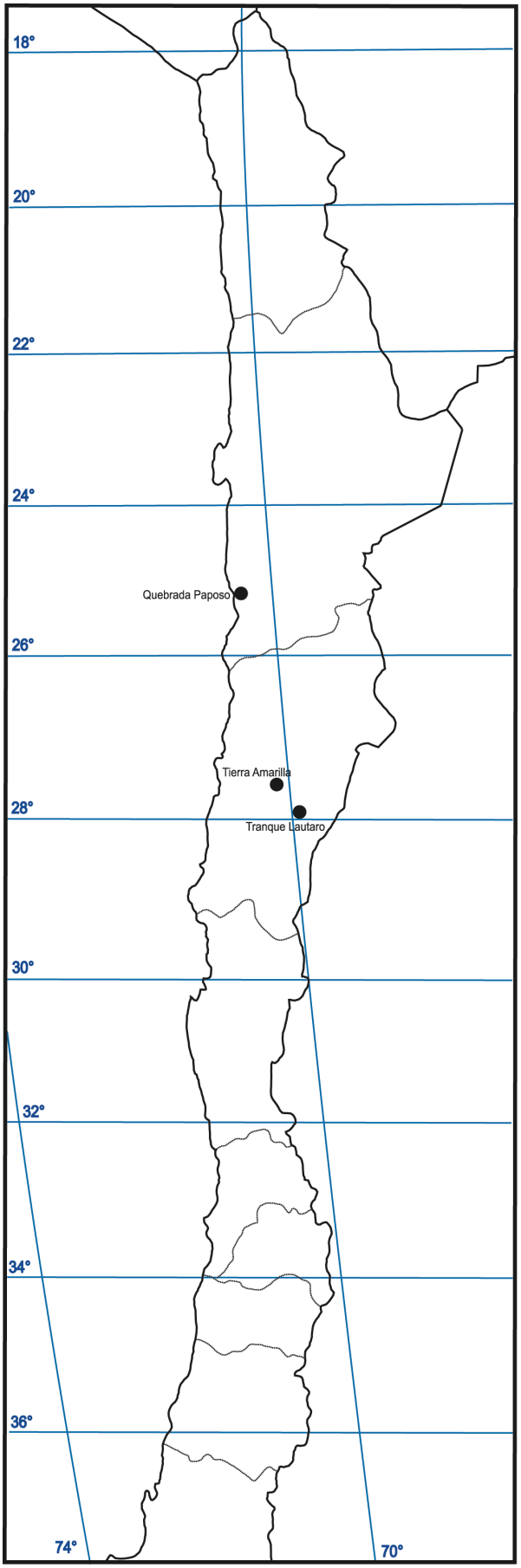
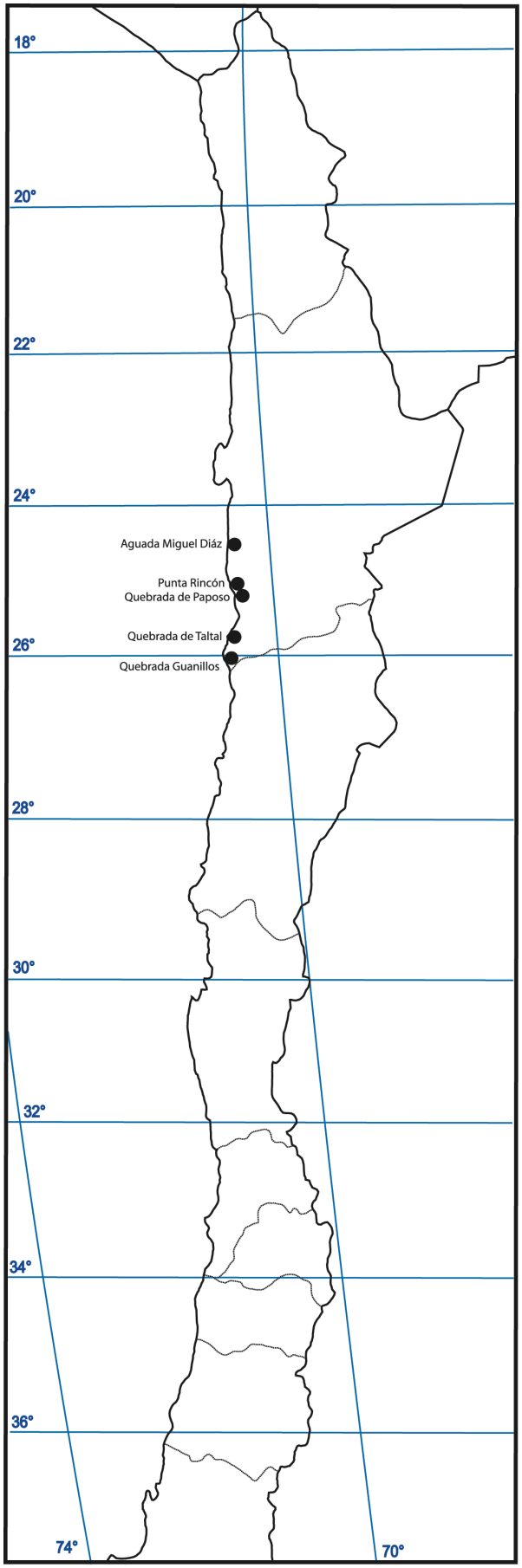
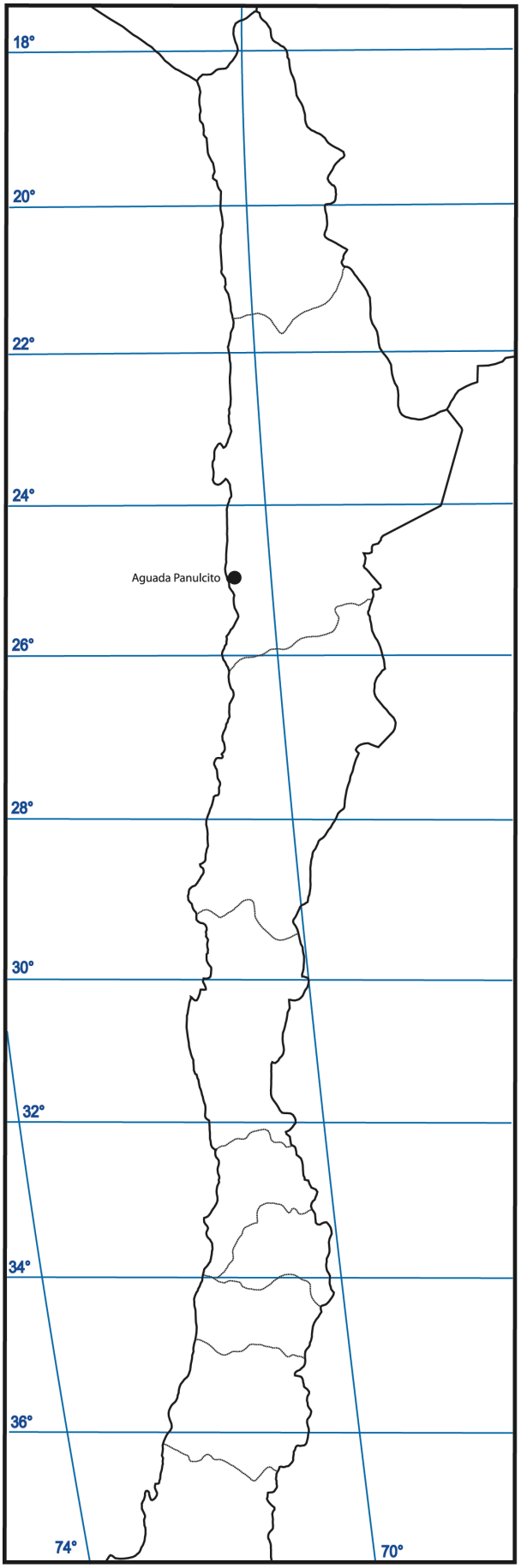


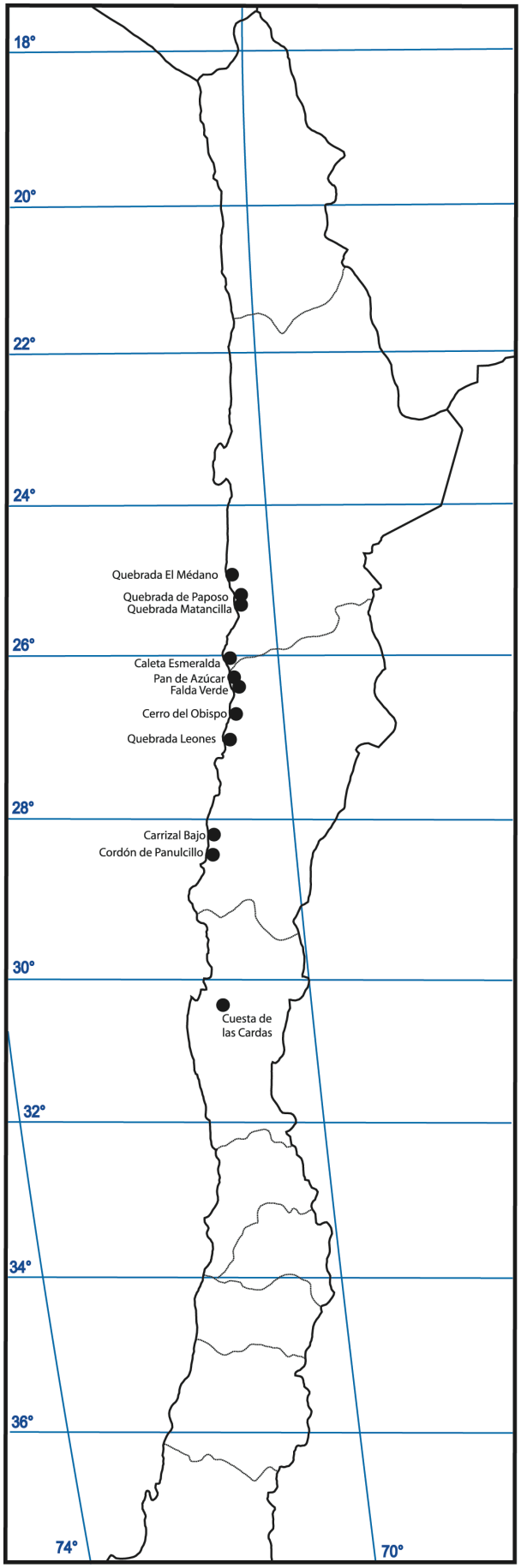
Map 1: Distribution of *Oxalis arbuscula* Barnéoud.



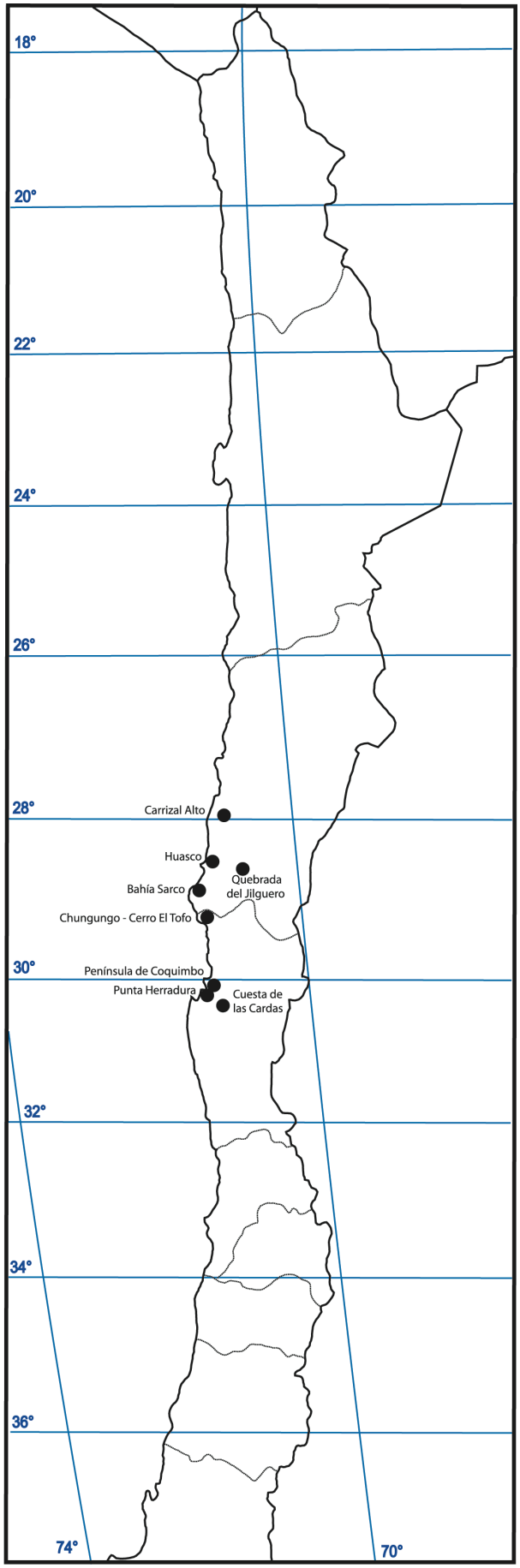
Map 2: Distribution of *Oxalis caesia* Philippi.



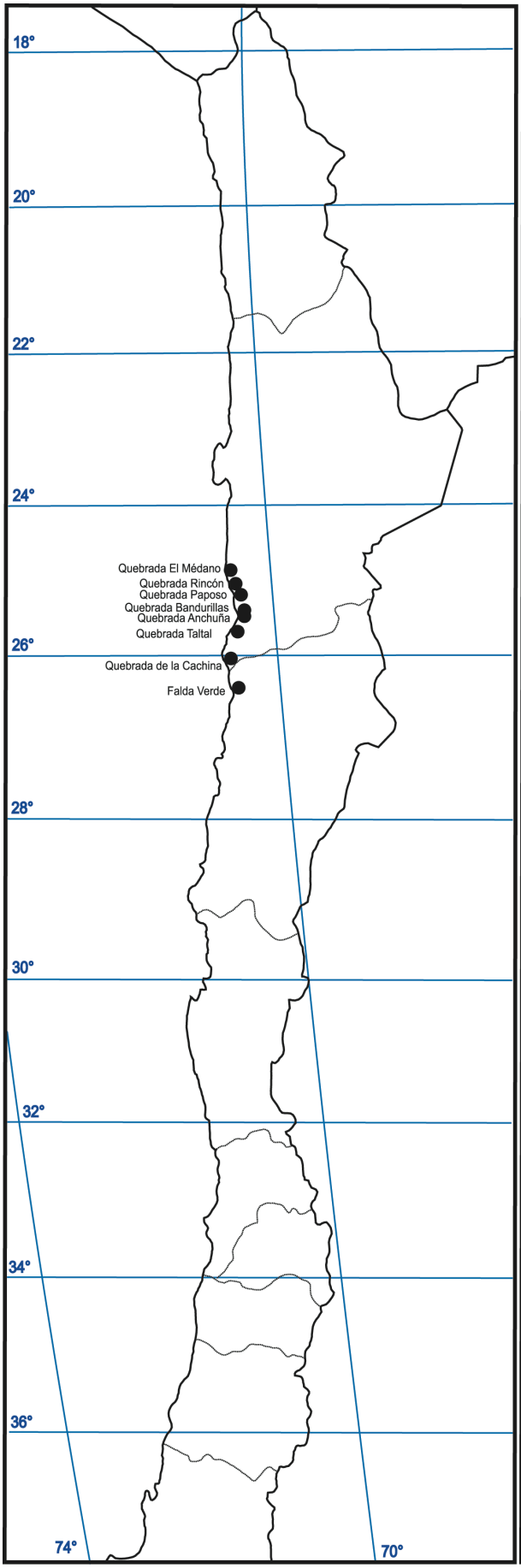
Map 3: Distribution of *Oxalis ericoides* Knuth.



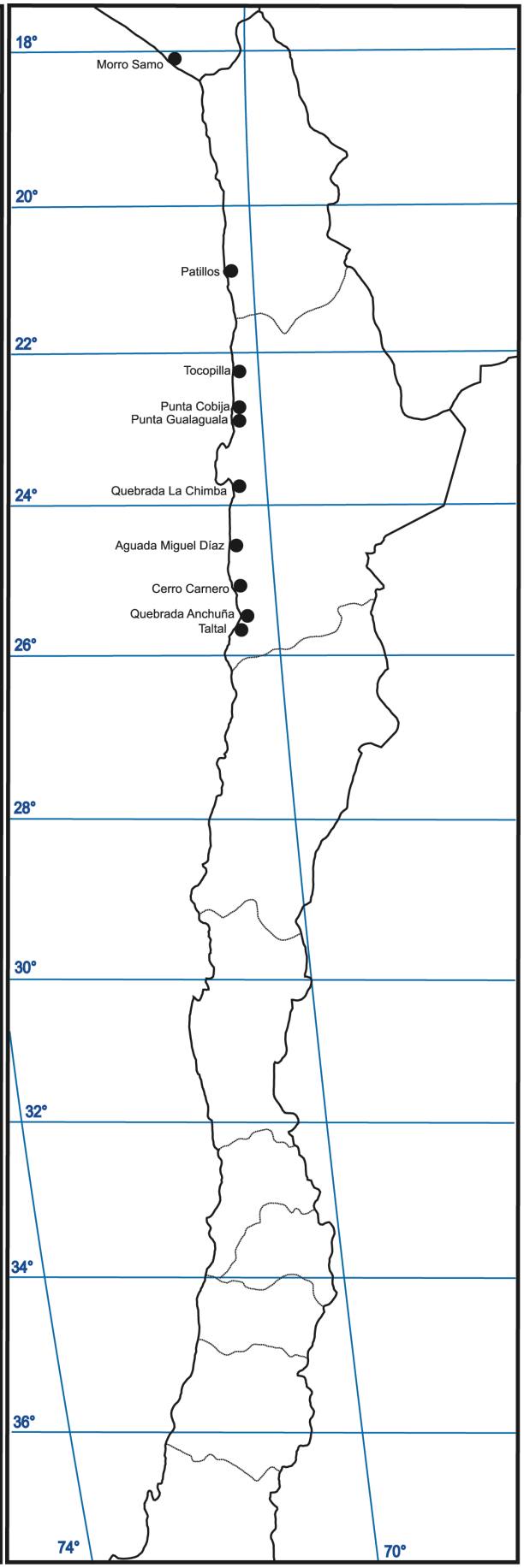
Map 4: Distribution of *Oxalis gigantea* Knuth.



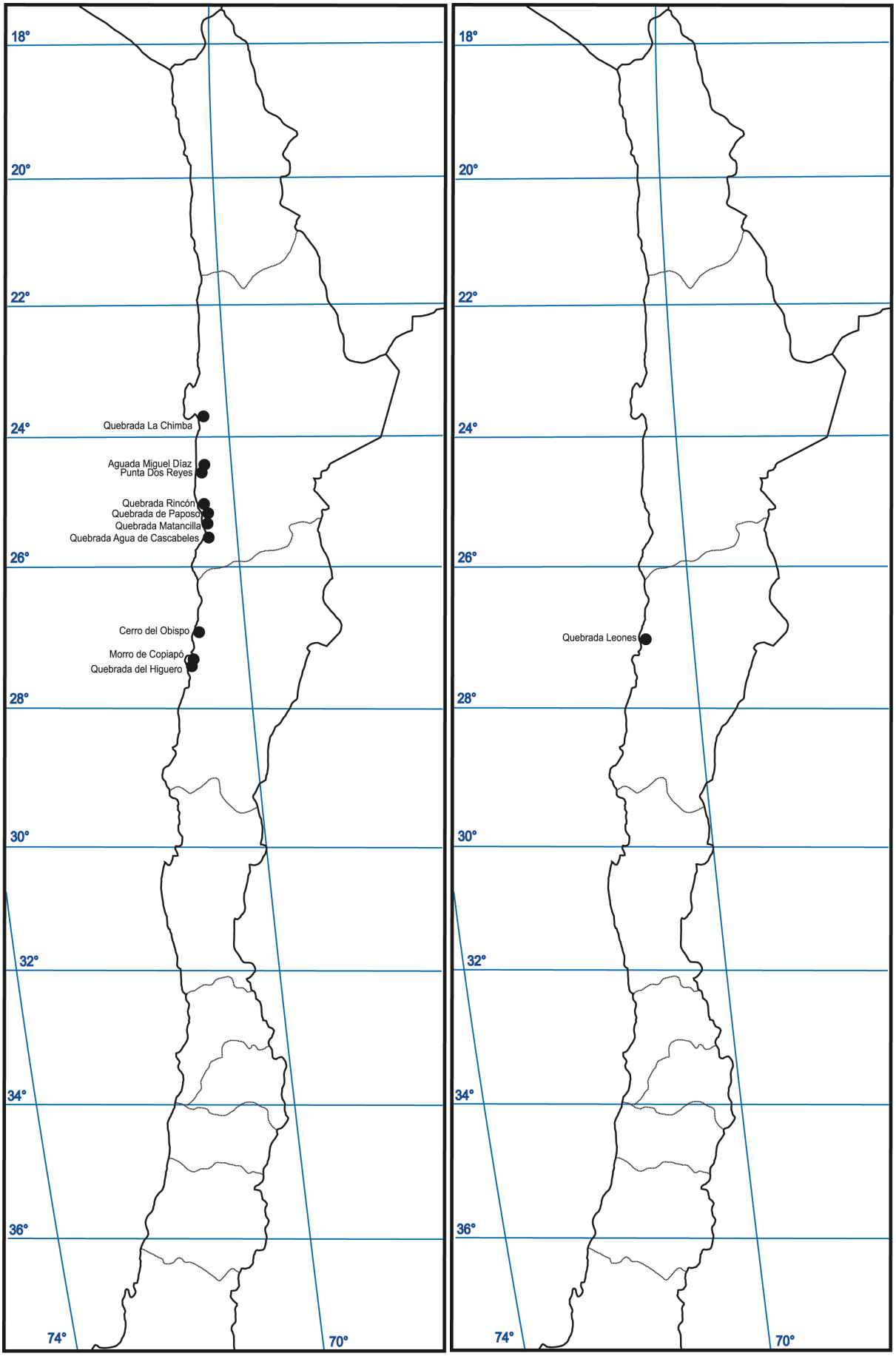
Map 5: Distribution of *Oxalis virgosa* Molina.



Map 6: Distribution of *Oxalis atacamensis* Reiche

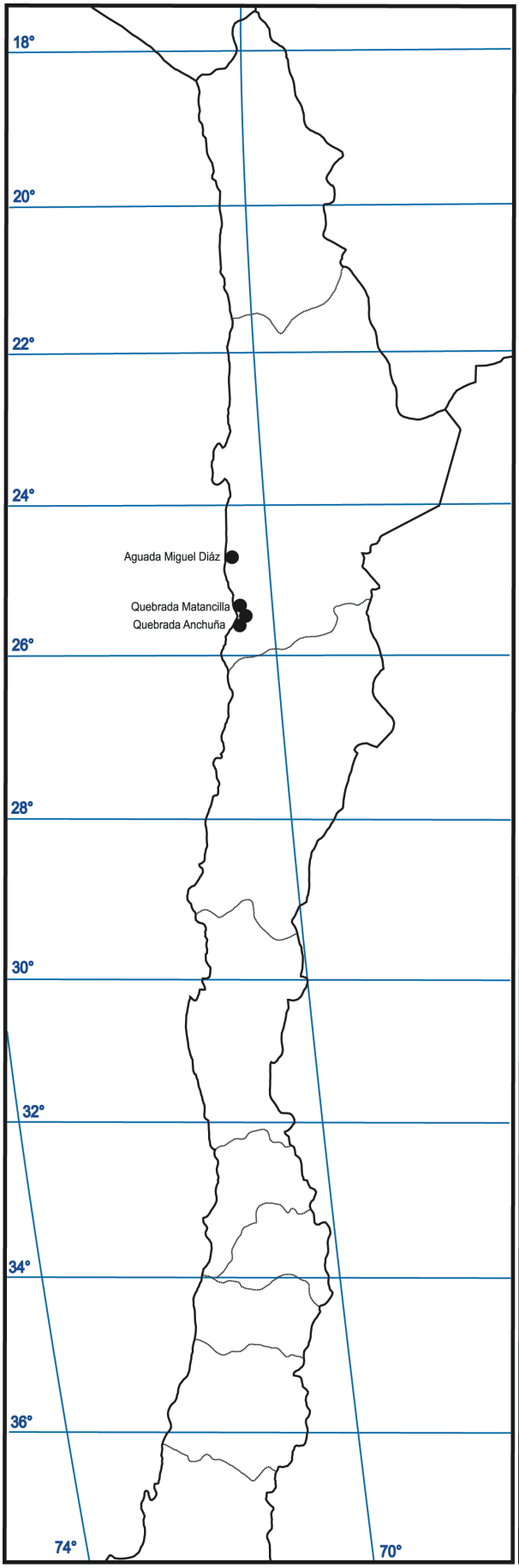


Map 7: Distribution of *Oxalis bulbocastanum* Philippi.

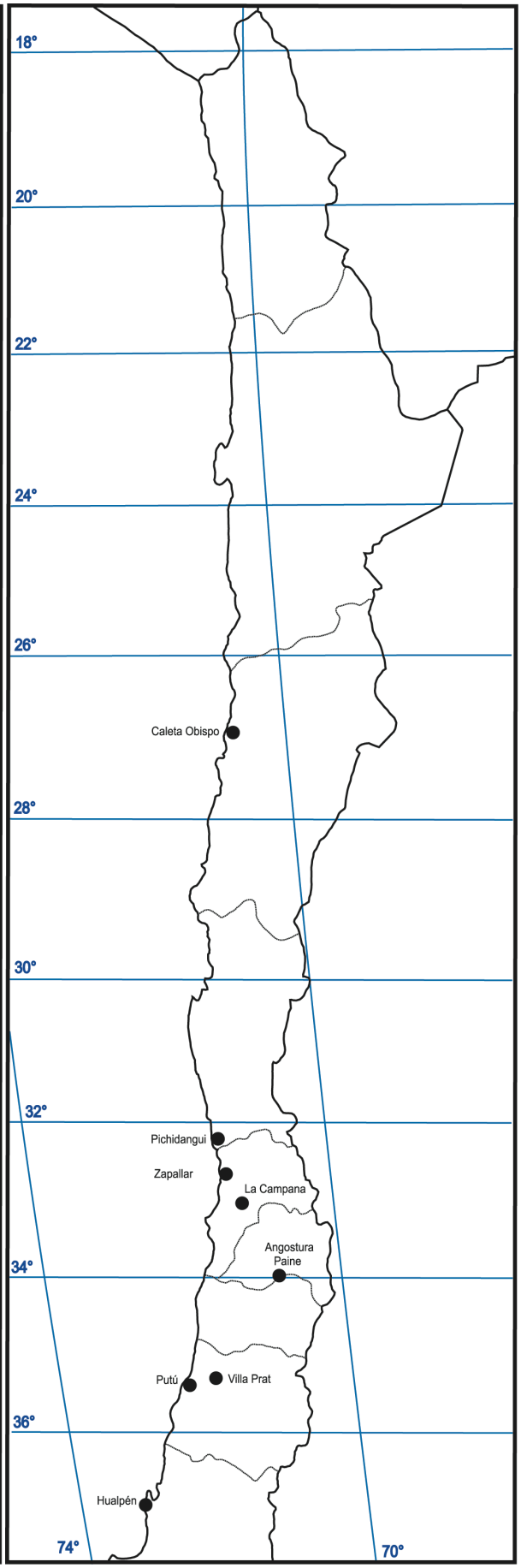


Map 8: Distribution of *Oxalis johnstonii* Knuth.

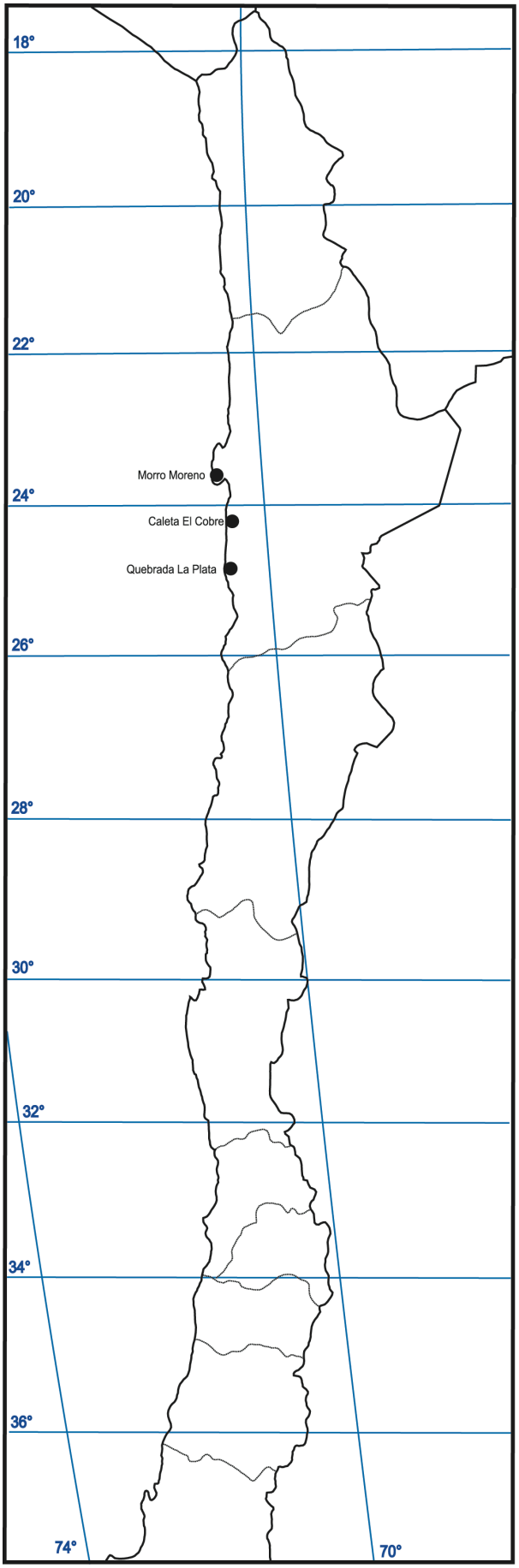
Map 9: Distribution of *Oxalis leucophylla* Philippi.



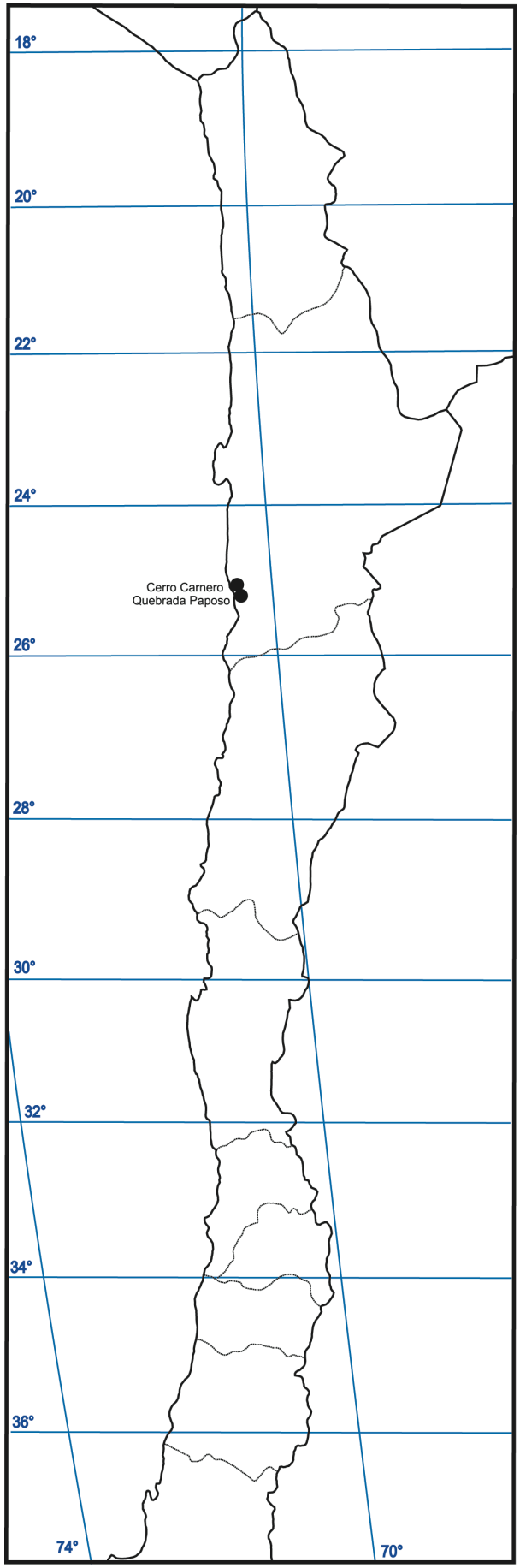
Map 10: Distribution of *Oxalis matancillae* Lourteig.



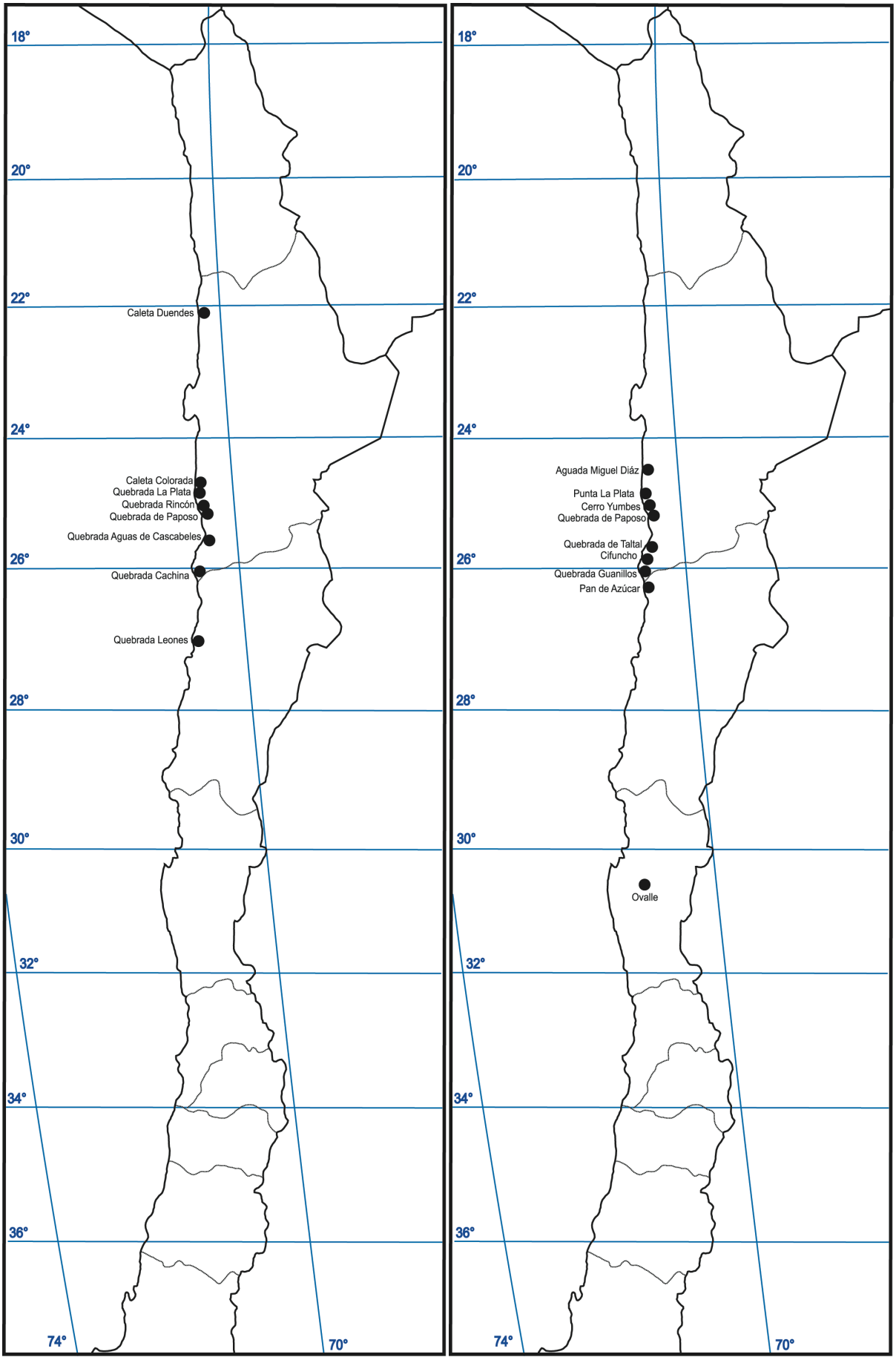
Map 11: Distribution of *Oxalis megalorrhiza* [Feuillée] Jacquin.



Map 12: Distribution of *Oxalis morenoensis* Lourteig.

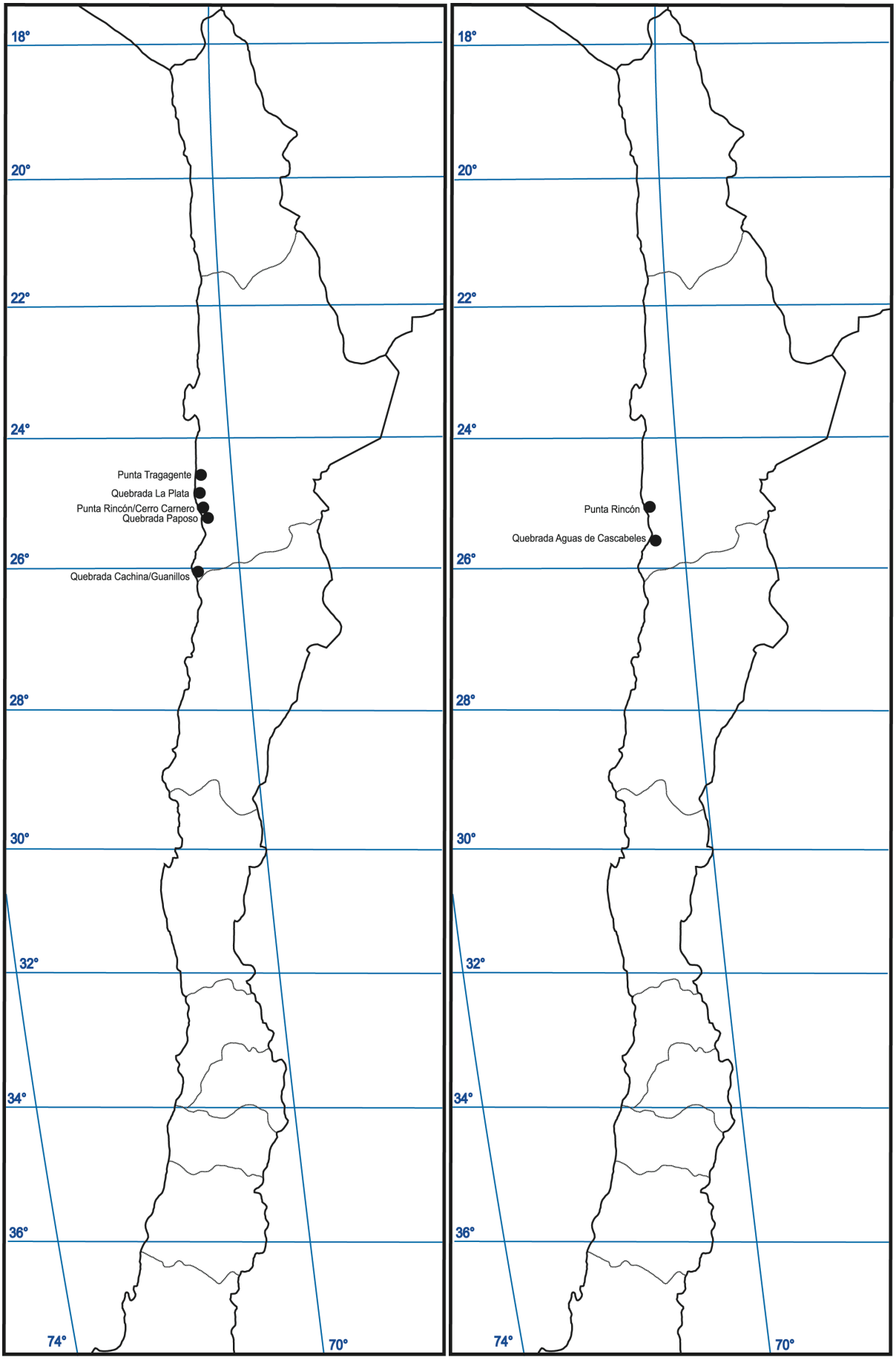


Map 13: Distribution of *Oxalis ornata* Philippi.



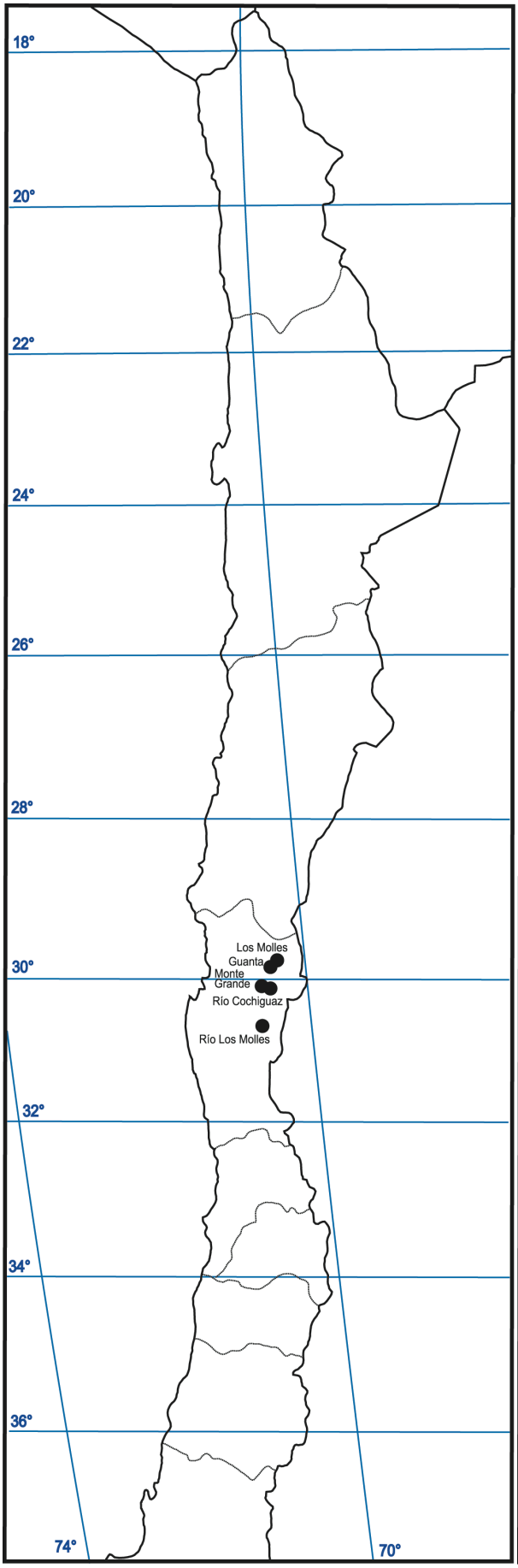
Map 14: Distribution of *Oxalis ornithopus* Philippi.

Map 15: Distribution of *Oxalis ovalleana* Philippi.

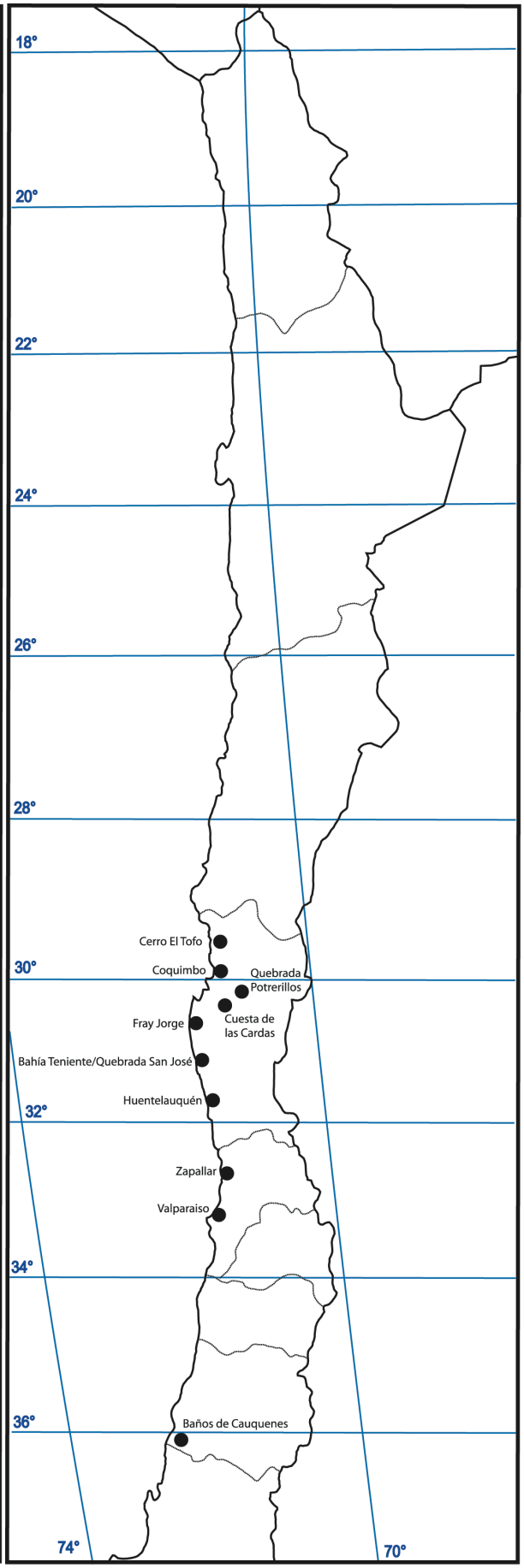


Map 16: Distribution of *Oxalis paposana* Philippi.

Map 17: Distribution of *Oxalis ricardii* Lourteig.



Map 18: Distribution of *Oxalis squarrosa* Barnéoud.



Map 19: Distribution of *Oxalis tortuosa* Lindley.

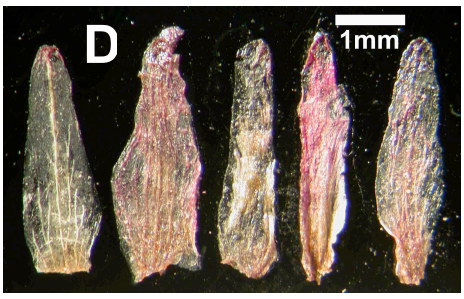


Figure 12: ***Oxalis arbuscula*** **Barnéoud**:
A Habit, **B** Inflorescence and leaves, **C** Flower, **D** Sepals.
A-D *leg*. Werdermann 400, Tierra Amarilla, Copiapó, 1924.

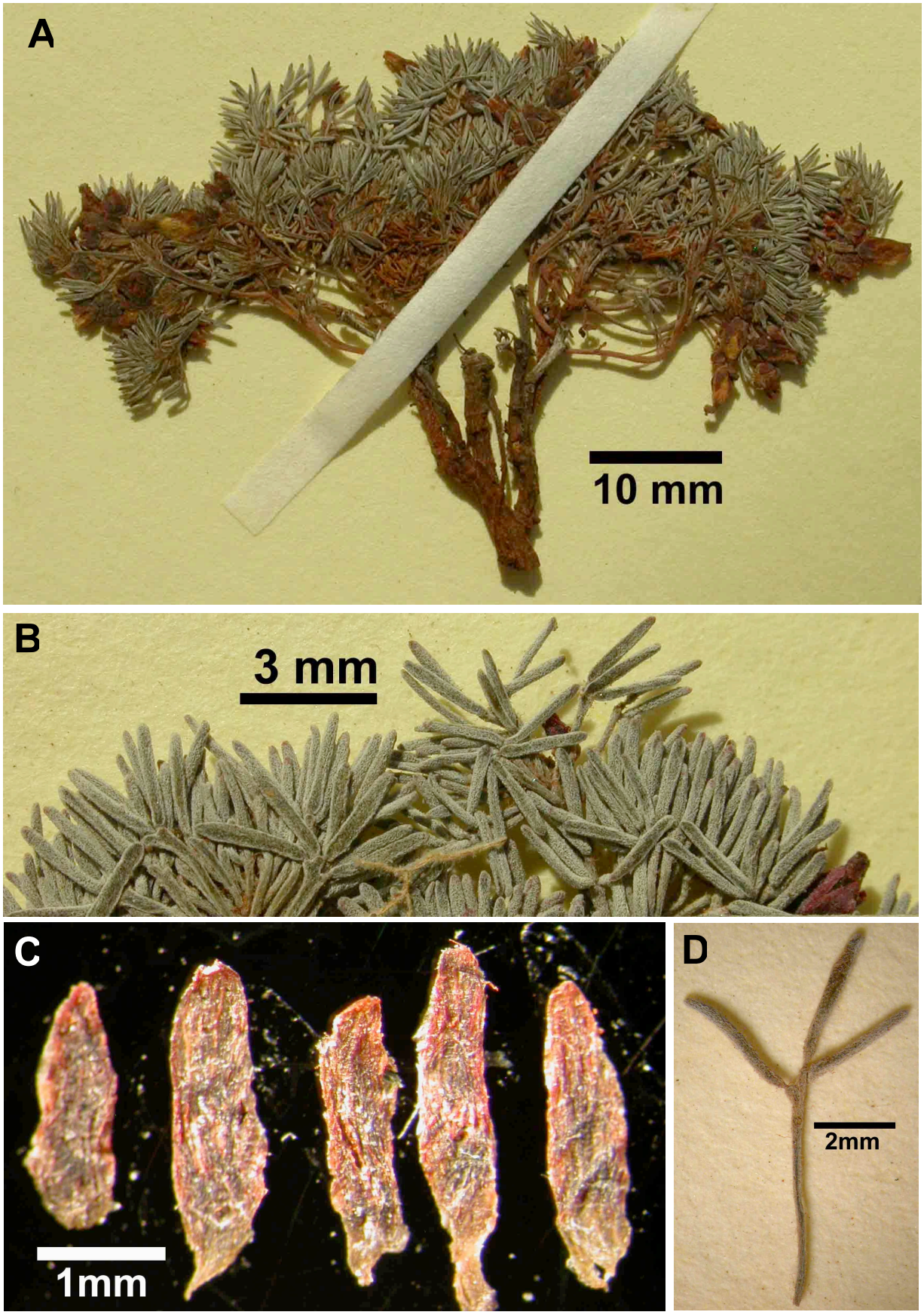


Figure 13: ***Oxalis caesia*** **Philippi**: **A** Habit, **B** Leaves, **C** Sepals, **D** Leave.
A-B *leg.* Grau 2149, Quebrada Paposo, 1980; C-D *leg.* Quezada & Ruiz, 210, Quebrada Paposo, 1991.

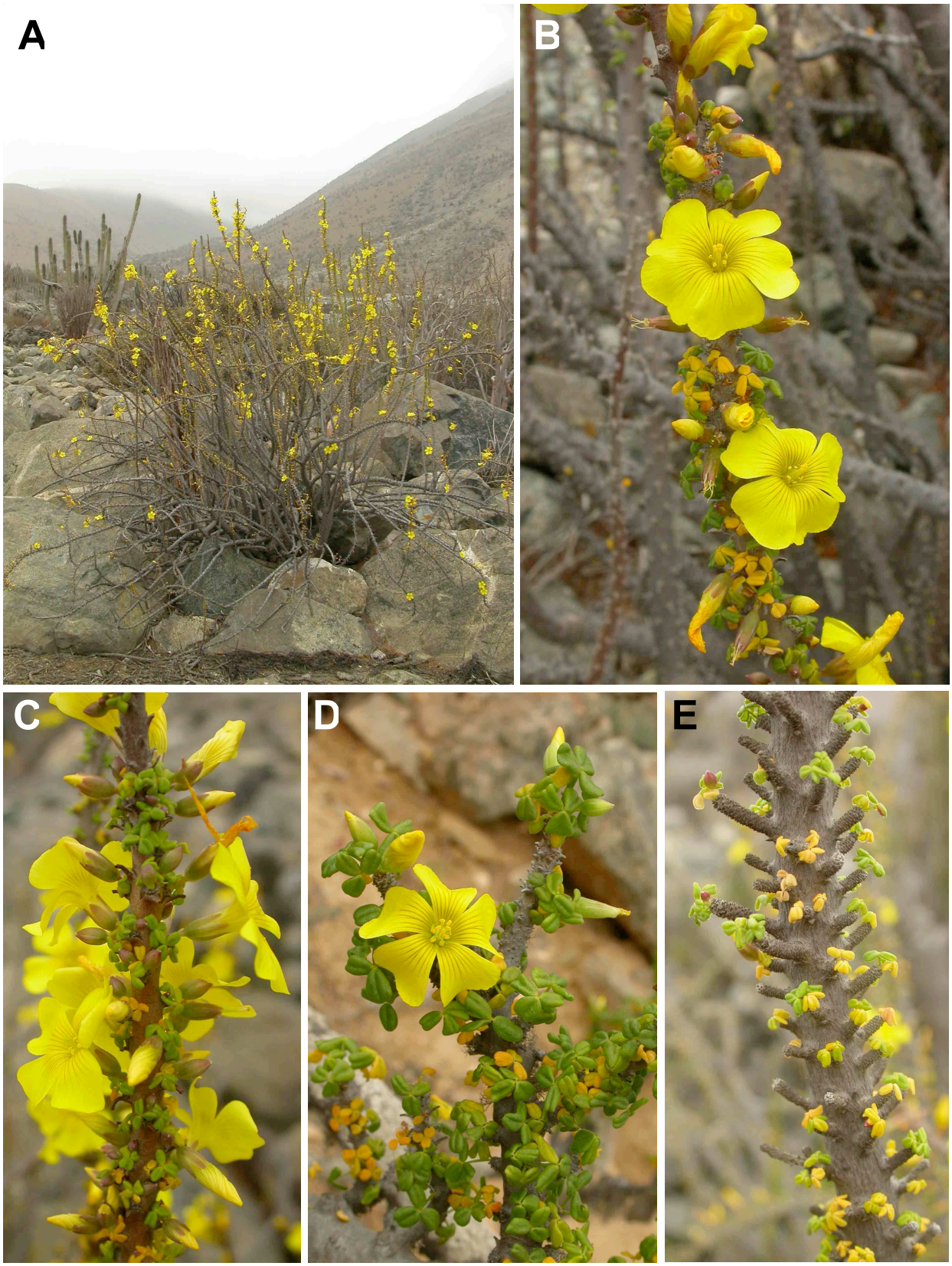


Figure 14: ***Oxalis gigantea*** **Barnéoud**: **A** Habit, **B-D** Flower and leaves, **E** Brachyblasts.
A-E *in situ* alluvial fan of Quebrada El Médano.

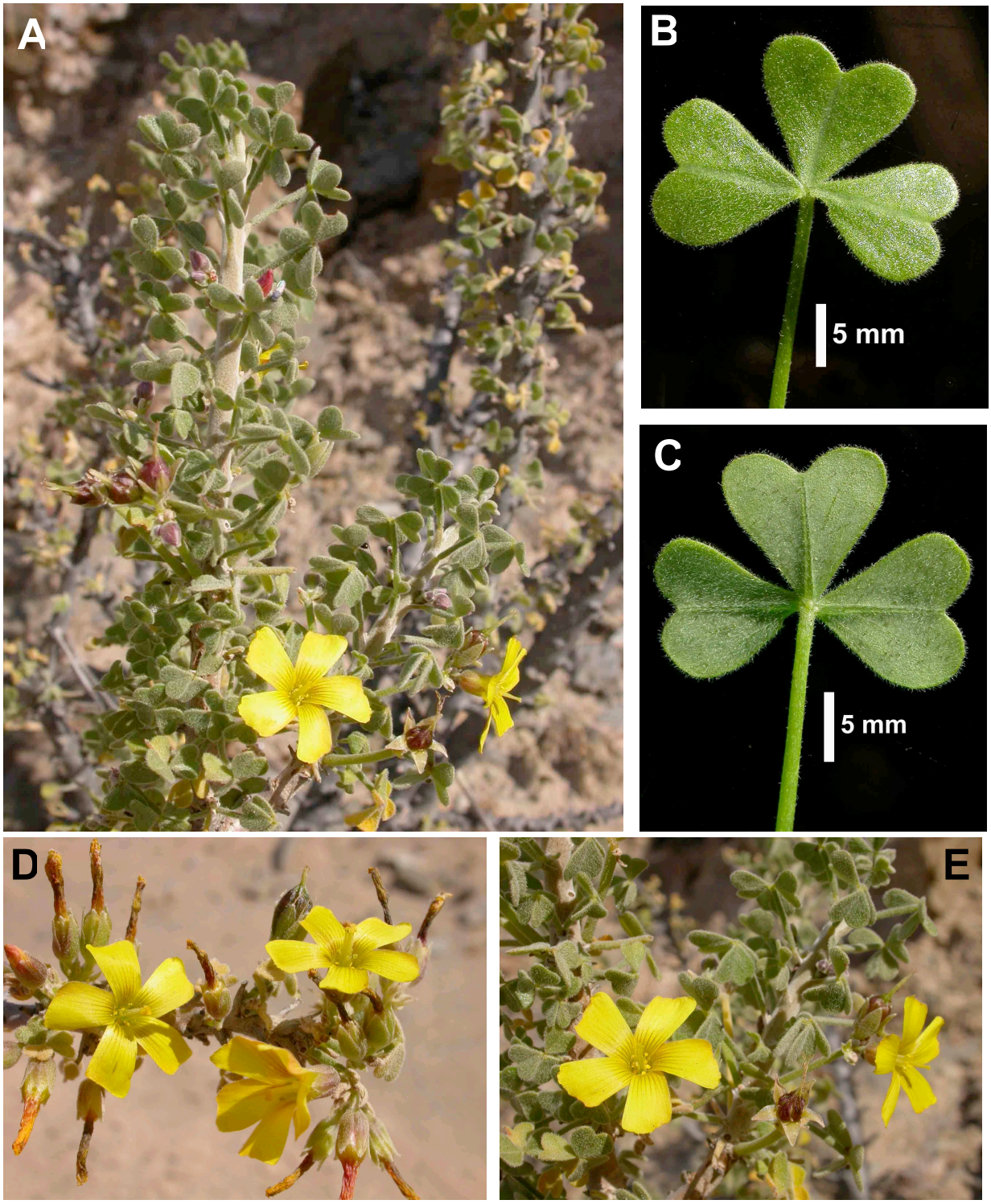
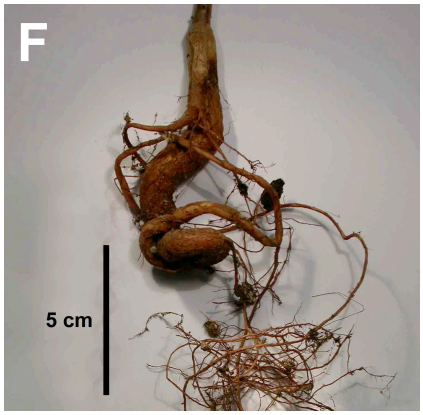


Figure 15: *Oxalis virgosa* Molina: **A** Habit, **B** Leaf, upper side, **C** Leaf, lower side, **D** Inflorescences, **E** Flowers and capsules, **F** Root tubers.
A, D-E *in situ* Quebrada del Totoral; B-C, F Greenhouse cultivation of accession Ehrhart 6-134, Bahía Sarco, 2002.



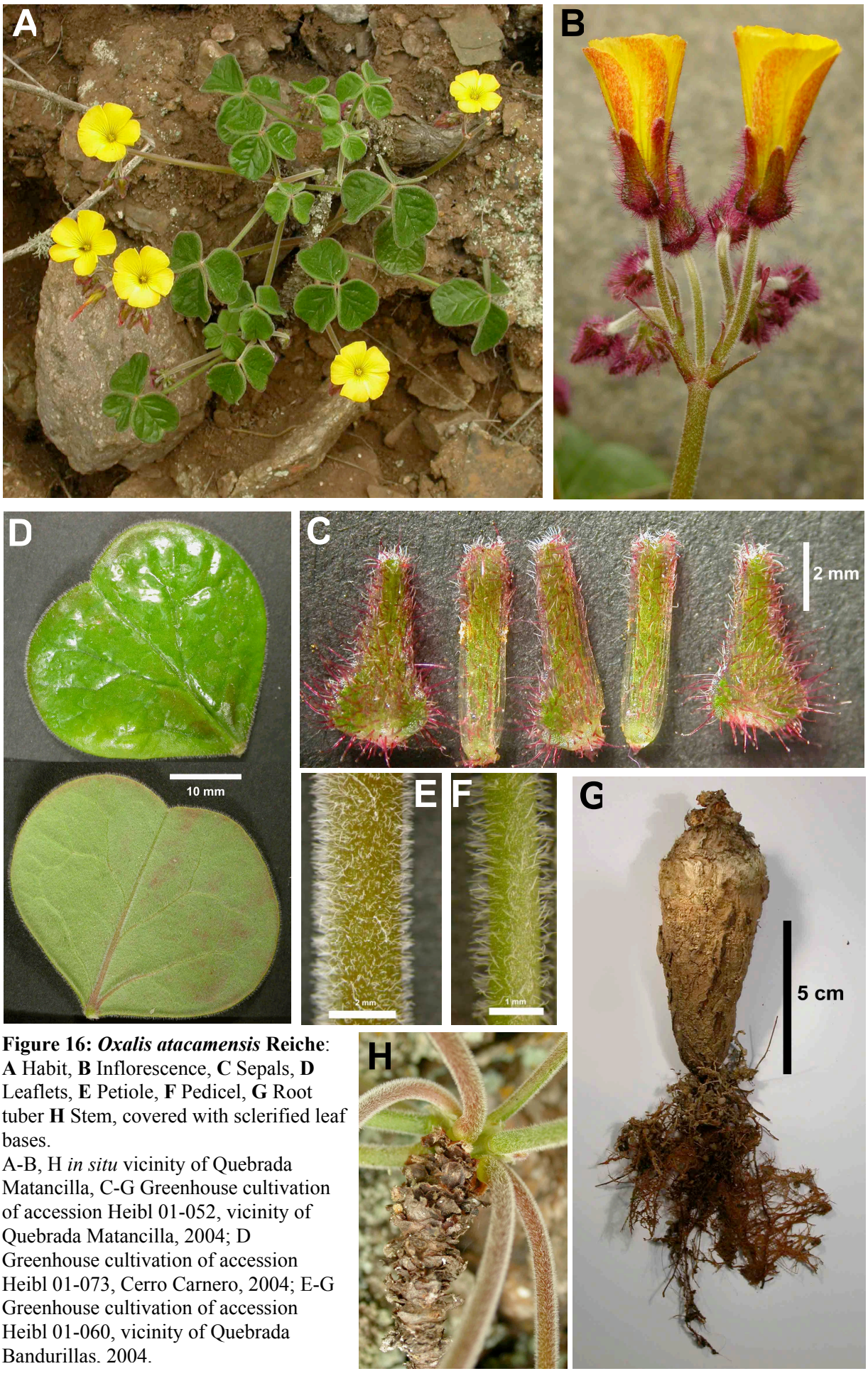


Figure 16: ***Oxalis atacamensis*** **Reiche**: **A** Habit, **B** Inflorescence, **C** Sepals, **D** Leaflets, **E** Petiole, **F** Pedicel, **G** Root tuber **H** Stem, covered with sclerified leaf bases.
A-B, H *in situ* vicinity of Quebrada Matancilla, C-G Greenhouse cultivation of accession Heibl 01-052, vicinity of Quebrada Matancilla, 2004; D Greenhouse cultivation of accession Heibl 01-073, Cerro Carnero, 2004; E-G Greenhouse cultivation of accession Heibl 01-060, vicinity of Quebrada Bandurillas. 2004.

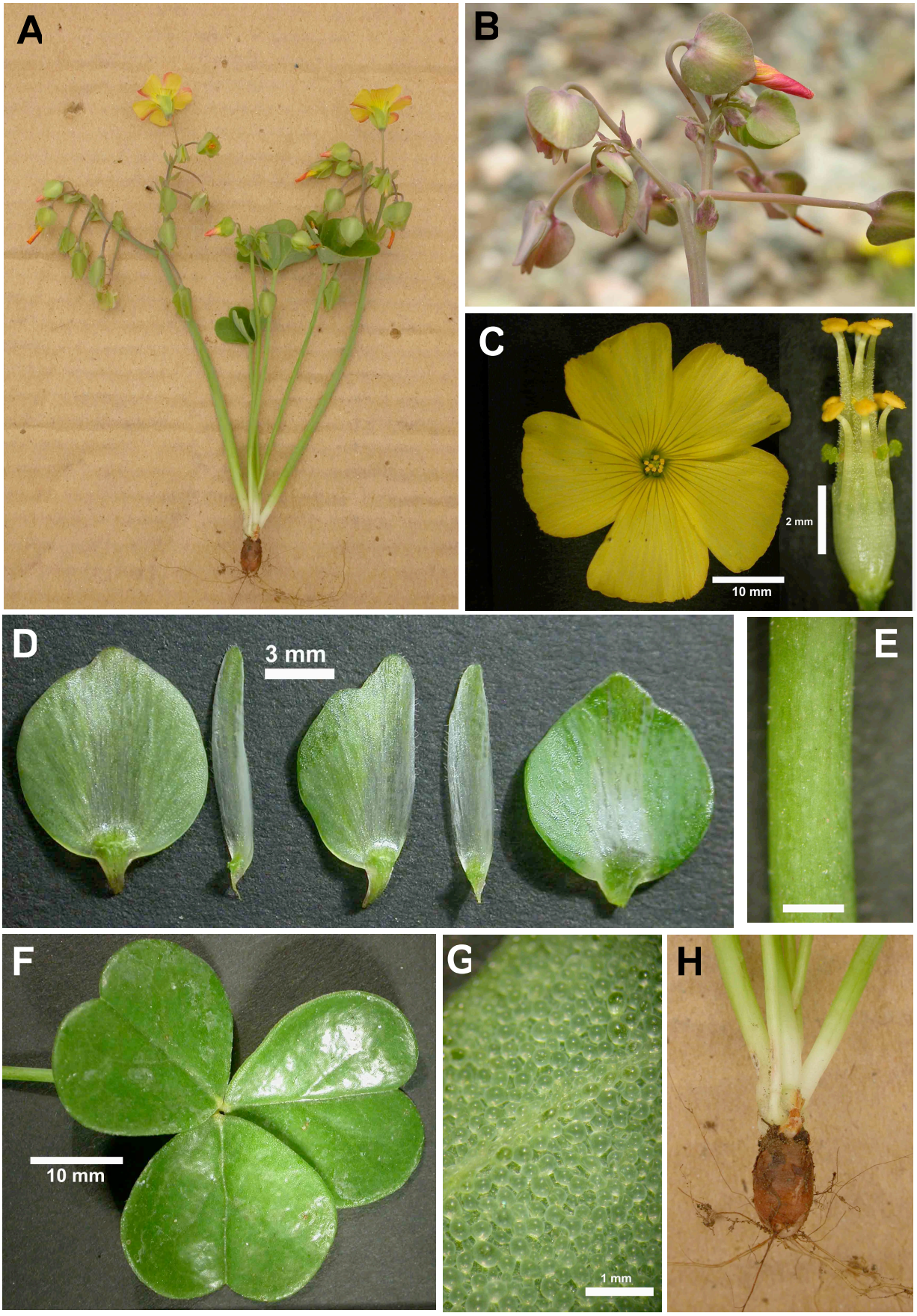


Figure 17: ***Oxalis bulbocastanum*** **Philippi**: **A** Habit, **B** Inflorescence, **C** Flower and pistil, **D** Sepals, **E** Petiole, **F** Leave, **G** Leaflet, lower side, **H** Root tuber. A-B, H *in situ* Cerro Carnero, C-G Greenhouse cultivation of accession Heibl 01-066, Quebrada Anchuña, 2004.

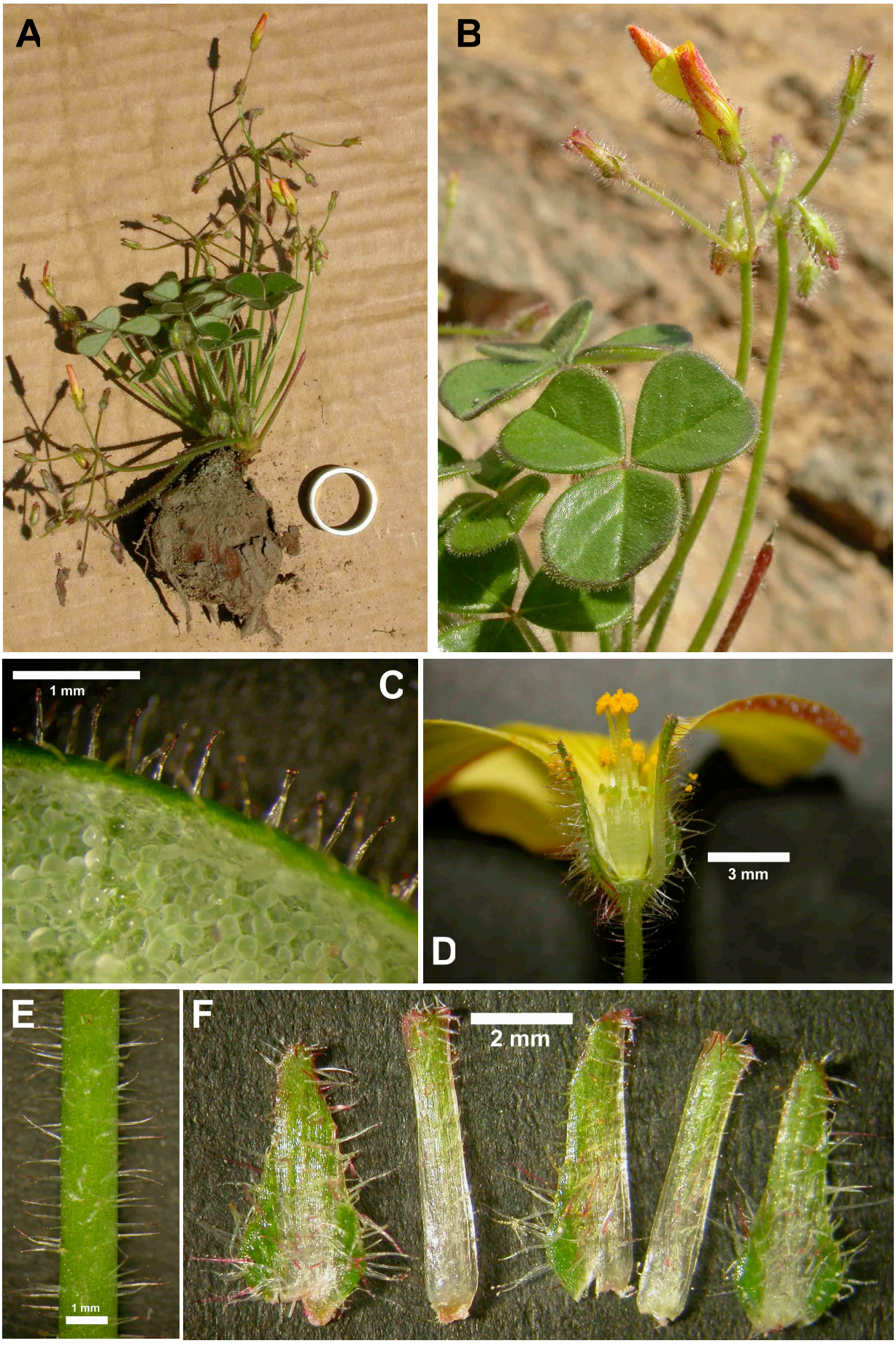


Figure 18: ***Oxalis johnstonii*** **Knuth**: **A** Habit, **B** Leaves and Inflorescence, **C** Leaflet margin, viewed from below **E** Sepals. A-B *in situ* Cerro del Obispo, C-F Greenhouse cultivation of accession Heibl 01-080, Cerro del Obispo, 2004.

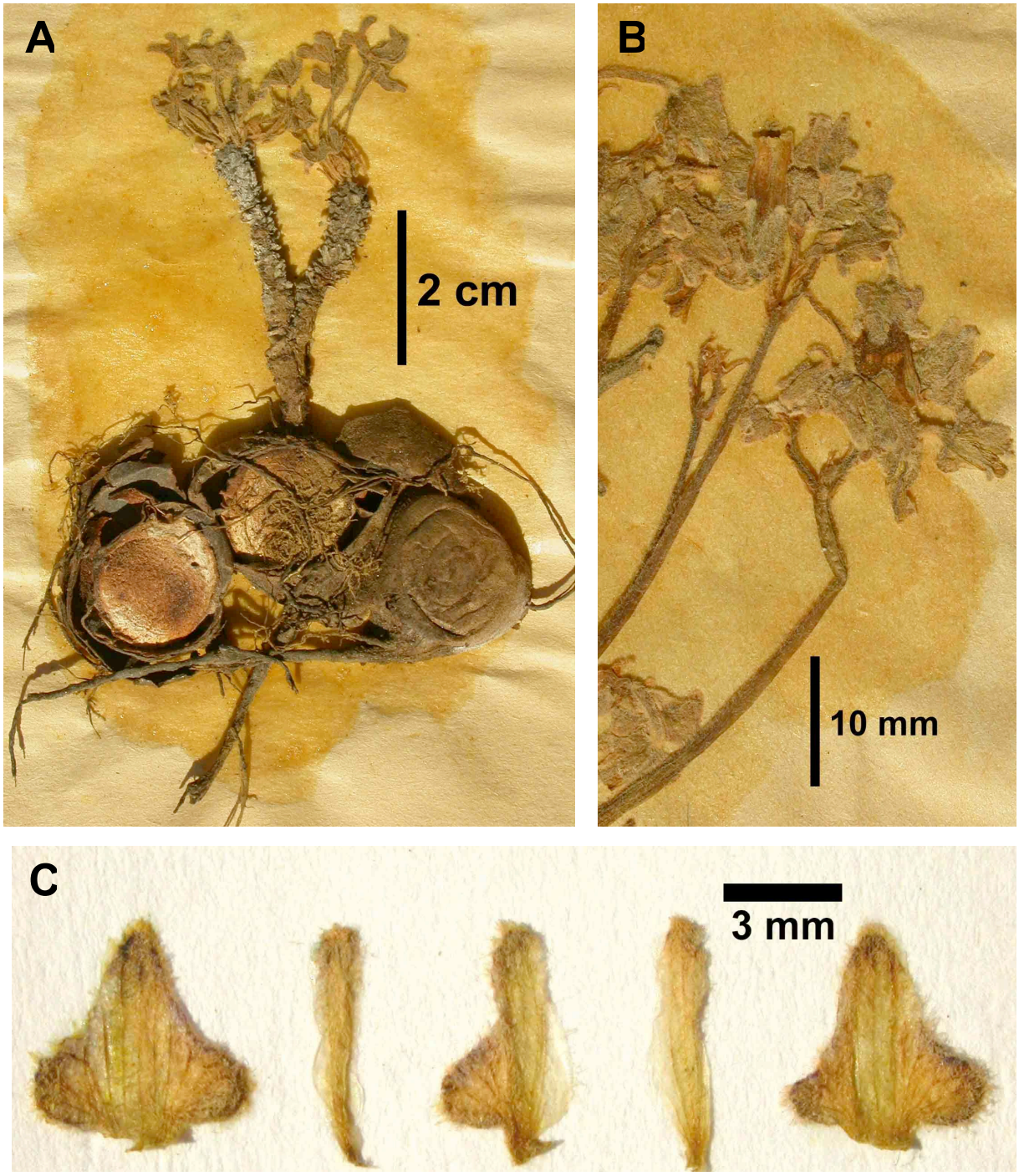


Figure 19: ***Oxalis leucophylla*** **Philippi**: **A** Habit, **B** Inflorescence, **C** Sepals, **D** Leaves. A-D *leg.* Werdermann 438, Quebrada León, 1924.

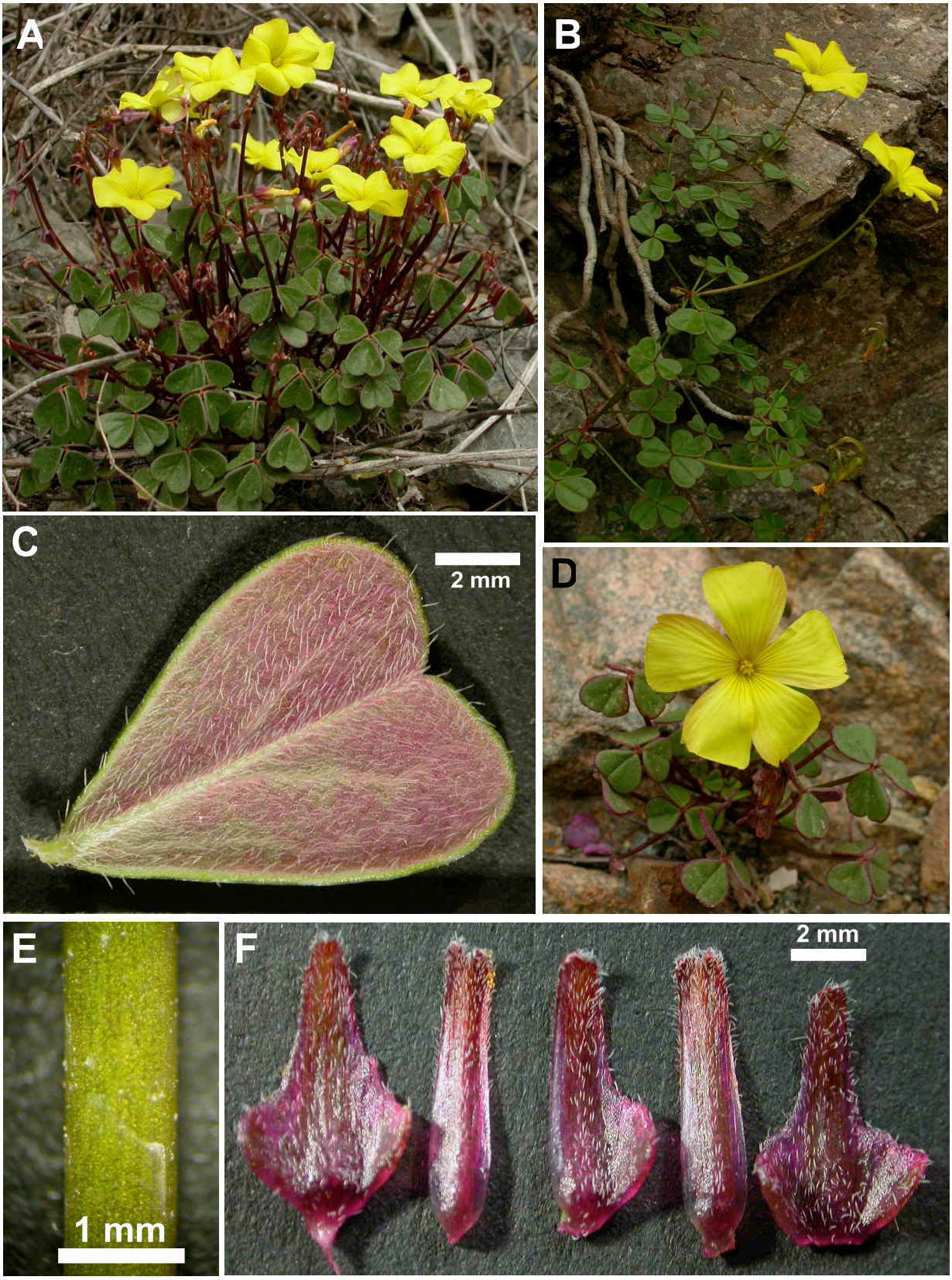


Figure 20: ***Oxalis matancillae*** **Lourteig**: **A-B, D** Habit, **C** Leaflet, lower side, **E** Petiole, **F** Sepals. A-B, D *in situ* Quebrada Anchuña; C, E-F Greenhouse cultivation of accession Heibl 01-064, Quebrada Anchuña, 2004.

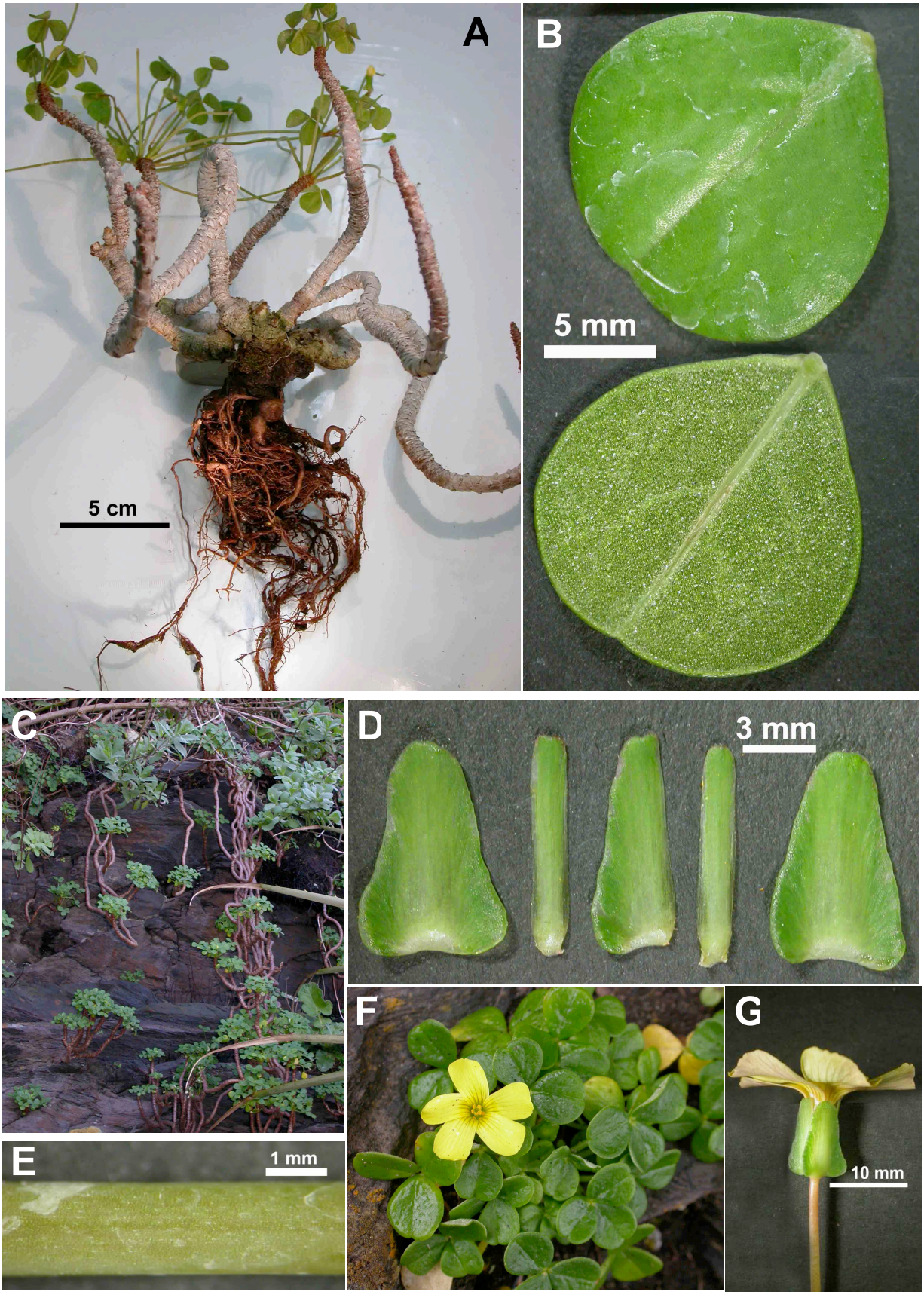


Figure 21: ***Oxalis megalorrhiza*** **[Feuillée] Jacquin**: **A, C, F** Habit, **B** Leaves, **D** Sepals, **E** Petiole, **E** Leaflet, **G** Flower. A, F *in situ* Hualpén, Concepción; B, D-E, G Greenhouse cultivation of accession Kraus 139, Hualpén, Concepción, 1992.

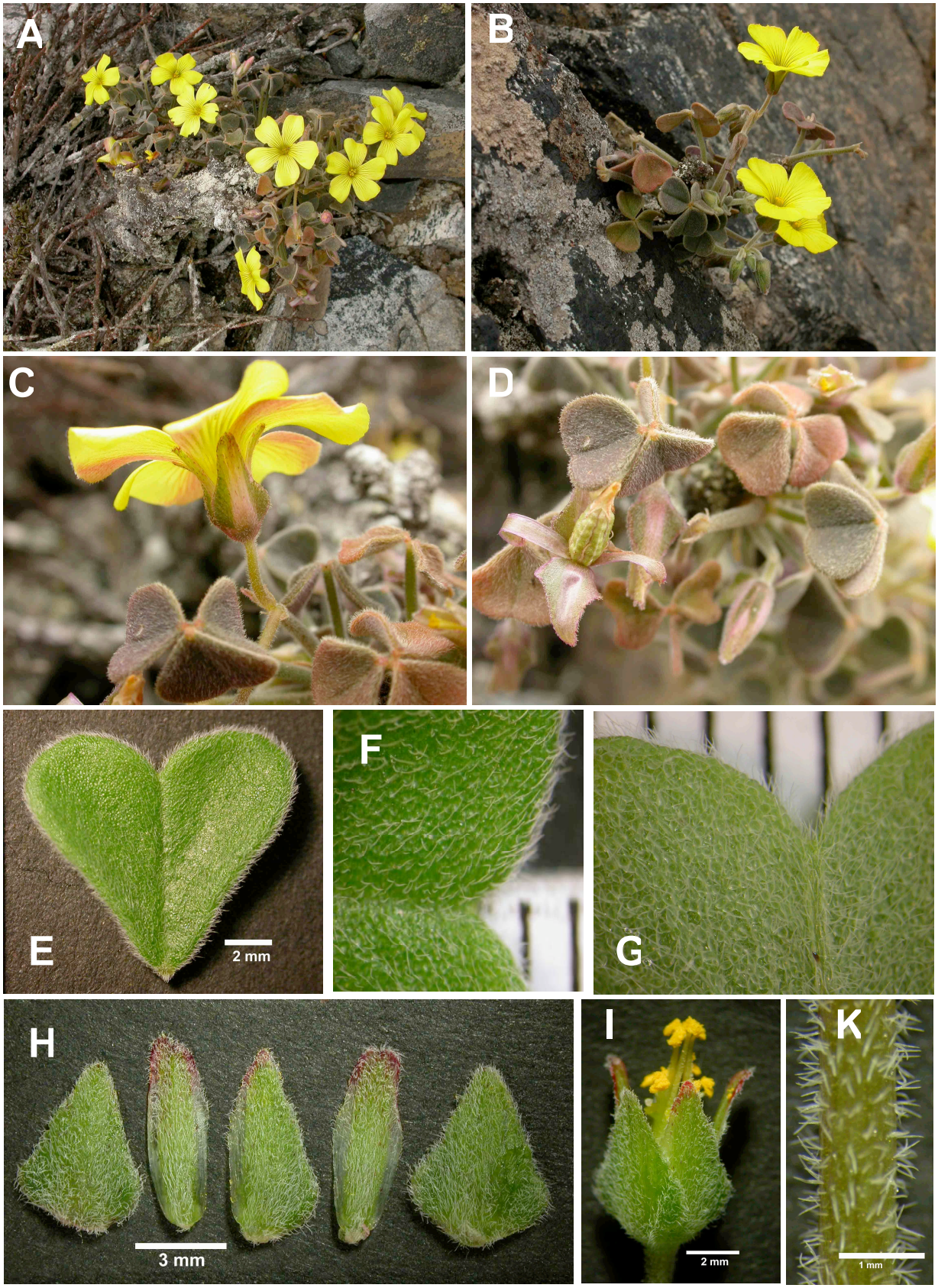


Figure 22: ***Oxalis morenoensis*** **Lourteig**: **A-B** Habit, **C** Flower and leaves, **D** Capsule, **E** Leaflet, **F** Leaflet, upper side, **G** Leaflet, lower side, **H** Sepals, **I** Calyx, **K** Pedicel. A-D *in situ* Morro Moreno; E-F Greenhouse cultivations of accession Heibl 01-026, Quebrada La Plata, 2004.

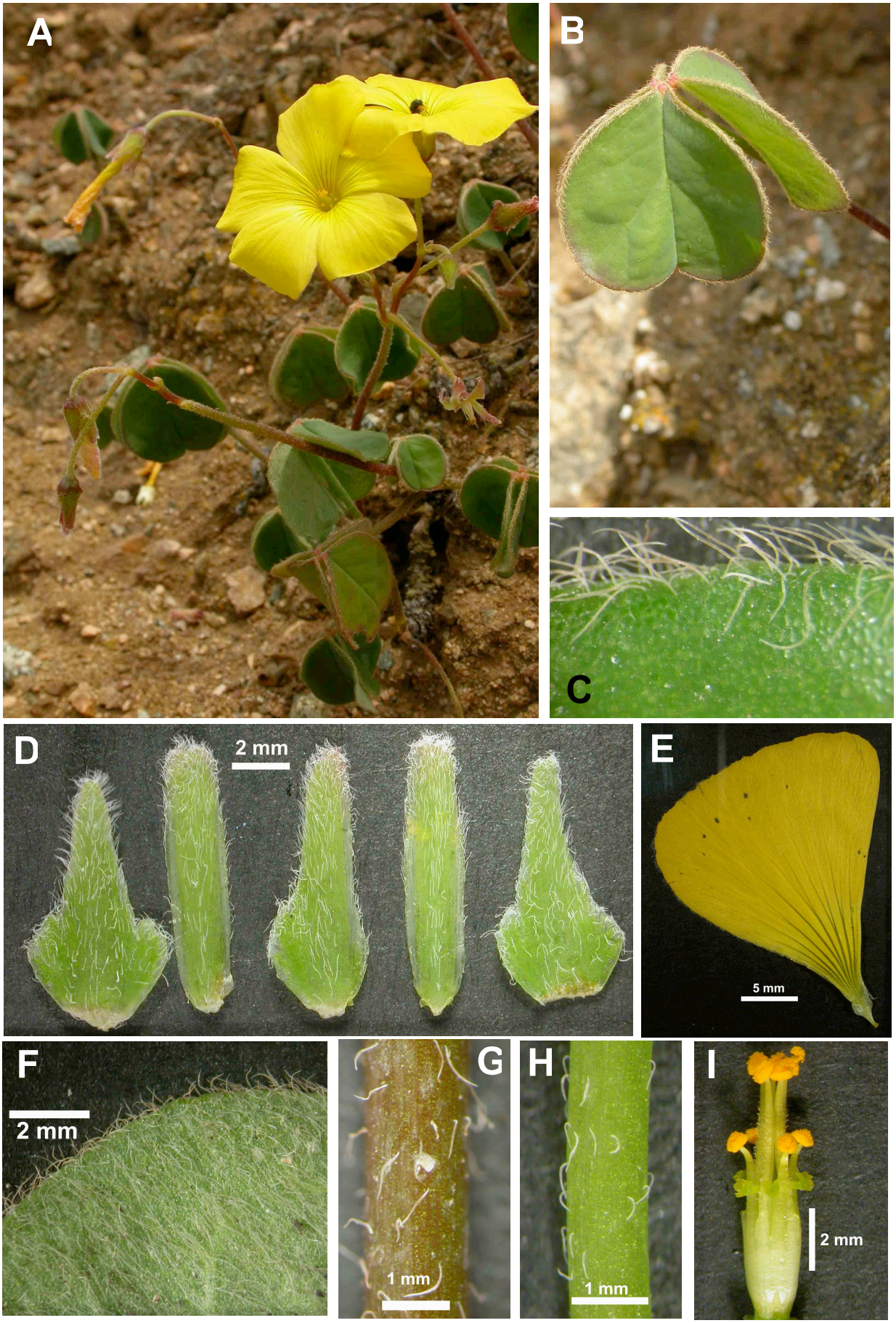


Figure 23: ***Oxalis ornata*** **Philippi**: **A** Habit, **B** Leaf, **C** Leaf margin, **D** Sepals, **E** Petal, **F** Leaflet, lower side, **G** Petiole, **H** Pedunculus, **I** Pistil. A-B *in situ* Cerro Carnero; C-I Greenhouse cultivation of accession Heibl 01-072, Cerro Carnero, 2004.

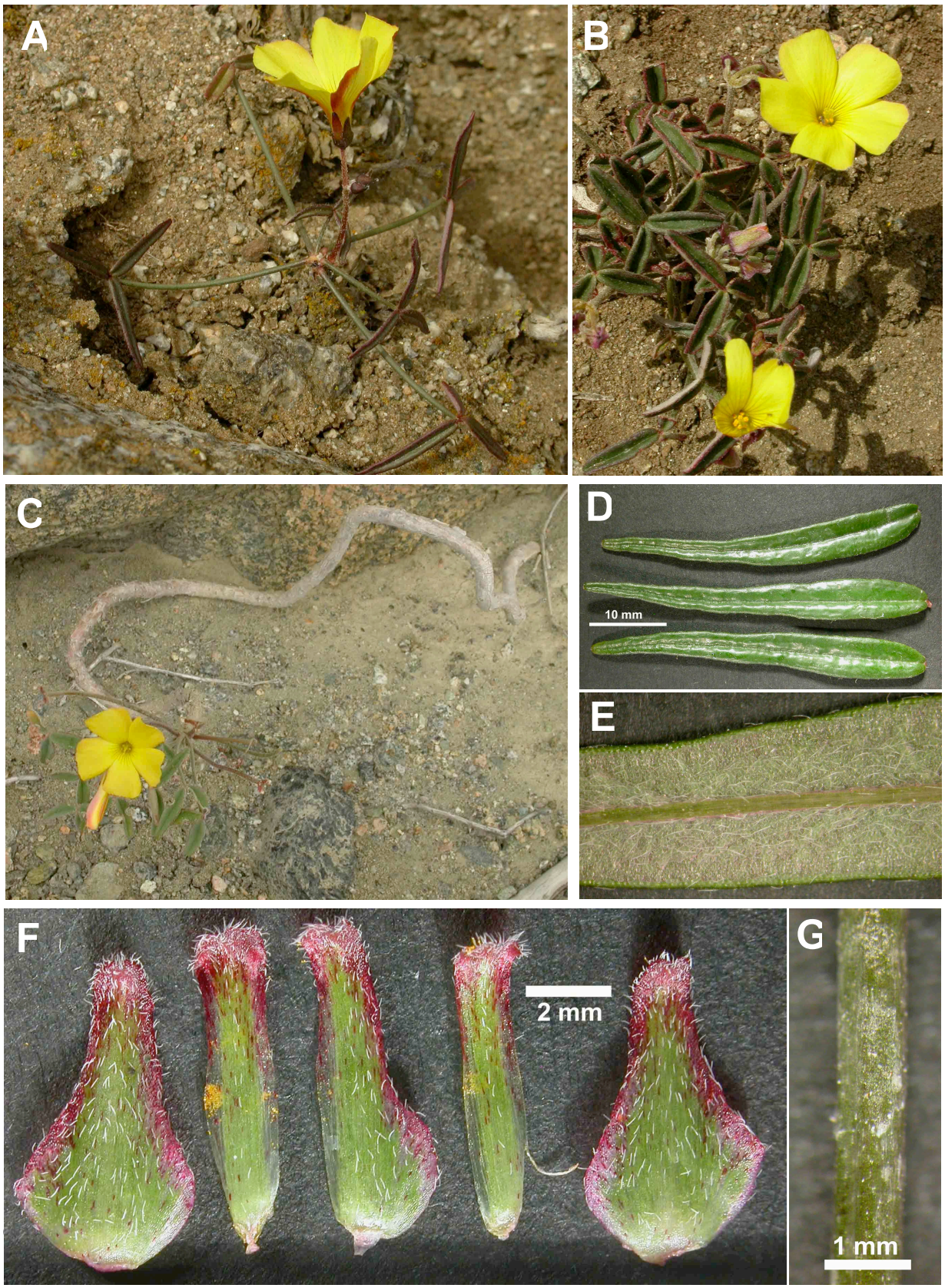


Figure 24: ***Oxalis ornithopus*** **Philippi**: **A-C** Habit, **D** Leaflets, **E** Leaflet, lower side, **F** Sepals, **G** Petiole. A-B *in situ* Caleta Colorada; C *in situ* Quebrada La Plata; D-G Greenhouse cultivation of accession Kraus 78, Quebrada Quiscuda, 1991.

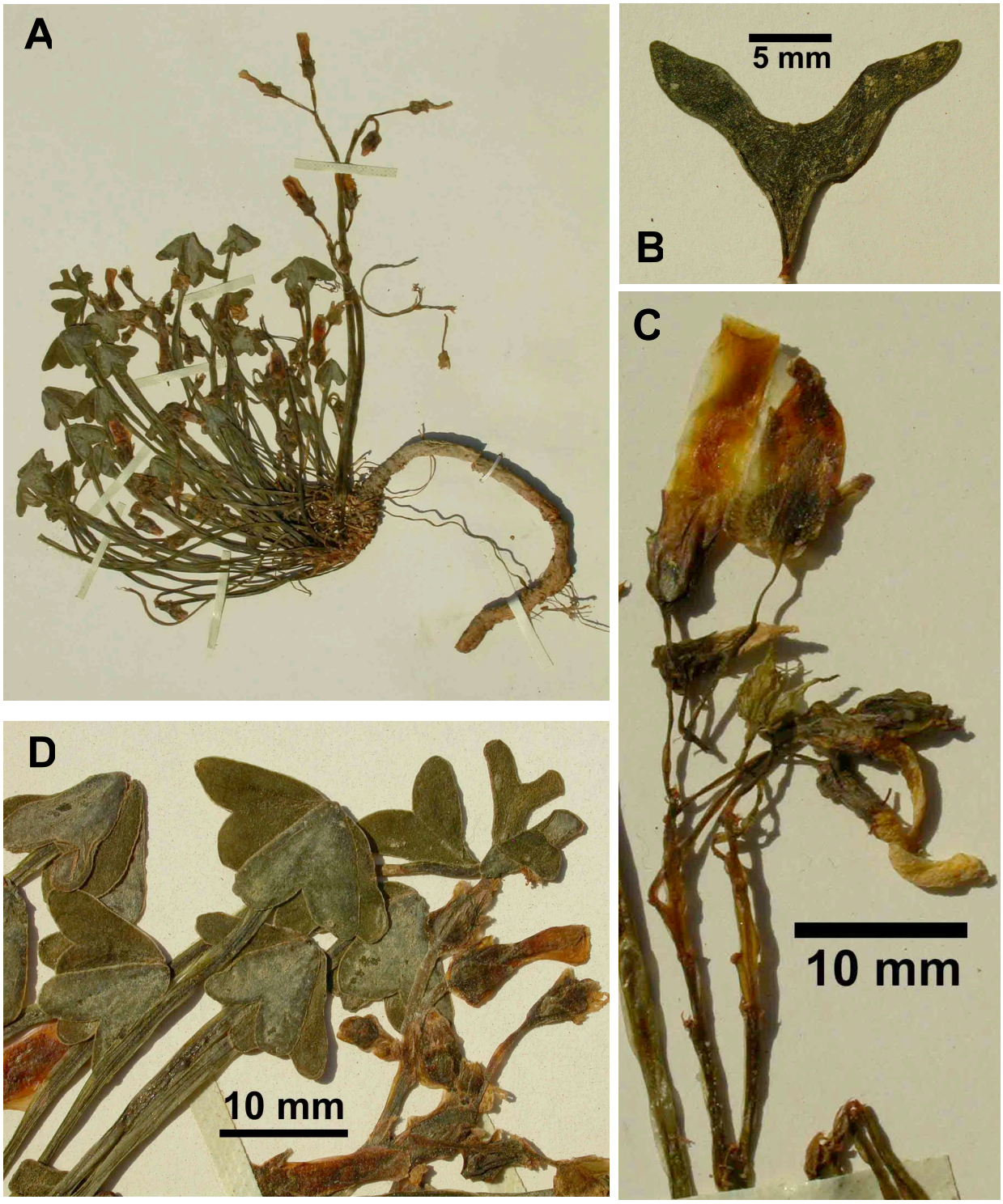


Figure 25: ***Oxalis ovalleana*** **Philippi**: **A** Habit, **B** Leaflet, **C** Inflorescence, **D** Leaves. A, D *leg.* Teillier et al. 2790, Quebrada Guanillos, 1992; B-C *leg.* Teillier et al. 2700, Quebrada Taltal, 1992.

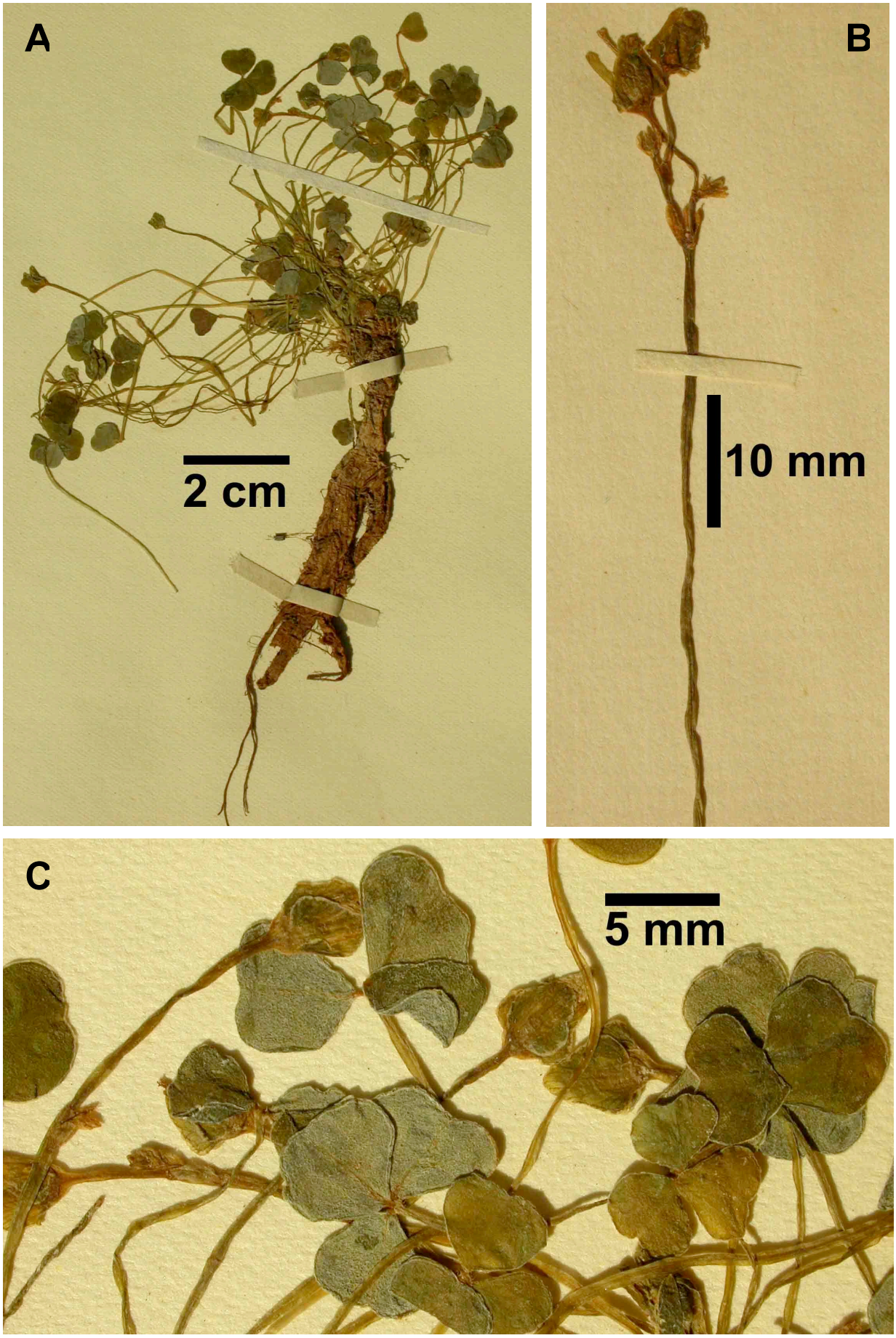


Figure 26: ***Oxalis pachyrhiza*** **Weddell**: **A** Habit with root tubers, **B** Inflorescence, **C** Leaves and calyces. A-D *leg.* Buchtien 614, La Paz, 1939.

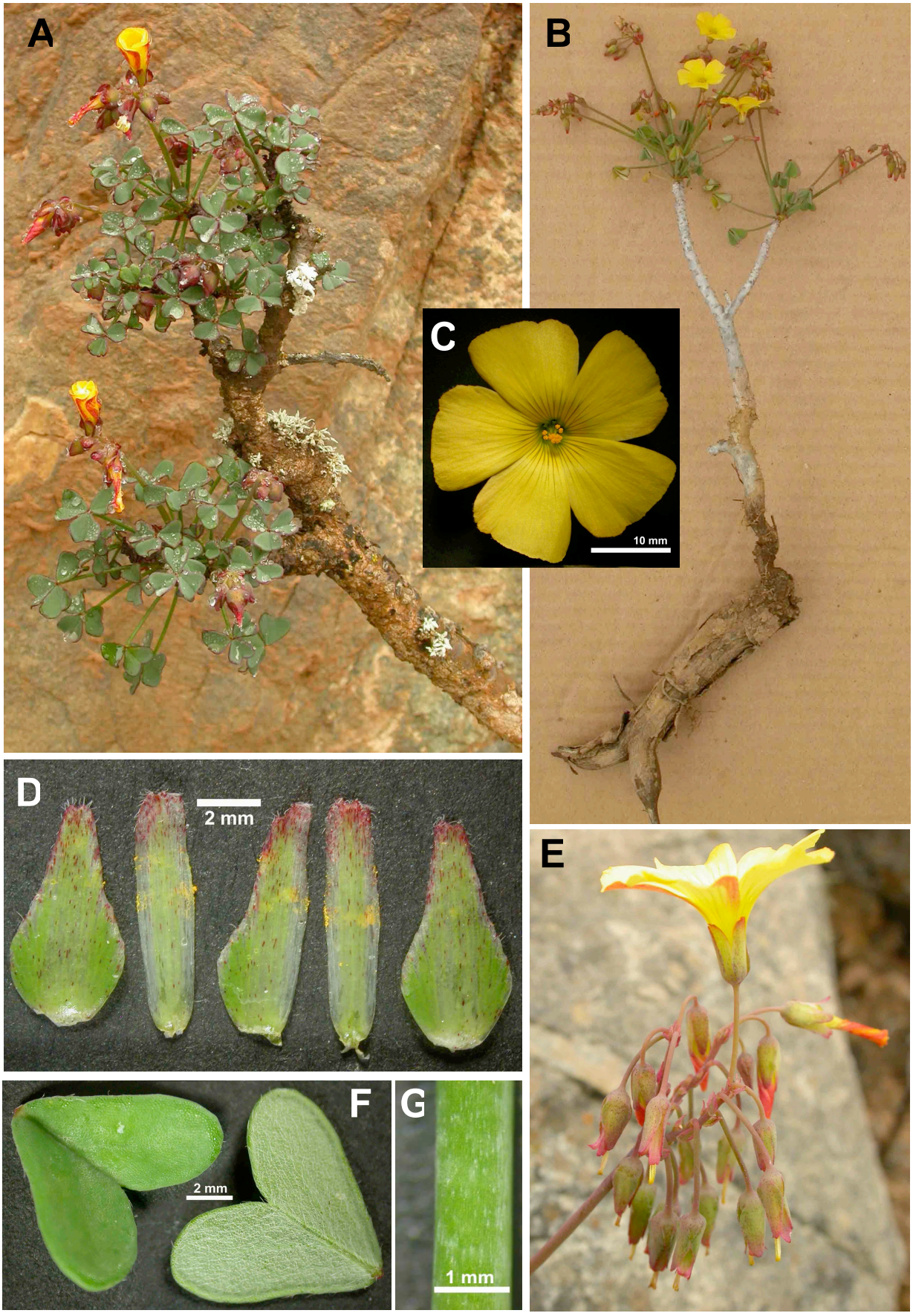


Figure 27: ***Oxalis paposana*** **Philippi**: **A** Habit, **B** Root tubers, **C** Flower, **D** Sepals, **E** Inflorescence, **F** Leaflets, **G** Petiole, **H** Sepals. A *in situ* Quebrada La Plata; B-E *in situ* Cerro Carnero; C-D, F-G greenhouse cultivation of accession Bayer & Grau 4920, Quebrada La Plata, 1990.

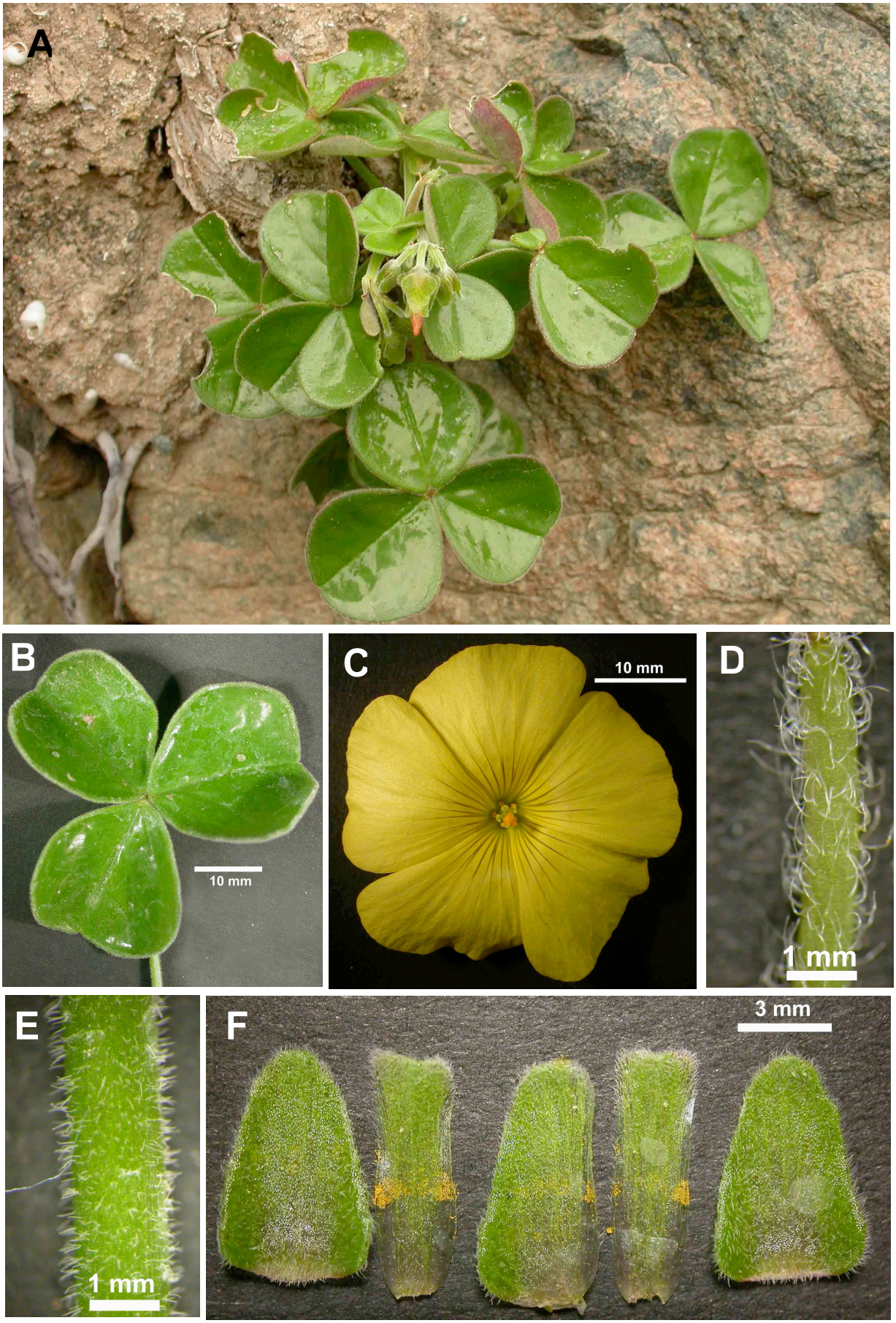


Figure 28: ***Oxalis ricardii*** **Lourteig**: **A** Habit, **B** Leave, **C** Flower, **D** Pedicel, **E** Petiole, **F** Sepals. A *in situ* Quebrada Bandurillas, B-F Greenhouse cultivations of accession Heibl 01-061, Quebrada Bandurillas, 2004.

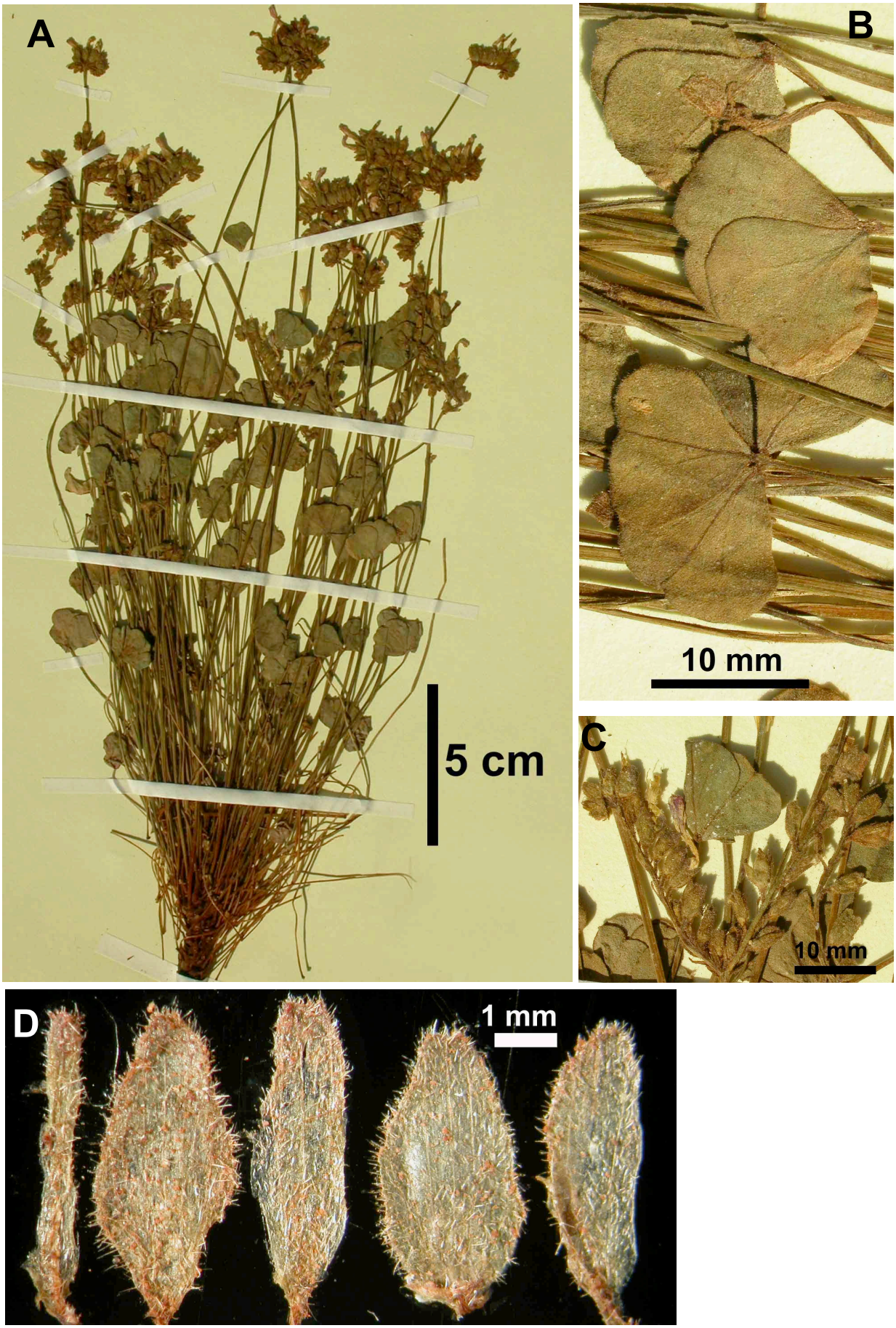


Figure 29: ***Oxalis squarrosa*** **Barnépud**: **A** Habit, **B** Leaves, **C** Inflorescence, **D** Sepals. A-D *leg.* Jiles 5814, Cerro Tololo, Coquimbo, 1971.

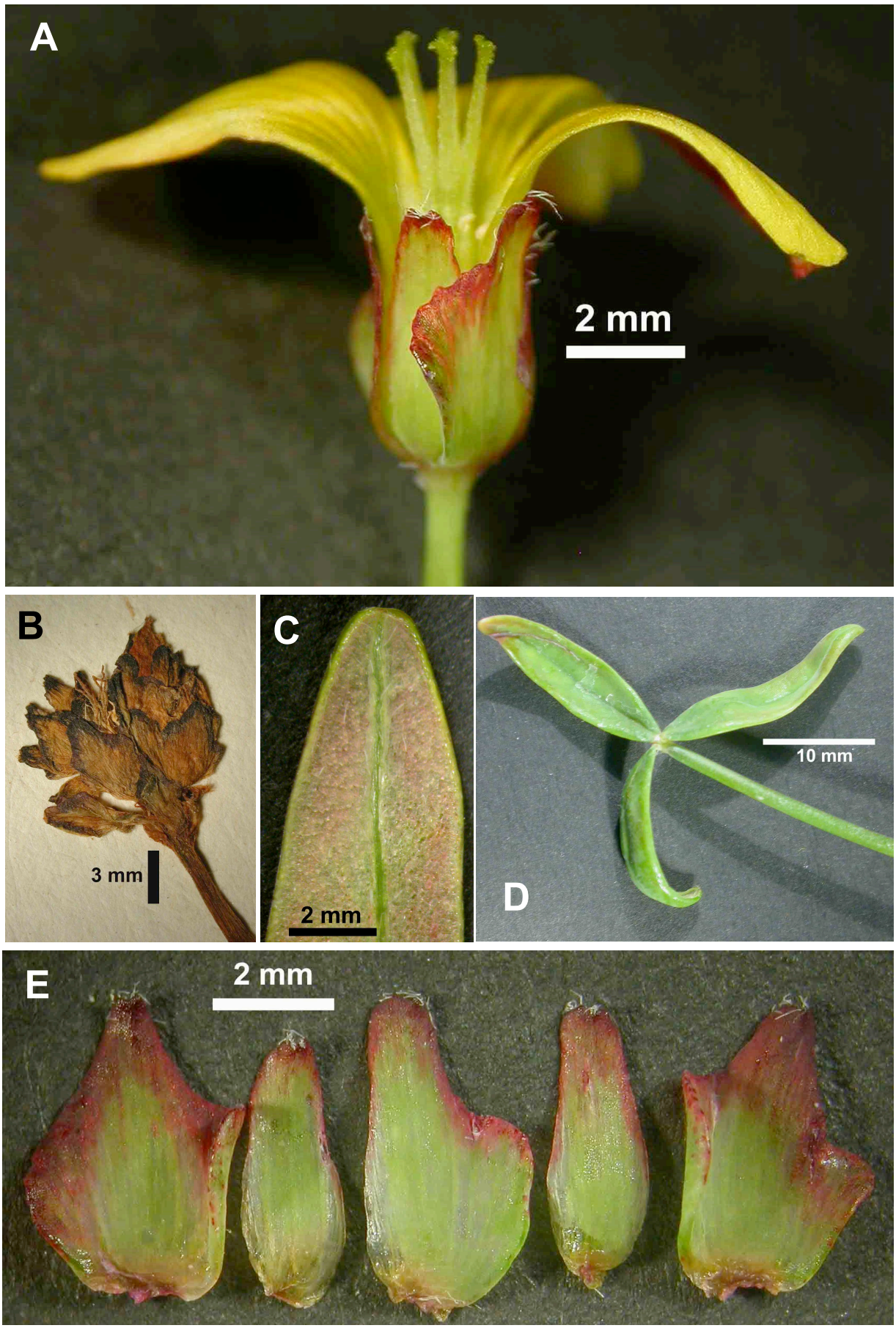


Figure 30: ***Oxalis tortuosa*** **Lindley**: **A** Flower, **B** Inflorescence, **C** Leaf apex, lower side, **D** Leave, **E** Sepals. A, C-E Greenhouse cultivation of accession Kraus 94, Zapallar, Valparaiso, 1991; B holotype *leg.* Bertero 1767, Playa Ancha, Valparaiso, 1830.

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Mein herzlicher Dank gilt all jenen, die mich bei dieser Arbeit unterstützt haben. Jeder hat auf seine Weise zum Gelingen beitragen.

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Selbständigkeitserklärung

Hiermit erkläre ich, daß ich die vorliegende Arbeit selbständig und nur unter Verwendung der angegebenen Hilfsmittel und Literatur angefertigt habe.

München,

Christoph Heibl