
THE SOLANACEAE OF THE LOMAS FORMATIONS OF COASTAL PERU AND CHILE

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ABSTRACT. The western coast of South America [5–30°S lat] is dominated by desert conditions that form a continuous, hyper-arid belt, broken only by occasional river valleys. The native, non-riparian vegetation of these deserts is largely confined to localities where recurring fogs meet the near-shore terrain. The fogs supply moisture for the development of plant communities here termed *lomas* formations. The *lomas* formations range over 3500 km and contain a combined vascular flora of over 1400 species. Individual *lomas* formations are isolated and endemism is high, reaching over 40% in some localities. This paper summarizes the current state of knowledge on the distribution and origin of the family Solanaceae within the *lomas* formations. The family is represented by 18 genera and 128 species arrayed in five subfamilies: Cestroideae, Nicotianoideae, Petunioideae, Schizanthoideae, and Solanoideae. Among the genera with endemic species are *Exodeconus*, *Grabowskia*, *Jaltomata*, *Leptoglossis*, *Lycium*, *Nicotiana*, *Nolana*, *Reyesia*, *Schizanthus*, *Salpiglossis*, and *Solanum* (including *Lycopersicon*). No fewer than 90 endemic species are recorded from the *lomas* formations, and *Nolana*, with 70 endemic *lomas* species, stands out as the largest and most wide-ranging genus of the *lomas* flora and the only genus to be encountered in all *lomas* formations. Different biogeographic patterns, i.e., autodisjunctions and allodisjunctions, are displayed and these reflect different arrival times and origins for the members of this specialized floristic community. Short-term climatic fluctuations, such as El Niño events, and long-term climatic change associated with glacial cycles have been influential in expansions and contractions in the floras of the Andean Cordillera.

Key words: Atacama Desert, biogeography, Chile, El Niño, *lomas* formations, Peru, Peruvian Desert, Solanaceae.

For nearly 3500 km along the western coast of South America [5°–30°S latitude], the Atacama and Peruvian Deserts form a continuous, hyper-arid belt, broken only by occasional river valleys from the Andean Cordillera. Though this is one of the driest places on Earth, it is home to an extraordinary type of vegetation termed *lomas* formations (Dillon, 1997; Dillon & Hoffmann, 1997; Rundel et al., 1991). These highly endemic plant communities occur in near-shore locations where ocean fog provides sufficient moisture for the development of vegetation. Each locality is an island of vegetation among a virtual ocean of arid desert, and over 100 such localities have been identified from northern Peru to central Chile (Fig. 1). The size and topography of individual formations vary greatly, as does the distance between formations. Rundel et al. (1991) provided a detailed discussion of the climate, geomorphology, and vegetation of this region, but a brief review of the major points is warranted for the current discussion.

COASTAL CLIMATE AND EL NIÑO EVENTS

Various factors are responsible for the development of the hyper-arid conditions along the coasts of Chile and Peru. All of western South America is isolated from weather patterns to the east by the Andean Cordillera, which reaches an average height of over 3500 m. Temperatures are homogeneous along the entire latitudinal extent of the deserts, which results from the influence of cool, sea surface temperatures associated with the south to north flow of the Humboldt (Peruvian) Current. This, combined with the positionally stable, subtropical anticyclone, results in a mild, uniform coastal climate where it nearly never rains, but there is the regular formation of thick stratus clouds below 1000 m usually during the months of September to December.

In addition to these seasonal fogs, the coastal region is also influenced by periodic and recurrent El Niño Southern Oscillation (ENSO) events. The frequency of El Niño events is roughly every 30 to 50 years for major events and every 3.5 to 7

years for minor events; however, two of the strongest El Niño events were recorded in 1982/1983 and 1997/1998. The El Niño phenomenon is complex and a complete explanation is beyond the scope of this paper (Allan et al., 1996). But simply put, El Niño conditions prevail when the normally cold waters off the coast of western South America are displaced by warmer water originating in the western Pacific. These conditions stimulate brief periods of heavy rainfall and relatively high temperatures. The increase in available moisture has profound effects upon the *lomas* formations and undoubtedly shapes their composition and structure. This is manifested by the stimulation of massive blooming events that replenish seed banks for annual and perennial plants. This phenomenon is illustrated with two photographs taken from approximately the same spot at the base of Cerro Cabezón in northern Peru. During a non-El Niño year (Fig. 2A), terrestrial *Tillandsia* (Bromeliaceae) dominates. But, during the 1997/1998 El Niño events, the foreground contains a dense population of *Exodeconus maritimus* (Solanaceae) (Fig. 2B). This white-flowered, prostrate annual can have branches reaching nearly three meters in length when sufficient moisture is available.

It is difficult to imagine what the coastal vegetation would resemble in the prolonged absence of El Niño events. One effect might be the reduction in levels of floristic diversity and elimination of migration and establishment within and between formations. Data relating to the historical onset of El Niño conditions suggest that the phenomenon can be accurately dated to between 5000 and 15,000 years ago (Fontugne et al., 1999; Rodbell et al., 1999). Longer-term records of El Niño events are more difficult to establish, but results from fossil coral suggest that El Niño-like conditions may have existed for over 100,000 years (Hughen et al., 1999). Authors have argued that the present extent of coastal aridity of the Atacama and Peruvian deserts is quite young (Arroyo et al., 1990), perhaps Holocene age (10,000 bp), while others suggest much greater antiquity but influenced by pluvial cycles (Alpers & Brimhall, 1988; Betancourt et al., 2000; Rundel

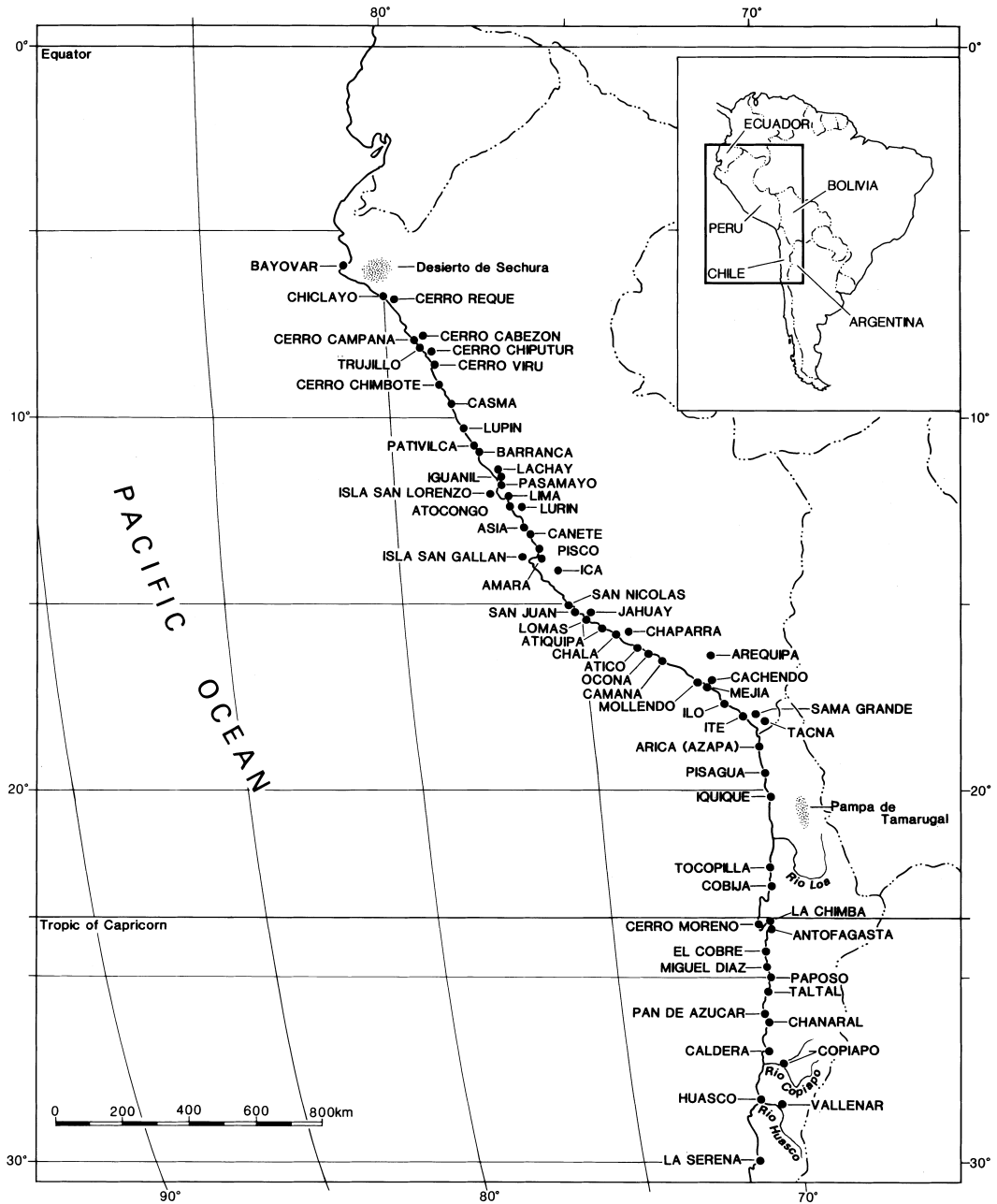


Figure 1. Geographic features, including *lomas* localities referred to within the Atacama and Peruvian Deserts.

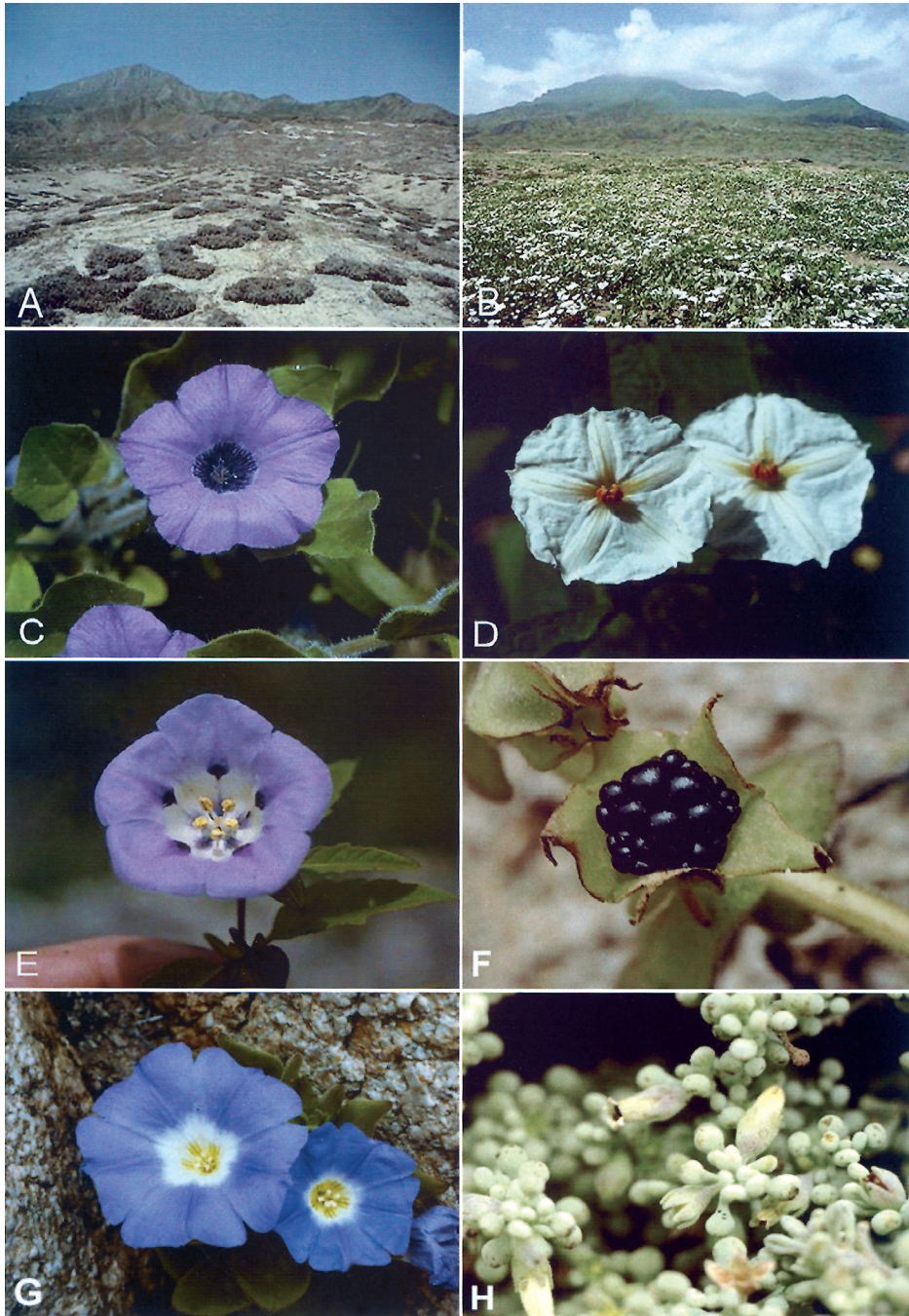


Figure 2. Solanaceae of the lomas formations. —A. Photograph of Cerro Cabezón (Dept. La Libertad, Peru) during a dry, “non-El Niño” period (June 1998). Only colonies of perennial, terrestrial *Tillandsia latifolia* are evident in the foreground. —B. Photograph of Cerro Cabezón during a wet, El Niño phase (February 1998) with annual, white-flowered *Exodeconus maritimus* in foreground. —C. *Exodeconus prostratus* flower (Lomas of Lupín, Peru). —D. *Lycianthes lycioides* flower from Cerro Campana. —E. *Nicandra physalodes* (Virú, Dept. La Libertad, Peru). —F. Mericarps in *Nolana rupicola* (Parque Nacional Pan de Azúcar, Antofagasta, Chile). —G. *Nolana rupicola* flowers (Parque Nacional Pan de Azúcar). —H. *Nolana peruviana* illustrating succulent, reduced leaves and reduced flowers (Caleta Buena, Antofagasta, Chile).

et al., 1991). Regardless of their age, recurrent El Niño events have surely helped shape the coastal communities present today (Dillon et al., 2003; Dillon & Rundel, 1990; Holmgren et al., 2001).

FLORISTIC STUDY

The study area, as defined here, is the *lomas* formations, which refers to fog-dependent, near-shore vegetational communities from northern Peru (ca. 7°S) to north-central Chile (ca. 28°S) (Dillon, 1997; Dillon & Hoffmann, 1997; Rundel et al., 1991). The plant communities are distributed between sea level and 1000 m, and usually within 1–30 km of the coast. Though the term *lomas* formations was originally proposed for southern Peruvian plant communities (Weberbauer, 1945), it is here used for all the communities along the coast that correspond to this definition. Other terms applied to these formations include “fertile belt” (Johnston, 1929), “meadows on the desert” (Goodspeed, 1961; Goodspeed & Stork, 1955), “oasis de niebla” (Ellenberg, 1959; Muñoz-Schick et al., 2001), and “desierto costero” (Gajardo, 1987).

The author’s study of the flora of the *lomas* formations has been under way since 1983, with the desert-blooming display during the 1982/1983 El Niño event. Over the last 20 years, fieldwork and collecting have been conducted throughout the extent of the *lomas* formations, including a series of collecting trips during and after El Niño events in Chile and Peru. Nearly 2100 collections have been made and all major herbaria with holdings from the region have been consulted. From these efforts, a database, called LOMAFLO, was established and currently contains nearly 9000 specimen records representing ferns, gymnosperms, monocotyledons, and dicotyledons recorded from the *lomas* formations. LOMAFLO is available via the internet <http://www.sacha.org/search_frame.htm>.

The native, non-riparian, vascular flora confined to these localities consists of 108 families, 520 genera, and ca. 1400 species. For this treatment, nearly 1600 herbarium sheets of Solanaceae have been consulted, and virtually all the species treat-

ed here have been observed, collected, and photographed in their respective environments. The Solanaceae of the coastal deserts of Chile and Peru comprise 18 genera and 128 species and rank as the second most species-rich family in the flora of the *lomas* formations. Only the Asteraceae, with 57 genera and nearly 150 species, contain more diversity within the *lomas* communities. The *lomas* formations contain pantropical species, a few Northern Hemisphere desert disjunctions, Andean Cordillera disjunctions, and a complement of genera and species endemic to the *lomas* formations. Endemic taxa can be widespread in several *lomas* formations or restricted to a single locality. Endemism in the overall flora often exceeds 40% in individual localities (Duncan & Dillon, 1991) and in the Solanaceae of the *lomas* formations, ca. 70% (90 of 128 species) are considered endemic (cf. Appendix 1).

Vegetation in the coastal deserts of western South America is not uniformly distributed (Rundel et al., 1991). It appears that there are at least three primary floristic segments within the coastal deserts that reflect independent histories: a northern Peruvian unit from ca. 7°S to 13°S latitude, a southern Peruvian unit from 13°S to 18°S latitude, and a northern Chilean unit from 20°S to 28°S latitude. The segment of coastal desert in extreme northern Chile, between 18° and 20°S latitude, is a hiatus, nearly devoid of vegetation, that lacks the proper, near-shore topography to develop *lomas* communities (cf. Rundel & Dillon, 1998; Rundel et al., 1991). In the overall *lomas* flora there are two centers of species endemism, one in southern Peru (13°–18°S) and the other in northern Chile (20°–28°S). There is a distributional hiatus between the modern desert floras of northern Chile and southern Peru. An analysis of the entire vascular plant flora from the coastal desert shows that only 112 species, from a total of ca. 1400, have distributions in both Peru and Chile. If widespread or weedy species are eliminated from the analysis, only 93 non-introduced species cross the 18°–20° latitude boundary, suggesting little active exchange over the hyper-arid barrier or hiatus. (An illustration

representing the sectoring of the coastal flora in Peru and Chile is available via the internet, <http://www.sacha.org/famil/nolana/Nolana_sectoring.htm>.)

BIOGEOGRAPHIC PATTERNS

The biogeography of the Solanaceae was analyzed and discussed by D'Arcy (1991). South America is a center of generic and species diversity (Hunziker, 1979, 2000), and the family is considered to be of Gondwanan origin (Symon, 1991). Studying the potential biogeographic relationships among *lomas* representatives allows the development and testing of hypotheses concerning the origins of these species. Our ability to reconstruct these events in an area the size of the Atacama and Peruvian Deserts requires information from many sources, including distributional patterns, information on past climates, and reconstructed phylogenies of member organisms.

There are few phylogenetic studies for genera represented within the Solanaceae of the *lomas* formations. At the family level, molecular studies (Olmstead & Palmer, 1992; Olmstead et al., 1999) have included 16 genera with *lomas* representatives. Species-level studies have been completed or are under way in several genera with *lomas* representatives (see below). The subfamilial and tribal circumscriptions are still being formulated (D'Arcy, 1991; Hunziker, 1979a, 2000a) and differences of opinion are evident (Olmstead et al., 1999; Hunziker, 2001). The categories presented here are intended for discussion of distributional patterns and potential biogeographic origins. Terminology for the description of disjunctions follows Turner (1972: 153). Autodisjunctions (autojuncts) are defined as "two or more morphologically similar populations that are widely separated spatially, the more remote elements having become isolated through the dissemination of appropriate colonizers from some *extant* population or gene pool." This type of disjunction is typically the result of a long-distance dispersal event, but vicariant events can accomplish the same distributional pattern (Wen et al., 2002). Continuing, allodisjunctions (allojuncts) are "two

or more closely related populations (i.e., more closely related to each other than either is to yet some other taxon) that are widely separated spatially, the various elements of which have been derived through phyletic divergence from populations now *extinct*."

The genera distributed in the *lomas* formations are arrayed in five subfamilies in the Solanaceae: Cestroideae, Petunioidae, Nicotianoideae, Schizanthoideae, and Solanoideae. Figure 3 provides a simplified tree, adapted from a strict consensus cladogram in the analysis conducted by Olmstead et al. (1999: 125). What follows here is a brief discussion of the Solanaceae of the *lomas* formations in relation to their classification in subfamilies, tribes, subtribes, and sections, and the current state of knowledge concerning their phylogenetic positions.

SCHIZANTHOIDEAE

The Schizanthoideae are monotypic with *Schizanthus* containing 12 species and distributed from northern to southern Chile and one species reaching Argentina (Coccuci, 1989). Four species range into northern Chile, where two species are endemic to the *lomas* formations and another two species are found immediately to the south, where they only just reach the edge of the Atacama Desert (Grau & Gronbach, 1984). Olmstead et al. (1999) concluded that *Schizanthus* is an early-diverging lineage within the Solanaceae and basal to the remainder of the family. Peña and Muñoz (2002) provided a species-level phylogeny for *Schizanthus* based upon morphological and alkaloid chemical characters. Their results suggested two species groups: one with white flowers without nectar guides, explosive pollen release, and pollination by nocturnal moths, and another with lavender flowers, nectar guides, passive pollen release, and pollination by bees. In the *lomas* formations, *S. integrifolius*, *S. lacteus*, and *S. candidus* are found in the white-flowered group, and *S. laetus* is found in the lavender-flowered group. Peña and Muñoz (2002) stated that the white-flowered species are the more primitive and likely ancestral to the lavender-flowered group. Further, they

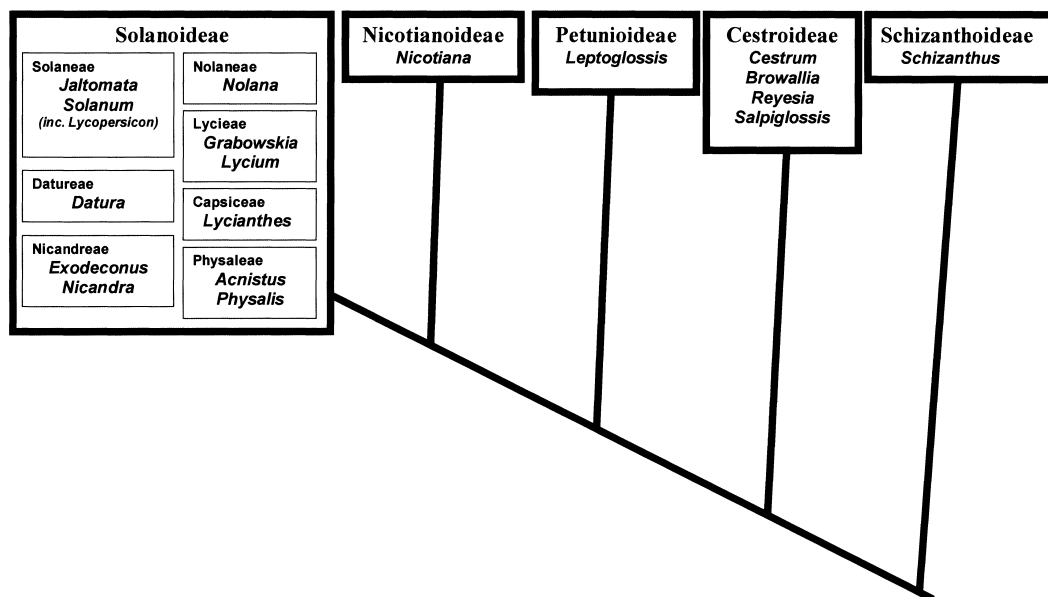


Figure 3. A simplified tree, adapted from a cladogram, to illustrate the representation of Solanaceae subfamilies, tribes, and genera recorded from within the *lomas* formations. Adapted from Olmstead et al. (1999).

stated (p. 50), “*Schizanthus* was emerging from the north part of present Chile, and extending south and to the Andes, finally reaching Argentina.” An alternative hypothesis is that the white-flowered clade (i.e., *S. integrifolius*, *S. lacteus*, and *S. candidus*) in northern Chile are allodisjuncts from the more southern species, *S. pinnatus*, and they have radiated into an unfilled niche in the north. The other *lomas* species, *S. laetus*, may be an allodisjunct of independent origin from ancestral stock not unlike *S. porrigens* or *S. tricolor*, both species restricted to central Chile (ca. 32°–33°S) with lavender flowers and bee pollination. Allodisjunctions of endemic Atacama Desert species derived from more southern Chilean congeners have been suggested in other families (Dillon & Muñoz-Schick, 1993; Gengler-Nowak, 2002). These two evolutionary hypotheses should be tested with other data.

CESTROIDEAE

The Cestroideae are represented in the *lomas* flora by three tribes and the following genera:

Browallieae (*Browallia*), Cestreae (*Cestrum*), and Salpiglossideae (*Reyesia* and *Salpiglossis*). The Browallieae are a minor element in the *lomas* formations with a single autodisjunct species, *Browallia americana*, likely derived from the Andean Cordillera where all other South American taxa are confined. The Cestreae are also a minor element with *Cestrum* represented by two widely distributed, apparently autodisjunct species from the Andean Cordillera: one from central Peru, *C. auriculatum*, and another in northern Chile, *C. parqui*. The Salpiglossideae contain two, primarily Chilean genera, *Salpiglossis* and *Reyesia*. *Salpiglossis* contains two taxa, *S. spinescens*, an Atacama Desert endemic species here considered an allodisjunct from stock similar to *S. sinuata*, the other species found in the Andean Cordillera of central Chile and adjacent Argentina (30°–40°S). *Reyesia* contains four taxa, two of which are endemic species in the *lomas* formations of northern Chile: *R. chilensis* and *R. cactorum*. These two species appear to be morphologically most similar to each other and

may represent allodisjunctions from ancestral stock similar to *R. parviflora*, a species of central Chile and adjacent Argentina.

NICOTIANOIDEAE

The Nicotianoideae are represented in the *lomas* formations by *Nicotiana* (tribe Nicotianeae), a genus of perhaps 95 species from North and South America and Australia with a center of diversity in the Andean Cordillera. Five species have been recorded from the *lomas* formations. These display two types of distributional patterns: autodisjuncts, such as *N. glauca*, *N. glutinosa*, and *N. paniculata* that have wider distributions in the Andean Cordillera, and allodisjunctions such as *N. knightiana* in Peru and *N. solanifolia* in Chile, both endemic species confined to a few sites. Goodspeed (1954) discussed the relationships of *Nicotiana* and suggested that most *lomas* species (*N. glauca*, *N. knightiana*, *N. paniculata*, and *N. solanifolia*) be placed in *Nicotiana* subg. *Rustica* sect. *Paniculatae* based upon tubular or salverform corollas and unwinged leaf petioles. The remaining *lomas* taxon, *N. glutinosa*, was placed in *Nicotiana* subg. *Tabacum* sect. *Tomentosae*, based upon infundibular corollas with expanded throats and winged leaf petioles. Olmstead and Palmer (1991) investigated *Nicotiana* with cpDNA restriction site analysis that included all the species found in the *lomas* formations with the exception of *N. solanifolia*. Their analysis presented a phylogeny with a well-supported, but largely unresolved clade containing *N. glutinosa*, *N. knightiana*, and *N. paniculata*. Goodspeed (1954: 341) has suggested that *N. knightiana* is "a vestige of a series of forms which once connected *N. paniculata* with *N. solanifolia* or a derivative of a hybrid between those two species."

Knapp et al. (2004) utilized nuclear and plastid genomes to test Goodspeed's sectional groupings and confirmed the placement of *Nicotiana glauca* in section *Noctiflorae* Goodsp., *N. glutinosa* in section *Undulatae* Goodsp., and *N. solanifolia*, *N. knightiana*, and *N. paniculata* in section *Paniculatae* Goodsp. It may be hypothesized that *Nicotiana* species reached the *lomas* via independent evolutionary routes and consequently at different times.

PETUNIOIDEAE

The Petunioideae are represented in the *lomas* formations by *Leptoglossis*, a genus of seven species, four of which are Peruvian endemic species. Three species, *L. darciana*, *L. ferreyraei*, and *L. lomana*, are allodisjuncts, and *L. schwenkioides* is widespread in the Andean Cordillera and is likely an autodisjunct from upland populations. Hunziker and Sublis (1979a) considered *Leptoglossis* to be closely related to *Hunzikeria*, a disjunction from the southern United States, Mexico, and Venezuela. While *Leptoglossis* has not been included in any molecular phylogenetic studies, *Hunzikeria* has been assigned to the Petunioideae by Olmstead et al. (1999) and it is placed in that subfamily here based upon the strong morphological relationship between these two genera (Hunziker, 2001). It should be mentioned that Hunziker and Sublis (1979b) considered *Salpiglossis* closely related to *Leptoglossis*, and recently Hunziker (2001) placed it in tribe Nicotianeae subtribe Leptoglossinae. The classification and relationships of *Leptoglossis* remain controversial.

SOLANOIDEAE

The Solanoideae are represented within the *lomas* formations by seven tribes: Capsiceae, Datureae, Lycieae, Nicandreae, Nolaneae, Physaleae, and Solaneae. The Capsiceae have a single widespread species, *Lycianthes lycioides*, which appears to be an autodisjunction from the adjacent Andean Cordillera. It is noteworthy, however, that the coastal populations in northern Peru possess white corollas (Fig. 2D), a floral color different from that found in the nearby Andean populations. The Datureae are represented by *Datura inoxia*, a weedy species originally from Mexico, but spread throughout South America (Jiao et al., 2002). In the *lomas* formations, this species is considered an example of an autodisjunction.

The Lycieae contain three Neotropical genera: *Grabowskia*, *Lycium*, and *Phrodus* (Hunziker & Bernardello, 1995; Hunziker, 2001). The sister-group relationship of the former two genera was supported by cpDNA data (Olmstead & Palmer, 1992; Olmstead et al., 1999). *Phrodus* is a mono-

typic, Chilean genus that only reaches the most southern boundary of the Atacama Desert, and it has not been recorded from the *lomas* formations (Hunziker, 2001). *Grabowskia* contains six species, primarily distributed in South America and with one species each in Chile and Peru. The Peruvian species, *G. boerhaaviaefolia*, is here considered an autodisjunct derived from populations in the Andean Cordillera, whereas the Chilean species, *G. glauca*, is a narrow endemic and considered here as an allodisjunct from congeneric stock in Argentina. *Lycium* has several species distributed in the *lomas* formations of both Chile and Peru, and their distributions suggest a combination of allopatrically derived endemic species and autodisjunctions from species found in the adjacent Andean Cordillera. Bernardello (1986) placed *lomas* species in two sections, *Lycium* sect. *Lycium* and *Lycium* sect. *Mescope*, based upon the presence of an inconspicuous green nectary or a conspicuously red nectary, respectively. Two recent molecular systematic studies (Fukuda et al., 2001; Miller, 2002) have been completed; however, they contained only one species found in the *lomas* formations. Miller (2002) suggested that the sections of *Lycium* proposed by Bernardello (1986) were not supported by molecular data. Further, Miller's sequence and morphological analysis nested *Grabowskia* within *Lycium*, and suggested that *Grabowskia* species may comprise a clade of very divergent *Lycium*.

The Nicandreae contain two Neotropical genera: *Exodeconus* and *Nicandra*. The sister-group relationship of these two genera was supported by cpDNA data (Olmstead & Palmer, 1992; Olmstead et al., 1999), and they occupied a basal position to the rest of the subfamily Solanoideae. Two *Exodeconus* species are found in the Peruvian *lomas* formations: *E. maritimus* (Fig. 2B) in northern and central Peru, and reaching southern Ecuador, and *E. prostratus* (Fig. 2C), an endemic to the *lomas* formations. *Nicandra physalodes* (Fig. 2E) is thought to have originated in Peru; however, it is widely dispersed in tropical and subtropical areas in both the Old and New World. In Peru, this species appears to be an autodisjunction from the Andean Cordillera and is restricted to a few northern Peruvian coastal sites.

The Nolaneae are here considered monotypic, with *Nolana* as the only genus, and an undisputable member of the Solanaceae (Olmstead et al., 1999; Tago & Dillon, 1999). With its inclusion in the Solanaceae, *Nolana*, with 85 total species, becomes the fifth largest genus in the family behind *Solanum*, *Lycianthes*, *Cestrum*, and *Nicotiana* (D'Arcy, 1991). Vegetative and floral morphology are not aberrant within the Solanaceae, though the unusual ovary formed from mericarps (Fig. 2F) is unique for the Solanaceae. Mesa (1986) proposed recognizing *Nolana* as a separate family with perhaps 18 species, but D'Arcy (1991) accepted *Nolana* in the Solanaceae at the subfamilial level, Nolanoideae, and recognized 22 species in two genera, *Alona* and *Nolana*. Later, Mesa (1997; Mesa et al., 1998) revised his species concept to accept ca. 70 species. Preliminary molecular data (Olmstead & Palmer, 1992; Olmstead & Sweere, 1994) supported observations made by previous taxonomists (Johnston, 1936) that *Nolana* shares relationships with *Lycium* and *Grabowskia*. The placement of *Nolana* within the Solanaceae changes the diagnosis of the family, adding mericarps to the possible fruit types, and Olmstead and Palmer (1992) consequently suggested that undue emphasis had been placed upon the gynoeceum morphology in defining taxonomic groups. *Nolana* exhibits extensive variation in habit, ecological preferences, and vegetative and floral morphology with both showy flowers, e.g., *Nolana rupicola* (Fig. 2G), and reduced forms, e.g., *Nolana peruviana* (Fig. 2H). Additional *Nolana* corollas may be observed via the internet <<http://www.sacha.org/Nolana/corollas.htm>>.

Species diversity in *Nolana* is nearly equally divided between Chile and Peru. At least one species of *Nolana* occurs in every *lomas* formation throughout Peru and Chile, and at some locations as many as 10 species occur sympatrically. There are 37 endemic species recorded from Peru (4 in Sector 1 and 37 in Sector 2), another 42 endemic species recorded from Chile (Sector 3), four species are found in both southern Peru and northern Chile, and one species is an endemic to

the Galápagos Islands, Ecuador. No fewer than 70 species are considered to be endemic to the *lomas* formations of Chile and Peru in about equal numbers. Another 13 species occur in upland habitats (> 1000 m) outside of the area normally included in the *lomas* formations (<http://www.sacha.org/famil/nolana/Nolana_sectoring.htm>). One species, *N. paradoxa*, has an extended distributional range from central Chile to southern coastal Chile (33°S–42°30'S).

Tago (1999) analyzed ITS and *matK* to estimate phylogenetic relationships within a sampling of 37 species of *Nolana*, including members from both Chile and Peru and two outgroup species, *Atropa belladonna* L. and *Grabowskia glauca* Schltdl. The preliminary data provided conflicting hypotheses of relationships with results largely incongruent between *matK* and ITS studies (Tago & Dillon, 1999). Further investigations are under way, and data from six molecular data sets including the nuclear ITS regions, 5S spacer, and GBSSI gene, and the chloroplast *trnC-trnD* region and *ndhF* gene have been accessed. There appears to be a strong biogeographic signal in preliminary data indicating a deep split between the *Nolana* species from Peru and Chile (J. Wen, pers. comm.), and this pattern is also reflected in the overall flora of these deserts (see FLORISTIC STUDY). As no other element within the flora, the evolutionary history of *Nolana* holds clues to the age and origin of the coastal deserts and their unique flora.

The Physaleae are represented by two tribes and genera: *Lochrominae* (*Acnistus*) and *Physalinae* (*Physalis*). *Acnistus* is a Neotropical, monotypic genus common from Mexico to Brazil, and the occurrence of *Acnistus arborescens* in the *lomas* formations is here considered an example of an autodisjunct from the Andean Cordillera populations. *Physalis* has two widely distributed species with rare occurrences within the *lomas* formations; both *P. angulata* and *P. peruviana* are considered to be cases of autodisjunct distributions from nearby Andean Cordillera populations.

The Solaneae are represented by *Jaltomata* and *Solanum* including *Lycopersicon*. These two gen-

era have species within the *lomas* formations considered as autodisjuncts from nearby Andean Cordillera species and allodisjuncts confined to the *lomas* formations. Molecular systematic studies have placed *Jaltomata* as basal to *Solanum*, and *Lycopersicon* grouped with *Solanum* species (Bohs & Olmstead, 1999; Olmstead & Palmer, 1992; Olmstead et al., 1999).

Jaltomata is under systematic study (Mione et al., 2000a, 2000b), but the relationships among its four species found in the Peruvian *lomas* formations have not been elucidated. *Jaltomata aspera* likely represents an autodisjunction from adjacent Andean Cordillera; however, it is possible that the population in *lomas* formations represents a distinct, endemic species (T. Mione, pers. comm.). The other three species, *J. hunzikeri*, *J. lomana*, and *J. umbellata*, are considered allodisjuncts and hypothesized to have been derived from ancestral stock from the adjacent Andean Cordillera. They may either have radiated from an initial introduction, in which case they would be expected to be more closely related to each other, or they may each represent independent introductions (Mione et al., 1994).

Solanum has 21 species within the *lomas* formations of Chile and Peru: 16 placed in subgenus *Solanum* and 5 species in section *Lycopersicon* (Peralta & Spooner, 2000, 2001). Molecular phylogenies (Olmstead & Palmer, 1992; Peralta & Spooner, 2001) reveal that *Lycopersicon* is not distinct from *Solanum* (Bohs & Olmstead, 1999), though its placement in *Solanum* is controversial and has not been accepted by all authors (Hunziker, 2001; Nee, 1999). The *lomas* species are all classified as *Solanum* sect. *Lycopersicon* subsect. *Lycopersicon*. In the phylogenetic analysis of the GBSSI gene sequences, Peralta and Spooner (2001) suggested that *S. pennellii* and *S. habrochaites* are a well-supported clade in the basal polytomy. *Solanum peruvianum* is considered paraphyletic and separates into two geographical groups, one in northern Peru (e.g., Cerro Campana, 7°58'S) and the other in central Peru (Dept. Ancash, 9°55'S), southern Peru (Dept. Arequipa, 17°02'S), and northern Chile (Prov. Tarapaca, 18°28'S). Further, they found that

Solanum pimpinellifolium was most closely related to *Solanum lycopersicum* (the cultivated tomato). Sacks et al. (1997) speculated that montane races of *S. peruvianum* (as *Lycopersicon peruvianum*) could be derived from coastal races and may form natural hybrids with *S. chilense* (as *Lycopersicon chilensis*) where their ranges overlap in southern Peru. The close relationship between these species invites speculation as to the timing of the arrival of each to the coastal environments. A vicariant origin of the *S. peruvianum* and *S. chilense* should be tested, certainly, and the origins of species with distributions within the *lomas* formations merits further investigation (Spooner et al., 2005).

The remaining 16 species are classified in *Solanum* subg. *Solanum* and display both autodisjunct and allodisjunct distributional patterns. Two species found in the *lomas* formations are considered autodisjunctions: *Solanum radicans* (sect. *Dulcamara*), distributed widely in South America, and *S. fragile* (sect. *Solanum*); both species are found at higher elevations in the Andean Cordillera of southern Peru. The remaining *Solanum* species are grouped into two sections, *Solanum* sect. *Regmandra* (Nee, 1999), which contains seven species, here considered allodisjuncts and confined to the *lomas* formations: *S. brachyantherum* (Chile), *S. ferreyrae* (southern Peru), *S. montanum* (Peru), *S. multifidum* (Peru), *S. murphyi* (southern Peru), *S. phyllanthum* (Chile and Peru), and *S. remyanum* (Chile). And the second, *Solanum* sect. *Petota* ser. *Tuberosa* (Nee, 1999), a suite of seven strictly Peruvian species: *S. chancayense*, *S. immite*, *S. medians*, *S. mochiquense*, *S. neoweberbaueri*, *S. tuberosum*, and *S. wittmackii*. The relationships of the second group of species have not been investigated, but most have distributions outside of the *lomas* formations and may be considered as autodisjunctions. The presence of *Solanum tuberosum* (cultivated potato) in the *lomas* formations may be attributed to human activities, since potatoes are cultivated in some coastal sites during El Niño events when sufficient moisture is available (pers. obs.).

DISCUSSION

The biogeographic patterns of the Solanaceae in the *lomas* formations of Chile and Peru reflect independent histories for various subfamilies, tribes, genera, and species, and it may be hypothesized that some members are long-time occupants of the deserts and others are potentially more recent introductions. Thirteen of 18 genera with *lomas* representatives are considered to be Neotropical in their overall distribution. Five subfamilies are represented in the *lomas* formations (Fig. 3) and each contains endemic species distributed among the following nine genera: *Exodeconus* (1 sp.), *Grabowskia* (1 sp.), *Jaltomata* (3 spp.), *Leptoglossis* (3 spp.), *Nolana* (70 spp.), *Reyesia* (2 spp.), *Salpiglossis* (1 sp.), *Schizanthus* (4 spp.), and *Solanum* (7 spp.). Of the 128 species recorded for the Solanaceae in the *lomas* formations, 90 species are considered endemic to these environments (70%). Endemism is equally divided between Chile and Peru, with an estimated 43 Chilean endemic species and 45 Peruvian endemic species. Of the total number of Solanaceae species reported from the *lomas* flora, only nine are recorded from both Chile and Peru, i.e., *Nolana* (4 spp.), *Solanum* (3 spp.), *Lycium* (1 sp.), and *Nicotiana* 1 (sp.). Of these, all four *Nolana* species and two *Solanum* species are considered *lomas* endemics as well. It is considered that the species that are endemic in the *lomas* formations represent allodisjuncts from ancestral, congeneric stocks now extinct, either derived from the proximal Andean Cordillera of Peru or semi-arid habitats in central Chile. Some 38 species may be considered examples of autodisjuncts most often originating from extant, conspecific populations in the adjacent Andean Cordillera in either Peru or Chile. There is a suite of 12 species in the northern Peruvian *lomas* formations (7°–13°S) in several genera that are all considered to be autodisjunctions with direct connections to nearby conspecific Andean populations. Without appropriate data, it cannot be determined with certainty which species are potentially original *lomas* dwellers that have dispersed into upland habitats within the Andean Cordillera.

The Solanaceae subfamily Schizanthoideae and subfamily Cestroideae tribe Salpiglossideae are primarily Chilean and adjacent Argentinean in distribution, with a number of endemic species reaching the *lomas* formations of the northern Atacama Desert. Solanaceae subfamily Cestroideae tribe Browallieae and subfamily Solanoideae tribes Datureae and Physaleae are prevalent in both North and South America and reach the northern and central Andean Cordillera of Peru. Solanaceae subfamily Petunioidae is primarily a Central and South American group, and *Leptoglossis* has four of its five taxa as endemic species confined to the *lomas* formations of Peru, and with one autodisjunct species in Argentina, a pattern found in other southern Peruvian taxa, e.g., *Bulnesia retama*, Zygophyllaceae (Solbrig, 1976). It has been suggested (Hunziker & Sublis, 1979a) that *Leptoglossis* shares relationships with *Hunzikeria*, an amphitropic disjunction from the southern United States, Mexico, and Venezuela. That these two taxa represent the product of an amphitropic disjunction is an interesting hypothesis that should be tested.

Allodisjuncts represented by endemic Peruvian *lomas* species are found in Solanaceae subfamily Solanoideae tribe Solaneae (*Jaltomata*, *Solanum*), Nicandreae (*Exodeconus*), and Nolaneae (*Nolana*). Allodisjuncts represented by endemic Chilean *lomas* species are found in Solanaceae subfamily Solanoideae tribes Lycieae (*Grabowskia*, *Lycium*) and Nolaneae (*Nolana*), and in each of these genera the most closely related species are distributed in habitats immediately south of the Atacama Desert in central to southern Chile and/or adjacent Argentina. As treated here, *Nolana* is considered to have 85 total species, and of these, 70 are restricted to the *lomas* formations, with approximately equal numbers of endemic species in Chile and Peru.

Olmstead and Palmer (1992) dated the early diversification of the Solanaceae at ca. 50 million years ago or early Eocene. The first appearance of *Nolana* was estimated using *matK* (Tago, 1999) or *rbcL* sequences (Olmstead & Sweere, 1994) as middle Miocene (10–11 mya). The constituents of the Solanaceae within the *lomas* formations rep-

resent a complex picture with multiple sources and origins for representative genera and species. These taxa offer many interesting examples of types and timing of disjunctions, including autojuncts and allodisjuncts formed via dispersal and subsequent modification (i.e., founder effects) or through vicariant events. Much remains to be accomplished in our search for modes of evolution and speciation in the *lomas* formations and the interplay of distributions with climatic, geological history, and potential vicariant events.

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APPENDIX I

The following is an annotated list of the species of Solanaceae encountered in the *lomas* formations in the coastal deserts of Chile and Peru. The subfamilial, tribal, and subtribal classification follows that proposed by Olmstead et al. (1999). Publication citations for each species, generic, specific and *lomas* formation distributions, relevant literature, and a voucher for each species are provided. Whenever possible, collections made by the author are cited and these have or will have duplicates distributed in appropriate South American herbaria. Additional vouchers may be found in the LOMAFLO database posted on the internet <<http://www.sacha.org/>>.

1. *Acnistus* Schott.

Solanoideae, Physaleae, Iochrominae

Generic distribution. *Acnistus* is a Neotropical, shrubby genus of one or perhaps two species distributed from Mexico, Central America, and the Caribbean to Andean South America, Galápagos Islands, and Brazil. The genus has been interpreted as monotypic by Hunziker.

Literature. D'Arcy (1991), Hunziker (1960, 1982, 2001), Macbride (1962).

1.1. *Acnistus arborescens* (L.) Schtdl., Linnaea 7: 67. 1832.

Species distribution. This species is a native to northwestern South America. In Peru, it is found in the northeastern Andes and has been recorded from the *lomas* formations of Dept. La Libertad (Cerro Campana) and Dept. Lima (Lachay, Atocongo, Pachacamac, Manzano).

Voucher. Knapp 8309 (F).

2. *Browallia* L.

Cestroideae, Browallieae

Generic distribution. *Browallia* is a Neotropical genus of two to seven species, distributed from the southern United States, Mexico, Central America, Antilles, and throughout the Andean Cordillera from Colombia to Bolivia. The genus occupies a wide range of environments, and the number of species accepted in the genus has varied greatly between seven species accepted by Dios, to four by Brako and Zarucchi, three by D'Arcy, and two by Hunziker.

Literature. Brako & Zarucchi (1993), D'Arcy (1991), Dios (1977), Hunziker (1995), Leiva-G. (1995), Macbride (1962), Sagástegui & Dios (1980).

2.1. *Browallia americana* L., Sp. Pl. 1: 631. 1753.

Species distribution. This species ranges widely in tropical America from Mexico to Peru and the Galápagos Islands. It is found in Andean locales from northern to central Peru and recorded from coastal *lomas* formations of Dept. La Libertad (Cerro Cabezón, Cerro Chipitur, Virú), Dept. Ancash (Lupín), and Dept. Lima (Amancaes, Asia, and Quilmaná).

Voucher. Dillon & Santisteban 4713 (F).

3. *Cestrum* L.

Cestroideae, Cestreae

Generic distribution. *Cestrum* is a woody genus of ca. 250 species distributed primarily in tropical America with ca. 150 species from South America. There are two species recorded from the *lomas* formations, one each in Chile and Peru.

Literature. Francey (1935, 1936), Macbride (1962), Matthei (1995).

3.1. *Cestrum auriculatum* L'Hérit., Stirp. Nov. 73, t. 35. 1788.

Species distribution. This species is widespread throughout Andean Ecuador and Peru, but rare within the *lomas* formations of Dept. Lima (Manzano, Pachacamac, Asia, Lurín) and Ica (Chincha Alto).

Voucher. Knapp 8333 (F).

3.2. *Cestrum parqui* L'Hérit., Stirp. Nov. 73, t. 36. 1788.

Species distribution. This species is widespread throughout southern South America from Brazil, Uruguay, Argentina, and Chile. Only one collection is recorded from the *lomas* formations of coastal Chile of Prov. Antofagasta (Miguel Díaz).

Voucher. Dillon et al. 8080 (F).

4. *Datura* L.

Solanoideae, Datureae

Generic distribution. *Datura* is a Neotropical genus of 8 to 10 annual species distributed from the southwestern United States, Mexico, Central America, and the Caribbean and introduced to the Galápagos Islands, Andean South America, Brazil, and Asia.

Literature. Avery et al. (1959), D'Arcy (1991), Macbride (1962), Persson et al. (1999), Symon & Haegi (1991).

4.1. *Datura innoxia* Mill., Gard. Dict. ed. 8, no. 5. 1768.

Species distribution. This species is distributed from Mexico, Central America, and South America from Venezuela to Paraguay. In Peru, it is considered an introduced herb and is rare within the *lomas* formations with only one collection record from Dept. Arequipa (Atiquipa).

Voucher. Ochoa & Salas 14903 (F).

5. *Exodeconus* Raf.

Solanoideae, Nicandreae

Generic distribution. *Exodeconus* is a Neotropical genus of six annual species distributed in northern Chile, Ecuador (mainland and Galápagos Islands), and coastal Peru. Though the genus does occur at high elevations in Chile, its species do not reach the coastal *lomas* formations.

Literature. Axelius (1994), Barboza et al. (1997).

5.1. *Exodeconus maritimus* (Benth.) D'Arcy, Solanaceae Newsl. 2(4): 19. 1986.

Species distribution. A species from near-ocean to upland Andean sites, ranging from northern to central Peru and one record from southern Ecuador. In the *lomas* formations, it is recorded from Dept. La Libertad (Cerro Campana, Cerro Cabezón, Virú), Dept. Ancash (Huarney), Dept. Lima, and Dept. Nasca.

Voucher. *Dillon & Whalen 4005* (F).

5.2. *Exodeconus prostratus* (L'Hérit.) Raf., *Sylva Tellur.* 57. 1838.

Species distribution. A Peruvian species endemic to coastal *lomas* formations of Dept. La Libertad (Cerro Cabezón, Cerro Campana, Virú), Dept. Ancash (Lupín), and Dept. Lima (Lachay, San Gerónimo, San Bartolomé, Amancaes, San Agustín).

Voucher. *Dillon & Santisteban 4697* (F).

6. *Grabowskia* Schldtl.

Solanoideae, Lycieae

Generic distribution. *Grabowskia* is a Neotropical, shrubby genus of ca. six species native to temperate South America with a disjunct of one species to Mexico (D'Arcy, 1991). There are two species recorded from the *lomas* formations, one each from Chile and Peru.

Literature. Bernardello (1982), Hunziker (1979).

6.1. *Grabowskia boerhaaviaefolia* (L.f.) Schldtl., *Linnaea* 7: 71. 1832.

Species distribution. A species of lower elevations and arid sites in Peru and the Galápagos Islands. It is recorded from northern Peruvian *lomas* formations of Dept. La Libertad (Cerro Cabezón, Cerro Campana, Cerro Chiputur, Cerro Negro, Virú).

Voucher. *Leiva & Dillon 2191* (F).

6.2. *Grabowskia glauca* (Phil.) I. M. Johnst., *Contr. Gray Herb.* 85: 112. 1929.

Species distribution. A Chilean species endemic to the *lomas* formations in two geographically adjacent populations of Prov. Antofagasta (Hueso Parado, Quebrada San Ramón).

Voucher. *Dillon & Teillier 5194* (F).

7. *Jaltomata* Schldtl.

Solanoideae, Solaneae

Generic distribution. *Jaltomata* is a Neotropical genus of about 45 species of herbs or shrubs distributed from the southwestern United States, Mexico, Central America, and Greater Antilles to Andean South America as far south as Bolivia; one species is disjunct in the Galápagos Islands. Four species are currently recorded from coastal Peru.

Literature. Gentry (1973), Mione (1999), Mione & Coe (1992), Mione et al. (1993, 2000a, 2000b).

7.1. *Jaltomata aspera* (Ruiz & Pav.) Mione, *Novon* 2: 383. 1992.

Species distribution. A Peruvian species recorded in near-coastal Andean habitats from central and southern Peru. In the *lomas* formations, it is recorded from sites in Dept. Lima (Atocongo, Amancaes, San Gerónimo) and Dept. Arequipa (Atiquipa).

Voucher. *Macbride 5912* (F).

7.2. *Jaltomata hunzikeri* Mione, *Rhodora* 102: 385. 2000.

Species distribution. A Peruvian species endemic to a single *lomas* formation from Dept. Lima (Pativilca).

Voucher. *Stork et al. 9228* (GH).

7.3. *Jaltomata lomana* Mione & S. Leiva, *Novon* 10: 54. 2000.

Species distribution. A Peruvian species endemic to a single *lomas* formation from Dept. Ancash (Mongon).

Voucher. *Leiva et al. 2140* (F).

7.4. *Jaltomata umbellata* (Ruiz & Pav.) Mione & M. Nee, *Brittonia* 45: 144. 1993.

Species distribution. A Peruvian species endemic to *lomas* formations from Dept. Lima (Lachay, Atocongo, San Agustín).

Voucher. *Dillon et al. 3626* (F).

8. *Leptoglossis* Benth.

Petunioideae, Leptoglossinae

Generic distribution. *Leptoglossis* is a Neotropical genus of seven annual to perennial species, mostly Peruvian in distribution, but with one disjunct endemic species in Argentina. Four species are known from the *lomas* formations of coastal Peru.

Literature. Hunziker & Subils (1979a, 1979b).

8.1. *Leptoglossis darcyana* Hunz. & Subils, *Lorentzia* 3: 15. 1979.

Species distribution. A Peruvian species endemic to *lomas* formations from Dept. Arequipa (Atico) and Dept. Tacna (Sama Grande, Tacna).

Voucher. *Dillon & Dillon 3895* (F).

8.2. *Leptoglossis ferreyraei* Hunz. & Subils, *Bot. Mus. Leaf.* 27: 16. 1979.

Species distribution. A Peruvian species endemic to *lomas* formations from Dept. Arequipa (Jahuay, Atiquipa, Pongo).

Voucher. *Dillon et al. 8198* (F).

8.3. *Leptoglossis lomana* (Diels) Hunz., *Bot. Mus. Leaf.* 27: 18. 1979.

Species distribution. A Peruvian species endemic to *lomas* formations from Dept. Arequipa (Camaná, Capac, Mejía).

Voucher. *Hutchison 1298* (F).

8.4. *Leptoglossis schwenkioides* Benth., *Bot. Voy. Sulphur* 143. 1845.

Species distribution. A Peruvian species found throughout the northern Andean Cordillera and coastal *lomas* formations from Dept. La Libertad (Cerro Chiputur), Dept. Lima (Cajamarquilla).

Voucher. *Hutchison 1032* (F).

9. *Lycianthes* (Dunal) Hassler.

Solanoideae, Capsiceae

Generic distribution. *Lycianthes* is a Neotropical, shrubby genus of ca. 200 species distributed from East Asia and South America. A single widespread species is reported from the *lomas* of northern Peru.

9.1. *Lycianthes lycioides* (L.) Hassl., *Annuaire Conserv. Jard.*

Bot. Genève 20: 181. 1917.

Species distribution. A species widespread throughout South America from Venezuela to Argentina, and common in Andean Peru. In the coastal *lomas* formations, it is recorded from Dept. La Libertad (Cerro Campana, Cerro Chiputur, Cerro Cabras, Virú).

Voucher. *Dillon et al. 2701* (F).

10. *Lycium* L.

Solanoideae, Lycieae

Generic distribution. *Lycium* is a cosmopolitan genus of shrubs and subshrubs with ca. 80 species distributed throughout tropical and extra-tropical North and South America and the Galápagos Islands. In the coastal *lomas* formations, five species are recorded from Peru and Chile.

Literature. Bernardello (1986).

- 10.1. *Lycium americanum* Jacq., Select. Stirp. Amer. Hist.: 50. 1763.

Species distribution. A widespread species found throughout the Caribbean and South America. In Peru, it is widespread in both the Andean Cordillera and in *lomas* formations from Dept. La Libertad (Cerro Campana) and Dept. Lima (San Agustín, Cañete, Lurín).

Voucher. *Weberbauer 5226* (F).

- 10.2. *Lycium deserti* Phil., Fl. Atacama. 43. 1860.

Species distribution. A Chilean species recorded from high-elevation localities and *lomas* formations from Prov. Antofagasta (Paposo, Hueso Parado) and Prov. Atacama (Pan de Azúcar).

Voucher. *Dillon et al. 5555* (F).

- 10.3. *Lycium distichum* Meyen, Reise 1: 448. 1834.

Species distribution. A species recorded from high-elevation localities in southern Peru and northern Chile. Bernardello listed the voucher cited here, a Peruvian collection from Dept. Arequipa (Mollendo).

Voucher. *Gourlay 133* (K).

- 10.4. *Lycium leiostrum* Wedd., Chlor. Andina 2: 108. 1850.

Species distribution. A species recorded from the Andean Cordillera of Peru and from several *lomas* formations in northern Chile from Prov. Tarapacá (Iquique) and Prov. Antofagasta (Cerro Moreno, La Chimba, Quebrada El Rincón, Cifuncho, Quebrada Cachina).

Voucher. *Pinto s.n.* (SGO #143002).

- 10.5. *Lycium stenophyllum* Remy, in Gay, Flora Chilena 5: 94. 1849.

Species distribution. A species recorded from southern Peru and northern Chile. It is known from *lomas* formations from Peru, Dept. Arequipa (Mollendo), and Chile, Prov. Antofagasta (Cobija) and Prov. Atacama (Copiapó).

Voucher. *Dillon & Dillon 3961* (F).

11. *Nicandra* Adans.

Solanoideae, Nicandreae

Generic distribution. *Nicandra* is a monotypic genus thought to have originated in Peru but now widely distributed and weedy in tropical and subtropical regions around the world.

Literature. Hunziker (1979), Macbride (1962).

- 11.1. *Nicandra physalodes* (L.) Gaertn., Fruct. 2: 237, pl. 131, fig. 2. 1791.

Species distribution. A species recorded from throughout the Andean Cordillera of Peru, and reaching *lomas* formations from Dept. La Libertad (Cerro Cabezon, Cerro Campana, Cerro Chiputur, Virú) and Dept. Lima (Lurín). It is cultivated in Chile, but has not been recorded from the *lomas* formations in that country.

Voucher. *Dillon et al. 2707* (F).

12. *Nicotiana* L.

Nicotianoideae, Nicotianeae

Generic distribution. *Nicotiana* is a genus of about 95 species primarily distributed in South America, Australia, and the islands of the South Pacific. Peru has 15 species recorded from throughout the Andean Cordillera, and Chile has 13 species in central and southern regions. Most species are small to large herbs but a few are shrubby. Five species are represented in the *lomas* formations, two recorded from Chile and four from Peru.

Literature. Goodspeed (1954).

- 12.1. *Nicotiana glauca* Graham, Edinburgh New Philos. J. 5: 175. 1828.

Species distribution. A species native to Argentina, but worldwide in distribution. It is recorded from *lomas* formations from Peru, Dept. Arequipa (Mollendo) and Dept. Tacna (Sama Grande), and Chile, Prov. Atacama (Vallenar).

Voucher. *Ferreyra 12074* (F).

- 12.2. *Nicotiana glutinosa* L., Sp. Pl. 1: 181. 1753.

Species distribution. A species found throughout the Andean Cordillera of Peru and the Galápagos Islands. It is recorded from *lomas* formations of northern Peru, Dept. La Libertad (Cerro Cabezon, Virú).

Voucher. *Sagastegui & López 10985* (F).

- 12.3. *Nicotiana knightiana* Goodspeed, Univ. Calif. Publ. Bot. 18: 139. 1938.

Species distribution. A Peruvian species endemic to the *lomas* formations from Dept. Arequipa (Mollendo).

Voucher. *Worth & Morrison 15696* (UC).

- 12.4. *Nicotiana paniculata* L., Sp. Pl. 1: 180. 1753.

Species distribution. A Peruvian species from the Andean Cordillera and the *lomas* formations from Dept. La Libertad (Cerro Cabezon, Cerro Campana, Cerro Chiputur, Virú), Dept. Ancash (Casma, Lupín), Dept. Lima (Lachay, Manzano, Atocongo, Quilmaná), and Dept. Arequipa (Caparra, Mejía).

Voucher. *Dillon et al. 3634* (F).

- 12.5. *Nicotiana solanifolia* Walp., Repert. Bot. Syst. 3: 12. 1844–1845.

Species distribution. A Chilean species endemic to *lomas* formations from Prov. Antofagasta (Miguel Díaz, Paposo, Hueso Parado, Taltal) and Prov. Atacama (Chañaral).

Voucher. *Dillon et al. 5741* (F).

13. *Nolana* L.f.

Solanoideae, Nolaneae

Generic distribution. *Nolana* is a Neotropical genus distributed from northern Peru to southern Chile and one disjunct, endemic species in the Galápagos Islands (Tago & Dillon, 1999). Most of its ca. 85 species are confined to the *lomas* formations where 70 species are recorded from Peru and Chile. A few range into higher elevation sites in Peru and Chile, well inland and outside of the influence of coastal fogs. Four *Nolana* species have distributions crossing from southern Peru to northern Chile: *N. adansonii*, *N. gracillima*, *N. lycioides*, and *N. jaffuelii*. All other species are confined to either Chile or Peru, and most have narrow distributions.

Literature. Ferreyra (1961, 1974), Johnston (1936), Mesa (1981, 1986, 1997), Mesa et al. (1998), Tago & Dillon (1999).

- 13.1. *Nolana acuminata* (Miers) Miers ex Dunal, Prodr. 13: 12. 1852.

Species distribution. A Chilean species endemic to the *lomas* formations from Prov. Antofagasta to Prov. Valparaíso.

Voucher. *Dillon 8100* (F).

- 13.2. *Nolana adansonii* (Roem. & Schult.) I. M. Johnston, Contr. Gray Herb. 112: 47. 1936.

Species distribution. An endemic species found in the *lomas* formations of southern Peru, Dept. Arequipa (Atico, Atiquipa), and one disjunct population in northern Chile, Prov. Tarapacá (Iquique).

Voucher. *Dillon & Dillon 3744* (F).

- 13.3. *Nolana albescens* (Phil.) I. M. Johnston, Contr. Gray Herb. 112: 66. 1936.

- Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (La Cachina) and Prov. Atacama (Caldera, Bahía Inglesa, Copiapó).
Voucher. *Dillon & Dillon* 6040 (F).
- 13.4. *Nolana amplexicaulis* Ferreyra, Publ. Mus. Nat. Hist. "Javier Prado", Ser. B. 10: 7. 1955.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Capac).
Voucher. *Ferreyra* 11747 (USM).
- 13.5. *Nolana aplocaryoides* (Gaudich.) I. M. Johnst., Contr. Gray Herb. 112: 57. 1936.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Tarapacá (Iquique), Prov. Antofagasta (Salar del Carmen, Caleta Botija, Paposo, Taltal, Hueso Parado; Tortolas), and Prov. Atacama (Pan de Azúcar, Chañaral, Caleta Obispio, Caldera).
Voucher. *Dillon & Dillon* 5660 (F).
- 13.6. *Nolana arenicola* I. M. Johnst., Contr. Gray Herb. 112: 29. 1936.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Jahuay) and Dept. Tacna (Sama Grande).
Voucher. *Dillon et al.* 3284 (F).
- 13.7. *Nolana aticoana* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 10: 13. 1955.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Atico).
Voucher. *Dillon & Dillon* 3838 (F).
- 13.8. *Nolana baccata* (Lindl.) Dunal, Prodr. 13: 14. 1852.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Caldera, Copiapó, Huasco).
Voucher. *Martcorena* 1869 (CONC).
- 13.9. *Nolana balsamiflua* (Gaudich.) Mesa, Fl. Neotrop. 26: 68. 1981.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Cobija, Tocopilla).
Voucher. *Dillon & Dillon* 5726 (F).
- 13.10. *Nolana carnosia* (Lindl.) Miers ex Dunal, Prodr. 13: 14. 1852.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Caldera, Bahía Inglesa).
Voucher. *Dillon & Trujillo* 8093 (F).
- 13.11. *Nolana cerrateana* Ferreyra, Publ. Mus. Nat. Hist. "Javier Prado," Ser. B. 10: 11. 1955.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Atico, Camaná, Mollendo, Cachendo).
Voucher. *Dillon et al.* 8215 (F).
- 13.12. *Nolana clivicola* (I. M. Johnst.) I. M. Johnst., Contr. Gray Herb. 112: 73. 1936.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Tocopilla, La Chimba).
Voucher. *Dillon & Dillon* 5721 (F).
- 13.13. *Nolana coelestis* (Lindl.) Miers ex Dunal, Prodr. 13: 13. 1852.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Travesía, Huasco Bajo) and Prov. Coquimbo (La Serena).
Voucher. *Dillon et al.* 5436 (F).
- 13.14. *Nolana confinis* I. M. Johnst., Contr. Gray Herb. 112: 78. 1936.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Ica (Nasca), Dept. Arequipa (Ocoña, Mollendo), and Dept. Tacna (Sama Grande).
Voucher. *Dillon et al.* 3383 (F).
- 13.15. *Nolana coronata* Ruiz & Pav., Fl. Peruv. 2: 7, tab. 112b. 1799.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Jahuay, Atiquipa, Atico, Capac, Chala, Mollendo).
Voucher. *Dillon et al.* 8200 (F).
- 13.16. *Nolana crassulifolia* Poepp., Forriep's Not. Natur-Heilk. 23: 276. 1829.
Species distribution. A Chilean species recorded in the *lomas* formations of Prov. Atacama (Carrizal Bajo), and extending to coastal sites in Prov. Coquimbo and Prov. Valparaíso (Concon).
Voucher. *Dillon et al.* 5435 (F).
- 13.17. *Nolana deflexa* (I. M. Johnst.) I. M. Johnst., Contr. Gray Herb. 112: 71. 1936.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Pan de Azúcar).
Voucher. *Harding* 2 (GH).
- 13.18. *Nolana diffusa* I. M. Johnst., Contr. Gray Herb. 112: 77. 1936.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Miguel Díaz, Hueso Parado).
Voucher. *Dillon & Dillon* 5644 (F).
- 13.19. *Nolana divaricata* (Lindl.) I. M. Johnst., Contr. Gray Herb. 112: 64. 1936.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (La Chimba, Hueso Parado, Taltal, Bahía Tórtolas).
Voucher. *Dillon & Teillier* 5339 (F).
- 13.20. *Nolana elegans* (Phil.) Reiche, Anales Univ. Chile 125: 487. 1910.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Tocopilla, La Chimba, Caleta Botija, El Rincón, Paposo, Hueso Parado, Esmeralda) and Prov. Atacama (Caleta Obispio).
Voucher. *Dillon et al.* 5483 (F).
- 13.21. *Nolana filifolia* (Hook. & Arn.) I. M. Johnst., Revista Chilena Hist. Nat. 34: 231. 1930.
Species distribution. A Chilean species recorded from Prov. Atacama (Pan de Azúcar) and extending to Prov. Coquimbo (Buenos Aires, Huentelauquén).
Voucher. *Dillon & Teillier* 4973 (F).
- 13.22. *Nolana flaccida* (Phil.) I. M. Johnst., Contr. Gray Herb. 112: 60. 1936.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Las Bombas, Pan de Azúcar).
Voucher. *Dillon et al.* 5608 (F).
- 13.23. *Nolana gayana* (Gaudich.) Koch, Ind. Sem. Berol. 12. 1855.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. La Libertad (Cerro Chiputur) and Dept. Lima (Pasamayo, Atocongo).
Voucher. *Dillon et al.* 4676 (F).
- 13.24. *Nolana glauca* (I. M. Johnst.) I. M. Johnst., Contr. Gray Herb. 112: 66. 1936.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Pan de Azúcar) and Prov. Coquimbo (Los Vilos).
Voucher. *Dillon & Trujillo* 8019 (F).

- 13.25. *Nolana gracilliana* (I. M. Johnst.) I. M. Johnst., Contr. Gray Herb. 112: 59. 1936.
Species distribution. A species ranging from the *lomas* formations of southern Peru, Dept. Arequipa (Arequipa), Dept. Moquegua (Moquegua), Dept. Tacna (Sama Grande) to northern Chile, Prov. Tarapacá (Arica) and Prov. Antofagasta (Tocopilla).
Voucher. *Dillon et al.* 4773 (F).
- 13.26. *Nolana guentherii* I. M. Johnst., Contr. Gray Herb. 112: 55. 1936.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Cachendo).
Voucher. *Guenther & Buchtien* 113 (GH).
- 13.27. *Nolana humifusa* (Gouan) I. M. Johnst., Contr. Gray Herb. 112: 50. 1936.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. La Libertad (Cerro Cabezón, Cerro Campana, Cerro Cabras, Cerro Chiputur, Cerro Negro, Virú), Dept. Ancash (Casma, Lupín), and Dept. Lima (Lachay, Iguanil, Pasamayo, Amancaes, Cerro Agustino, Atocongo, Lurín).
Voucher. *Dillon et al.* 4654 (F).
- 13.28. *Nolana incana* (Phil.) I. M. Johnst., Contr. Gray Herb. 112: 68. 1936.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Mantancilla, Bandurrias, San Ramón) and Prov. Atacama (Esmeralda, Pan de Azúcar, Caleta Obispio).
Voucher. *Dillon & Trujillo* 8010 (F).
- 13.29. *Nolana inconspicua* (I. M. Johnst.) I. M. Johnst., Contr. Gray Herb. 112: 73. 1936.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Cobija, Tocopilla, Cerro Moreno, La Chimba).
Voucher. *Teillier* 457 (CONC).
- 13.30. *Nolana inflata* Ruiz & Pav., Fl. Peruv. 2: 7, tab. 112a. 1799.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Cháparra, Atiquipa, Atico).
Voucher. *Dillon et al.* 3844 (F).
- 13.31. *Nolana insularis* (I. M. Johnst.) I. M. Johnst., Contr. Gray Herb. 112: 49. 1936.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Ica (Isla de San Gallán).
Voucher. *Murphy* 3472 (GH).
- 13.32. *Nolana intonsa* I. M. Johnst., Contr. Gray Herb. 112: 34. 1936.
Species distribution. A Chilean species endemic to the *lomas* formations of Tarapacá (Iquique).
Voucher. *Pinto s.n.* (SGO #142968).
- 13.33. *Nolana ivaniana* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 10: 3. 1955.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Mollendo).
Voucher. *Dillon et al.* 8219 (F).
- 13.34. *Nolana jaffuelii* I. M. Johnst., Contr. Gray Herb. 112: 39. 1936.
Species distribution. A species endemic to the *lomas* formations of Chile, Prov. Tarapacá (Iquique), Prov. Antofagasta (Tocopilla) and Peru, Dept. Tacna (Tacna).
Voucher. *Pinto s.n.* (SGO #142973).
- 13.35. *Nolana johnstonii* Vargas, Rev. Univ. (Cuzco) 107: 155. 1954.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Moquegua (Ilo).
Voucher. *Dillon et al.* 8225 (F).
- 13.36. *Nolana latipes* I. M. Johnst., Contr. Gray Herb. 112: 30. 1936.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Mollendo, Mejía).
Voucher. *Worth* 15709 (F).
- 13.37. *Nolana leptophylla* (Miers) I. M. Johnst., Contr. Gray Herb. 112: 73. 1936.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Cobija, El Cobre, Quebrada Médano, Taltal) and Prov. Atacama (Carrizal Bajo), and can range to interior sites above 2000 m.
Voucher. *Dillon et al.* 5730 (F).
- 13.38. *Nolana linearifolia* Phil., Anales Univ. Chile 91: 28. 1895.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Tocopilla, Punta Hornos, Cuesta Barriles, Cerro Moreno, La Chimba, Paposo, Quebrada San Ramón).
Voucher. *Dillon et al.* 5890 (F).
- 13.39. *Nolana lycioides* I. M. Johnst., Contr. Gray Herb. 112: 70. 1936.
Species distribution. A species endemic to the *lomas* formations of Chile, Prov. Tarapacá (Iquique), and Peru, Dept. Moquegua (Ilo) and Dept. Tacna (Sama Grande).
Voucher. *Dillon et al.* 8227 (F).
- 13.40. *Nolana mariarosae* Ferreyra, Bol. Soc. Peruana Bot. 7(1–2): 3. 1974.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Atico, Ocoña).
Voucher. *Ferreyra* 12490 (USM).
- 13.41. *Nolana minor* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 10: 4. 1955.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Camaná), possibly extinct due to habitat destruction at type locality.
Voucher. *Ferreyra* 2535 (USM).
- 13.42. *Nolana mollis* (Phil.) I. M. Johnst., Contr. Gray Herb. 112: 61. 1936.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Paposo, Taltal, Tórtolas) and Prov. Atacama (Pan de Azúcar, Copiapó).
Voucher. *Dillon & Trujillo* 8015 (F).
- 13.43. *Nolana pallida* I. M. Johnst., Contr. Gray Herb. 112: 69. 1936.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Ica (Marcona) and Dept. Arequipa (Jahuay, Atico, Capac, Atiquipa).
Voucher. *Dillon et al.* 8205 (F).
- 13.44. *Nolana pallidula* I. M. Johnst., Contr. Gray Herb. 112: 31. 1936.
Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Atiquipa, Atico, Camaná), Dept. Moquegua (Ilo), and Dept. Tacna (Sama Grande, Tacna).
Voucher. *Dillon et al.* 8226 (F).
- 13.45. *Nolana parviflora* (Phil.) Phil., Anales Univ. Chile 91: 29. 1895.
Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Pajonales, Caldera, Monte Amargo).
Voucher. *Werdermann* 460 (GH).

- 13.46. *Nolana pearcei* I. M. Johnst., Contr. Gray Herb. 112: 58. 1936.
Species distribution. A Peruvian species endemic to the lomas formations of Dept. Tacna (Tacna).
Voucher. *Pearce s.n.* (BM #21199).
- 13.47. *Nolana peruviana* (Gaudich.) I. M. Johnst., Contr. Gray Herb. 112: 66. 1936.
Species distribution. A Chilean species endemic to the lomas formations of Prov. Tarapacá (Iquique), Prov. Antofagasta (Tocopilla, Cerro Moreno, La Chimba, El Cobre, Paposo), and Prov. Atacama (Carrizal Bajo).
Voucher. *Dillon & Dillon 5622* (F).
- 13.48. *Nolana pilosa* I. M. Johnst., Contr. Gray Herb. 112: 79. 1936.
Species distribution. A Peruvian species endemic to the lomas formations of Dept. Arequipa (Mollendo, Mejía, Cachendo).
Voucher. *Dillon & Dillon 3908* (F).
- 13.49. *Nolana platyphylla* (I. M. Johnst.) I. M. Johnst., Contr. Gray Herb. 112: 60. 1936.
Species distribution. A Peruvian species endemic to the lomas formations of Dept. Moquegua (Moquegua).
Voucher. *Weberbauer 7455* (F).
- 13.50. *Nolana plicata* I. M. Johnst., Contr. Gray Herb. 85: 174. 1929.
Species distribution. A Peruvian species endemic to the lomas formations of Dept. Ica (Marcona), Dept. Arequipa (Jahuay, Atiquipa).
Voucher. *Dillon et al. 3225* (F).
- 13.51. *Nolana polymorpha* Gaudich., Voy. Bonite, Bot., pl. 101. 1851.
Species distribution. A Peruvian species endemic to the lomas formations of Dept. Lima (Isla San Lorenzo).
Voucher. *Gaudichaud s.n.* (F #1000362).
- 13.52. *Nolana pterocarpa* Phil., Anales Univ. Chile 91: 27. 1895.
Species distribution. A Chilean species endemic to the lomas formations of Prov. Atacama (Copiapó, Carrizal Bajo).
Voucher. *Dillon & Teillier 5040* (F).
- 13.53. *Nolana ramosissima* I. M. Johnst., Contr. Gray Herb. 112: 72. 1936.
Species distribution. A Chilean species endemic to the lomas formations of Prov. Antofagasta (Miguel Díaz, Paposo, La Rinconada, Mantancilla).
Voucher. *Dillon et al. 8085* (F).
- 13.54. *Nolana rostrata* (Lindl.) Miers ex Dunal, Prodr. 13: 14. 1852.
Species distribution. A Chilean species endemic to the lomas formations of Prov. Atacama (Bahía Inglesa, Carrizal Bajo) and Prov. Coquimbo (El Tofo).
Voucher. *Dillon & Teillier 5051* (F).
- 13.55. *Nolana rupicola* Gaudich., Voy. Bonite, Bot., pl. 28. 1841.
Species distribution. A Chilean species endemic to the lomas formations of Prov. Antofagasta (Cerro Moreno, La Chimba, Taltal), Prov. Atacama (Pan de Azúcar, Chañaral, Flamenco, Travesía), and Prov. Coquimbo (Fray Jorge, Coquimbo).
Voucher. *Dillon & Trujillo 8005* (F).
- 13.56. *Nolana salsoloides* (Lindl.) I. M. Johnst., Contr. Gray Herb. 112: 62. 1936.
Species distribution. A Chilean species endemic to the lomas formations of Prov. Antofagasta (Paposo, Taltal), Prov. Atacama (Pan de Azúcar, Carrizal Bajo), and Prov. Coquimbo (Ovalle).
Voucher. *Dillon & Trujillo 8047* (F).
- 13.57. *Nolana scaposa* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 10: 5. 1955.
Species distribution. A Peruvian species endemic to the lomas formations of Dept. Arequipa (Jahuay, Atiquipa, Atico, Camaná).
Voucher. *Dillon et al. 8209* (F).
- 13.58. *Nolana sedifolia* Poepp., Froriep's Not. Natur-Heilk. 23: 276. 1829.
Species distribution. A Chilean species endemic to the lomas formations of Prov. Tarapacá (Iquique), Prov. Antofagasta (Cobija, Cerro Moreno, La Chimba, Mantancilla, Hueso Parado, Taltal), Prov. Atacama (Caleta Obispio, Travesía), and Prov. Coquimbo (Papudo).
Voucher. *Dillon & Trujillo 8007* (F).
- 13.59. *Nolana spathulata* Ruiz & Pav., Fl. Peruv. 2: 7, tab. 113a. 1799.
Species distribution. A Peruvian species endemic to the lomas formations of Dept. Arequipa (Jahuay, Atico, Atiquipa, Mollendo, Cachendo), Dept. Moquegua (Ilo), and Dept. Tacna (Sama Grande, Tacna).
Voucher. *Dillon et al. 4784* (F).
- 13.60. *Nolana spergularioides* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 10: 8. 1955.
Species distribution. A Peruvian species endemic to the lomas formations of Dept. Arequipa (Camaná).
Voucher. *Weigend & Förther 971766* (F).
- 13.61. *Nolana sphaerophylla* (Phil.) Mesa, Soc. Biol. Chile, Not. Biol. 6: 199. 1998.
Species distribution. A Chilean species endemic to Prov. Atacama (Quebrada Flamenco, El Salado).
Voucher. *Marticorena 9893* (CONC).
- 13.62. *Nolana stenophylla* I. M. Johnst., Contr. Gray Herb. 85: 103. 1929.
Species distribution. A Chilean species endemic to the lomas formations of Prov. Antofagasta (Tocopilla, La Chimba, Miguel Díaz, Paposo).
Voucher. *Dillon & Dillon 5664* (F).
- 13.63. *Nolana thinophila* I. M. Johnst., Contr. Gray Herb. 112: 61. 1936.
Species distribution. A Peruvian species endemic to the lomas formations of Dept. Ica (Marcona), Dept. Arequipa (Jahuay, Lomas, Atico, Ocoña, Camaná, Mollendo, Mejía).
Voucher. *Dillon & Dillon 3851* (F).
- 13.64. *Nolana tocopillensis* (Phil.) I. M. Johnst., Contr. Gray Herb. 112: 78. 1936.
Species distribution. A Chilean species endemic to the lomas formations of Prov. Antofagasta (Cobija, Tocopilla).
Voucher. *Johnston 3603* (GH).
- 13.65. *Nolana tomentella* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 10: 10. 1955.
Species distribution. A Peruvian species endemic to the lomas formations of Dept. Arequipa (Jahuay).
Voucher. *Dillon et al. 8159* (F).
- 13.66. *Nolana tovariana* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 10: 14. 1955.
Species distribution. A Peruvian species endemic to Dept. Arequipa (Camaná, Ocoña).
Voucher. *Ferreyra 8861* (GH).
- 13.67. *Nolana villosa* (Phil.) I. M. Johnst., Contr. Gray Herb. 112: 70. 1936.
Species distribution. A Chilean species endemic to the lomas formations of Prov. Antofagasta (Cerro Moreno, Punta

Plata, Paposo, San Ramón, Hueso Parado, Taltal, Los Zanjones, Tórtolas) and Prov. Atacama (Caldera), and can range to interior sites above 2000 m.

Voucher. *Dillon et al.* 5136 (F).

13.68. *Nolana volcanica* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 12: 3. 1960.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Mollendo).

Voucher. *Dillon et al.* 4835 (F).

13.69. *Nolana weissiana* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 10: 9. 1955.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Chala, Cháparra, Capac).

Voucher. *Hutchison* 1326 (F).

13.70. *Nolana willeana* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 12: 1. 1960.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Ica (Lomas de Amará).

Voucher. *Kore s.n.* (USM).

14. *Physalis* L.

Solanoideae, Physaleae, Physalinae

Generic distribution. *Physalis* is a Neotropical genus with perhaps 80 species; its highest diversity is in Mexico with ca. 70 species, and a few species are found in the United States, Central America, and the Caribbean. In South America, 12 species are recorded in tropical and subtropical regions; two widespread species are recorded from the *lomas* formations of coastal Peru.

Literature. Macbride (1962), Martínez (1999).

14.1. *Physalis angulata* L., Sp. Pl. 1: 183. 1753.

Species distribution. A species ranging from the United States, Mexico, the Galápagos Islands, and throughout Andean South America to Peru. In Peru, it is widespread in the Andean Cordillera, but only recorded in one *lomas* formation, Dept. La Libertad (Cerro Cabezón).

Voucher. *Leiva et al.* 2172 (F).

14.2. *Physalis peruviana* L., Sp. Pl. 2: 1670. 1763.

Species distribution. In Peru, it is widespread in the Andean Cordillera and often cultivated, but only recorded in one *lomas* formation, Dept. Lima (Chorillos).

Voucher. *Gentry & Prance* 16455 (F).

15. *Reyesia* Gay

Cestroideae, Salpiglossideae

Generic distribution. *Reyesia* is a Neotropical genus of four species confined to northern Chile, with one reaching adjacent western Argentina.

Literature. Hunziker & Subils (1979b).

15.1. *Reyesia chilensis* Gay, Flora Chilena 4: 418, lam. 52. 1849.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Tocopilla, Taltal) and Prov. Atacama (Copiapó, Huasco, Coquimbo).

Voucher. *Dillon & Teillier* 5215 (F).

15.2. *Reyesia cactorum* (L. M. Johnston.) D'Arcy, Ann. Missouri Bot. Gard. 65: 712. 1978.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Aguada del Cardon).

Voucher. *Johnston* 5258 (GH).

16. *Salpiglossis* Ruiz & Pav.

Cestroideae, Salpiglossideae

Generic distribution. *Salpiglossis* is a Neotropical genus with only two species, both endemic to Chile.

Literature. D'Arcy (1978), Hunziker & Subils (1979b, 1986).

16.1. *Salpiglossis spinescens* Clos, in Gay, Fl. Chilena 5: 127. 1849.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Tierra Amarilla, Chañarillo).

Voucher. *Werdermann* 419 (F).

17. *Schizanthus* Ruiz & Pav.

Schizanthoideae, Schizanthaceae

Generic distribution. *Schizanthus* is a Neotropical genus of 9 to 12 annual species largely confined to Chile; two species are disjunct to adjacent Argentina.

Literature. Grau & Gronbach (1984), Hunziker (1979, 2000).

17.1. *Schizanthus candidus* Lindl., Bot. Reg. 29, t. 45. 1843.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Carrizal Bajo).

Voucher. *Philippi s.n.* (SGO #55393).

17.2. *Schizanthus integrifolius* Phil., Anales Univ. Chile 43: 530. 1873.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Chañaral) and Prov. Coquimbo (Vicuña), and occurring in both high and low elevations.

Voucher. *Martcorena et al.* 1586 (F).

17.3. *Schizanthus lacteus* Phil., Reise Atacama 46. 1860.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Paposo, Taltal).

Voucher. *Dillon et al.* 5744 (F).

17.4. *Schizanthus laetus* Phil., Reise Atacama 45. 1860.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Tocopilla, Paposo, Taltal).

Voucher. *Dillon & Teillier* 5173 (F).

18. *Solanum* L.

Solanoideae, Solaneae

Generic distribution. *Solanum* is a cosmopolitan genus of ca. 1250 species, with estimates of 850 species from South America. Within the *lomas* formations of Chile and Peru, 21 species are represented, and among these, five have traditionally been treated under *Lycopersicon*.

Literature. Correll (1967), D'Arcy (1972), Edmonds (1972), Hawkes (1990), Johnston (1931), Macbride (1962), Nee (1999), Ochoa (1962), Olmstead & Palmer (1997), Rick (1986), Rick & Lamm (1955), Rick & Tanksley (1981), Rick et al. (1977, 1979), Ugent (1975).

18.1. *Solanum brachyantherum* Phil., Anales Univ. Chile 43: 522. 1873.

Species distribution. A Chilean species endemic to *lomas* formations of Prov. Tarapacá (Iquique) and Prov. Antofagasta (Tocopilla, La Chimba, El Cobre, Miguel Díaz, Paposo, Taltal).

Voucher. *Dillon et al.* 5534 (F).

18.2. *Solanum chancayense* Ochoa, Agronomía (Lima) 26: 316. 1959.

Species distribution. A Peruvian species endemic to *lomas*

formations of Dept. La Libertad (Cerro Cabras, Cerro Chipitir) and Dept. Lima (Lachay, Chancay, Quilmaná).

Voucher. Ochoa 11765 (F).

18.3. *Solanum chilense* (Dunal) Reiche, Fl. Chile 5: 358. 1910.

Species distribution. A species widely distributed in coastal localities from southern Peru to northern Chile. Within the *lomas* formations of Peru, it ranges from Dept. Moquegua and Dept. Tacna, south to Prov. Tarapacá (Azapa, Iquique) and in Chile, Prov. Antofagasta (Tocopilla, Paposo, Taltal). In floras recognizing *Lycopersicon*, this species is treated as *L. chilense* Dunal, *L. atacamensis* Phil., or *L. bipinnatifidum* Phil.

Voucher. Dillon et al. 5560 (F).

18.4. *Solanum ferreyrae* Ugent, Phytologia 31: 18. 1975.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Jahuay).

Voucher. Ferreyra 1523 (USM).

18.5. *Solanum fragile* Wedd., Chlor. Andina 2: 105. 1859.

Species distribution. A species widely distributed throughout the Andean Cordillera from Ecuador, Peru, Chile, and Argentina. The type was collected in southern Peru (Dept. Tacna) at elevations > 3000 m. Though collections from the *lomas* formations have been annotated as *S. fragile*, the species encountered from Dept. Arequipa (Atiquipa) appear distinct and possibly represent an undescribed species.

Vouchers. Ochoa & Salas 14901 (F), Weigend & Förther 97/925 (F), Worth & Morrison 15704 (F).

18.6. *Solanum habrochaites* S. Knapp & D. M. Spooner, Novon 9: 375. 1999.

Species distribution. A widespread species from southwestern Ecuador to south-central Peru. Within the *lomas* formations, it is restricted to Dept. La Libertad (Cerro Campana, Cerro Cabezón, Cerro Cabras). This species has been treated as *Solanum agrimoniifolium* Dunal, or in treatments recognizing *Lycopersicon* as *L. hirsutum* Dunal.

Voucher. Dillon et al. 4665 (F).

18.7. *Solanum immite* Dunal, Prodr. 13: 32. 1852.

Species distribution. A widespread Peruvian species from the Andean Cordillera and coastal habitats. In the *lomas* formations, it is recorded from Dept. La Libertad (Virú) and Dept. Lima (Supe, Chancay).

Voucher. Bernardi 16413 (F).

18.8. *Solanum medianis* Bitter, Repert. Spec. Nov. Regni Veg. 11: 366. 1912.

Species distribution. A widespread Peruvian species from the Andean Cordillera and coastal habitats. In the *lomas* formations, it is recorded from Dept. Lima (Quilmaná, Cerro Agustino), Dept. Arequipa (San Juan, Camaná, Atiquipa, Chala), Dept. Moquegua (Ilo), and Dept. Tacna (Sama Grande).

Voucher. Ochoa & Salas 14900 (F).

18.9. *Solanum mochiquense* Ochoa, Agronomía (Lima) 26: 111. 1959.

Species distribution. A widespread Peruvian species from the eastern lowlands to coastal habitats. In the *lomas* formations, it is known from Dept. La Libertad (Cerro Campana, Cerro Chipitir, Cerro Cabras, Virú).

Voucher. Angulo 1213 (F).

18.10. *Solanum montanum* L., Sp. Pl. 1: 186. 1753.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Lambayeque (Cerro Reque), Dept. La Libertad (Cerro Chipitir, Cerro Campana, Cerro Cabras, Virú), Dept. Ancash (Casma), Dept. Lima (Lachay, Pasamayo, Chorrillos, Amancaes, Atocongo, Manzano, Lupín, Pachacamac), and Dept.

Arequipa (Capac, Atiquipa). The synonym *S. tuberiferum* Dunal has been applied to this species.

Voucher. Dillon et al. 4685 (F).

18.11. *Solanum multifidum* Lam., Tabl. Encycl. 2: 17. 1794.

Species distribution. A widespread Peruvian species from the Andean Cordillera to coastal habitats. In the *lomas* formations, it is recorded from Dept. La Libertad (Cerro Cabezón, Cerro Campana, Cerro Cabras), Dept. Ancash (Lupín), Dept. Lima (Pasamayo), Dept. Arequipa (Caravelí, Atico, Mollendo, Cachendo), and Dept. Tacna (Tacna). The synonym *S. senecioides* Dunal has been applied to this species.

Voucher. Dillon et al. 4741 (F).

18.12. *Solanum murphyi* I. M. Johnston, Contr. Gray Herb. 95: 34. 1931.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Ica (Isla San Gallán, Islas de las Viejas).

Voucher. Murphy 3219 (GH).

18.13. *Solanum neoweberbaueri* Wittm., Bot. Jahrb. Syst. 50 (Suppl.): 540. 1914.

Species distribution. A Peruvian species ranging from high-elevation localities in the central Andean Cordillera and recorded from the *lomas* formations of Dept. Lima (Morro Solar, Chorrillos).

Voucher. Weberbauer 5683 (F).

18.14. *Solanum pennellii* Correll, Madroño 14: 233. 1958.

Species distribution. A widespread Peruvian species from the Andean Cordillera and recorded from the *lomas* formations of Dept. La Libertad (Cerro Cabezón, Virú), Dept. Ica (Nasca), and Dept. Arequipa (Chala). In floras recognizing *Lycopersicon*, this species has been treated as *Lycopersicon pennellii* (Correll) D'Arcy.

Voucher. Leiva et al. 2193 (F).

18.15. *Solanum peruvianum* L., Sp. Pl. 186. 1753.

Species distribution. A species recorded from the Andean Cordillera and coastal habitats. It is widespread in the *lomas* formations, occurring in Peru from Dept. La Libertad (Cerro Cabezón, Cerro Campana, Cerro Prieto, Cerro Chipitir, Virú), Dept. Lima (Lachay, Iguanil, Amancaes, Cerro Agustino, Atocongo), Dept. Arequipa (Atiquipa, Capac, Atico, Camaná, Mollendo), and Dept. Tacna (Pampa Mogollo), and in northern Chile, Prov. Tarapacá (Azapa). In floras recognizing *Lycopersicon*, this species has been treated as *L. hirsutum* Dunal or *L. peruvianum* (L.) Mill.

Voucher. Dillon et al. 4665 (F).

18.16. *Solanum phyllanthum* Cav., Ic. 4: 35, tab. 359, fig. 2. 1797.

Species distribution. A widespread species recorded from the *lomas* formations of northern Chile, Prov. Antofagasta (Paposo) and Peru from Dept. La Libertad (Cerro Campana) and Dept. Lima (Chancay, Amancaes). The synonym *S. paposanum* Phil. has been applied to this species.

Voucher. Dillon et al. 2720 (F).

18.17. *Solanum pimpinellifolium* L., Cent. Pl. 1: 8. 1755.

Species distribution. A widespread species ranging from the Andean Cordillera of southern Ecuador to Peru. In the *lomas* formations, it is recorded from Dept. La Libertad (Cerro Campana), Dept. Lima (Atocongo, Amancaes, Pachacamac), and Dept. Tacna (Sama Grande). In treatments recognizing *Lycopersicon*, this species has been treated as *L. pimpinellifolium* (L.) Mill.

Voucher. Dillon et al. 2703 (F).

18.18. *Solanum radicans* L.f., Dec. Pl. Horti Upsal. 1, tab. 10. 1762.

Species distribution. A Peruvian species widespread from

the eastern lowlands, Andean Cordillera, and coastal habitats. In the *lomas* formations it is recorded from Dept. La Libertad (Cerro Campana), Dept. Arequipa (Mollendo), Dept. Moquegua (Ilo), and Dept. Tacna (Pampa Mogollo).

Voucher. *Dillon et al.* 4755 (F).

18.19. *Solanum remyanum* Phil., *Anales Univ. Chil.* 91: 17. 1895.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (El Cobre, Paposo, Taltal), Prov. Atacama (Pan de Azúcar, Pampa de Caracoles), and Prov. Coquimbo (Punta Arrayán).

Voucher. *Dillon et al.* 5477 (F).

18.20. *Solanum tuberosum* L., *Sp. Pl.* 1: 185. 1753.

Species distribution. A widespread species in the Andean Cordillera as a cultivated herb and the source of potatoes. It is a rare in Peruvian *lomas* formations, but has been encountered as a cultivated species during El Niño events when local inhabitants take advantage of increased soil moisture to cultivate various crops.

Voucher. No voucher seen, but the author has observed it cultivated in Dept. La Libertad (Cerro Cabezón).

18.21. *Solanum wittmackii* Bitter, *Repert. Spec. Nov. Regni Veg.* 12: 54. 1913.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Lima (Amancaes, San Gerónimo).

Voucher. *Macbride* 5890 (F).