## Geographic Variation among Closely Related, Highly Variable Species with a Wide Distribution Range: the South Andean-Patagonian *Nassauvia* subgenus *Strongyloma* (Asteraceae, Nassauvieae)

# Marcela V. Nicola,<sup>1,3</sup> Leigh A. Johnson,<sup>2</sup> and Raúl Pozner<sup>1</sup>

<sup>1</sup>Instituto de Botánica Darwinion, Casilla de Correo 22, B1642HYD, San Isidro, Buenos Aires, Argentina. <sup>2</sup>Department of Biology and Bean Life Science Museum, 401 WIDB, Brigham Young University, Provo, Utah 84602, U. S. A. <sup>3</sup>Author for correspondence (mnicola@darwin.edu.ar)

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Abstract—Morphological variation among the five species of Nassauvia subgenus Strongyloma was assessed through statistical analyses of morphometric traits in populations throughout the southern Andean-Patagonian region. Uni- and multivariate analyses were used to identify patterns of morphological variation in relation to geography. Additionally, species distribution modeling was implemented to relate these patterns to climatic conditions. No well-defined groups could be recovered through multivariate analyses, although we observed some geographic structure. Latitudinal variation was found in leaves, phyllaries and cypselas, with a cline towards the south, where these structures become shorter and wider. Towards the east, the number of flowers per capitulum decreases, and abaxial corolla lips and cypselas become anarower and shorter. Distribution modeling showed several areas of contact and a large overlap of suitable conditions for more than one species, which is mainly related to the mean temperature of winter. Despite an association between morphological variation with geography and climate. Further genetic analyses are still needed to identify the probable processes that led to the complex patterns of observed variation.

Keywords—Morphological variation, multivariate analyses, populations, South America, species complex, species distribution modeling.

The study of variation within species that are widely distributed at extensive spatial scales provides an opportunity to observe evolution in progress and understand systematic diversity (Judd et al. 2002; Mascó et al. 2004; Chalcoff et al. 2008). Morphological variation is expected in plants that are widely distributed through different environments because they often respond to direct and indirect environmental factors with changes in phenology, vegetative growth, and reproductive traits. This response gives rise to changes in phenotypic characteristics between populations of the same or related species (Paruelo et al. 1998; Jobbágy et al. 2002) as polymorphisms within populations increase or decrease in frequency along geographic transects (Grant 1989). A taxonomically perplexing case of a polymorphic taxon with wide geographical range is Nassauvia Comm. ex Juss. subgenus Strongyloma (DC) Cabrera (Asteraceae, Nassauvieae), an early diverging Asteracean group from the South Andean-Patagonian region.

Nassauvia is one of the most widely distributed genera in the South Andean-Patagonian region. It comprises 38 species endemic to South America, distributed from southern Bolivia, through the Andes and the Patagonian steppe of Chile and Argentina, to Tierra del Fuego and The Malvinas/ Falkland Islands (Cabrera and Willink 1973; Cabrera 1982; Arroyo and Marticorena 1988; Katinas et al. 2009). The genus is divided into two subgenera and four sections, including herbs and small shrubs with imbricate leaves, solitary to aggregate capitula of one to five flowers, bilabiate corollas, style branches crowned by apical papillae, the pappus usually narrowly paleaceous, and gametic chromosome numbers of *n* = 11, 22, ca. 44 (Cabrera 1982; Hunziker et al. 1991; Katinas et al. 2009). Nassauvia subgen. Strongyloma is a welldefined group of small shrubs with a tendency toward heteroblastic development, subulate leaves with a vaginate base accompanied, when brachyblasts are present, by small leaves in rosettes, and with pubescent cypselas. Alpha taxonomy studies discern five species within subgen. Strongyloma (Cabrera 1982): N. axillaris (Lag. ex Lindl.) D. Don, N. fuegiana (Speg.) Cabrera, N. glomerulosa (Lag. ex Lindl.) D. Don,

N. maeviae Cabrera, and N. ulicina (Hook. f.) Macloskie. These species are defined on the basis of the number of flowers per capitulum, type of capitulescence, presence or absence of brachyblasts, and shape and longitude of leaves (Cabrera 1982; Table 1). Variation in these morphological traits does not, however, strictly follow species boundaries. Wide morphological variation within and among these species of this subgenus was observed (Cabrera 1982), suggesting that experimental analyses were needed to refine the species circumscription. Subsequently, a morphological cladistic analysis showed no resolution among these species (Freire et al. 1993). We have observed many plants in the field with differing combinations of the diagnostic morphological characters of these taxa (Table 1). Furthermore, herbarium specimens have been identified differently by various specialists, reinforcing the confusing species boundaries encountered in this group. Thus, interspecific variation in subgen. Strongyloma seems to be extensive, in part due to its geographic distribution, which is as wide as the distribution of the entire genus (excluding the Malvinas/Falkland Islands), including diverse climatic conditions and habitats (Paruelo et al. 1998).

A morphological cladistic analysis supported the monophyly of subgen. Strongyloma (Freire et al. 1993). However, a more recent molecular phylogenetic study based on the ITS region of nuclear ribosomal DNA, showed that subgen. Strongyloma is polyphyletic (Maraner et al. 2012), with N. axillaris placed separately from N. fuegiana, N. glomerulosa, and N. ulicina (N. maeviae was not included in the analysis). However, Maraner et al. (2012: p. 404) explained that "although N. axillaris is placed in section Mastigophorus [i.e. subgen. Nassauvia] by analyses of ITS data, it groups with other representatives of subgen. Strongyloma in a plastid phylogeny (Maraner and Stuessy, unpublished). Indeed, the preponderance of evidence [i.e. several morphological traits], including the inflorescence type, places *N. axillaris* in subgen. Strongyloma". Possible reasons for the discordant placement of N. axillaris by the ITS sequences of Maraner et al. (2012) are an error in sample or sequence identity, or the availability of divergent sequence paralogs. Indeed, their ITS sequence of

Species	Cabrera (1982)	Personal observations						
N. axillaris	Dimorphic leaves.	Dimorphic leaves.						
	Linear-subulate macroblast leaves (10–30 mm long).	Macroblast leaves with narrow, long, triangular blade, crowning a wide sheath (10.4–31.4 mm total length).						
	Linear brachyblast leaves (3–10 mm long).	Brachyblast leaves with narrow, long triangular blade, and narrow sheath (2.7–16.0 mm total length).						
	Lateral dichasia with 1–3 capitula.	Lateral or terminal solitary capitula, or lateral or terminal dichasia with 2–4 capitula.						
	5 flowers per capitulum.	5 flowers per capitulum.						
	Corolla 5 mm long.	Corolla 4.1–7.0 mm long.						
N. fuegiana	Isomorphic leaves.	Isomorphic leaves to foliar dimorphism little evident.						
,	Linear-subulate leaves (6–15 mm long).	Macroblast leaves with narrow, long, triangular blade, crowning a wide sheath (6.5–25.7 mm total length).						
	Lateral and solitary capitula.	Brachyblast leaves absent or similar to those of <i>N. axillaris</i> (1.8–12.4 mm total length).						
	5 (exceptionally fewer) flowers per capitulum.	Lateral or terminal solitary capitula, or lateral or terminal dichasia with 2–4 capitula.						
	Corolla 5.5 mm long.	3–5 flowers per capitulum.						
	0	Corolla 4.4–6.8 mm long.						
N. glomerulosa	Dimorphic leaves.	Dimorphic leaves.						
n gronier meen	Linear-subulate macroblast leaves (5–10 mm long).	Macroblast leaves with narrow, long, triangular blade, crowning a wide sheath (2.3–16.8 mm total length).						
	Elliptic brachyblast leaves (1 mm long).	Brachyblast leaves with wide, short, triangular blade, crowning a wide sheath (1.9–10.2 mm total length).						
	Lateral or terminal capitula, and solitary or in dichasia with 2–3 capitula.	Lateral or terminal solitary capitula, or lateral dichasia with 2–3 capitula.						
	5 flowers per capitulum.	2–5 flowers per capitulum.						
	Corolla 5–6 mm long.	Corolla 3.5–6.1 mm long.						
V. maeviae	Isomorphic leaves.	Isomorphic leaves to foliar dimorphism little evident.						
	Oblong-linear leaves (1–3 mm long).	Macroblast leaves with narrow, short, triangular blade, crowning a wide sheat (2.3–4.3 mm total length).						
	Terminal and solitary capitula.	Brachyblast leaves absent or similar to those of <i>N. glomerulosa</i> (2.4–3.0 mm total length).						
	3 flowers per capitulum.	Terminal and solitary capitula.						
	Corolla 3.2 mm long.	3 flowers per capitulum.						
		Corolla 4.1–4.4 mm long.						
N. ulicina	Dimorphic leaves.	Dimorphic leaves.						
	Linear-subulate macroblast leaves (5–12 mm long).	Macroblast leaves with narrow, long, triangular blade, crowning a wide shea (3.9–17.1 mm total length).						
	Linear brachyblast leaves (1–3 mm long).	Brachyblast leaves with narrow, short triangular blade, crowning a wide sheat (1.1–5.2 mm total length).						
	Lateral or terminal dichasia with 2-4 capitula.	Lateral or terminal solitary capitula, or lateral or terminal dichasia with 2–4 capitula.						
	1–3 flowers per capitulum.	2–3 flowers per capitulum.						
	Corolla 4–4.5 mm long.	Corolla 2.7–5.6 mm long.						

TABLE 1. Distinguishing traits of the five species traditionally recognized for *Nassauvia* subgen. *Strongyloma*, contrasting the descriptions of Cabrera (1982; left column) and our personal observations (right column).

*N. axillaris* differs by at least 26 base pairs (4.3%) from 10 *N. axillaris* sequences we have obtained for this species. A re-analysis of the ITS data set of Maraner et al. (2012) with 53 ITS sequences obtained from multiple populations of species of subgen. *Strongyloma* (including the 10 *N. axillaris* sequences), recovers a monophyletic subgen. *Strongyloma* with our sequences of *N. axillaris* placed among other members of subgen. *Strongyloma*, corroborating our expectations based on morphology (tree not shown). A preliminary phylogeographic analysis of subgen. *Strongyloma* based on two plastid molecular markers (Nicola et al. in prep.) further supports the inclusion of *N. axillaris* within subgen. *Strongyloma*.

In this context, the present study intended to improve our understanding of the patterns of morphological variation in *Nassauvia* subgen. *Strongyloma*. More specifically, we were interested to see if: (1) the five recognized species of subgen. *Strongyloma* can be consistently identified using multivariate analyses based on morphological data; (2) the distinctive traits of species belonging to subgen. *Strongyloma* are correlated geographically; and (3) biologically relevant climatic data can help illuminate patterns of morphological variation in these species. To accomplish these goals, we used uni- and multivariate analyses to statistically identify patterns of morphological variation (Jensen 2003; Henderson 2006 and literature therein) of Nassauvia subgen. Strongyloma. We also applied statistical analyses to assess relationships between morphological variation and geographic or climatic gradients. Additionally, we used geographic and environmental data and new modeling techniques (Graham et al. 2004; Hijmans et al. 2005; Soberón and Peterson 2005; Elith et al. 2006) to further understand how abiotic factors impact the geographic limits of lineages and species (Graham et al. 2004; Wiens and Graham 2005; Rissler and Apodaca 2007). For that, we performed species distribution modeling as a means to understand how temperature, precipitation, or seasonality might influence the patterns of geographic variation encountered in this subgenus and possible associations with putative species limits.

#### MATERIALS AND METHODS

Sampling Procedures and Traits Measured—We sampled 65 localities distributed throughout the range of the five species of Nassauvia subgen.

Strongyloma, from southern Bolivia (ca. 21° S) to southern Argentina (ca. 53° S), and from western Chile (ca. 74° W) to eastern Argentina (ca. 64° W), mainly in the Patagonian steppe but also in the Andean region, from sea level to 4,250 m above sea level (a. s. l.) (Fig. 1; Appendix 1). Taxonomic identity of each population was established following Cabrera (1982). A total of 172 individuals approximately at the same stage of development were collected: samples of 131 individuals (five to eight plants per locality) were preserved in 70% ethanol, while 37 individuals were sampled from herbarium specimens (from CORD, CONC, and SI) to augment the field collected specimens. Four individuals were based on type images (from G, K, and LP). Samples were dissected under a Zeiss 47 50 52-9901 stereomicroscope, and morphometric measurements (n = 516) were taken with a calibrated eyepiece micrometer. Herbarium material was hydrated with hot water and detergent, and type images were measured using Image Tool 3.0 (UTHSCSA 2000). A single person obtained three measurements (pseudo-replicates) per plant.

Thirty-one morphological traits were considered in this study (abbreviations given between brackets; Appendix 2). The variables examined were: habit (H; 1 = shrub, 2 = cespitose, and 3 = cushion; Halloy 1990), presence or absence of foliar dimorphism (FD), total macroblast leaf length (MLL), total brachyblast leaf length (BLL), brachyblast leaf width (BLW), brachyblast leaf length/brachyblast leaf width ratio as an estimator of leaf shape (BLS), brachyblast leaf length × brachyblast leaf width ratio as an estimator of leaf area (BLA), presence or absence of lateral (LC) or terminal (TC) solitary capitula, and lateral (LD) or terminal dichasia (TD), peduncle length (PL), number of outer phyllaries (NOP), length of outer phyllaries (LOP), width of outer phyllaries (WOP), outer phyllaries length/outer phyllaries width ratio as an estimator of outer phyllaries shape (OPS), outer phyllaries length × outer phyllaries width ratio as an estimator of outer phyllaries area (OPA), number of inner phyllaries (NIP), length of inner phyllaries (LIP), width of inner phyllaries (WIP), inner phyllaries length/inner phyllaries width ratio as an estimator of inner phyllaries shape (IPS), inner phyllaries length × inner phyllaries width ratio as an estimator of inner phyllaries area (IPA), number of flowers per capitulum (NFC), abaxial lip length (ALL), abaxial lip width (ALW), abaxial lip length/abaxial lip width ratio as an estimator of abaxial lip shape (ALS), abaxial lip length × abaxial lip width ratio as an estimator of abaxial lip area (ALA), cypsela length (CL), cypsela width (CW), cypsela length/cypsela width ratio as an estimator of cypsela shape (CS), and cypsela length × cypsela width ratio as an estimator of cypsela area (CA). We included morphological characters used by Cabrera (1982) to distinguish subgen. Strongyloma species to test their discriminative value (FD, MLL, BLL, BLS, and NFC). We also included a wide selection of vegetative and reproductive characters (selected because of their independence and variability among individuals) to see if additional traits supported the delimitation of species in this subgenus, and to characterize, for the first time, leaf, flower, and fruit variation in this group of plants across its geographic range.

Both brachy- and macroblast leaves of subgen. Strongyloma are sessile with a sheathing base. Even though different brachyblast leaf shapes were previously described for species belonging to subgen. Strongyloma (Cabrera 1982; ovate in N. glomerulosa and linear in the remaining species), this was due to the inclusion of both base and blade in the general outline of N. glomerulosa leaves, but not for the other species. Our preliminary observations showed that the blade is always triangular (wide, short to narrow, long) with inwards folded margin when young, expanded at maturity. As brachyblast leaves have uniform shapes, we used the length/width ratio to measure variation of proportions within the same basic shape avoiding the general size effect. The same criterion was applied to phyllaries, abaxial corolla lips, and cypselas. In spite of being a tridimensional structure, we also used length and width as descriptors of cypsela variation because cypselas are not compressed, having a circular transverse section that is uniform across these taxa. Nevertheless, because we are characterizing this tridimensional structure in just two dimensions, we approached our interpretation of variation with caution.

*Morphometric Analyses*—To comply with assumptions of normality and homocedasticity, log<sub>10</sub> transformation was applied to BLL, BLW, BLS, BLA, OPS, LIP, WIP, IPS, IPA, ALS, ALA, CL, and CS, and square root transformation to MLL, PL, OPA, CL, CW, and CA data, although multivariate procedures are considered to be relatively insensitive to deviations from normality (Tabachnik and Fidell 2001; Henderson 2006). We standardized variables prior to all analyses. In addition, we reduced some data because of multicolinearity among morphological variables using a consensus between principal component analysis (PCA), Spearman's rank correlation coefficients (r<sub>S</sub>), and variance inflation factors (VIF). Finally, we selected a subset of 18 morphological variables (H, MLL, BLS, LC, TC, LD, TD, PL, NOP, LOP, OPS, IPS, NFC, ALW, ALS, ALA, CL, and CS) to conduct the statistical analyses. For multivariate analyses referred to populations, a data matrix was prepared with mean values of all variables for each population.

Cluster analysis (CA) of populations was performed using the 18 morphological variables selected above, to gain insights into the natural structure of the observations under study. Hierarchical clustering used the average linkage method, and distances between clusters were calculated using Euclidean distances. The highest value of the cophenetic correlation coefficient was used to select one of several alternative groupings. From the resulting phenograms of the CA, we applied a modified Population Aggregation Analysis (PAA; Davis and Nixon 1992) proposed by Henderson (2004, 2005) for the identification of phylogenetic species. Under this technique species are recognized by unique combinations of qualitative character states and varieties are based on significant mean value differences of quantitative characters. We performed PCA using the quantitative morphological variables to describe the multivariate pattern of the morphological variability among populations and to identify the variables that most contribute to the variability between observations.

Discriminant analysis (DA) of quantitative morphological variables was used to discriminate the five species defined a priori (following Cabrera 1982) in a space where differences between groups are maximized and variation within groups is minimized. DA was also used to assess the relative importance of the variables for discriminating amongst groups. Morphological variables selected by PCA and DA as contributing to the majority of the variables in box plots to show variability between the five species. All statistical analysis and graphs were carried out in InfoStat 2.0 (Di Rienzo et al. 2011) and implemented in the software package R 2.13 (R Development Core Team 2011).

Analyses of Climatic and Geographic Patterns of Variation-We recorded altitude (Alt), and latitudinal (LatS) and longitudinal (LonW) coordinates from localities for N. axillaris (43 populations), N. fuegiana (19 populations), N. glomerulosa (135 populations), and N. ulicina (26 populations), covering the entire distribution range of each species using a handheld Geographical Positioning System (GPS) unit. The remaining 36 point localities of N. fuegiana and N. ulicina obtained from herbarium specimens were geo-referenced using Google Earth 6.0 (http://www .google.com/earth/index.html). Given that geographic and taxonomic mistakes can produce a first error source in the models (Feeley and Silman 2010; Newbold 2010), we reviewed carefully the identification of specimens and their associated geographic data. The software based on the maximum-entropy approach for species habitat modeling, Maxent (Phillips et al. 2004), has little sensitivity to sample size, but no algorithm predicts consistently well with small sample sizes (n < 30). Therefore, we considered these two predictions as exploratory models (Wisz et al. 2008) that can be compared later according to the quality of the data (Pliscoff and Fuentes-Castillo 2011).

Environmental information represented by 19 bioclimatic variables derived from the monthly temperature and rainfall values with a spatial resolution of 2.5 arc-minutes (5 km<sup>2</sup>) were downloaded from the WorldClim 1.4 database (http://www.worldclim.org/current; Hijmans et al. 2005). These were: annual mean temperature (Bio1), mean diurnal range (Bio2), isothermality (Bio3), temperature seasonality (Bio4), maximum temperature of warmest period (Bio5), minimum temperature of coldest period (Bio6), temperature annual range (Bio7), mean temperature of wettest quarter (Bio8), mean temperature of driest quarter (Bio9), mean temperature of warmest quarter (Bio10), mean temperature of coldest quarter (Bio11), annual precipitation (Bio12), precipitation of wettest period (Bio13), precipitation of driest period (Bio14), precipitation seasonality (Bio15), precipitation of wettest quarter (Bio16), precipitation of driest quarter (Bio17), precipitation of warmest quarter (Bio18), and precipitation of coldest quarter (Bio19). These environmental variables were extracted for each locality using Diva-Gis 7.3 (Hijmans et al. 2001; Appendix 3).

To avoid over-estimation of climatic data that can lead to misleading results (Elith et al. 2002, 2011; Phillips et al. 2004; Peterson and Nakazawa 2008) we reduced some data because of multicolinearity among climatic variables following a procedure implemented by various authors (e.g. Rissler et al. 2006; Werneck et al. 2011; Sede et al. 2012). We generated 2,000 random points from across Argentina, Bolivia, and Chile using Geo Midpoint (http://www.geomidpoint.com/random/), extracted environmental data in Diva-Gis 7.3 (Hijmans et al. 2001), and conducted a series of correlation tests using a Pearson correlation coefficient  $\geq 0.75$  ( $p \leq 0.001$ ). We also implemented PCA and VIF, and determined a consensus between these three multicolinearity tests to identify highly correlated variables. Finally, we selected ten variables that were considered more

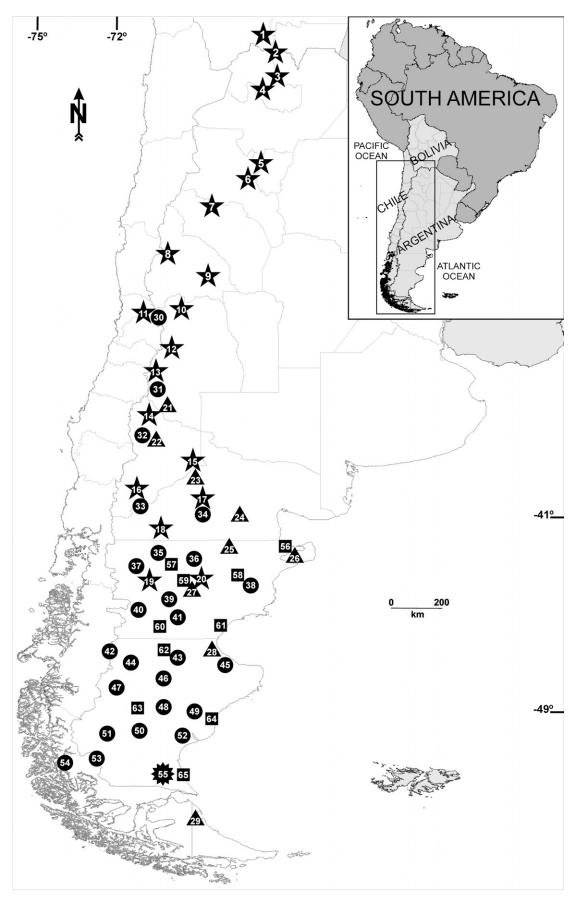


FIG. 1. Location of the 65 populations of *Nassauvia* subgen. *Strongyloma* in the South Andean-Patagonian region. Full locality names are provided in Appendix 1. Symbols indicate the five species according to Cabrera (1982): star *N. axillaris*, triangle *N. fuegiana*, circle *N. glomerulosa*, sun *N. maeviae*, and square *N. ulicina*.

TABLE 2. Spearman correlation coefficients (r<sub>S</sub>) between selected morphological variables, and environmental and geographical data. Significance levels: \* *p*, 0.05; \*\* *p*, 0.01; \*\*\* *p*, 0.001.

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	MLL	BLS	PL	NOP	LOP	OPS	IPS	NFC	ALW	ALS	ALA	CL	CS	Alt	LatS	LonW
Bio1	0.19	0.25*	0.05	-0.18	-0.08	0.24*	0.32**	-0.35**	-0.16	0.11	-0.11	-0.10	0.23	-0.34**	0.15	0.47***
Bio3	0.59***	0.38**	-0.07	-0.12	0.10	0.30*	0.32**	0.33**	0.12	0.09	0.16	-0.19	0.10	0.72***	0.82***	0.15
Bio7	0.68***	0.50***	0.18	-0.01	0.07	0.35**	0.40**	0.23	0.15	0.06	0.24*	-0.05	0.12	0.56***	0.76***	0.32**
Bio8	0.23	0.18	-0.22	-0.26*	-0.19	0.14	0.18	-0.24	-0.28*	0.16	-0.26*	-0.34**	0.27*	-0.08	0.20	0.59***
Bio9	0.09	0.18	0.28*	0.00	0.07	0.13	0.40***	-0.22	0.15	-0.04	0.22	0.26*	0.05	-0.29*	0.04	-0.04
Bio11	0.15	0.20	-0.02	-0.22	-0.07	0.21	0.27*	-0.35**	-0.18	0.12	-0.14	-0.11	0.25*	-0.40***	0.10	0.46***
Bio12	-0.01	-0.02	0.02	0.02	0.22	0.05	0.06	0.21	0.24	-0.05	0.25*	0.12	0.00	0.14	0.12	-0.37**
Bio15	0.43***	0.28*	-0.01	-0.06	0.15	0.21	0.15	0.28*	0.05	0.02	0.10	-0.24*	-0.09	0.65***	0.69***	0.00
Bio18	0.07	-0.06	-0.33**	-0.06	0.02	-0.03	-0.08	0.09	-0.15	0.13	-0.18	-0.25*	0.13	0.13	0.12	0.27*
Bio19	-0.17	-0.05	0.27*	0.10	0.22	-0.02	0.07	0.06	0.38**	-0.20	0.39**	0.39**	-0.07	-0.18	-0.20	-0.62***
Alt	0.50***	0.24	0.02	0.11	0.12	0.11	-0.01	0.54***	0.14	0.03	0.19	-0.16	-0.19			
LatS	0.73***	0.45***	0.01	-0.13	0.09	0.39**	0.37**	0.30**	0.06	0.12	0.15	-0.22	0.06			
LonW	0.29*	0.26*	-0.21	-0.23	-0.05	0.33**	0.26*	-0.25*	-0.32**	0.15	-0.33**	-0.39**	0.30*			

biologically meaningful and directly relevant to these species. These were: Bio1, Bio3, Bio7, Bio8, Bio9, Bio11, Bio12, Bio15, Bio18, and Bio19. Multicolinearity tests were performed in InfoStat 2.0 (Di Rienzo et al. 2011) and implemented in the software package R 2.13 (R Development Core Team 2011).

We first measured the degree of association between the morphological variables with the environmental and geographic data selected above for each of the 63 populations individually (Table 2). We then modeled the present potential geographic distribution of each species of *Nassauvia* subgen. *Strongyloma* using known point locality information and the environmental data selected in Diva-Gis 7.3 (Hijmans et al. 2001) and Maxent 3.3.3, with the maximum entropy machine-learning algorithm (Phillips et al. 2004). A model for *N. maeviae* could not be achieved due to extremely low number of known localities (only one with certainty). Nonetheless, we considered point locality information and relevant trends of this species.

The bioclimatic layers were trimmed to the areas surrounding each species and then projected over a larger region that included latitude  $17^{\circ}41'$  S to  $55^{\circ}49'$  S and longitude  $57^{\circ}31'$  W to  $75^{\circ}43'$  W for all species in Diva-Gis. Projections in Maxent were run using the following settings for all models: 10 replicates with auto features, response curves, jackknife tests, logistic output format, random seed, random test percentage = 10, replicate run type = crossvalidate, regularization multiplier = 1, maximum iterations = 1,000, convergence threshold = 0.00001, and maximum number of background points = 10,000 following a similar procedure described by Fontanella et al. (2012) and Sede et al. (2012). To determine the threshold value for each projection, we used the minimum training value averaged over the 10 runs. Variable importance was determined comparing percent contribution values and jackknife plots.

#### Results

Cluster Analysis—Considerable heterogeneity exists across the entire dataset used in the cluster analysis (CA, Fig. 2). Populations of N. axillaris tend to group together, although most stepparian populations within this species are well separated from a separate cluster of mostly Andean populations. Andean populations of N. axillaris are closer to N. glomerulosa populations than stepparian populations of N. axillaris. Populations of N. glomerulosa were grouped together in one large cluster, with the exception of the southernmost population from Chile, which was grouped with populations of N. ulicina. Furthermore, populations of N. ulicina remained grouped in one cluster, with the exception of a population located in northern Santa Cruz Province, which was grouped with stepparian populations of N. axillaris. Lastly, populations of N. fuegiana were distributed throughout the different clusters defined above, and the sample of N. maeviae was grouped with populations of N. ulicina. Population Aggregation Analysis failed to recover any major cluster characterized by a unique combination of qualitative character states, or with significant differences in mean values of quantitative traits.

Principal Component Analysis-In the principal component analysis (PCA), the first three principal components (PC) accounted for 70% of the variation across populations (Fig. 3). The first PC expressed mainly variation in macroblast leaf length (MLL; eigenvector = +0.32), brachyblast leaf length (BLL; +0.37), outer phyllaries shape (OPS; +0.41), inner phyllaries shape (IPS; +0.35), and cypsela shape (CS; +0.39), generally contrasting longer leaves and longer and narrower phyllaries and cypselas in populations at the right extreme of the scatter plot with shorter leaves and shorter and wider phyllaries and cypselas in populations at the left extreme of the resulting scatter plot (Fig. 3A). The second PC expressed mainly variation in abaxial corolla lip area (ALA; +0.51), abaxial corolla lip width (ALW; +0.43), and cypsela length (CL; +0.42), with larger areas of abaxial corolla lips, wider abaxial corolla lips, and longer cypselas at the upper extreme of the scatter plot; and smaller areas of abaxial corolla lips, narrower abaxial corolla lips, and shorter cypselas at the lower extreme of the resulting scatter plot (Fig. 3A). The third PC expressed mainly variation in abaxial corolla lip shape (ALS; +0.59), number of flowers per capitulum (NFC; +0.48), and ALW (-0.46), contrasting populations with longer and narrower abaxial corolla lips and higher number of flowers per capitulum at the upper extreme of the scatter plot; and populations with shorter and wider abaxial corolla lips and lower number of flowers per capitulum at the lower extreme of the resulting scatter plot (Fig. 3B). We observed relatively undifferentiated data clouds consistent with the unclear clustering revealed in the CA, and a mixture of populations relative to the five species traditionally recognized by Cabrera (1982).

**Discriminant Analysis**—In the discriminant analysis (DA), the first two canonical axes accounted for 95% of the overall variation among populations (Fig. 4). Because the third canonical axis explained less than 4% of the variation, only results from the first two axes were reported. Prediction ellipses with 95% confidence for the five groups defined a priori overlapped in the plane and their centroids lie close to one another along each of the first two axes. Cross-validation obtained from the discriminant function gave an average error rate of 5%, meaning that one sample of *N. axillaris* should be clustered with *N. fuegiana*, one sample of *N. glomerulosa* should be grouped with *N. maeviae*, and one sample of *N. ulicina* should be clustered with *N. maeviae*. Although the average error rate was low, when we successively included more populations in the analysis, the overlap of the ellipses was

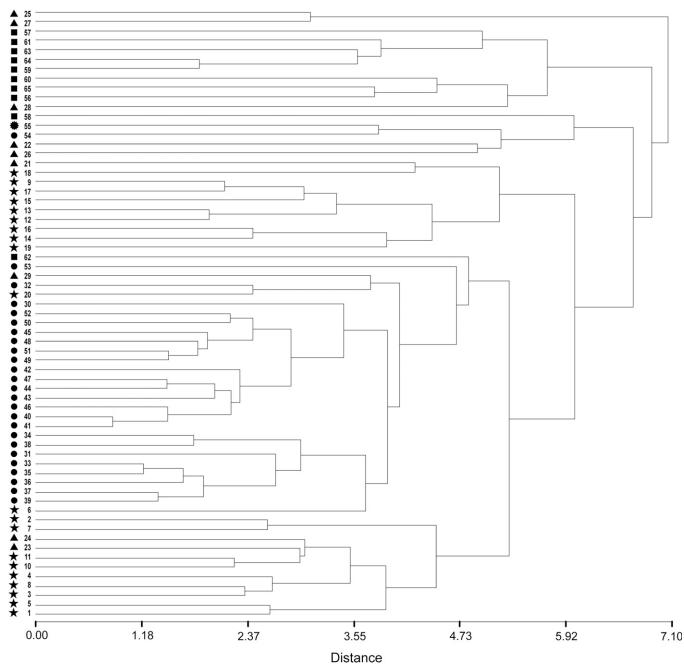


FIG. 2. Resulting phenogram of cluster analysis (CA) of the 65 populations of *Nassauvia* subgen. *Strongyloma* studied based on 18 morphological variables. Full locality names are provided in Appendix 1. Symbols indicate the five species according to Cabrera (1982): star *N. axillaris*, triangle *N.* 

correspondingly greater. Populations of *N. axillaris* are well differentiated from populations of *N. maeviae–N. ulicina* on the first axis, based on differences in ALW (wider abaxial corolla lips in populations at the right extreme of the scatter plot) and ALA (larger areas of abaxial corolla lips in populations at the left extreme of the resulting scatter plot). Differences in ALW (wider abaxial corolla lips in populations at the upper extreme of the scatter plot) and ALA (larger areas of abaxial corolla lips in populations at the upper extreme of the scatter plot) and ALA (larger areas of abaxial corolla lips in populations at the lower extreme of the resulting scatter plot) allowed discriminating the observations between the *N. glomerulosa* group and the *N. ulicina* group on the second axis. Populations of *N. axillaris* remained clearly separated from populations of *N. glomerulosa* and *N. ulicina*. Populations of *N. glomerulosa* remained separated from pop-

fuegiana, circle N. glomerulosa, sun N. maeviae, and square N. ulicina.

ulations of *N. ulicina*, with the exception of two populations of *N glomerulosa*; one from eastern Chubut Province and other from the center of Río Negro Province. Finally, we observed that populations of *N. fuegiana* were distributed through the groups of populations of *N. axillaris* and *N. ulicina*, and the population of *N. maeviae* was grouped with populations of *N. ulicina*. These results were consistent with the resulting phenogram obtained from the CA and with the resulting scatter plot of the PCA.

Descriptive Statistics and Correlation Coefficients— Variation within the five species traditionally recognized by Cabrera (1982) based on the 65 populations examined and the ten quantitative characters (MLL, BLS, OPS, IPS, NFC, ALW, ALS, ALA, CL, and CS) selected by PCA and DA as most

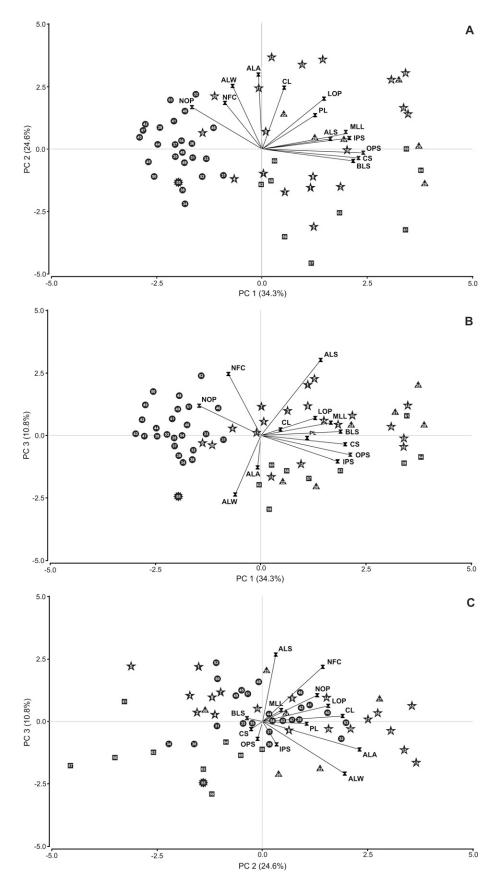


FIG. 3. Scatter plots of the first three principal components of the principal component analysis (PCA) of the 65 populations of *Nassauvia* subgen. *Strongyloma* studied based on 13 quantitative morphological variables. The eigenvalues associated with each PC are provided in parentheses. Full names of populations are provided in Appendix 1 and acronyms for the different morphological variables are in Materials and Methods. Arrows show the contribution of each variable to the PCs. Symbols indicate the five species according to Cabrera (1982): star *N. axillaris*, triangle *N. fuegiana*, circle *N. glomerulosa*, sun *N. maeviae*, and square *N. ulicina*. A. PC1 versus PC2. B. PC1 versus PC3. C. PC2 versus PC3.

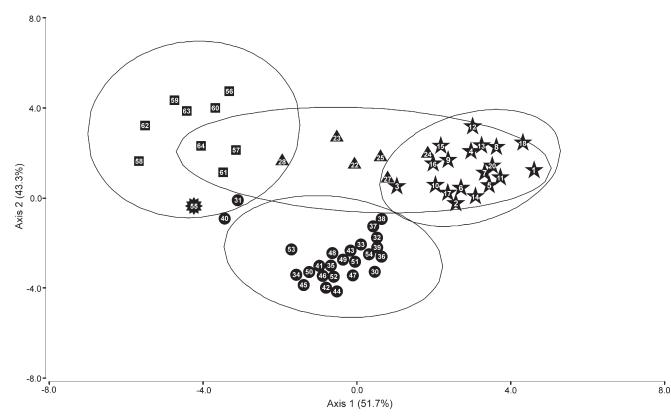


FIG. 4. Representation of multivariate observations into five groups defined a priori according to the five species recognized by Cabrera (1982) in the discriminant space formed by the first two canonical axes of the discriminant analysis (DA) using the 65 populations of *Nassauvia* subgen. *Strongyloma* studied and 13 quantitative morphological variables. The eigenvalues associated with each axis are provided in parentheses. Outlines correspond to ellipses of prediction. Symbols indicate the five species according to Cabrera (1982): star *N. axillaris*, triangle *N. fuegiana*, circle *N. glomerulosa*, sun *N. maeviae*, and square *N. ulicina*.

informative, reveals ranges of variation in each character that overlap to such an extent that none of them can be used individually to reliably delimit species in this subgenus (Fig. 5). In general, leaf traits showed higher coefficients of variation (52.7–130.6%) than floral traits (13.8–70.5%; Appendix 2).

Like other statistical values, correlation values do not explain causality; we therefore only report significant values with apparent biological meaning for some of the selected variables. MLL was significantly and positively correlated with isothermality (Bio3;  $r_S = +0.59$ , p < 0.001), the temperature annual range (Bio7;  $r_s = +0.68$ , p < 0.001), and the precipitation seasonality (Bio15;  $r_S = +0.43$ , p < 0.001). BLS was also significantly and positively correlated with Bio3 ( $r_s = +0.38$ , p < 0.01), Bio7 ( $r_s = +0.50$ , p < 0.001), and Bio15 ( $r_s = +0.28$ , p < 0.05). OPS and IPS were significantly and positively correlated with the annual mean temperature (Bio1;  $r_S = +0.24$ , p < 0.05 and  $r_S =$ +0.32, p < 0.01 respectively), Bio3 ( $r_S = +0.30$ , p < 0.05 and  $r_S =$ +0.32, p < 0.01 respectively), and Bio7 ( $r_s = +0.35$ , p < 0.01 and  $r_{\rm S}$  = +0.40, p < 0.01 respectively). NFC was significantly and positively correlated with Bio3 ( $r_s = +0.33$ , p < 0.01) and Bio15 ( $r_s = +0.28$ , p < 0.05), and negatively correlated with Bio1 ( $r_s =$ -0.35, p < 0.01) and the mean temperature of the coldest quarter (Bio11;  $r_s = -0.35$ , p < 0.01). ALW, ALA, and CL were significantly and negatively correlated with the mean temperature of the wettest quarter (Bio8;  $r_{\rm S} = -0.28$ , p < 0.05;  $r_{\rm S} = -0.26$ , p < 0.05 and  $r_{\rm S} = -0.34$ , p < 0.01 respectively) and positively correlated with the precipitation of the coldest quarter (Bio19;  $r_{\rm S}$  = +0.38, *p* < 0.01;  $r_{\rm S}$  = +0.39, *p* < 0.01 and  $r_{\rm S}$  = +0.39, *p* < 0.01 respectively; Table 2). In the principal component analysis, the first PC showed a weak correlation with South latitude (LatS;

 $\mathbf{r}_{\rm S}$  = +0.44, p < 0.001), West longitude (LonW;  $\mathbf{r}_{\rm S}$  = +0.34, p < 0.01), Bio3 ( $\mathbf{r}_{\rm S}$  = +0.31, p < 0.05), and Bio7 ( $\mathbf{r}_{\rm S}$  = +0.39, p < 0.01). The second PC showed a weak correlation with LonW ( $\mathbf{r}_{\rm S}$  = -0.43, p < 0.001), Bio8 ( $\mathbf{r}_{\rm S}$  = -0.41, p < 0.01), Bio11 ( $\mathbf{r}_{\rm S}$  = -0.28, p < 0.05), and Bio19 ( $\mathbf{r}_{\rm S}$  = +0.43, p < 0.001). The third PC showed a weak correlation with the mean temperature of the driest quarter (Bio 9;  $\mathbf{r}_{\rm S}$  = -0.30, p < 0.05) and Bio19 ( $\mathbf{r}_{\rm S}$  = -0.30, p < 0.05) and Bio19 ( $\mathbf{r}_{\rm S}$  = -0.30, p < 0.05) and Bio19 ( $\mathbf{r}_{\rm S}$  = -0.30, p < 0.05) and Bio19 ( $\mathbf{r}_{\rm S}$  = -0.30, p < 0.05) and Bio19 ( $\mathbf{r}_{\rm S}$  = -0.30, p < 0.05) and Bio19 ( $\mathbf{r}_{\rm S}$  = -0.30, p < 0.05) and Bio19 ( $\mathbf{r}_{\rm S}$  = -0.30, p < 0.05) and Bio19 ( $\mathbf{r}_{\rm S}$  = -0.30, p < 0.05) and Bio19 ( $\mathbf{r}_{\rm S}$  = -0.30, p < 0.05).

In general, plants with longer and narrower leaves, phyllaries, and cypselas were associated with a wider annual temperature range, as registered in northern Patagonia. Variation moved clinally towards the south, where those structures were shorter and wider, and annual temperature range was narrower. Plants with greater number of flowers per capitulum (five or, less commonly, four), longer cypselas, and wider abaxial corolla lips with larger area were associated with lower temperatures and higher precipitation of winter, as occurs in western Patagonia. Towards the east, the number of flowers per capitulum was lower (three or, less commonly, one or two), cypselas were shorter, and abaxial corolla lips were narrower with a smaller area, while registered temperature in winter was higher and precipitation was lower. As values mentioned above were relatively low and the correlations were relatively weak in all cases, the results should be interpreted cautiously. Groups of populations resulting from the multivariate analyses were not clearly related to any geographical and/or ecological range.

*Species Distribution Modeling*—Species distribution models show the minimum presence threshold for the five named entities that constitute *Nassauvia* subgen. *Strongyloma* 

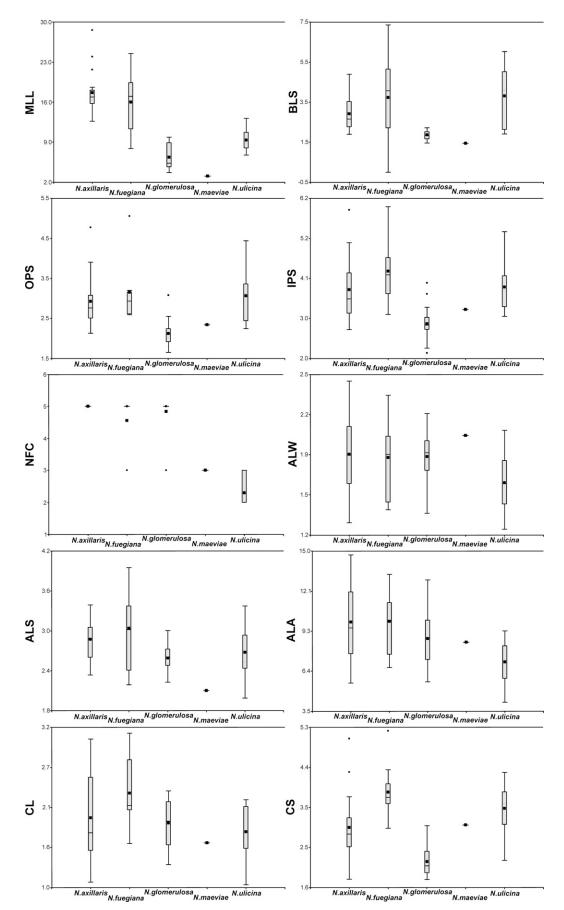


FIG. 5. Box-plots describing the variation of quantitative characters in *Nassauvia* subgen. *Strongyloma* according to the five species traditionally recognized by Cabrera (1982). Acronyms for the different morphological variables are in Materials and Methods.

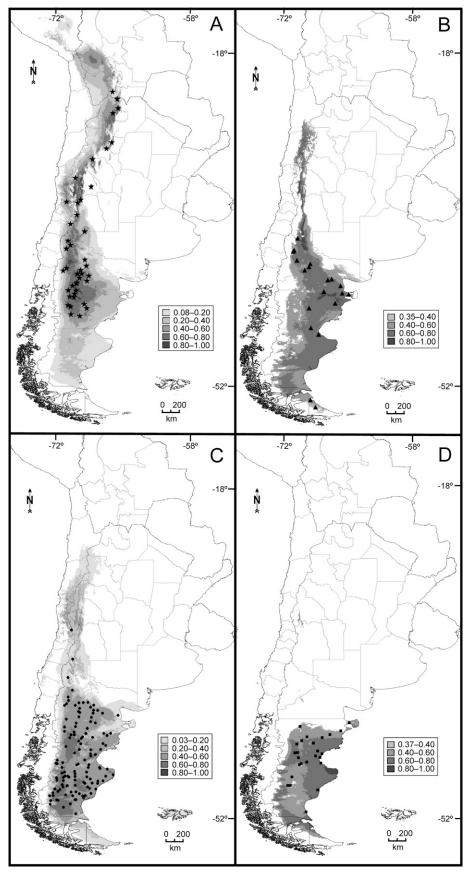


FIG. 6. Predictive distribution models for the species that traditionally constitute *Nassauvia* subgen. *Strongyloma* showing habitat suitability in southern South America. Darker colors indicate regions with a higher probability of species occurrence; lowest values correspond to the minimum training presence logistic threshold. Symbols refer to point localities on which the models are based: A. *N. axillaris*, B. *N. fuegiana*, C. *N. glomerulosa*, and D. *N. ulicina*. *N. maeviae* was not analyzed.

(Fig. 6). The mean values of the area under the curve (AUC) of the receiver-operating characteristic (ROC) were 99.5% ( $\pm 4\%$ ), 99.6% ( $\pm 2\%$ ), 99.2 ( $\pm 2\%$ ), and 99.7% ( $\pm 1\%$ ) for *N. axillaris*, *N. fuegiana*, *N. glomerulosa*, and *N. ulicina*, respectively.

For *N. axillaris*, some overprediction between projected and realized distribution areas was found, mainly in northwestern Bolivia, southwestern Perú, and Santa Cruz Province in Argentina, where this species has never been observed. Although the highest percent contribution (pc) was from variable Bio3 (pc = 43.1%) and the largest permutation importance (pi) was from Bio1 (pi = 45.2%), Jackknife tests showed Bio11 to have the most useful information when used in isolation (pc = 0.9%; pi = 30.7%) and Bio7 to have the most information than other variables (pc = 4.8%; pi = 5.9%). In addition, some overprediction was found for the distribution model of N. fuegiana, mainly in the Andes of western Argentina and eastern Chile, and in Santa Cruz Province in Argentina, where the species has never been collected. The environmental variable with the most useful information by itself and not present in the other variables was Bio11 (pc = 4.1%; pi = 84.3%). The projection of the distribution model for N. glomerulosa was a fairly good representation of the extant geographical distribution of this species, although some discordances with the known distribution were found, particularly in the Andes of western Argentina and eastern Chile, in the Islas Malvinas/ Falkland Islands, and in Tierra del Fuego Province in Argentina. Nevertheless, it has been recorded in the latter. Jackknife tests showed Bio11 to have the most useful information when used in isolation (pc = 12.2%; pi =1.6%) and Bio18 to have the most unique information (pc = 32.2%; pi = 27.9%). For *N. ulicina*, the distribution model showed great similarity with the current distribution of the species. Jackknife tests showed Bio11 to have the most useful information when used in isolation (pc = 1.1%; pi = 56%) and Bio7 to have the most unique information (pc = 6.6%; pi = 19.3%).

Considering relevant trends, suitable conditions for *N. axillaris* occurred mostly in the Andes of Argentina, Bolivia, and Chile from  $18^{\circ}$  S to  $45^{\circ}$  S. Appropriate environments for *N. fuegiana* were in the Andes of Argentina from  $31^{\circ}$  S to  $38^{\circ}$  S and also in the steppe, in northeastern Chubut Province, in Argentina. For *N. glomerulosa*, suitable habitats occur in Chubut and Santa Cruz, mainly in the southwestern parts of these two provinces. *N. maeviae* was recorded only for its type locality in the southeastern of Santa Cruz Province, in Argentina, in the surroundings of Laguna La Leona. Some specimens cited for southern Chile have been misidentified and actually correspond to what is traditionally recognized as the cushioned form of *N. glomerulosa*. Appropriate environments for *N. ulicina* were principally in northeastern Santa Cruz Province.

#### DISCUSSION

Our data did not allow an overall and clear separation of the species of *Nassauvia* subgen. *Strongyloma* due to overlapping ranges of morphological variation. Although some structure was detected in our data, there was no single character set allowing a clear discrimination of the species, according to the initial determinations following Cabrera (1982). Traits traditionally used to distinguish the five species that constitute subgen. *Strongyloma* (FD, MLL, BLL, BLS, and NFC) account for most of the sample variation, but they do not have significant morphological discontinuities along the large distribution range of the group. In addition, abaxial corolla lip width and area also contribute substantially to the total sample variation, but, like the traditional distinguishing features noted above, they also lack discontinuities that would make these features useful diagnostically. Our results indicate that variation in morphological traits in subgen. *Strongyloma* is clinal, and it is possible that a larger sampling might further emphasize the continuity of character variation.

Despite some association between morphological variation with geography and climate, the actual geographic distribution of the samples identified to species following Cabrera (1982) does not entirely match that clinal pattern of morphology, geography, and climate. Diagnostic traits of N. axillaris (longest and narrowest leaves, phyllaries, and cypselas, 5-flowered capitula, and widest abaxial corolla lips with largest area) are frequently found in populations from northwestern Patagonia, but some populations of N axillaris also occur in central southern Chubut. On the opposite end of the range, in southeastern Patagonia, we found N. maeviae with the shortest and widest leaves, phyllaries, and cypselas, 3-flowered capitula, and narrowest abaxial corolla lips with smallest area. Diagnostic traits of N. ulicina are frequently found in populations from central eastern Patagonia, but some populations occur both in the northeast (morphologically close to N. fuegiana) and the southeast (morphologically close to N. maeviae). Although both diagnostic traits of N. glomerulosa and N. fuegiana occur throughout Patagonia, traits of N. glomerulosa are highly frequent while traits of N. fuegiana appear in a few scattered populations.

In considering these results, we examined the nomenclatural types for each of the five putative species. These type specimens appear to be morphologically different from each other and certainly suggest the presence of five distinct species. However, it is interesting to note that the type localities of N. fuegiana, N. maeviae, and N. ulicina are located at the southernmost end of the geographical distribution of the subgenus. These three sites are located fairly close together, although the biological communities and soils are somewhat different. The type locality of N. fuegiana is located in northern Tierra del Fuego Province, where humid grasslands of Festuca gracillima dominate this great continental island (Cabrera and Willink 1973; León et al. 1998). N. maeviae is found with certainty only in its type locality, in a very particular area in the southeast of Santa Cruz Province with chalky and stony soil in a community dominated by Frankenia microphylla and Lepidophyllum cupressiforme, although these edaphic communities with hygrophilous vegetation are present across the Patagonian steppe, in some low-lying parts of the grasslands or coastal areas (Cabrera and Willink 1973). The type locality of *N. ulicina* is located in southeastern Santa Cruz Province, where xeric grasslands of Festuca pallescens dominate the Gallegos River Basin (Cabrera and Willink 1973; León et al. 1998). On the other hand, the two remaining type localities, for N. axillaris and N. glomerulosa, are very close together, in the Cordillera of the Andes in central Chile, but the labels of the specimens are not very detailed. This area corresponds to the northwestern end of the geographical distribution of N. glomerulosa, and to a midpoint within the distribution of N. axillaris. Thus, except for N. axillaris, the type localities for each putative species are located almost at the extremes of the geographical distribution of the subgenus. These extreme locations also have marked differences in altitude (Appendix 1), soil types, and plant communities. Our results demonstrate clinal variation in vegetative and

reproductive characters within subgen. *Strongyloma*, such that the morphological differences originally observed in the type specimens of the putative species of subgen. *Strongyloma* may be more related to the environmental and latitudinal differences of the type locations rather than reflecting well-

established taxonomic boundaries. Based on our sampling and species distribution modeling, suitable geographic and climatic areas for each species are greater than previously considered (Fig. 6); adequate conditions for each species overlap considerably. Species distribution modeling identifies the mean temperature of the coldest quarter as the environmental variable that most influences the geographical distribution of this group of plants. This variable is biologically significant because it is associated with the beginning of the growing period, with the growing period delayed as the mean temperature of winter decreases (Paruelo et al. 1998; Jobbágy et al. 2002). Temperature appears to be the primary control of phenology in Patagonia with a NW-SE distribution of the isotherms, while solar radiation and photoperiod present a latitudinal cline (Paruelo et al. 1998). Several areas exist with suitable environmental conditions for these species that largely overlap, and syntopy of two or three of these species in several areas of Patagonia has been documented. There are multiple areas of contact in the southern Andean-Patagonian region, namely: (i) some areas located in southern Mendoza, in north-central Neuquén, in west-central Río Negro, and in the center of Chubut where N. axillaris, N. glomerulosa, and often N. fuegiana coexist; (ii) the center of Chubut where N. axillaris, N. fuegiana, and N. ulicina coexist; (iii) the center of Chubut where N. glomerulosa and N. ulicina coexist; and (iv) eastern Chubut and northeastern Santa Cruz where N. fuegiana and N. glomerulosa, N. fuegiana and N. ulicina, or N. glomerulosa and N. ulicina coexist. It is of special interest that many individuals with intermediate morphological characteristics were encountered in southern Mendoza Province and in the center of Chubut Province, suggesting that these are particularly dynamic areas for evolution and possible gene exchange among this group of plants.

Nassauvia subgen. Strongyloma is taxonomically problematic, with considerable and complex morphological variation. This subgenus cannot be clearly divided into well-defined groups. Based on the results presented here, we conclude that Nassauvia subgen. Strongyloma should be considered a large, highly polymorphic species complex composed of a set of five entities, distributed over a large geographical area, with clinal morphological variation. Ecological and morphological differences among the members of the species complex from extreme locations have led to their classification as distinct taxonomic species. Some evidence, such as the intermediacy observed in statistical analyzes graphs and overlap of suitable areas of species distributions suggest the possibility of gene exchange between populations of different named entities. The biological structure of subgen. Strongyloma may be the result of incipient speciation or the consequence of hybridization in contact areas of distribution. However, further analyses are still needed to test those hypotheses, especially using molecular and chromosomal techniques at population level, to test horizontal gene transfer, incomplete lineage sorting, and the delimitation of genetically cohesive groups.

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APPENDIX 1. Specimens examined. Entries are in the order of species and authors (last identification according to Cabrera, 1982), population code number (in bold), country (in capital letters), province, locality, geographic coordinates and altitude (between square brackets), collector and number (in italics; if not: s. n. = sine numero - without number), and herbarium acronym (between parentheses; TI = type image and T = type).

N. axillaris (Lag. ex Lindl.) D. Don. 1; BOLIVIA. Potosí: Tupiza [21°28' S, 65°43' W, 2,970 m], Fiebrig 3114 (SI). 2; ARGENTINA. Ŝalta: Santa Victoria [22°12' S, 65°13' W, 4,250 m], Zuloaga 10678 (SI). 3; Jujuy: Pucará [23°10' S, 65°09' W, 3,500 m], Kiesling 3653 (SI). 4; Abra de Lipán [23°41' S, 65°41' W, 4,200 m], Zuloaga 3559 (SI). 5; Tucumán: Ojo de Agua [26°42' S, 65°48' W, 2,900 m], Gómez-Sosa 236 (SI). 6; Catamarca: Mina Capillitas [27°22' S, 66°20' W, 3,740 m], Zuloaga 11934 (SI). 7; La Rioja: Famatina [28°27' S, 67°49' W, 3,000 m], Hunziker 1877 (SI). 8; San Juan: Agua Negra [30°23' S, 69°35' W, 3,000 m], Cabrera 30130 (SI). 9; San Juan: Pie de Palo [31°17' S, 67°57' W, 3,130 m], Kiesling 6292 (SI). 10; Mendoza: Quebrada del Toro [32°38' S, 69°02' W, 1,580 m], Nicora 4441 (SI). 11; CHILE. Valparaíso: Andes [32°51' S, 70°29' W, 1,000 m], s. n. (K, TI). 12; ARGENTINA. Mendoza: Refugio Cruz de Piedra [34°14' S, 69°25' W, 2,622 m], Zavala 57 (SI). 13; Las Leñas Amarillas [35°09' S, 70°04' W, 2,203 m], Cabrera 33389 (SI). 14; Neuquén: Vegas del Pelán [36°54' S, 70°20' W, 1,750 m], Boelcke 11107 (SI). 15; Primeros Pinos [38°52' S, 68°35' W, 518 m], Cabrera 32869 (SI). 16; Junín de los Andes [40°00' S, 70°50' W, 670 m], Merrill King 9385 (SI). 17; Río Negro: Sierra de Queupuniyeu [40°32' S, 68°11' W, 1,156 m], Nicola 109 (SI). 18; Ojo de Agua [41°33' S, 69°52' W, 1,115 m], Burkart 19763 (SI). 19; Chubut: Estancia Quichaura [43°35' S, 70°20' W, 910 m], Soriano 2429 (SI). 20; Los Altares [43°53' S, 68°25' W, 364 m], Cabrera 33293 (SI).

*N. fuegiana* (Speg.) Cabrera. **21**; ARGENTINA. Mendoza: Ranquil de Lirkay [36°39′ S, 69°47′ W, 1,161 m], *Ruiz Leal 21922* (SI). **22**; Neuquén: Churriaca [37°54′ S, 70°08′ W, 1,390 m], *Ruiz Leal 18019* (SI). **23**; Río Negro: Ruta Provincial 74 [39°18′ S, 68°28′ W, 637 m], *Cosacov s. n.* (SI). **24**; Meseta de Somuncurá [40°58′ S, 66°40′ W, 618 m], *Zanotti 23* (SI). **25**; Chubut: Telsen [42°09′ S, 67°05′ W, 613 m], *Arroyo* 465 (SI). **26**; Isla de los Pájaros [42°25′ S, 64°31′ W, 7 m], *Daciuk 60* (SI). **27**; Paso de Indios [43°50′ S, 68°35′ W, 250 m], *Nicola 76* (SI). **28**; Santa Cruz: Caleta Olivia [46°34′ S, 67°38′ W, 300 m], *Donat s. n. c* (SI). **29**; Tierra del Fuego: Golfo de San Sebastián [53°18′ S, 68°27′ W, 15 m], *s. n.* (LP, *TI*).

N. glomerulosa (Lag. ex Lindl.) D. Don. 30; CHILE. Valparaíso: Cordillera del Portillo [32°50' S, 70°08' W, 2,870 m], Née s. n. (G, TI). 31; ARGENTINA. Mendoza: Bardas Blancas [35°50' S, 70°00' W, 1,540 m], Zuloaga 12419 (SI). 32; Neuquén: El Huecú [37°43' S, 70°30' W, 1,483 m], Nicola 127 (SI). 33; Collón Curá [40°25' S, 70°39' W, 604 m], Sérsic 4122 (CORD). 34; Río Negro: Los Menucos [40°46' S, 68°11' W, 874 m], Zanotti 35 (SI). 35; Chubut: ColánConhué [42°45' S, 69°43' W, 584 m], Nicola 8 (SI). 36; Laguna Fría [42°56' S, 68°31' W, 1,025 m], Nicola 5 (SI). 37; Los Rifleros [43°15' S, 70°52' W, 676 m], Nicola 17 (SI). 38; Dique Florentino Ameghino [43°41' S, 66°29' W, 260 m], Nicola 62 (SI). 39; Estancia Cañadón Grande [44°15' S, 69°24' W, 900 m], Nicola 33 (SI). 40; Alto Río Senguer [44°48' S, 70°42' W, 643 m], Nicola 28 (SI). 41; Sierra del Castillo [45°07' S, 69°20' W, 854 m], Nicola 29 (SI). 42; CHILE. Aysén: Chile Chico [46°32' S, 71°45' W, 300 m], García 4191 (CONC). 43; ARGENTINA. Santa Cruz: Las Heras [46°36' S, 69°27' W, 343 m], Biganzoli 2345 (SI). 44; Puesto Lebrún [46°58' S, 71°06' W, 1,353 m], Paiaro s. n. (SI). 45; Fitz Roy [46°58' S, 67°16' W, 242 m], Biganzoli 2343 (SI). 46; Estancia Piedra Grande [47°36' S, 69°46' W, 775 m], Paiaro s. n. (SI). 47; Estancia Cerro Beltza [48°00' S, 71°41' W, 912 m], Paiaro s. n. (SI). 48; Gobernador Gregores [48°48' S, 69°45' W, 331 m], Zanotti 66 (SI). 49; Estancia Cerro Perdido [48°58' S, 68°29' W, 241 m], Zanotti 64 (SI). 50; Cerro Mank Aike [49°46' S, 70°44' W, 807 m], Paiaro s. n. (SI). 51; Hotel La Leona [49°51' S, 72°02' W, 294 m], Zanotti 93 (SI). 52; Luis Piedra Buena [49°54' S, 69°00' W, 108 m], Zanotti 70 (SI). 53; CHILE. Magallanes: Sierra de los Baguales [50°44' S, 72°20' W, 700 m], Arroyo 841140 (CONC). 54; Torres del Paine [51°02' S, 73°45' W, 200 m], Domínguez 297 (CONC).

*N. maeviae* Cabrera. 55; ARGENTINA. Santa Cruz: Laguna La Leona [51°31' S, 69°47' W, 63 m], *Correa s. n.* (SI, *T*).

*N. ulicina* (Hook. f.) Macloskie. **56**; ARGENTINA. Chubut: Isla de los Pájaros [42°25′ S, 64°31′ W, 7 m], *Daciuk 61* (SI). **57**; Paso del Sapo [42°48′ S, 69°34′ W, 387 m], *Zanotti 59* (SI). **58**; Las Chapas [43°38′ S, 66°31′ W, 261 m], *Botta 436* (SI). **59**; Paso de Indios [43°52′ S, 68°51′ W, 285 m], *Arroyo 64* (SI). **60**; Río Senguer [45°28′ S, 69°50′ W, 421 m], *Nicola 170* (SI). **61**; Bahía Solano [45°35′ S, 67°19 W, 190 m], *de Marco 207* (SI). **62**; Santa Cruz: Las Heras [46°36′ S, 69°27′ W, 343 m], *Biganzoli 2347* (SI). **63**; Gobernador Gregores [48°50′ S, 70°49′ W, 430 m], *Ruiz Leal 24214* (SI). **64**; Puerto San Julián [49°17′ S, 67°47′ W, 40 m], *Dusén 5328* (SI). **65**; Cabo Buen Tiempo [51°32′ S, 68°57′ W, 60 m], *Capt. King s. n.* (K, *TI*).

APPENDIX 2. Mean values (SD) of the 31 morphological traits measured for the 65 populations of *Nassauvia* subgen. *Strongyloma* studied. See Appendix 1 for the full names of population codes and Materials and Methods for full names of trait acronyms. Mean and CV are the average values (SD) and coefficient of variation of population means for each one of the species (n. c. = not correspond; CV does not correspond for categorical variables). Total means and total CVs for the entire data set are also shown.

Code	Н	FD	MLL	BLL	BLW	BLS	BLA	LC	TC	LD	TD
1	1	1	17.6 (1.7)	4.6 (1.5)	2.4 (0.2)	1.9 (0.7)	11.1 (3.4)	1	0	0	0
2	1	1	16.4 (5.1)	6.5 (0.5)	1.6 (0.4)	4.1 (0.9)	10.7 (2.7)	1	1	0	0
3	1	1	18.6 (4.0)	3.4 (0.8)	1.4 (0.6)	2.6 (0.8)	5.2 (2.9)	1	0	1	0
4	1	1	16.2 (3.2)	5.7 (0.8)	2.5 (0.5)	2.4 (0.9)	13.8 (1.3)	1	0	1	0
5	1	1	17.2 (1.3)	6.1 (1.5)	1.7 (0.2)	3.6 (0.6)	10.2 (3.2)	1	0	0	0
6	2	1	16.9 (3.3)	7.9 (1.1)	2.9 (0.5)	2.7 (0.4)	23.6 (6.7)	1	0	1	0
7	1	1	16.2 (3.7)	5.5 (0.3)	2.6 (0.5)	2.2 (0.5)	14.2 (2.4)	1	1	0	0
8	1	1	28.6 (2.9)	5.2 (0.8)	2.2 (0.5)	2.4 (0.3)	11.4 (4.0)	1	0	1	0
9	1	1	14.7 (2.1)	5.4 (0.3)	2.1 (0.1)	2.6 (0.2)	11.6 (0.6)	1	0	1	0
10	1	1	24.0 (3.6)	7.3 (1.8)	1.7 (0.6)	4.9 (2.7)	11.9 (5.1)	1	0	1	0
11	1	1	15.7 (3.0)	4.3 (0.6)	1.0 (0.1)	4.1 (0.4)	4.4 (0.9)	1	0	1	0
12	2	1	21.6 (2.4)	12.1 (2.3)	4.5 (1.0)	2.8 (0.8)	55.5 (18.9)	1	0	1	0
13	2	1	13.7 (3.0)	4.7 (0.5)	1.9 (0.2)	2.5 (0.2)	8.9 (1.9)	1	0	1	0
14	1	1	18.1 (3.0)	4.7 (0.1)	1.3 (0.3)	3.8 (0.7)	6.1 (1.4)	1	0	1	0
15	1	1	16.7 (1.6)	4.4 (0.2)	2.0 (0.2)	2.2 (0.3)	8.5 (1.0)	1	0	1	0
16	1	1	17.5 (0.4)	4.7 (0.2)	1.7 (0.3)	2.8 (0.4)	8.0 (1.5)	1	0	1	0
17	1	1	15.2 (1.5)	4.7 (0.6)	2.5 (0.6)	2.0 (0.4)	11.9 (3.8)	1	0	1	0
18	1	1	16.9 (0.4)	5.0 (1.3)	1.6 (0.4)	3.1 (0.1)	8.3 (3.9)	1	0	1	1
19	1	1	12.7 (1.8)	3.9 (0.6)	1.9 (0.1)	2.0 (0.2)	7.6 (1.6)	1	0	0	0
20	1	1	12.7 (1.8)	3.9 (0.6)	1.9 (0.1)	2.0 (0.2)	7.6 (1.6)	1	0	0	0
N. axillaris mean	1	1	17.6	5.7	2.1	2.9	12.9	1	0	1	0
N. axillaris CV	n. c.	n. c.	20.3	33.8	35.8	28.4	84.4	n. c.	n. c.	n. c.	n. c.
21	1	1	23.0 (0.8)	8.2 (0.9)	1.4 (0.2)	5.6 (0.2)	11.3 (3.0)	0	0	1	1
22	1	1	14.1 (1.7)	5.4 (0.6)	1.3 (0.2)	4.1 (0.3)	7.3 (1.6)	0	1	0	0
23	1	1	19.4 (1.2)	6.5 (1.0)	3.0 (0.5)	2.2 (0.1)	19.7 (6.1)	1	0	0	0
24	1	1	17.9 (1.9)	7.6 (0.2)	1.5 (0.2)	5.2 (0.5)	11.4 (1.7)	1	0	0	0
25	1	1	17.0 (0.9)	8.1 (0.9)	1.1 (0.2)	7.4 (1.6)	9.1 (1.5)	1	1	0	0
26	2	1	9.1 (1.1)	2.1 (0.4)	2.0 (0.3)	1.1 (0.3)	4.1 (0.7)	0	1	0	0
27	1	1	24.5 (1.5)	10.2 (2.6)	2.0 (0.3)	5.0 (1.0)	21.0 (7.7)	1	1	0	0
28	2	1	7.9 (1.9)	2.8 (0.0)	0.9 (0.1)	3.1 (0.5)	2.6 (0.3)	0	0	1	1
29 N. Guariana	2	0	11.3 (2.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1	0	0	0
<i>N. fuegiana</i> mean	1	1	16.0	5.7	1.5	3.7	9.6	1	0	0	0
N. fuegiana CV 30	n. c. 2	n. c. 1	36.8 5.4 (0.2)	59.3	55.7 0.5 (0.1)	62.9 1.8 (0.1)	74.9	n. c. 1	n. c. 0	n. c. 0	n. c. 0
31	2	1	9.8 (1.8)	1.0 (0.0) 1.6 (0.4)	0.8 (0.2)	2.1 (0.6)	0.5 (0.1) 1.2 (0.4)	1	0	0	0
32	2	1	9.2 (1.4)	1.8(0.4) 1.8(0.3)	0.9 (0.2)	2.0 (0.6)	1.2(0.4) 1.7(0.4)	1	0	0	0
33	1	1	9.2 (1.4) 9.6 (2.7)	1.5 (0.4)	0.8 (0.2)	2.0 (0.0)	1.2 (0.4)	1	0	0	0
34	1	1	7.2 (1.6)	1.5 (0.4)	0.7 (0.1)	2.2 (0.3)	1.0 (0.2)	1	0	0	0
35	1	1	9.6 (1.2)	1.4 (0.2)	0.7 (0.1)	2.0 (0.4)	1.1 (0.3)	1	0	0	0
36	1	1	9.4 (1.9)	1.5 (0.2)	0.7 (0.1)	2.2 (0.4)	1.1 (0.3)	1	0	0	0
37	1	1	9.9 (1.1)	1.4(0.1)	0.6 (0.0)	2.2 (0.2)	0.9(0.41)	1	0	0	0
38	1	1	8.9 (1.5)	1.4 (0.2)	0.7 (0.1)	2.0 (0.3)	1.0 (0.3)	1	0 0	Ő	Ő
39	1	1	7.7 (1.0)	1.6 (0.1)	0.8 (0.1)	2.1 (0.4)	1.2 (0.3)	1	0 0	Ő	Ő
40	3	1	4.7 (0.6)	1.7 (0.2)	0.9 (0.1)	1.8 (0.2)	1.6 (0.4)	1	0 0	Ő	Ő
41	3	1	4.4 (1.0)	1.9 (0.2)	0.9 (0.1)	2.2 (0.4)	1.7 (0.2)	1	Õ	Õ	Õ
42	3	1	4.5 (0.2)	1.8 (0.2)	1.2 (0.1)	1.6 (0.2)	2.1 (0.3)	1	Õ	Õ	Õ
43	2	1	4.7 (1.3)	1.4 (0.2)	0.9 (0.1)	1.7 (0.3)	1.2 (0.2)	1	Õ	Õ	Õ
44	3	1	4.8 (0.2)	1.9 (0.2)	1.0 (0.1)	1.9 (0.3)	2.0 (0.3)	1	0	0	0
45	2	1	3.7 (0.6)	1.4 (0.2)	1.0 (0.1)	1.5 (0.2)	1.4 (0.3)	1	0	0	0
46	3	1	6.6 (0.7)	1.7 (0.2)	0.9 (0.2)	1.8 (0.4)	1.6 (0.3)	1	0	0	0
47	3	1	5.0 (0.9)	1.7 (0.3)	1.1 (0.2)	1.6 (0.2)	1.9 (0.6)	1	0	0	0
48	3	1	4.6 (0.7)	1.5 (0.2)	1.0 (0.2)	1.5 (0.2)	1.5 (0.3)	1	0	0	0
49	2	1	4.3 (0.9)	1.4 (0.1)	0.8 (0.1)	1.8 (0.3)	1.2 (0.2)	1	0	0	0
50	3	1	4.9 (1.1)	1.5 (0.2)	1.0 (0.2)	1.6 (0.3)	1.5 (0.4)	1	0	0	0
51	2	1	5.8 (0.4)	1.7 (0.1)	1.0 (0.1)	1.8 (0.3)	1.6 (0.2)	1	0	0	0
52	2	1	5.8 (0.5)	1.6 (0.2)	0.9 (0.1)	1.8 (0.2)	1.4 (0.2)	1	0	0	0
53	3	1	4.6 (0.1)	2.1 (0.2)	1.5 (0.1)	1.5 (0.2)	3.0 (0.1)	1	0	1	0
54	3	1	4.2 (0.4)	2.0 (0.1)	1.1 (0.2)	1.8 (0.2)	2.3 (0.4)	0	1	0	0
N. glomerulosa mean	2	1	6.4	1.6	0.9	1.9	1.5	1	0	0	0
N. glomerulosa CV	n. c.	n. c.	34.2	15.0	22.1	12.6	35.5	n. c.	n. c.	n. c.	n. c.
55	3	1	3.1 (1.1)	2.7 (0.3)	1.9 (0.2)	1.4 (0.1)	5.1 (1.0)	0	1	0	0
N. maeviae mean	3	1	3.1	2.7	1.9	1.4	5.1	0	1	0	0
N. maeviae CV	n. c.	n. c.	0.0	0.0	0.0	0.0	0.0	n. c.	n. c.	n. c.	n. c.
56	2	1	7.0 (3.2)	2.1 (0.5)	0.8 (0.3)	2.7 (0.6)	1.8 (0.9)	1	0	1	1
57	2	1	11.7 (3.2)	3.2 (0.7)	0.6 (0.1)	5.5 (1.8)	1.9 (0.6)	0	0	1	0
58	2	1	8.0 (1.8)	1.8 (0.1)	0.8 (0.1)	2.1 (0.1)	1.5 (0.3)	1	1	1	1

(Continued)

## APPENDIX 2. (Continued).

											:
Code	Н	FD	MLL	BLL	BLW	BLS		BLA	LC		D TD
59	2	1	13.2 (4.9)	4.0 (1.1)	1.0 (0.2)	4.1 (0.3	/	4.0 (2.0)	0		1 0
60	2 2	1	7.9 (2.6)	2.7(0.3)	1.5(0.3)	1.9 (0.3		4.0 (1.0)	0		l 1
61 62	2	1 1	10.6 (3.1) 8.3 (2.2)	3.3 (0.1) 2.0 (0.4)	0.6 (0.1) 0.9 (0.2)	6.0 (0.8 2.1 (0.4		1.8 (0.2) 1.9 (0.6)	0 1		L 0 L 0
63	2	1	10.7 (4.5)	4.5 (0.5)	1.0(0.2)	4.6 (0.9		4.5 (0.4)	0		L 0
64	2	1	9.3 (3.9)	3.0 (0.3)	0.6 (0.2)	5.0 (1.6		1.9 (0.8)	Õ		L Ő
65	2	1	6.8 (0.2)	2.2 (0.3)	0.5 (0.1)	4.1 (0.4		1.2 (0.4)	1	0	l 1
N. ulicina mean	2	1	9.4	2.9	0.8	3.8		2.5	0	0	1 0
N. ulicina CV	n. c.	n. c.	22.7	31.1	33.2	39.7		48.8	n. c.	n. c. n.	
Total mean	2	1	8.9 52.7	3.6	1.3	2.7	1	6.2	1		) 0
Total CV	n. c.	n. c.	52.7	68.6	56.0	50.2	1	30.6	n. c.	n. c. n.	c. n. c.
Code	PL	NOP	LOP	WOP	OPS	OPA	NIP	LIP	WIP	IPS	IPA
1	0.8 (0.3)	3 (1)	4.1 (0.4)	1.3 (0.0)	3.1 (0.3)	5.5 (0.7)	5 (0)	4.8 (0.1)	1.4 (0.2)	3.5 (0.5)	6.7 (1.1)
2 3	0.5 (0.0) 0.5 (0.1)	2 (0) 3 (1)	3.9 (0.5) 3.3 (0.3)	1.1 (0.1) 1.3 (0.2)	3.5 (0.1) 2.7 (0.5)	4.5 (1.0) 4.2 (0.9)	5 (0) 5 (0)	4.8 (0.2) 4.9 (0.1)	1.4(0.3)	3.6 (0.7) 3.6 (0.2)	6.6 (1.5) 6.8 (0.6)
4	1.3(0.0)	3 (1)	3.9 (0.1)	1.5(0.2) 1.6(0.1)	2.7 (0.3) 2.4 (0.1)	4.2 (0.9) 6.2 (0.2)	5 (0)	4.9 (0.1)	1.4(0.1) 1.5(0.1)	3.0 (0.2)	7.0 (0.5)
5	0.4(0.1)	2 (0)	3.9 (0.2)	1.6 (0.2)	2.5 (0.3)	6.3 (0.5)	5 (0)	5.7 (0.5)	1.6 (0.2)	3.5 (0.7)	9.2 (0.5)
6	2.9 (0.5)	5 (1)	4.0 (0.4)	1.6 (0.2)	2.4 (0.2)	6.6 (1.2)	5 (0)	5.0 (0.5)	1.7 (0.3)	3.0 (0.4)	8.7 (2.2)
7	0.5 (0.0)	3 (1)	4.4 (0.2)	1.7 (0.2)	2.5 (0.2)	7.6 (1.1)	5 (0)	5.3 (0.5)	1.9 (0.4)	2.8 (0.4)	10.1 (2.8)
8	1.8 (0.5)	2(1)	3.3 (0.2)	1.2 (0.3)	2.8 (0.9)	4.0 (0.9)	5 (0)	4.8 (0.5)	1.4 (0.1)	3.5 (0.5)	6.6 (0.6)
9	2.9(0.0)	4(1)	4.4(0.2)	1.8 (0.0)	2.4(0.1)	8.1 (0.4)	5 (0)	5.4(0.5)	1.7(0.3)	3.2(0.3)	9.2 (2.4)
10 11	4.1 (0.1) 3.8 (0.0)	2 (1) 3 (0)	3.7 (0.4) 3.5 (0.5)	1.4 (0.4) 1.2 (0.0)	2.8 (0.7) 2.8 (0.5)	5.2 (1.8) 4.4 (0.6)	5 (0) 5 (0)	5.8 (0.4) 5.4 (0.8)	1.7 (0.2) 1.1 (0.0)	3.5 (0.1) 5.0 (0.8)	9.7 (1.7) 5.7 (0.7)
12	5.4 (2.1)	3 (0) 4 (0)	4.6 (0.6)	1.2 (0.0)	2.7 (0.3)	7.9 (1.8)	5 (0)	6.6 (0.8)	1.8 (0.3)	3.8 (0.6)	11.7 (2.4)
13	5.5 (0.0)	5 (1)	4.7 (0.4)	1.8 (0.2)	2.6 (0.1)	8.3 (1.5)	5 (0)	7.3 (0.7)	1.6 (0.5)	4.8 (1.3)	11.8 (4.3)
14	3.1 (1.0)	3 (1)	5.9 (0.5)	1.7 (0.1)	3.4 (0.1)	10.4 (1.5)	5 (0)	7.1 (0.4)	1.8 (0.1)	4.0 (0.4)	12.9 (0.9)
15	3.2 (0.5)	5 (1)	5.4 (0.5)	1.8 (0.3)	3.0 (0.4)	9.8 (2.4)	5 (0)	8.6 (0.3)	2.0 (0.2)	4.4 (0.6)	17.3 (1.6)
16	4.4 (1.4)	4(1)	5.3 (0.6)	1.6 (0.1)	3.2 (0.5)	8.6 (1.1)	5 (0)	7.6 (0.4)	1.7 (0.1)	4.4 (0.5)	13.2 (0.5)
17 18	4.0 (0.6) 4.4 (1.6)	5 (0) 3 (0)	4.6 (0.6) 5.3 (0.3)	1.8 (0.2) 1.4 (0.2)	2.6 (0.3) 3.9 (0.4)	8.3 (1.7) 7.3 (1.3)	5 (0) 5 (0)	6.1 (0.7) 8.5 (0.9)	1.8 (0.2) 1.5 (0.1)	3.5 (0.3) 5.9 (0.9)	10.9 (2.3) 12.4 (1.2)
19	0.9(0.0)	4 (1)	4.5 (0.7)	2.1 (0.3)	2.1(0.2)	9.6 (2.7)	5 (0)	7.1 (0.5)	2.6 (0.2)	2.8 (0.2)	12.4 (1.2)
20	0.9 (0.0)	4(1)	4.5 (0.7)	2.1 (0.3)	2.1 (0.2)	9.6 (2.7)	5 (0)	7.1 (0.5)	2.6 (0.2)	2.8 (0.2)	18.4 (2.9)
N. axillaris mean	2.9	3	4.4	1.5	2.9	6.9	5	6.1	1.6	3.8	10.2
N. axillaris CV	67.6	31	16.5	18.2	20.7	29.0	0	20.8	18.9	21.0	34.0
21	8.0 (2.8)	4(0)	4.7 (1.1)	1.7(0.1)	2.8 (0.7)	7.9 (1.8)	5(0)	7.3 (0.4)	1.8 (0.1)	4.0 (0.4)	13.2 (0.6)
22 23	0.5 (0.0) 3.4 (0.2)	2 (1) 2 (0)	4.3 (0.6) 3.6 (0.6)	1.7 (0.1) 1.3 (0.3)	2.6 (0.5) 2.7 (0.5)	7.3 (0.9) 4.9 (1.6)	5 (0) 5 (0)	5.5 (0.4) 5.7 (0.5)	1.5(0.1) 1.4(0.1)	3.7 (0.2) 4.2 (0.2)	8.1 (1.0) 7.8 (1.4)
23	4.7(0.2)	$\frac{2}{4}(0)$	3.7 (0.1)	1.2 (0.1)	3.2 (0.3)	4.4 (0.6)	5 (0)	6.0 (0.6)	1.7 (0.2)	3.5 (0.7)	10.5(1.4)
25	2.0 (0.0)	3 (1)	4.2 (0.2)	1.6 (0.0)	2.6 (0.1)	6.9 (0.3)	5 (0)	6.8 (0.3)	1.3 (0.1)	5.1 (0.5)	8.9 (0.2)
26	0.5 (0.0)	2 (1)	4.3 (0.4)	1.4 (0.2)	3.2 (0.1)	6.0 (1.4)	5 (1)	6.0 (0.2)	1.0 (0.1)	6.0 (0.6)	6.0 (0.6)
27	6.0 (0.4)	?	?	?	?	?	5 (0)	9.4 (0.9)	2.0 (0.2)	4.6 (0.7)	19.0 (1.8)
28	9.0 (0.0)	2(1)	4.4 (0.6)	0.9(0.1)	5.1 (1.0)	3.9 (0.4)	3 (0)	5.6 (0.1)	1.4 (0.3)	4.2 (0.9)	7.7 (1.3)
29 <i>N. fuegiana</i> mean	? 4.3	3 (0) 3	3.9 (0.0) 4.2	1.2 (0.0) 1.4	3.1 (0.0) 3.2	4.8 (0.0) 5.8	5 (0) 5	5.1 (0.0) 6.4	1.6 (0.0) 1.5	3.1 (0.0) 4.3	8.3 (0.0) 10.0
N. fuegiana CV	76.2	32	4.2 9.1	20.5	25.6	25.7	14	20.5	20.4	20.4	40.0
30	?	3 (0)	4.4 (0.0)	1.4 (0.0)	3.1 (0.0)	6.4 (0.0)	5 (0)	5.1 (0.0)	1.8 (0.0)	2.8 (0.0)	9.0 (0.0)
31	1.6 (0.1)	3 (0)	3.6 (0.5)	1.5 (0.1)	2.4 (0.4)	5.2 (0.6)	5 (0)	5.2 (0.5)	1.3 (0.1)	4.0 (0.6)	6.7 (0.1)
32	2.3 (0.1)	5 (1)	4.2 (0.5)	1.9 (0.2)	2.2 (0.2)	7.9 (1.6)	5 (0)	6.0 (0.7)	2.0 (0.2)	3.0 (0.3)	12.1 (2.6)
33	2.0(0.6)	4(1)	3.0(0.4)	1.3 (0.2)	2.4 (0.4)	3.9 (1.0)	5 (0)	5.1 (0.6)	1.4 (0.2)	3.7 (0.5)	7.2 (1.5)
34 35	1.5 (0.2) 2.0 (0.5)	4(1) 4(0)	2.9 (0.4) 3.2 (0.4)	1.3 (0.2) 1.6 (0.2)	2.3 (0.5) 2.1 (0.3)	3.6 (0.6) 5.0 (1.2)	3 (0) 5 (0)	4.6 (0.4) 5.0 (0.6)	1.5 (0.3) 1.6 (0.2)	3.2 (0.7) 3.1 (0.4)	7.0 (1.9) 8.2 (1.6)
36	1.9(0.3)	4 (0) 4 (0)	3.6 (0.5)	1.6(0.2) 1.4(0.1)	2.6 (0.3)	5.2 (1.1)	5 (0)	4.9 (0.6)	1.6(0.2) 1.5(0.1)	3.1(0.4) 3.3(0.3)	7.4 (1.4)
37	2.3 (0.5)	5 (1)	3.1 (0.5)	1.5 (0.2)	2.1 (0.3)	4.7 (1.3)	5 (0)	5.1 (0.5)	1.6 (0.2)	3.1 (0.3)	8.5 (1.3)
38	1.6 (0.5)	4 (0)	2.8 (0.5)	1.5 (0.2)	1.9 (0.4)	4.2 (1.0)	3 (0)	4.8 (0.5)	1.7 (0.1)	2.8 (0.2)	8.3 (1.2)
39	2.2 (0.2)	6 (0)	3.6 (0.5)	1.6 (0.2)	2.2 (0.2)	5.9 (1.5)	5 (0)	5.4 (0.3)	1.8 (0.2)	3.0 (0.3)	9.9 (1.1)
40	2.7 (0.7)	5 (1)	4.4 (0.4)	2.1 (0.4)	2.1 (0.4)	9.2 (1.8)	5 (0)	6.4 (0.3)	2.3 (0.3)	2.8 (0.3)	15.1 (2.2)
41	2.8(1.0)	5 (0)	4.3 (0.4)	2.2(0.2)	1.9(0.2)	9.4 (1.3)	5 (0)	5.9 (0.5)	2.2(0.2)	2.7(0.3)	13.4(1.7)
42 43	0.9 (0.1) 2.3 (0.4)	4 (0) 5 (1)	4.0 (0.4) 3.7 (0.4)	2.1 (0.0) 1.9 (0.3)	2.0 (0.2) 2.0 (0.3)	8.3 (0.7) 7.0 (1.7)	5 (0) 5 (0)	7.0 (0.1) 5.5 (0.6)	2.9 (0.3) 2.0 (0.2)	2.4 (0.3) 2.8 (0.4)	20.6 (1.9) 11.0 (2.0)
43 44	2.3(0.4) 2.0(0.6)	$\frac{3(1)}{4(1)}$	3.4 (0.5)	1.9(0.3) 1.9(0.3)	1.8 (0.2)	6.7 (1.9)	5 (0)	5.9 (0.6)	2.0 (0.2)	2.8(0.4) 2.7(0.4)	13.3 (2.1)
45	1.9 (0.4)	6 (0)	3.9 (0.6)	1.9 (0.3)	2.1 (0.5)	7.4 (1.6)	5 (0)	5.2 (0.9)	1.7 (0.2)	3.1 (0.8)	8.9 (1.3)
46	3.4 (1.2)	5 (0)	4.3 (0.5)	2.1 (0.2)	2.1 (0.2)	9.1 (1.7)	5 (0)	6.4 (0.4)	2.2 (0.3)	2.9 (0.3)	14.3 (2.2)
47	1.5 (0.6)	5 (0)	3.7 (0.3)	2.1 (0.2)	1.8 (0.3)	7.7 (1.2)	5 (0)	5.4 (0.6)	1.9 (0.3)	2.9 (0.3)	10.3 (2.6)
48	2.0 (0.8)	5(1)	4.2 (0.4)	2.0 (0.2)	2.1 (0.2)	8.6 (1.1)	5 (0)	5.8 (0.6)	1.9 (0.2)	3.0 (0.3)	11.3 (2.3)
49	1.6(0.7)	5(1)	3.8(0.3)	1.7(0.4)	2.3(0.5)	6.8(1.7)	5 (0)	5.7 (0.6)	2.0(0.2)	2.8(0.2)	11.6 (2.2)
50 51	1.1 (0.2) 2.1 (0.7)	4(0) 4(1)	3.5 (0.3) 4.1 (0.4)	1.9 (0.3) 1.9 (0.3)	1.9 (0.3) 2.2 (0.3)	6.6 (1.2) 7.8 (1.7)	5 (0) 5 (0)	4.9 (0.5) 5.6 (0.1)	2.2 (0.2) 2.0 (0.3)	2.3 (0.3) 2.9 (0.4)	10.8 (1.5) 11.0 (1.6)
U1	2.1 (0.7)	т(1)	ч.1 (0. <del>4</del> )	1.7 (0.3)	2.2 (0.3)	7.0 (1.7)	5 (0)	5.0 (0.1)	2.0 (0.3)	2.7 (U. <del>4</del> )	11.0 (1.0)

345

(Continued)

## APPENDIX 2. (Continued).

$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	Code	PL	NOP	LOP W	OP OP	S OPA	NIP	LIP	WIP	IPS	IPA
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	52		4 (1)	7 (0.5) 1.9			) 5(0)	5.4 (0.3)	2.1 (0.3)	2.7(0.7)	11.3 (1.4)
$ \begin{split} & \text{generalises} \\ \textbf{M} & \text{generalises} \\ & \textbf{M} & \textbf{M} & \textbf{M} \\ \textbf{Secondsolver} & \textbf{M} & \textbf{M} \\ & \textbf{Secondsolver} & \textbf{M} & \textbf{M} \\ & \textbf{Secondsolver} & \textbf{M} & \textbf{M} \\ & \textbf{Secondsolver} & \textbf{M} \\ \textbf{Secondsolver} & \textbf{M} & \textbf{M} \\ \textbf{Secondsolver} & \textbf{M} & \textbf{M} \\ & \textbf{M} & \textbf{M} \\ \textbf{M} & \textbf{M} \\ \textbf{M} & \textbf{M} \\ \textbf{M}$			( )				, ,	. ,	· · ·	· · ·	19.0 (3.4)
N. N. Discretion of Constraints TI 11 106 20.9 135 31.3 31.6 77.0		· · ·					, ,	. ,	· · ·	· · ·	12.4 (1.8)
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	0										
$\begin{split} N. macriate mean begin for the second se$	0										
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		· · ·	· · /	· · ·	· · ·			. ,	· · ·	· · ·	· · ·
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $											
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $											4.6 (0.5)
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	57	2.7 (0.3)	2 (0) 3					4.7 (0.3)	1.5 (0.3)	3.3 (0.8)	6.9 (1.4)
				( )	· · ·		, , ,	. ,	· · ·	· · ·	7.2 (1.6)
		· · ·					, , ,	. ,	· · ·	· · ·	9.4 (2.7)
$\begin{array}{cccccccccccccccccccccccccccccccccccc$							, ,	. ,		· · ·	
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		· · ·		· · ·	· · ·		, , ,	. ,	· · ·	. ,	
		· · ·		· · ·	· · ·		, , ,	. ,	· · ·	. ,	
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		· · ·		· · ·	· · ·		, , ,	. ,	· · ·	. ,	10.9 (3.6)
	65			.3 (0.0) 1.8	(0.0) 2.3 (			5.6 (0.0)	1.1 (0.0)	5.3 (0.0)	6.0 (0.0)
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $										3.9	
$\begin{array}{c c c c c c c c c c c c c c c c c c c $											
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$											
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	Total CV	70.5	34 16	5.2 21.8	25.9	29.5	18	17.6	23.2	23.3	34.6
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	Code	NFC	ALL	ALW	ALS	ALA	CL		CW	CS	СА
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	1	5 (0)	4.7 (0.3)	1.4 (0.0)	3.4 (0.3)	6.5 (0.3)	1.5 (0	.5) 0.1	5 (0.1)	3.1 (1.4)	0.8 (0.1)
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$											0.6 (0.2)
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	3	5 (0)	4.8 (0.3)								0.5 (0.1)
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$			4.4 (0.2)	1.7 (0.2)		7.7 (1.3)	1.3 (0	.2) 0.	6 (0.0)	2.3 (0.2)	0.7 (0.1)
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$\begin{array}{cccccccccccccccccccccccccccccccccccc$				· · ·	· · ·					. ,	· · ·
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		5 (0)	6.1 (0.6)	2.4 (0.2)	2.6 (0.3)	14.7 (1.9)	2.3 (0	.3) 0.9	9 (0.2)	2.7 (0.4)	2.1 (0.7)
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$						· · ·					2.1 (0.2)
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$\begin{array}{cccccccccccccccccccccccccccccccccccc$			( )	( )				,	· /	· · ·	· · ·
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$\begin{array}{c c c c c c c c c c c c c c c c c c c $		5 (0)	5.2 (0.0)	2.1 (0.0)	2.4 (0.0)	11.0 (0.0)	3.0 (0	.2) 1.	3 (0.5)	2.7 (1.2)	3.9 (1.6)
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$\begin{array}{cccccccccccccccccccccccccccccccccccc$											1.8 (0.6)
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	26		5.6 (0.3)	2.0 (0.2)		11.3 (1.5)	2.1 (0			3.6 (0.6)	1.3 (0.3)
$\begin{array}{cccccccccccccccccccccccccccccccccccc$											1.9 (0.4)
N. fuegiana mean55.41.83.010.02.30.63.81.4N. fuegiana CV1914.016.819.723.420.915.717.630.9305 (0)4.1 (0.0)1.9 (0.0)2.2 (0.0)7.7 (0.0)2.1 (0.0)1.1 (0.0)1.8 (0.0)2.3 (0.0315 (0)4.3 (0.1)1.7 (0.4)2.5 (0.6)7.5 (1.5)1.5 (0.1)0.7 (0.1)2.0 (0.3)1.1 (0.0325 (0)5.0 (0.2)2.1 (0.3)2.4 (0.2)10.9 (1.7)2.3 (0.4)0.9 (0.1)2.5 (0.4)2.1 (0.6335 (0)4.8 (0.3)1.8 (0.1)2.6 (0.2)8.8 (1.0)1.6 (0.2)0.8 (0.1)2.1 (0.3)1.2 (0.2343 (0)4.1 (0.3)1.7 (0.2)2.4 (0.4)7.0 (1.3)1.3 (0.1)0.7 (0.1)2.0 (0.4)0.9 (0.2355 (0)4.6 (0.5)1.9 (0.2)2.5 (0.3)8.6 (1.7)1.6 (0.2)0.8 (0.1)1.9 (0.3)1.4 (0.3)365 (1)4.7 (0.3)2.0 (0.2)2.3 (0.2)9.7 (1.3)1.5 (0.2)0.8 (0.1)1.8 (0.3)1.2 (0.2)375 (0)4.9 (0.6)2.0 (0.3)2.5 (0.3)10.0 (2.4)1.4 (0.2)0.7 (0.2)2.2 (0.6)1.0 (0.3)383 (0)4.4 (0.4)1.8 (0.2)2.4 (0.2)7.9 (1.3)1.5 (0.1)0.8 (0.1)1.9 (0.2)1.3 (0.2)395 (0)5.1 (0.2)2.0 (0.1)2.5 (0.2)10.3 (0.9)1.5 (0.1)0.8 (0.1)1.9 (0.2											
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33 5 (0) 4.8 (0.3) 1.8 (0.1) 2.6 (0.2) 8.8 (1.0) 1.6 (0.2) 0.8 (0.1) 2.1 (0.3) 1.2 (0.2)   34 3 (0) 4.1 (0.3) 1.7 (0.2) 2.4 (0.4) 7.0 (1.3) 1.3 (0.1) 0.7 (0.1) 2.0 (0.4) 0.9 (0.2)   35 5 (0) 4.6 (0.5) 1.9 (0.2) 2.5 (0.3) 8.6 (1.7) 1.6 (0.2) 0.8 (0.1) 1.9 (0.3) 1.4 (0.3)   36 5 (1) 4.7 (0.3) 2.0 (0.2) 2.3 (0.2) 9.7 (1.3) 1.5 (0.2) 0.8 (0.1) 1.8 (0.3) 1.2 (0.2)   37 5 (0) 4.9 (0.6) 2.0 (0.3) 2.5 (0.3) 10.0 (2.4) 1.4 (0.2) 0.7 (0.2) 2.2 (0.6) 1.0 (0.3)   38 3 (0) 4.4 (0.4) 1.8 (0.2) 2.4 (0.2) 7.9 (1.3) 1.5 (0.2) 0.6 (0.1) 2.7 (0.7) 0.9 (0.2)   39 5 (0) 5.1 (0.2) 2.0 (0.1) 2.5 (0.2) 10.3 (0.9) 1.5 (0.1) 0.8 (0.1) 1.9 (0.2) 1.3 (0.2)   40 5 (1) 5.2 (0.2) 2.0 (									· /		2.1 (0.6)
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38 3 (0) 4.4 (0.4) 1.8 (0.2) 2.4 (0.2) 7.9 (1.3) 1.5 (0.2) 0.6 (0.1) 2.7 (0.7) 0.9 (0.2)   39 5 (0) 5.1 (0.2) 2.0 (0.1) 2.5 (0.2) 10.3 (0.9) 1.5 (0.1) 0.8 (0.1) 1.9 (0.2) 1.3 (0.2)   40 5 (1) 5.2 (0.2) 2.0 (0.2) 2.7 (0.3) 10.2 (1.2) 2.3 (0.3) 1.0 (0.1) 2.3 (0.4) 2.3 (0.4)				· · · ·							1.2(0.2)
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											2.3 (0.2)
								,	· · ·		2.2 (0.5)

(Continued)

Code	NFC	ALL	ALW	ALS	ALA	CL	CW	CS	CA
42	5 (0)	5.5 (0.1)	2.0 (0.1)	2.8 (0.1)	10.7 (0.9)	2.2 (0.1)	1.2 (0.1)	1.8 (0.2)	2.6 (0.3)
43	5 (0)	4.8 (0.3)	1.9 (0.2)	2.5 (0.2)	9.3 (1.4)	1.7 (0.2)	0.9 (0.1)	1.8 (0.3)	1.6 (0.2)
44	5 (0)	5.0 (0.3)	1.9 (0.2)	2.6 (0.2)	9.6 (1.1)	1.9 (0.2)	0.9 (0.2)	2.2 (0.5)	1.6 (0.4)
45	5(1)	4.1 (0.2)	1.6 (0.1)	2.6 (0.2)	6.5 (0.7)	1.6 (0.2)	0.9 (0.1)	1.9 (0.2)	1.4 (0.2)
46	5 (0)	4.8 (0.4)	1.7 (0.1)	2.8 (0.2)	8.2 (0.8)	2.2 (0.2)	0.9 (0.2)	2.6 (0.6)	2.0 (0.4)
47	5 (0)	4.7 (0.4)	1.9 (0.1)	2.4(0.2)	9.1 (1.2)	2.2 (0.2)	0.8 (0.2)	2.3 (0.4)	2.1 (0.5)
48	5 (0)	4.5 (0.3)	1.6 (0.2)	2.8 (0.2)	7.2 (1.1)	1.9 (0.3)	0.9 (0.1)	2.1 (0.4)	1.8 (0.3)
49	5 (0)	4.1 (0.2)	1.6 (0.2)	2.6 (0.2)	6.6 (0.9)	2.0 (0.3)	0.8 (0.1)	2.5 (0.4)	1.5 (0.4)
50	5 (0)	4.3 (0.2)	1.5 (0.1)	2.8 (0.2)	6.6 (0.6)	2.0 (0.1)	0.9 (0.1)	2.2 (0.2)	1.8 (0.2)
51	5 (0)	4.4 (0.4)	1.6 (0.2)	2.7 (0.3)	7.2 (1.2)	1.9 (0.3)	0.9 (0.1)	2.0 (0.3)	1.8 (0.4)
52	5 (0)	4.1 (0.1)	1.4 (0.2)	3.0 (0.4)	5.6 (0.9)	2.2 (0.1)	0.9 (0.1)	2.4(0.4)	2.1 (0.3)
53	5 (0)	5.9 (0.2)	2.2 (0.2)	2.7 (0.1)	12.9 (1.5)	2.2 (0.3)	0.7 (0.1)	3.0 (0.2)	1.7 (0.4)
54	5 (0)	5.2 (0.1)	2.0 (0.4)	2.7 (0.6)	10.3 (2.1)	2.3 (0.3)	0.9 (0.3)	2.6 (0.7)	2.2 (1.0)
N. glomerulosa mean	5	4.7	1.8	2.6	8.7	1.9	0.9	2.2	1.7
N. glomerulosa CV	11	10.2	10.9	7.1	20.0	17.0	15.9	14.8	28.8
55	3 (0)	4.2 (0.2)	2.0 (0.1)	2.1 (0.1)	8.5 (0.9)	1.6 (0.1)	0.5 (0.1)	3.0 (0.3)	0.9 (0.2)
N. maeviae mean	3	4.2	2.0	2.1	8.5	1.6	0.5	3.0	0.9
N. maeviae CV	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
56	2(1)	3.8 (0.3)	1.5 (0.0)	2.5 (0.2)	5.8 (0.4)	1.5 (0.1)	0.4(0.1)	3.4 (0.6)	0.6 (0.1)
57	2 (0)	2.8 (0.2)	1.4 (0.2)	2.0 (0.3)	4.1 (0.8)	1.0 (0.0)	0.3 (0.1)	3.2 (0.5)	0.3 (0.1)
58	3 (1)	4.5 (0.1)	2.0 (0.1)	2.2 (0.0)	9.3 (0.4)	1.9 (0.1)	0.5 (0.1)	3.8 (1.3)	1.0 (0.2)
59	2(1)	5.1 (0.5)	1.7 (0.2)	2.9 (0.1)	8.9 (1.8)	2.2 (0.2)	0.6 (0.1)	3.6 (0.2)	1.3 (0.3)
60	3 (1)	4.5 (0.1)	1.8 (0.2)	2.5 (0.2)	8.2 (0.8)	2.2 (0.1)	0.8 (0.0)	2.8 (0.2)	1.7 (0.1)
61	2 (0)	4.2 (0.2)	1.2 (0.2)	3.3 (0.2)	5.2 (0.9)	1.5 (0.2)	0.4(0.0)	3.7 (0.0)	0.6 (0.1)
62	2 (1)	4.4 (0.3)	1.8 (0.2)	2.4 (0.2)	8.2 (1.5)	1.7 (0.2)	0.8 (0.1)	2.2 (0.4)	1.3 (0.2)
63	2 (0)	4.0 (0.2)	1.6 (0.1)	2.5 (0.2)	6.4 (0.3)	1.8 (0.2)	0.4 (0.1)	4.1 (0.4)	0.8 (0.2)
64	2(1)	4.8 (0.8)	1.6 (0.3)	2.9 (0.3)	7.9 (2.5)	2.1 (0.4)	0.5 (0.1)	4.2 (0.2)	1.1 (0.3)
65	3 (0)	4.6 (0.0)	1.4 (0.0)	3.4 (0.0)	6.2 (0.0)	1.7 (0.0)	0.6 (0.0)	3.0 (0.0)	1.0 (0.0)
N. ulicina mean	2	4.3	1.6	2.7	7.0	1.8	0.5	3.4	1.0
N. ulicina CV	21	14.4	14.8	17.0	24.2	20.5	27.5	17.8	40.6
Total mean	4	4.9	1.8	2.7	9.0	1.9	0.7	2.9	1.5
Total CV	24	14.7	14.5	13.8	26.2	23.8	29.5	28.6	45.8

APPENDIX 3. Values of the 19 bioclimatic variables obtained for the 65 populations of *Nassauvia* subgen. *Strongyloma* studied. See Appendix 1 for the full names of population codes and Materials and Methods for full names of environmental data acronyms.

Code	Bio1	Bio2	Bio3	Bio4	Bio5	Bio6	Bio7	Bio8	Bio9	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	Bio16	Bio17	Bio18	Bio19
1	15.0	17.1	62.3	372.0	27.2	-0.2	27.4	18.2	9.7	18.4	9.7	311.0	79.0	0.0	117.9	208.0	0.0	171.0	0.0
2	5.9	19.7	63.6	410.0	19.6	-11.3	30.9	9.8	0.5	9.8	0.2	263.0	70.0	0.0	118.0	183.0	3.0	183.0	4.0
3	7.7	18.9	62.7	418.3	21.0	-9.2	30.2	11.8	2.1	11.8	1.9	233.0	60.0	0.0	115.5	160.0	4.0	160.0	5.0
4	6.8	18.3	62.9	403.8	19.7	-9.3	29.0	10.9	1.5	10.9	1.3	165.0	47.0	0.0	122.7	119.0	2.0	119.0	4.0
5 6	10.9 10.1	13.5 13.9	53.8 54.4	414.9 429.0	22.9 22.4	-2.1 -3.2	25.0 25.6	15.7 15.1	5.8 4.9	15.7 15.1	5.6 4.6	233.0 203.0	$56.0 \\ 48.0$	1.0 2.0	110.2 106.0	155.0 129.0	5.0 7.0	155.0 129.0	7.0 9.0
7	10.1	14.4	58.2	429.0 398.1	22.4	-2.5	23.0	14.3	7.1	15.0	5.3	203.0 165.0	40.0	1.0	100.0	129.0	9.0	129.0	9.0
8	3.4	13.9	60.8	358.3	15.3	-7.6	22.9	-0.3	2.8	7.9	-0.9	136.0	20.0	7.0	37.3	49.0	22.0	33.0	44.0
9	7.0	14.9	54.1	477.2	21.1	-6.4	27.5	12.1	1.2	13.0	1.2	257.0	44.0	5.0	64.1	120.0	23.0	120.0	23.0
10	11.0	15.1	53.8	480.6	25.9	-2.1	28.0	16.1	6.0	17.2	5.2	252.0	33.0	8.0	39.8	93.0	33.0	89.0	36.0
11	14.0	16.0	59.4	429.2	29.0	2.1	26.9	9.6	19.3	19.3	8.9	381.0	89.0	2.0	99.7	226.0	13.0	13.0	223.0
12	3.9	14.8	55.5	473.5	18.5	-8.2	26.7	-1.2	9.7	9.7	-1.9	474.0	75.0	15.0	60.4	220.0	53.0	53.0	207.0
13 14	6.0 6.9	15.0 15.4	55.3 55.3	474.2 500.1	21.2 23.0	-5.9 -4.8	27.1 27.8	0.9 1.5	11.9 13.1	11.9 13.1	0.2 0.9	626.0 510.0	120.0 93.0	$14.0 \\ 14.0$	76.5 70.5	327.0 256.0	48.0 47.0	48.0 47.0	317.0 247.0
15	13.2	14.8	48.5	601.1	29.6	-0.9	30.5	12.8	19.7	20.6	5.9	142.0	16.0	9.0	18.0	41.0	30.0	32.0	33.0
16	9.7	13.2	52.8	476.3	24.3	-0.6	24.9	4.6	15.6	15.6	3.9	503.0	101.0	12.0	74.4	267.0	44.0	44.0	245.0
17	9.2	14.8	50.0	586.4	25.4	-4.2	29.6	9.0	15.3	16.3	2.0	175.0	21.0	10.0	21.6	52.0	36.0	39.0	43.0
18	7.5	13.6	50.4	535.3	22.8	-4.2	27.0	1.6	13.0	14.0	0.9	242.0	44.0	8.0	61.9	117.0	27.0	30.0	100.0
19	7.1	12.4	49.6	486.1	21.0	-3.9	24.9	3.9	12.0	13.1	1.1	166.0	25.0	5.0	46.5	65.0	21.0	24.0	59.0
20	11.9	12.4	47.4	530.7	26.4	0.2	26.2	5.9	17.4	18.5	5.4	185.0	26.0	9.0	37.8	72.0	29.0	31.0	62.0
21	12.3	16.1	52.4	571.8	29.2	-1.5	30.7	6.1	18.4	19.4	5.4	246.0	37.0	11.0	49.8	106.0	37.0	37.0	101.0
22 23	9.7 12.4	15.8 14.7	55.1 48.8	532.4 597.9	26.2 28.7	-2.5 -1.5	28.7 30.2	3.8 12.0	16.3 18.8	16.3 19.7	3.3 5.1	318.0 141.0	56.0 15.0	10.0 9.0	64.9 20.9	154.0 42.0	33.0 28.0	33.0 30.0	144.0 33.0
23 24	12.4	14.7	48.8 49.2	597.9 575.6	28.2	-1.5 -0.9	30.2 29.1	12.0	6.8	19.7 19.4	5.1 5.4	213.0	15.0 24.0	9.0 12.0	20.9 19.7	42.0 62.0	28.0 43.0	50.0 50.0	48.0
25	11.0	13.9	48.7	566.7	26.6	-1.9	28.5	10.9	16.9	18.0	4.1	183.0	20.0	11.0	19.8	54.0	38.0	42.0	46.0
26	13.7	11.5	48.2	482.7	26.4	2.5	23.9	14.2	18.2	19.6	7.7	194.0	25.0	10.0	27.3	63.0	35.0	39.0	48.0
27	12.0	12.4	47.3	532.2	26.5	0.2	26.3	5.9	17.4	18.5	5.4	191.0	27.0	9.0	39.1	75.0	29.0	32.0	65.0
28	10.9	10.3	46.3	473.5	23.3	1.0	22.3	5.7	13.8	16.7	5.1	205.0	27.0	11.0	33.7	76.0	36.0	36.0	67.0
29	6.0	7.1	46.1	326.0	14.7	-0.8	15.5	6.2	4.1	10.0	2.0	315.0	35.0	16.0	23.8	94.0	55.0	91.0	75.0
30	5.3	13.2	54.7	435.0	18.4	-5.7	24.1	0.8	10.5	10.5	0.1	345.0	79.0	3.0	91.7	189.0	17.0	17.0	184.0
31	7.6	15.3	54.0	505.9	23.4	-5.0	28.4	2.1	13.9	13.9	1.4	480.0	83.0	16.0	64.2	230.0	52.0	52.0	226.0
32 33	8.6 10.5	15.6 12.9	55.9 50.9	501.9 496.7	25.0 25.2	-2.8 -0.2	27.8 25.4	3.1 5.2	14.8 16.6	14.8 16.6	2.6 4.4	521.0 525.0	96.0 102.0	13.0 16.0	72.0 69.6	266.0 270.0	45.0 52.0	45.0 52.0	251.0 241.0
34	10.3	14.7	49.4	490.7 590.7	26.6	-0.2	29. <del>4</del> 29.7	10.2	16.5	17.5	3.1	180.0	21.0	11.0	22.2	55.0	37.0	40.0	44.0
35	10.0	13.2	49.4	527.6	25.0	-1.8	26.8	4.1	15.4	16.5	3.5	198.0	34.0	6.0	55.6	88.0	24.0	25.0	74.0
36	8.8	13.5	49.1	548.4	24.0	-3.4	27.4	2.6	14.4	15.5	2.0	168.0	22.0	8.0	31.5	60.0	26.0	31.0	53.0
37	8.6	12.3	50.1	463.2	22.4	-2.1	24.5	5.6	14.3	14.3	2.9	320.0	55.0	11.0	54.7	136.0	38.0	38.0	117.0
38	12.6	12.4	47.4	526.1	26.6	0.5	26.1	8.9	12.8	19.0	6.1	178.0	24.0	11.0	29.7	62.0	33.0	38.0	52.0
39	7.8	12.3	48.7	510.4	21.8	-3.5	25.3	1.9	13.0	14.0	1.5	140.0	20.0	4.0	41.6	53.0	17.0	19.0	50.0
40	8.2	10.9	47.8	463.2	20.8	-2.0	22.8	2.9	12.9	13.9	2.4	265.0	38.0	9.0	42.9	104.0	37.0	37.0	92.0
41 42	8.0 7.8	11.8 8.9	48.1 44.7	502.6 433.6	21.4 18.3	-3.1 -1.7	24.5 20.0	2.2 2.7	14.1 12.9	14.1 12.9	1.7 2.3	133.0 367.0	18.0 60.0	5.0 11.0	37.0 62.8	49.0 167.0	19.0 36.0	19.0 36.0	45.0 157.0
43	12.4	11.0	44.6	433.0 539.4	25.9	1.2	20.0 24.7	12.4	12.9	12.9	5.8	250.0	40.0	13.0	36.1	88.0	45.0	49.0	61.0
44	4.0	10.4	46.3	472.9	15.6	-6.9	22.5	4.2	8.7	9.6	-1.9	202.0	28.0	6.0	37.0	69.0	29.0	29.0	62.0
45	10.4	10.1	46.3	463.4	22.4	0.6	21.8	5.2	13.1	16.0	4.7	204.0	26.0	12.0	30.4	74.0	37.0	38.0	66.0
46	8.5	11.1	45.2	527.0	21.5	-3.0	24.5	8.5	13.9	14.8	2.0	192.0	30.0	10.0	33.4	64.0	35.0	36.0	50.0
47	4.8	9.8	45.7	447.8	15.9	-5.5	21.4	4.9	9.3	10.0	-0.8	256.0	37.0	12.0	31.7	88.0	47.0	47.0	63.0
48	9.0	10.9	44.8	517.6	21.4	-2.9	24.3	2.7	6.7	14.9	2.5	172.0	20.0	10.0	18.2	51.0	36.0	44.0	43.0
49 50	9.3	10.9	46.8	494.4	21.7	-1.6	23.3	3.4	9.8	15.1	3.1	212.0	25.0	13.0	20.5	68.0	42.0	52.0	59.0
50 51	5.3 7.8	10.7 9.5	$46.5 \\ 45.4$	477.7 445.1	17.1 18.8	-5.9 -2.0	23.0 20.8	5.1 4.7	6.0 12.4	10.8	-0.8 2.2	151.0 238.0	18.0 32.0	9.0 11.0	19.9 33.6	48.0 86.0	30.0 40.0	35.0 43.0	38.0 73.0
51 52	7.8 8.5	9.5 10.8	45.4 47.4	445.1 483.1	20.5	-2.0	20.8 22.7	4.7 4.9	12.4 9.3	13.1 14.0	2.2	238.0 180.0	32.0 24.0	9.0	26.1	86.0 54.0	40.0 33.0	43.0 51.0	44.0
53	1.4	9.6	49.1	485.1 386.4	11.7	-7.8	19.5	1.4	1.9	5.9	-3.5	541.0	24.0 59.0	37.0	15.8	165.0	117.0	122.0	137.0
54	6.0	7.3	48.3	299.8	14.1	-1.1	15.2	8.1	4.6	9.6	2.2	2010.0	206.0	141.0	10.8	562.0	463.0	517.0	468.0
55	7.1	10.4	49.8	425.3	18.0	-2.8	20.8	11.4	5.3	11.8	1.6	202.0	24.0	10.0	24.1	64.0	35.0	64.0	43.0
56	13.7	11.5	48.2	482.7	26.4	2.5	23.9	14.2	18.2	19.6	7.7	194.0	25.0	10.0	27.3	63.0	35.0	39.0	48.0
57	11.1	13.2	48.8	533.9	26.2	-0.8	27.0	5.1	16.6	17.7	4.5	203.0	34.0	7.0	51.0	87.0	27.0	28.0	73.0
58	12.4	12.5	47.6	527.7	26.5	0.3	26.2	8.7	12.6	18.8	5.9	178.0	24.0	11.0	29.7	62.0	33.0	38.0	52.0
59 60	11.9	12.5	47.2	531.9	26.6	0.2	26.4	5.8	17.4	18.5	5.4	195.0	28.0	8.0	41.8 26 5	78.0	27.0	30.0	68.0
60 61	10.0 12.4	11.3 10.3	46.9 47.0	502.3 454.2	23.0 24.6	-1.0 2.6	24.0 22.0	4.2 9.4	16.0 15.0	16.0 17.9	3.6 6.8	162.0 217.0	21.0 32.0	7.0 11.0	36.5 37.9	60.0 83.0	24.0 36.0	24.0 40.0	53.0 69.0
62	12.4	10.5	47.0 44.6	434.2 539.4	24.6 25.9	2.6 1.2	22.0 24.7	9.4 12.4	15.0 15.4	17.9	6.8 5.8	250.0	32.0 40.0	13.0	37.9 36.1	83.0 88.0	36.0 45.0	40.0 49.0	69.0 61.0
63	7.9	10.5	44.5	495.9	19.9	-3.6	23.5	7.8	11.3	13.6	1.7	164.0	19.0	10.0	20.3	51.0	32.0	36.0	43.0
64	9.7	10.7	47.3	465.8	22.1	-0.6	22.7	4.1	10.0	15.1	4.0	245.0	29.0	15.0	24.1	82.0	46.0	64.0	71.0
65	6.9	10.1	51.3	401.7	17.4	-2.2	19.6	10.9	5.0	11.4	1.7	235.0	33.0	11.0	30.1	80.0	38.0	77.0	51.0